From Neuroscience to Social Science

Volume 1 Mechanisms of Imitation and Imitation in Animals

edited by Susan Hurley and Nick Chater

Perspectives on Imitation

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Volume 1: Mechanisms of Imitation and Imitation in Animals

Introduction: The Importance of Imitation

Susan Hurley and Nick Chater

Imitation is often thought of as a low-level, cognitively undemanding, even childish form of behavior, but recent work across a variety of sciences argues that imitation is a rare ability that is fundamentally linked to characteristically human forms of intelligence, in particular to language, culture, and the ability to understand other minds. This burgeoning body of work has important implications for our understanding of ourselves, both individually and socially. Imitation is not just an important factor in human development, it also has a pervasive influence throughout adulthood in ways we are just starting to understand.

These two volumes present papers by researchers working in disciplines that include neuroscience and brain imaging, psychology, animal behavior, philosophy, computer science, education studies, anthropology, media studies, economics, sociology, and law. Among the authors are many who are leading figures in imitation research and who have produced seminal work on imitation. They also include younger researchers and scholars commenting on work in disciplines other than their own. One of our main aims in these volumes has been to provide a resource that brings together important work on this topic from various disciplines, makes it accessible across disciplines, and fosters interdisciplinary cross-fertilization. In particular, we want to convey why imitation is a topic of such intense current interest in the cognitive sciences and how important this work is for the social sciences and for philosophy, where it has yet to be assimilated.

This introduction surveys the central themes of the volumes, chapter by chapter, and then distills some of the important issues on which they bear, both methodological and substantive. En route, the following questions are addressed:

Which actions count as imitation and which are better understood in other terms?

What is imitated—the goals of action or the movements that are the means to goals, or both?
How is imitation achieved? By what neural mechanisms, in the contexts of what cognitive architectures or social environments?
Who imitates—only human beings, or other animals?
When does imitation occur—only in development, or also in adulthood?
Why does imitation occur—what are its evolutionary and cultural functions?

The structure of this introduction largely follows the structure of the two volumes. In volume 1, part I focuses on the subpersonal mechanisms by which imitation is achieved, and part II on imitation in animals. In volume 2, part I is on the role of imitation in human development and part II is on the role of imitation in human culture. This introduction concludes with a broad view of why imitation matters and highlights themes and questions that unite the two volumes.

Volume 1, Part I Mechanisms of Imitation

What exactly is imitation? Imitation may be presumed to require at least *copying* in a generic sense. The observer's perception of the model's behavior causes similar behavior in the observer, in some way such that the similarity between the model's behavior and that of the observer plays a role, though not necessarily at a conscious level, in generating the observer's behavior.[1] More than that we will not try to say at the outset. As we will explain below, imitation needs to be distinguished from other forms of social learning that may look superficially similar, and there are different accounts, in part motivated by the aims of different disciplines, of what is distinctive about imitation. However, even the generic idea of copying perceived behavior poses a certain immediate problem, which thus provides a natural starting place.

Imitation appears to require the solution to a difficult *correspondence problem*. How is the perceived action of another agent translated into similar performance by the observer? When I imitate your hand movements at least I can see my own hands, even though my visual perspective on the

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[1] Although even this generic formulation may include controversial elements. See W. Prinz in vol. 1, ch. 5 on how similarity can be functional in imitation, and Meltzoff in vol. 2, ch. 1 cf. Heyes in vol. 1, ch. 6 who questions the role of similarity in generating the observer's response, and Whiten's comments on Heyes in vol. 1, ch. 8.

two actions is different; but when I imitate your facial gestures, I cannot see my own face. How is the perceptual-to-motor mapping achieved? Moreover, when an infant imitates an adult, the two have very different body structures and dynamics. What information and mechanisms are needed to solve this problem?

Striking discoveries in neuroscience suggest a possible answer. Certain neurons appear to constitute a direct link between perception and action; their firing correlates with specific perceptions as well as specific actions. Some of these, *canonical neurons*, can be thought of as reflecting affordances (in Gibson's sense, 1986); they fire when a certain type of action is performed, but are also triggered by perception of objects that afford such actions. Others, *mirror neurons*, fire when a certain type of action is performed, but also when another agent is observed performing the same type of action. That is, mirror neurons are sensitive both to others' actions and to equivalent actions of one's own. They can be very specifically tuned. For example, certain cells fire when a monkey sees an experimenter bring food to her own mouth with her own hand *or* when the monkey brings food to its own mouth (even in the dark, so that the monkey cannot see its hand).

When mirror neurons were discovered by a group of scientists in Parma, Italy, it was tempting to suggest that they enable imitation by avoiding the correspondence problem. If the same neurons code for perceived action and matching performance, it may seem that no neural translation is needed. However, things are not quite that simple. Neuroscientist Giacomo Rizzolatti, one of the Parma group, addresses the relationship between the ability to understand another agent's action and the ability to replicate it, both of which he holds are required for imitation. In his view, action understanding phylogenetically precedes imitation and is subserved by mirror systems, which are necessary but not sufficient for imitation. Indeed, imitation has not been demonstrated in the macaque monkeys in which mirror neurons were discovered (but see Voelkl & Huber 2000). Rizzolatti suggests that the motor resonance set up by mirror neurons makes action observation meaningful by linking it to the observer's own potential actions.

Mirror neurons were discovered in monkeys by single-cell recording. Evidence for human mirror systems includes brain imaging work, as well as demonstrations that observing another agent act primes the muscles the observer would need to do the same thing. Rizzolatti describes mirror neurons in the monkey frontal brain area F5 as part of a neural circuit, including also parietal area PF and the superior temporal sulcus (STS) visual area. In human beings, he suggests, a similar circuit constitutes a comparator system in which an intended imitative movement is controlled by reference to an observed target movement, enabling imitative learning. (Others have postulated similar control systems, although they differ on details; e.g., Rizzolatti locates the comparator site in PF, while Marco Iacoboni locates it in STS.) In monkeys, mirror neurons display *high-level resonance;* they code for the goals or ends of performed or observed actions. By contrast, in human beings, the mirror system displays both high-level resonance and *low-level resonance;* it extends to the specific movements that are the means to achieving goals.

This difference between mirroring the ends of action and mirroring the means of action is important for Rizzolatti's argument that action understanding precedes imitation. His view faces the objection that many animals to whom it would be implausible to attribute action understanding can nonetheless replicate movements. Consider response priming, by which observing a movement "primes" the same movement by the animal, independently of any understanding of the goal of the movement (as in the flocking of birds). In response to this objection Rizzolatti suggests that such low-level mirroring of movements could be present without high-level mirroring of goals, or vice versa. Action understanding requires high-level mirroring of goals, which is found in macaque monkeys. However, genuine imitative learning has not been found in these monkeys and would require the interplay of mirroring for both the ends and the means of action, which is found in human mirror systems (again see and cf. Voelkl & Huber 2000). Rizzolatti's argument here finds an ally in the views of Michael Tomasello, who links the phylogenetically rare capacity for imitative learning to the flexible recombinant means and ends structure of intentional action: the ability to use a given movement for different ends and pursue a given end by a variety of means.

Psychologist Paul Harris has suggested an experimental assessment of the extent to which mirror neurons subserve action understanding in monkeys.[2] Monkey mirror neurons fire when a monkey reaches for an apple, or when it sees the experimenter reach for the apple. The same mirror neurons also fire when a monkey sees a screen come down in front of the apple, so that it is no longer visible, and then sees the experimenter's hand reach behind the screen to where the apple is hidden. But they do not fire when the monkey first sees that there is no apple, and then the screen comes down and the monkey sees the experimenter's hand reach behind

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[2] This was in a discussion at the Royaumont conference, 2002.

the screen in the same way. The mirror neurons, that is, appear to code for the goal of the action. Harris suggests a variant that would address how insightfully the monkey attributes goals to others. Suppose the monkey and experimenter look at a nut and see the screen come down in front of it. Then the experimenter leaves the room. The monkey is permitted to remove the nut. Now the experimenter returns and the monkey sees the experimenter reach behind the screen for the nut, which the monkey knows is no longer there. Will the monkey's mirror neuron for reaching for the nut fire? If so, this would suggest that the monkey attributes the goal of reaching for the nut to the experimenter, who "doesn't know" that the nut is no longer there. Or will it not fire, because the nut is not there? Does the mirror neuron, that is, code for the *intended goal* of the observed action, or merely its *result?*[3]

Neuroscientist Marco Iacoboni also characterizes the ends-means comparator structure of the neural circuit for imitation, drawing on human brain imaging studies. He suggests a division of labor within the mirror system—that frontal areas of the mirror system code for the ends or goals of action, and parietal areas for movements and means. To enable imitation, both areas generate motor signals relating to a planned imitative action for comparison with the observed action; the motor plan is then adjusted until a match is obtained. Iacoboni compares this neural architecture for imitation to current ideas about functional motor control architectures that combine inverse and forward models. *Inverse models* estimate what motor plan is needed to reach a certain goal from a given state of affairs. They can be adjusted by comparison with real feedback from motor activity, but this is slow. It is often more efficient to use real feedback to train *forward models*, which take copies of motor plans as input and simulate or predict their consequences. Forward models can then be used with inverse models to control goal-directed behavior more efficiently. In particular, forward models can predict the consequences of a planned imitative action for comparison with the observed action, so that the motor plan can be adjusted until a match is obtained. Iacoboni is optimistic that imaging work will contribute to mapping this functional architecture for motor control onto the neural mirror system.

Mirror neurons were discovered in the monkey homologue of part of Broca's area, one of the primary language areas of the human brain. Broca's

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[3] See Nicholas Rawlins in vol. 1, ch. 8.1 for another means of assessing mind reading by animals, via recordings from hippocampal place cells rather than mirror neurons.

area is among those areas activated when human participants perform imitative tasks, and Iacoboni's group has recently shown that transient lesions of this area made by transcranial magnetic stimulation interfere with imitative tasks. As Iacoboni explains, when imaging techniques are used to morph a chimp brain onto a human brain, the areas that expand most are the perisylvian brain areas occupied by the mirror system, which are extremely important for language. Now a broadly nativist view of language *could* motivate a kind of protectiveness about Broca's area as the best candidate for an innate language module in the brain. However, the discovery that Broca's area is occupied by the mirror system and has an essential role in imitation has underscored questions about how language might depend on the capacity for imitation, either in evolutionary or developmental time frames. To what extent might language acquisition exploit imitative learning mechanisms rather than expressing innate linguistic knowledge? Iacoboni argues that evolution leads from action recognition through imitation to language.

What are the key features of imitation and the human mirror system that language might build on or exploit? First, if imitative learning requires flexible relations between means and ends, such flexibility could be an evolutionary precursor of the arbitrary relations between symbol and referent. Second, as Iacoboni (vol. 1, ch. 2) and Michael Arbib (2002, and in press) argue in different ways, the mirror system provides a common code for the actions of self and other, hence for production and perception of language. By thus enabling action understanding, the mirror system may be the basis for the intersubjective "parity" or sharing of meaning that is essential to language. Third, as Arbib has suggested, the flexible recombinant structure of ends and means in imitation may be a basis for recombinant grammatical structure in language. Here Iacoboni provides an alternative suggestion. He regards actual conversation as more like a dance than a formal structure, an embodied practice of social interaction with essential motor elements, and in this way dependent on action recognition and the mirror system.[4]

Vittorio Gallese, another member of the Parma group who discovered mirror neurons, concurs with Rizzolatti, Iacoboni, and Jean Decety and Thierry Chaminade in hypothesizing that extensions of the mirror system provide a plausible neural basis for emotional understanding and em-

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[4] See also the comments by Pickering on Pepperberg in vol. 1, ch. 12.4; Donald in vol. 2, ch. 14 and Christiansen's comments in vol. 2, ch. 19.8; Claxton's comments on Kinsbourne in vol. 2, ch. 8.9; and Chater in vol. 2, ch. 18.

pathy.[5] Gallese's *shared manifold hypothesis* generalizes the empathic role of the mirror system, postulating a primitive intersubjective information space that develops out of the modeling of environmental interactions in biological control systems. This shared manifold arises prior to self–other distinctions, both phylogenetically and ontogenetically, softening the contrast between adult human mind reading and mere responses to others' behavior as found in other social animals. Nevertheless, the shared manifold is preserved in human adults. It supports automatic intersubjective identifications, not just across different perceptual modalities and action, but also for sensations and emotions. There is evidence, for example, of mirror mechanisms for pain and disgust, and hearing an expression of anger increases the activation of muscles used to express anger. Gallese argues that the extended mirror system is the neural basis of the shared manifold.

Neuroscientists Decety and Chaminade invoke single-cell, imaging, and behavioral evidence in support of the shared neural coding of action and the perception of action in a mirror system. They also regard such automatic motor resonance as a necessary basis for intersubjectivity in understanding action and in emotional empathy. But while Gallese's focus is on how the blended intersubjective space that precedes the self–other distinction is established, Decety and Chaminade focus on the characteristically human self–other distinction, and the way it is imposed on what is common to the representation of self and other. They report imaging experiments that probe the neural bases of the self–other distinction and reveal the relevance of left-right lateralization.

As Marcel Kinsbourne comments, their work dissects out the neural substrate of the self–other distinction by setting up conditions that differ only in this respect, so that the few nonoverlapping areas of brain activation they observe code for this difference. For example, they compare participants imagining performing an act themselves with participants imagining someone else performing the same act. In addition to the mostly common areas of activation, they find differential left inferior parietal activation for imagining oneself performing an act and differential right inferior parietal activation for imagining someone else performing the same act. Similarly, they compare participants imitating an act with participants being imitated in performing the same act, and again find mostly common activation but also some lateralized differential activation. Left inferior parietal areas enable you to imitate, they suggest, while right inferior parietal

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[5] Susan Jones in vol. 1, ch. 8.4, likes the idea that mirror neurons underlie intersubjective empathy, but is skeptical about their role in imitation.

areas enable you to recognize that you are being imitated. Decety and Chaminade regard the capacity to identify with others as especially dependent on right hemisphere resources.

Well before mirror neurons were discovered and invoked in neuroscientific arguments for the common coding of perception and action, psychologists argued for common coding from behavioral evidence. Meltzoff and Moore (1977) postulated a common "supramodal" code underlying early imitation (see Meltzoff, vol. 2, ch. 1). Wolfgang Prinz (1990) developed an argument for common coding to explain the reaction time advantage of imitative tasks and imitative interference effects, and related it to William James's views on ideomotor action. Common coding, Prinz reasoned, would facilitate imitation by avoiding the need for sensory-to-motor translation.[6] Here Prinz provides a definitive statement of his common coding view applied to imitation and further behavioral evidence for it from recent experiments.

In imitation, when an observed act *a* leads to performance of a similar act *b*, it seems to be no accident that *a* and *b* are similar. How, Prinz asks, can the similarity of observed and performed acts have a functional role in imitation? An approach that conceives of actions as responses to prior stimuli and of perceptions and actions as separately coded faces the problem of how correspondence between perceptions and similar actions is achieved. By contrast, the *ideomotor approach* Prinz favors conceives of actions as the means to realizing intentions and postulates the common coding of perception and action, so that a representation of movement observed in another agent tends inherently to produce a similar movement by the observer. The regular concurrence of action with perceived effects enables the prediction of the effects of an action (as in a forward model) and the selection of an action, given an intention to produce certain effects (as in an inverse model). As a result, the representation of a regular effect of action, whether proximal or distal, acquires the power to evoke a similar action if it is not inhibited. By explaining how perception and action share representational resources, the ideomotor view avoids the correspondence problem and explains the functionality of similarity in imitation.

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[6] Prinz argued that we should expect common codes for perception and action to code for distal events rather than for proximal events, such as patterns of activation of sensory receptors or of muscle neurons. Note that the mirror neurons discovered in monkeys appear to code distally, although, as Rizzolatti (vol. 1, ch. 1) and Iacoboni (vol. 1, ch. 2) explain, the human mirror system appears to code for the results or goals of action in some brain areas and the movements that are the behavioral means to such goals in others.

In this view, as Kinsbourne comments, when automatic imitative effects are held covert, inhibition occurs at the level of motor output rather than centrally, between separate perceptual processing and action processing. This point has implications for how we understand failures to inhibit imitation, whether pathological or normal. More generally, the common coding approach challenges standard Humean assumptions about the intrinsic motivational inertness of perception.

The consequences of damage to the mechanisms that normally inhibit automatic imitative tendencies in adults are revealed in classic studies of patients with frontal or prefrontal lesions. Luria's patients[7] found it very difficult not to imitate what the experimenter was doing, even when they were instructed to do something else. Lhermitte's imitation syndrome patients[8] imitated gestures the experimenter made, although they were not instructed to do so, and even when these gestures were socially unacceptable or odd. When asked why they did this, they did not disown their behavior but explained that they felt that the gestures they saw somehow included an order to imitate them; that their response was the reaction called for.

However, there are both theoretical and empirical reasons to hold that the automatic tendency of human adults to imitate is not confined to those with brain damage. The philosopher, and proponent of the idea that we understand other minds by mental simulation, Robert Gordon (1995a) argues that it takes a special containing mechanism to keep the emotion recognition process from reverting to ordinary emotional contagion, and this mechanism is not fail-safe. If simulation theory is right, he holds, there is only a delicate separation between one's own mental life and one's representation of the mental life of another; "offline" representations of other people have an inherent tendency to go "online." Moreover, striking similarities have been observed between the behavior of Lhermitte's patients and that of normal college students in priming experiments by social psychologists.[9]

Normal adults are studied in three experimental paradigms described by Prinz that provide evidence for the ideomotor approach. This work shows how an action by normal adults is spontaneously induced or modulated by the perception of a similar action. Perception has effects on action that are automatic but nevertheless have cognitive depth in that they

[7] See Kinsbourne, vol. 2, ch. 7; see also L. Eidelberg (1929).

[8] Lhermitte (1986), Lhermitte et al. (1986).

[9] As Bargh (in press) comments; see also Dijksterhuis in vol. 2, ch. 9.

depend on the way participants understand what they are perceiving and doing.

First, in imitative interference paradigms, both the initiation and selection of gestures are faster when participants are primed by perception of similar gestures or of their results or goals, even if such primes are logically irrelevant to their task.

Second, induction paradigms examine when spontaneous movements are induced by actions you actually perceive (perceptual induction, or involuntary imitation) as well as when movements are induced by actions you would like to perceive (intentional induction, as when moviegoers or sports fans in their seats make gestures they would like to see made). Both types of induction are found and are modulated by various contextual factors. It is interesting that perceptual induction is stronger than intentional induction when participants observe the results of a task performed by another person, especially when the participants have practiced the task earlier, but it is absent when participants believe that otherwise similar observed results have been generated by a computer rather than a person! Thus, perceptual induction appears to depend in part on background beliefs about whether what is perceived is the result of agency.

Third, coordination paradigms adapt imitative interference paradigms to tasks in which labor is divided and coordinated across two persons. Participants are asked to press the left key when a red cue is given and the right key when a green cue is given, while also observing irrelevant but distracting pointing cues. When a single participant does this task, the responses are faster and the errors less frequent when the irrelevant cues point toward the key called for by the relevant color cues. What happens when two participants sit side by side and one is asked to respond to red, the other to green? The interference effect persists, as if the two participants composed one agent with a unified action plan. The left-right response dimension extends across the two participants, and the irrelevant pointing cues interfere with both participants' responses. Remarkably, the interference effect disappears if the participants sit side-by-side but one is asked to respond to red only and the other to do nothing. While the "red" participant's partial task is unchanged, in the absence of coordination across the two participants, the left-right response dimension is lost and the irrelevant pointer cues no longer produce interference.

These results suggest that the automatic effects of perception on action depend on social context in a strong sense. Whether an individual's action is subject to interference by given perceptions can depend on whether her actions are part of a collective action with which those perceptions interfere. Understanding what you are doing in terms of a team effort can alter the ways in which your actions are automatically influenced by perception (see Bacharach, 1999; Hurley, 1989).

The correspondence problem posed by imitation is also addressed by the psychologist Celia Heyes in her *associative sequence learning model*. By what mechanism are perceptions linked to similar actions in imitation? Must such correspondences be innate? Heyes thinks not, and aims to show how they could be acquired, in the right environment, through general-purpose associative learning mechanisms whereby "neurons that fire together, wire together." In this respect her account allies her with the minority[10] who are skeptical about influential evidence[11] of imitation by human newborns. Her account is compatible with the common coding of perception and action, but regards neural mirror properties as acquired through association rather than based on intrinsic similarity. In effect, from this point of view Humean associationism may be on the right track, even if a Humean view of perception as inert turns out not to be.

A general solution to the correspondence problem must cover imitation of *perceptually opaque* acts such as facial gestures, which cannot be seen by their agent, as well as of *perceptually transparent* acts such as hand gestures, which can be seen by their agent. It must cover imitative learning of novel acts, as well as imitation of acts already in an agent's repertoire. Heyes's account aims to satisfy these demands. It characterizes both direct and indirect routes by which sensorimotor associations can be acquired. Direct associations are formed when someone watches her own hand gesture, for example. But this won't work when the agent cannot perceive her own actions, as in facial gestures. Here the association can be mediated by a third item, such as a mirror, an action word, or a stimulus that evokes the same behavior in the actor and in other agents the actor observes. Moreover, adult imitation of infants is common, and can perform the associative function of a mirror (see also Meltzoff, vol. 2, ch. 1 on the importance of being imitated).

In effect, the associative mechanism that enables opaque imitation extends into the cultural environment. Novel acts can be learned by

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[10] Including Moshe Anisfeld in vol. 2, ch. 4 and Susan Jones, commenting on Whiten in vol. 1, ch. 12.6.

[11] From work by Andrew Meltzoff and others; see Meltzoff, vol. 2, ch. 1. Note that Meltzoff argues that the correspondence between perception and action expressed by mirror neurons may be learned rather than innate, and that it remains an open question what the role of experience is in forming mirror neurons.

observing another agent perform an unfamiliar sequence of familiar elements of an act, where each perception of an element already has a motor association, resulting in a new sequence of motor elements that become linked through repetition to give rise to a novel act. Thus, given interactions with the right environment, imitation emerges.

Heyes sharpens issues faced by other views, but as she recognizes, her account also faces several challenges. If imitation does not require dedicated evolved mechanisms, why is it so rare in the animal kingdom? It is greatly facilitated, she suggests, by cultural environments; enculturated chimps raised like human children are better imitators than other chimps. By arguing that the emergence of imitation from general learning mechanisms may depend on cultural environments, Heyes turns the tables on the view that imitation is the copying mechanism that drives cultural accumulation and evolution.[12] In her view, the similarity of what is perceived and what is done in imitation is emergent rather than functional, in Prinz's sense. But can imitation both emerge from culture in this way and provide its engine in some complex dynamic process? (Does it help in considering this question to consider analogies to genetic copying and evolution?)

Philosopher Susan Hurley's *shared circuits hypothesis* draws together various threads from early chapters and elsewhere, concerning the relationships among control, imitation, and simulation within a complex comparator architecture. Her shared circuits model can be regarded as a dynamic descendent of the common coding theory, and is also a close relative of Gallese's shared manifold hypothesis.

Hurley describes a subpersonal functional architecture in five layers, starting with adaptive feedback control such as that found in a thermostat, where real sensory feedback is compared with a target behavior and motor output is adjusted until feedback and target match. At the second layer, internally simulated motor-to-sensory feedback or "prediction" is added to speed and smooth motor control; affordance neurons with both sensory and motor fields are predicted at this layer. At the third layer, the sensorimotor links between one's own actions and one's observations of them or their consequences are instead activated in reverse, so that one's observation of others' actions results in the priming of similar movements, emulation of similar goals, and imitation. Mirror systems are predicted at this layer, which realizes a version of the primitive intersubjective space

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[12] For discussion see Sugden (vol. 2, ch. 15), Gil-White (vol. 2, ch. 16), Greenberg (vol. 2, ch. 17), Chater (vol. 2, ch. 18) and comments by Blackmore (vol. 2, chs. 19.9, 19.12, 19.13).

postulated by Gallese (see also Meltzoff, vol. 2, ch. 1 on the fundamental self–other equivalence exploited by early imitation). Via indirect links, associations could also be formed between one's own perceptually opaque acts, such as facial gestures, and similar acts by others. At the fourth layer, the tendency to copy the acts of others can be inhibited or "taken offline," so that observing another's act creates a simulation of that act. Simulation for action understanding requires the system to track whether copying is offline or not, so that a self–other distinction would come to overlay the self–other similarities registered in the more basic intersubjective space.

Finally, at the fifth layer, input can be simulated as well. A distinction between the imagined and the real requires the system to track whether an input is simulated, so that counterfactual situations can be simulatively entertained and assessed in deliberation, planning, and hypothetical and instrumental reasoning. Variations of the specified structure could be repeatedly implemented in a linked network of such circuits, yielding the flexible recombinant properties characteristic of intentional action.

Hurley is concerned to advance understanding of the way descriptions of the mind at neural, functional, and personal levels can be related to one another while avoiding oversimple assumptions of isomorphism between levels of description. Her midlevel, functional subpersonal architecture holds promise here. It lends itself to neural mapping exercises and also raises issues concerning mind reading and higher cognitive abilities. It shows how an intersubjective space can be distilled out of the shared information space for perception and action and used in simulation. Moreover, it suggests how the self–other and the imagined/real distinctions, which are essential to the cognitive abilities of persons, can emerge from these prior shared information spaces. Hurley's hypothesis provides a subpersonal parallel to Robert Gordon's[13]; understanding other agents depends at the most fundamental level on multiplying first person information through simulation rather than on building an inferential bridge between first person and third person information. Subpersonal information about persons arrives in the first person plural, without distinction or inference between self and other.

Volume 1, Part II Imitation in Animals

Vol. 1, part I discusses work in neuroscience and psychology concerning what mechanisms could solve the perception-action correspondence

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[13] Gordon (1995a,b, 2002) and volume 2, chapter 3.

problem for imitation. By contrast, studies of social learning in animals often focus on distinguishing true imitation from other superficially similar behaviors, and in particular on the requirement of novelty for imitative learning. Sophisticated experimental and theoretical work on different kinds of copying behavior in animals helps to clarify the nature and varieties of imitation in human development (see vol. 2, part I) and in human adults, as well as in nonhuman animals. It also sheds light on the role of varieties of imitative behavior in the generation and transmission of culture (see vol. 2, part II) and poses the question of how far imitation can explain what is distinctive about human cultural transmission.

It has proved remarkably difficult to find evidence of true imitation in nonhuman animals, and for a long while sceptics who regarded the capacity for imitation as exclusively human had the upper hand. A new consensus is emerging as a result of painstaking work showing imitation in some great apes and monkeys (see Byrne, vol. 1, ch. 9 and Whiten et al., vol. 1, ch. 11; see also Voelkl & Huber, 2000), dolphins (Herman, 2002), and birds such as some parrots, corvids, and quail (Pepperberg, 1999; G. Hunt & Gray, 2003; Weir et al., 2002; Akins & Zentall, 1996). Cautious moves are being made to describe continuities along a spectrum from the capacities of other social animals to the interrelated capacities for imitation, mind reading, and language that appear to be characteristically human. To understand the significance of this work with animals, it is necessary to understand some of the distinctions that have been drawn between imitation and other forms of social learning.

The concept of "true imitation" is contested, owing in part to the different theoretical aims and methodologies of those concerned with imitation.[14] What matters for present purposes is not what deserves this label, but that relevant distinctions be recognized. The most restrictive understanding of true imitation requires that a novel action be learned by observing another perform it, and in addition to novelty, requires a means/ends structure. You copy the other's means of achieving her goal, not just her goal or just her movements.

A variety of other less cognitively demanding forms of learning in social contexts might look superficially similar. For example, in *stimulus enhancement*, another's action draws your attention to a stimulus that triggers an innate or previously learned response; you do not thereby learn a novel action by observing the other. In *emulation*, by contrast, you observe an-

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[14] See Rizzolatti (vol. 1, ch. 1), Byrne (vol. 1, ch. 9), and Thomas Zentall's comments on Byrne (vol. 1, ch. 12.1); Heyes (2001) and Heyes and Galef (1996).

other achieving a goal in a certain way, find that goal attractive, and attempt to achieve it yourself by whatever means (cf. the very different sense of "emulation" used in Grush, 1995 and forthcoming). Individual trial-and-error learning may then lead you to the other's means of achieving the goal. In both stimulus enhancement and emulation, any coincidence of the movements between learner and model is incidental. A further contrast is with mere *response priming*, as in flocking behavior or contagious yawning, where bodily movements are copied but not as a learned means to a goal.

Goal emulation and response priming can be thought of as the ends and means components, respectively, of full-fledged imitation. The distinction between ends and means is not absolute; a movement can be a means to adopting a posture, for example, which may in turn be a means to bring about an effect on an external object or conspecific. We can understand more complex forms of imitation in terms of a structured sequence of means/ends relationships in which one acquires a goal, learns how to achieve it by achieving several subgoals, learns how to achieve the subgoals by certain means, and so on. More complex forms of imitation are methodologically important for animal research (and, as we will see in part III, for research on imitation in human development) because they reduce the plausibility of explanations of mirroring behaviors in terms of mere stimulus enhancement, emulation, or response priming. For example, the more complex the movements modeled in a goal-directed behavior that is emulated, the more implausible it is that trial-and-error learning would reproduce these specific movements. Similarly, certain complex patterns of movement are unlikely to be reproduced by response priming because the learner is unlikely to have a prespecified matching response that merely needs to be triggered. True imitation can make sense of the copying of such complex patterns of movement as the learned means to an end.

Response priming, goal emulation, and stimulus enhancement are certainly found in nonhuman animals, and careful experiments are needed to obtain evidence of imitation in a more restricted sense. For this purpose, the *two-action* experimental paradigm has become the tool of choice. When two models illustrate two different means of obtaining the same attractive result, will animals who observe one or the other model differentially tend to copy the specific method they have seen demonstrated? If not—if they use either method indifferently to achieve the goal, or converge on one method despite the different methods modeled—they may be displaying mere goal emulation plus trial-and-error learning, or stimulus enhancement, rather than imitative learning.

Psychologist and primatologist Richard Byrne explains some of the limitations of the two-action experimental criterion for imitative learning and in particular questions its usefulness in demonstrating novelty. Success on the two-action criterion, Byrne suggests, is consistent with an alternative account in which a modeled action primes rare preexisting acts in a large repertoire, which may be further amplified by individual trial-and-error learning, so that no imitative learning of a genuinely novel skill has occurred.[15] We may note, in addition, that with merely *two* actions to be distinguished by the learner, even a very partial grasp of the means used by the model may suffice to bias the learner toward that means—and the rest might then be acquired by individual trial-and-error learning.

What naturally occurring examples of imitative learning might resist such an alternative explanation? The persistence of a less efficient method of performing a given task in a particular population, such as apes using one short stick instead of two long sticks to fish out insects, might be evidence for imitative as opposed to trial-and-error learning. But, as Byrne explains, it will be hard to rule out the possibility that environmental differences rather than imitation explain such behavioral differences among populations.

He finds better evidence for imitative learning of novel skills in his field observations of what he calls *program-level imitation*, in which animals imitatively learn a specific organization of a complex process. Gorillas, he argues, learn to prepare particular types of plants for eating using a standardized, complex organization of manual processing stages, despite idiosyncratic lower-level differences among individual gorillas; the standard processing pattern is even learned by gorillas whose hands have been maimed by snares, who might be expected to find different processing techniques through individual trial-and-error learning. Byrne argues that such program-level imitation cannot be explained in terms of socially guided priming, emulation, and trial-and-error learning; it illustrates imitative learning of genuinely novel skills.[16] This capacity to transmit complex techniques for processing food, he suggests, may have helped apes compete with monkeys in exploiting shared food resources, despite the lesser mobility and other feeding disadvantages of apes.

From the question of what behavior distinguishes imitation from other forms of social learning, Byrne returns to the question of subpersonal

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[15] See and cf. Meltzoff on infant imitation of novel acts in volume 2, chapter 13.

[16] See various comments on Byrne and Russon (1998) for assessments of the evidence for program-level imitation in gorillas and orangutans.

mechanisms of imitation. His focus is on the mechanisms needed to enable program imitation rather than those needed to solve the correspondence problem. A mirror mechanism could recognize elements in fluid movements and find corresponding units in the existing action repertoire, which could be strung together in observed new ways. But Byrne argues that for program-level imitation, a further *behavior parsing* mechanism is also needed, which would statistically parse many such observed strings to extract their shared organization or deep structure from the idiosyncratic surface variation. Skilled action has a modular structure that facilitates flexible recombinant functioning. The behavior parsing mechanism could detect module boundaries in observed behavior, the points at which links between behavior strings are weakest, by registering points of smooth resumption after interruption of behavior; clusters of pauses; and patterns of substitution, omission, or repetition. Alternatively, as the developmental psychologist Birgit Elsner suggests on the basis of work with human children, modules might be parsed by reference to subgoals. Byrne sees behavior parsing capacities as an important precursor to more sophisticated human abilities for high-level perception of an underlying structure of intentions and causes in the surface flux of experience.

It is tempting also to regard behavior parsing and the recombinant structure of program-level imitation as precursors of syntactic parsing and the recombinant structure of language. Michael Arbib (2002) explains the neural intertwining of human mirror and language systems along related lines. Moreover, the problem of finding recombinant units of action in apparently smooth streams of bodily movement has many parallels with the problem of finding linguistic units such as words in the apparently continuous acoustic stream of speech.

A quite different slant on the relations between imitation and language is provided by the psychologist Irene Pepperberg's pioneering work with the African Grey parrot Alex. African Greys have walnut-sized brains with very little that resembles primate cortex. Yet Alex does what bigger-brained animals cannot; he acquires significant fragments of English speech by listening in on conversations between human trainers, and he uses it to perform cognitive tasks put to him in English. Alex's well-known accomplishments are described in detail elsewhere (Pepperberg, 1999). He can both comprehend and produce words for fifty objects; seven colors; five shapes; numerals up to 6; the categories of color, shape, material, and number; plus the words "no," "come," "go," "want," etc. He can combine these words in new ways to identify, request, comment, refuse, alter his environment, add objects to categories, or process queries. For example, from an array of red and blue balls and blocks, he can quantify a subarray, such as the set of blue blocks, on request.

Does Alex imitate? He learns the specific vocalizations of another species and uses them functionally. Such exceptional vocalizations are unlikely to occur in normal development and cannot plausibly be explained as the priming or evoking of innate behaviors. Pepperberg locates Alex's vocal abilities in relation to three different levels of imitation and shows that the similarity of African Grey speech to human speech is not an artifact of human perception, but shares acoustic characteristics with human speech. Alex derives new sounds from old ones by babbling, but in ways that respect English rules for building words. Byrne considers whether Alex's copying of the structure of English speech can be regarded as emulation or as program-level imitation comparable to that displayed by human children.

One of the most thought-provoking aspects of Pepperberg's work is the model/rival training method on which Alex's success depends. Standard behavioral training techniques were unsuccessful. Moreover, just being part of a standard referential triangle, in which two participants refer to the same object, does not enable Alex to learn as he does. Rather, what is essential is that Alex be able to eavesdrop on a referential triangle composed of two human English users referring to an object. One plays the role of trainer, the other models the learning process and acts as a rival to Alex for the trainer's attentions and rewards. The trainer gives feedback to the model, scolding for errors such as the bird might make, or providing rewards for correct responses, and the pair demonstrate the referential and functional use of the label. It is essential that the bird observe role reversal between trainer and model; otherwise, the bird does not learn both parts of the interaction, and does not learn to transfer responses to new trainers. Moreover, it is essential that the objects referred to are themselves used as rewards, to avoid confusion between labeled objects and different rewards. When any of these elements of model/rival training are omitted, training is unsuccessful. When such birds are given model/rival training for some labels and other training techniques are used for other labels, the birds practice only the model/rival trained labels when alone! Pepperberg suggests that observing a model responding to a trainer may enable the parrot to represent the required response separately from the "do-as-I-do" command. As she notes, promising work is under way using the model/rival technique to facilitate learning for some autistic children.[17]

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[17] See also Jones's comments on Whiten et al. in volume 1, chapter 12.6 for a different angle on imitation and therapy for autism.

The dependence of Alex's learning on exposure to a very specific training regimen recalls Heyes's view that imitative learning can depend on particular cultural environments. More generally, observations of nonhuman animals in different environments or using different, apparently reasonable, testing methods may lead to very different estimates of their cognitive abilities. Because of the way environmental structure and input can affect the manifestation of cognitive capacities, great care is needed in determining what capacities are present and how they compare with human capacities.

This point is underscored by the way skepticism about chimp imitation has been overcome, as explained by the psychologists Andrew Whiten, Victoria Horner, and Sarah Marshall-Pescini, as well as by Bennett Galef, a former skeptic. Imitation was regarded through most of the nineteenth century as a low-level ability, characteristic of the mentally weak or childish, and as less rationally demanding than individual trial-and-error learning. But at the end of the nineteenth century Edward Thorndike showed that many animals who could learn through trial and error could not imitate, and argued that imitation is in fact the rarer and more cognitively demanding ability. This view is now generally accepted. While early fieldwork with chimps appeared to provide evidence of their imitative abilities, critics such as Galef, Heyes, and Michael Tomasello challenged this interpretation effectively. Many subsequent experimental studies reported a lack of chimp imitation. Only recently has evidence of chimp imitation won over most critics; the relevant questions now are what, how, and why they imitate, rather than whether they can do so at all.

Whiten and colleagues have played a prominent role in demonstrating chimp imitation and comparing it with imitation in children. Their innovative experiments using ingenious "artificial fruits" extend the two-action method, revealing that chimps sometimes emulate and sometimes imitate. For example, Whiten's pin-apple is a box containing food that can be opened in two ways: by poking or pulling its bolts, and then pulling or twisting a handle. One way of opening it is modeled for one group of chimps, the other way for another group. The chimps imitate the specific means modeled to remove the bolts, but merely emulate using the handle to achieve the goal of reaching the food. Children, by contrast, imitate the specific means modeled for both parts of the task, even when this is less efficient. Using a more complex pin-apple, the two-action method shows that chimps imitate sequential structure but not details of component techniques, suggesting program-level imitation. Yet another artificial fruit, the key-way, is used with the two-action method to contrast imitation of the hierarchical structure of a task with imitation of left-right versus right-left sequence. Here, young chimps, like children, ignore the modeled sequence direction but do imitate hierarchical structure. They organize the multiple moves needed to open the key-way by rows or by columns, according to what they have seen modeled.

Why do chimps sometimes imitate and sometimes emulate? Do they imitate selectively, or do they have only a limited ability to imitate? Whiten and colleagues argue that chimps imitate selectively, selecting aspects of a modeled task to be imitated or not according to their appraisal of the significance of these aspects for achieving their goal. For example, a hierarchical task structure is not transparently irrelevant to success, while left-right sequence direction is. Using a variant of a task used by Paul Harris and Stephen Want to demonstrate selective imitation in children, Whiten and colleagues show that chimps imitate more selectively than 3-year-old children.[18] A model shows chimps how to obtain food in a box by using a tool to stab the food though tunnels in the box. The model first stabs down a tunnel and hits a barrier, which blocks the food from reach, but then stabs through a different tunnel and reaches the food. This "mistake" is modeled using both a transparent box, in which it is obvious that the initial downward stab will not reach the food, and an opaque box, in which it is not obvious. As predicted, chimps imitate the futile first downward stab less when the transparent box is used. Three-year-old children, by contrast, imitate the futile downward stab in both versions of the task, even if they are left alone to remove social pressure to conform.

Even if chimps *can* imitate, children are "imitation machines," as Michael Tomasello (1999, p. 159) has put it and as Andrew Meltzoff also argues (in vol. 2, ch. 1). Children have a stronger tendency than chimps to imitate rather than emulate, even when doing so is transparently inefficient. For example, after seeing a demonstrator use a rake inefficiently, prongs down, to pull in bait, chimps tend to turn the rake over and use it more efficiently, edge down, to pull in the bait. Two-year-old children in a parallel experiment almost never do so; they go right on imitating the inefficient means of obtaining the bait they have seen demonstrated, with prongs down (Nagell et al., 1993; cf. Gergely et al., 2002). Human imitation is flexible, ubiquitous, effortless, and intrinsically rewarding (see Jones, vol. 1, 12.6, p. 298). Chimps may appear to be better off in this comparison, at least in the short run. Why might it be beneficial to humans in the long run to imitate with such determination? Tomasello (1999) explains this in

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[18] See and cf. Harris and Want in volume 2, chapter 6.

terms of the *ratchet effect*. Imitation preserves rare one-off insights about how to achieve goals, which would not be rediscovered readily by independent trial-and-error learning, and so would be lost without imitation. Imitation spreads these discoveries around, makes them available to all as a platform for further development. Through the ratchet effect, imitation is the mechanism that drives cultural and technological transmission, accumulation, and evolution.[19]

We have discussed the mechanisms that may underlie and enable the strong imitative tendencies that are so characteristically human, and we will go on to consider their possible functions and effects in relation to human culture. But first we turn to the role of imitation in human development, and in particular in the development of another distinctive human capacity, the ability to understand other minds.

Volume 2, Part I Imitation and Human Development

Human beings are distinctive among animals in their capacities for language and for understanding other minds, or *mind reading*. Whether these are innate as *capacities*, the skilled behavioral expression of these capacities develops over years of interaction between infants and their environments, in well-studied stages during which much learning occurs. The same could be said about a third distinctive human capacity, the ability to imitate. This, however, begins to be manifested very early—indeed, at birth, according to highly influential work by the developmental psychologist Andrew Meltzoff and others on imitation in human infants, including newborns.

The relationships among this trio of capacities—for language, mind reading, and imitation—are of fundamental importance for understanding the transition of human infants into adult persons. Does the development of either language or mind reading depend on imitation? If so, at what levels of description and in what senses of "depend"? Or does dependence run the other way or both ways, dynamically? The answers are controversial, and may of course differ for language and mind reading. Several of the chapters in vol. 2, part I focus on the question of how imitation is related to the understanding of other minds and in particular other *agents*. This question brings into play the further controversy about whether mind reading is best understood as theorizing about other minds or as

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[19] See and cf. Harris (vol. 2, ch. 6), Sugden (vol. 2, ch. 15), Gil-White (vol. 2, ch. 16), Greenberg (vol. 2, ch. 17), Chater (vol. 2, ch. 18) and Blackmore (vol. 2, ch. 19).

simulating them. How does the theory–simulation controversy concerning the mechanism by which we understand other minds bear on the relationships between imitation and mind reading, or vice versa?

Meltzoff surveys his work on early imitation and draws on it to argue that early imitation and its enabling mechanisms beget the understanding of other agents, not the other way around.[20] In a series of famous experiments, Meltzoff and Moore studied imitation in newborns and infants under 1 month, including facial and manual imitation. Since infants can see others' facial acts but not their own, newborn facial imitation suggests an innate, supramodal correspondence between observed acts and an observer's similar acts.[21] Moreover, very young infants defer imitation across a delay of 24 hours and correct their imitative responses, homing in on a match without external feedback. The *active intermodal mapping* (AIM) hypothesis interprets this evidence in terms of the comparison and matching of proprioceptive feedback from an observer's own acts to an observed target act, where these are coded in common, supramodal terms. Elsewhere, Meltzoff and Moore (1997) explicate this common code as initially coding for relations among bodily organs such as lips and tongue, and developing through experience of body babbling toward more dynamic, complex, and abstract coding.

Meltzoff emphasizes that various further imitative and related behaviors are not present from birth, but are acquired at stages throughout infancy. Infants from 6 weeks to 14 months recognize that they are being imitated,[22] but only older infants act in ways that apparently purposively test whether they are being imitated. Since only people can imitate systematically, an ability to recognize being imitated provides a means of recognizing that an entity is a person. By 14 months, infants imitate a modeled novel act after a week's delay; they turn on a light by touching a touch-sensitive light panel with their foreheads instead of their hands, differentially copying the novel means modeled as well as the result (see Meltzoff, vol. 2, ch. 13, p. 59, and Tomasello and Carpenter, vol. 2, ch. 17, p. 138.) Note that in a follow-up to the Meltzoff's light-pad experiment,

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[20] In contrast to Rizzolatti (vol. 1, ch. 1) and Tomasello (1999), who argue in their different ways that understanding an action precedes imitation.

[21] See Nicholas Humphrey (vol. 2, ch. 8.2) for some intriguing speculations on possible pathological phenomenological manifestations in adulthood of such supramodal mappings.

[22] With differential activation of the right inferior parietal lobe; see Decety and Chaminade (vol. 1, ch. 4).

children do use their hands to touch the light-pad when they see a demonstrator whose hands are occupied by doing something else touch it with her head (Gergely et al., 2002). Children *can* emulate as well as imitate. Nevertheless, their tendency to imitate rather than emulate appears to be considerably greater than that of chimps when direct comparisons have been made, as in Nagell et al., 1993. By 15 or 18 months, infants recognize the underlying goal of an unsuccessful act they see modeled and produce it using various means. For example, after seeing an adult try but fail to pull a dumbbell apart in her hands, they succeed in pulling it apart using their knees as well as their hands. However, they do not recognize and attempt to bring about the goals of failed "attempts" from similar movements by inanimate devices.

Thus, in Meltzoff's view, the ability to understand other minds has innate foundations but develops in stages. Imitation plays a critical role in his arguments for a middle ground between Fodorian nativism and Piagetian theory. Infants have a primitive ability to recognize being imitated and to imitate, and hence to recognize people as different from other things and to recognize equivalences between the acts of self and other. The initial bridge between self and other provides a basis for access to people that we do not have to things, which is developed in an early three-stage process.

First, an infant's own acts are linked to others' similar acts supramodally, as evidenced by newborns' imitation of others' facial acts. Second, own acts of certain kinds are linked bidirectionally to own experiences of certain kinds through learning. Third, others' similar acts are linked to others' similar experiences. This process gets mind reading started on understanding agency and the mental states most directly associated with it: desires, intentions, perceptions, and emotions. The ability to understand other minds is not all or nothing, as Meltzoff emphasizes.[23] An understanding of mental states that are further from action, such as false beliefs, comes later in development.

Meltzoff claims here that the early three-stage process he describes is not a matter of formal reasoning, but rather one of processing the other as "like me." Meltzoff is often interpreted as viewing mind reading in terms of theoretical inferences from first-person mind-behavior links to similar third-person links, in an updating of classical arguments from analogy. There are clear elements of first-to-third-person inference in his view of

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[23] The same point can be made for other animals; see Tomasello (1999) on levels of mind-reading ability.

how mind reading develops. As he states in vol. 2, ch. 1, "the crux of the 'like-me' hypothesis is that infants may use their own intentional actions as a framework for interpreting the intentional actions of others" (p. 75). For example, 12-month-old infants follow the "gaze" of a model significantly less often when the model's eyes are closed than when they are open, but do not similarly refrain from following the "gaze" of blindfolded models until they are given first-person experience with blindfolds. Similarly, as Paul Harris comments, giving 3-month-old infants Velcro mittens to enhance their grasping abilities also enhances their ability to recognize others' goals in grasping. Nevertheless, the initial self–other linkage that Meltzoff postulates, expressed in imitation by newborns, is via a supramodal common code for observed acts and the observer's acts, which is direct and noninferential (see Meltzoff & Moore, 1997). In a graded view of mind reading such as Meltzoff's, the role of theoretical inference from the first to the third person in mind reading can enter at later stages and increase significantly with development.

Philosopher Alvin Goldman also considers the relationship between imitation and mind reading, first from the perspective that understands mind reading in terms of theorizing, which he attributes to Meltzoff, and then from his preferred view of mind reading in terms of simulation. The *"theory theory"* approach to mind reading regards commonsense psychology as a kind of protoscientific theory in which knowledge is represented in the form of laws about mental states and behavior; to the degree that these are not innate, they are discovered by testing hypotheses against evidence. People's specific mental states and behaviors are inferred from other mental states and behaviors by means of such laws. No copying is involved. By contrast, *simulation theories* understand mind reading to start with the mind reader taking someone else's perspective and generating pretend mental or behavioral states that match the other person's. These are not made the object of theoretical inference, but rather are used as inputs to the simulator's own psychological processes, including decision-making processes, while these are held offline, producing simulated mental states and behavior as output. The simulated outputs are then assigned to the other person; these may be predicted behaviors by the other, or mental states of the other that explain the observed behaviors. This is an extension of practical abilities rather than a theoretical exercise. The simulator copies the states of the other and uses the copies as inputs to her own psychological equipment, instead of formulating laws and making inferences from them about the other. Within this broad theory versus simulation contrast, many finer distinctions have rightly been drawn among various versions, levels of description, and aims within each category.[24]

Consider the role of imitation in Meltzoff's version of a theory-theory approach to mind reading. One could restate Meltzoff's three-stage process, described earlier, in explicitly theory-theory terms, as follows. At stage one, the innate equivalence between my own acts and others' acts (exploited by early imitation and the recognition of being imitated) makes it possible to recognize that some acts (by myself) are similar to other acts (by another). At stage two, first-person experience provides laws that link one's own acts and mental states. At stage three, it is inferred that another's act that is similar to mine is lawfully linked to the other's mental states in the same way that my act is lawfully linked to my mental states. As Meltzoff points out (personal communication), there is no inference from the first person to the third person at stage one of this account; the initial bridge between the self and other expressed in imitation and recognition of being imitated is bidirectional. However, an inference from the first person to the third person does enter as we proceed through stages two and three of this account. It resembles traditional arguments from analogy in inferring laws linking third-person acts and mental states from laws linking first-person acts and mental states.

Goldman does not object here to the first-to-third-person inference per se. He notes that psychologists could be correct to attribute such an analogical inference to mind readers, even if, as philosophers have often argued, it is epistemologically unsound. Nor does he object to making understanding of other minds depend on direct first-person knowledge of one's own mental states; his own simulationist account does this. However, he regards such dependence as internally incompatible with a theory-theory approach to self-knowledge, according to which knowledge of first-person mental states relies on theoretical inference in the same way that knowledge of third-person mental states does. Thus, he argues that the argument from analogy makes knowledge of one's own mind asymmetrically prior to knowledge of other minds, while a theory-theory of self-knowledge treats them symmetrically, as equally dependent on theoretical inference. Thus, the argument from analogy and the theory-theory of self-knowledge are incompatible.

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[24] For some of these, and challenges to the distinction, see Davies and Stone (1995a,b), and Carruthers and Smith (1996). See also Millikan (vol. 2, ch. 8.4), who distinguishes ontological, ontogenetic, and epistemological questions about thoughts of other minds, on which theory-theory and simulation theory may differ.

Meltzoff might respond by rejecting this kind of theory-theory for self-knowledge while retaining his account of how mind reading builds on imitation, with its first-to-third-person inference. Philosopher Ruth Millikan argues, referring to Wilfrid Sellars, that theory theorists have other resources to draw on in characterizing self-knowledge, and that a critique of theory-theory needs to go deeper than Goldman's. She traces the theory-theory of mind reading back to a more general philosophical view of Willard Van Orman Quine and Sellars about the nature of thoughts, which was then applied to thoughts about other minds in particular, or mind reading. Undermining the theory-theory of mind reading, she argues, requires showing either that the more general view of thoughts is mistaken, or that thoughts about other minds are peculiar in some way, so that the more general view does not apply straightforwardly to them.

Quine and Sellars held that thoughts acquired their content in the same general way as theoretical terms in a scientific theory: in virtue of their inferential relations to one another, as well as to inputs and outputs. Millikan's own view is that this general view of thought is wrong (Millikan, 2000). But even if we assume that this general view is correct and that thoughts are in general identified by their inferential or functional roles, what should we say about the specific case of thoughts about another's thoughts, that is, mind reading? Surely, Millikan urges, thought about inferential roles and their relations rests on our own inferential dispositions, not on entirely independent beliefs about laws that govern inferential roles. Millikan's suggestion is that thinking about a thought requires me to be able to entertain that thought, which can be regarded as a kind of offline processing, or simulation. However, other mental processes in addition to mind reading, such as imagining and hypothetical thinking, also require offline simulation. She is skeptical that such simulative processes in general, or mind reading in particular, are directly linked to imitation.

Goldman finds a simulationist approach to the links between imitation and mind reading more promising than a theory-theory approach. He considers two compatible proposals: first, that simulationist mechanisms guide some imitation as well as mind reading, and second, that imitation plays a pivotal role in the development of advanced mind reading via simulationist mechanisms.[25]

To motivate the first proposal, Goldman notes that autists tend to be deficient in imitative skills, especially those requiring perspective switching, as well as in mind-reading skills. The two deficits may have a common

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[25] Compare the links described by Hurley (vol. 1, ch. 7).

cause: dysfunction in simulation mechanisms that normally enable perspective taking and thus underlie both abilities. He regards mirror neurons as a plausible neural substrate of such simulation mechanisms, since by means of them the observation of an action activates a similar goal-related plan (although that activity may be inhibited elsewhere). Thus, dysfunction of the mirror system may be at the root of a cascade of related problems in autism—problems with perspective-taking, imitation, and mind reading (see J. Williams et al., 2001).

Goldman's second proposal is that imitation contributes to advanced mind reading through role-play. Role-play is simulation that can be understood as a kind of extended imitation, in which an action type rather than an action token is copied creatively, with novel embellishments and including the mental states or processes appropriate to the action type. Children who engage in more role-play early on are better at advanced mind-reading tasks later, such as understanding that others may have false beliefs. Goldman sketches a progression in which action imitation extends to role-play, including mental simulation, which in turn contributes to mastery of advanced mind-reading skills.

Unlike Goldman, Wolfgang Prinz objects to the idea that we have direct, privileged access to our own minds, which we use to infer or simulate other minds. Organisms, Prinz argues, are designed to know the world at the expense of knowing themselves; perceptual mechanisms cancel out information deriving from the self in order to distill information about the world from the total information available. While we must, of course, use our own minds to know the world, our privileged access is to the world, not to our own minds. We come to understand ourselves as like others in part as a result of our experience as infants of being imitated by adults; the infant needs such a "mirror" to get to know herself.[26] Being imitated enables the infant to overcome the tendency to cancel out self-information in order to know the world; it allows an infant to perceive her own actions through the other. But, as Prinz admits, this view of self-knowledge does not address the question of how being imitated is recognized (see Decety and Chaminade, vol. 1, ch. 4), or indeed of how other minds are understood in the first place.

Philosopher Robert Gordon's radical version of simulation theory, which is quite different from Goldman's, explicitly rejects the first-to-third-person direction of explanation in understanding other minds. Note that it is a

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[26] Compare the role of being imitated in addressing the correspondence problem, in Heyes's account of imitation (vol. 1, ch. 6).

mistake to associate simulation theories too closely with the first-to-third-person arguments from analogy (Gordon's view is a counterexample) or theory theories with rejection of this type of argument (Meltzoff's view is a counterexample). The theory versus simulation distinction cuts across acceptance or rejection of the first-to-third-person direction of explanation.

Gordon here examines the links between imitation and mind reading from his own simulationist perspective on mind reading. Goldman finds no link between imitation and what he calls the "rationality" or "charity" approach to understanding other minds, versions of which are associated especially with Donald Davidson (1982, 1984) and Daniel Dennett (1987). However, Gordon's version of simulation theory is at the same time a variant of the rationality approach.[27] The role of rationality in Gordon's view of mind reading as simulation turns out to be important for understanding both how he connects imitation with mind reading and how he aims to avoid the first-to-third-person move in his account of mind reading.

In the course of comparing Meltzoff's and Gallese's views, Gordon distinguishes two kinds of mirroring response. In constitutive mirroring, a copied motor pattern is part of the very perception of the other person's action, although the motor pattern may be inhibited and thus not produce overt movement. By contrast, in imitative mirroring, a motor pattern that was active when the other person's action was observed is reactivated without inhibition. The same mirror neurons may be active in both.

Gordon finds constitutive mirroring in Gallese's account of the primitive intersubjective "we" space or shared manifold, which is the basis of empathy and which implicitly expresses the similarity of self and other (but not, as Gallese points out, their distinctness). Gallese understands empathy to involve, not the recognition of others as bodies endowed with minds, but rather the assumption of a common scheme of reasons by reference to which persons, self and others alike, are intelligible (vol. 1, ch. 3; see and cf. Strawson, 1959). Gordon proposes, in more detail, that when constitutive mirroring imposes first-person phenomena, a process of analysis by synthesis occurs in which the other's observed behavior and the self's matching response—part of the very perception of the other's behavior—become intelligible together in the same process. For example, when I see you reach to pick up a ringing phone, your act and my matching response are made sense of together, within a scheme of reasons that is part of the funda-

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[27] See also Gallese (vol. 1, ch. 3), for implied links among imitation, a simulationist approach to mind reading, and rationality assumptions.

mental commonality of persons. I don't infer from the first to the third person, but rather multiply the first person.

Gordon finds the first-to-third-person inference in Meltzoff's account problematic, not because it attributes *similarity* to one's own and others' acts or experiences, but because it requires that they be *identified* and *distinguished*. In the first stage of Meltzoff's account, the similarity between acts of self and other is supposed to be established by their innate equivalence, which is exploited by early imitation; this stage may involve constitutive mirroring, as in Gallese's primitive shared manifold. But the second and third stages of Meltzoff's account, where the analogical inference occurs, requires that self and other also be distinguished. If this kind of act *of mine* is linked to *my* experiences of a certain kind, then a similar (as established in stage one) kind of act *by another person* is also linked to that person's experiences of a similar kind. As Gordon says, if I cannot distinguish *a* and *b*, I cannot make an analogical inference from *a* to *b*. While such an inference may sometimes be a feature of mature imitative mirroring, Gordon regards it as beyond the capacities of infants.

However, a standard charge against pure simulation theories of mind reading has been that they lack the resources to explain how mature mind readers distinguish and identify different people and keep track of which actions and mental states belong to which people. Gordon suggests that multiple first persons are distinguished and tracked in the process of making them intelligible as persons, to avoid incoherence and disunity under the common scheme of reasons (see and cf. Hurley, 1998, part I). Mental states that do not make sense together are assigned to different persons. But can this be done in pure simulation mode, with no overlay of theory and inference? Simulation is supposed to be offline use of practical abilities, in contrast to theorizing about the actions and thoughts of others. But what exactly is the difference between making sense of an action and theorizing about it? When I use practical reason offline in mind reading, I don't formulate normative laws from which I make inferences; rather, I activate my own normative and deliberative dispositions. As Millikan might say, my thought about another's action is not wholly separate from my entertaining that action.

A suggestion worth considering here is this: The fundamental *similarity between self and other* may best be understood, not in terms of theorizing, but rather in terms of simulation (as in Gordon's constitutive mirroring, Gallese's shared manifold, Hurley's level three, or the innate self–other equivalence exploited by early imitation, in Meltzoff's view; a question that needs further attention is whether this fundamental intersubjectivity should be understood to hold at the subpersonal level, at the personal level, or both). Such primitive intersubjectivity may persist into adulthood and remain an essential aspect of mature empathy and mind reading, as Gallese suggests. But as mind reading develops, it also employs a *self–other distinction*, as when an older child attributes to the other false beliefs, different from her own, or distinguishes imitating from being imitated (see Decety and Chaminade in vol. 1, ch. 4 and Hurley's stage 4 in vol. 1, ch. 7). More generally, mature mind reading requires the ability to distinguish, identify, and track different persons and to assign acts and mental states to them. The full range of distinctions and identifications that mature mind reading requires may indeed draw on theoretical and inferential resources, even while the simulative foundation remains essential.

Developmental psychologist Moshe Anisfeld represents a minority (including Celia Heyes and Susan Jones) who remain skeptical about evidence for very early and newborn imitation. He defends here a more extended, Piagetian timetable for representationally mediated imitation (as opposed to mere contagion effects, such as contagious crying by very young infants). Piaget regarded facial imitation as representational, since the imitator cannot see his own act and so must infer its correspondence to the observed act. Anisfeld finds evidence of facial imitation persuasive only for infants more than 6 months old. Work claiming to show earlier facial imitation, he argues, is subject to various methodological criticisms; in his view, there is convincing evidence only for tongue protrusion effects, but these are better understood as arousal effects than as imitation. Piaget regarded deferred imitation as representational when a novel activity is copied after a delay and without any immediate practice having occurred. Anisfeld finds evidence of deferred imitation persuasive only for infants that are more than 11 months old. He argues that work purporting to show earlier deferred imitation suffers from inappropriate controls, or fails to meet the novelty requirement. Moreover, Anisfeld finds support for Piaget's views about the development of representational abilities in work showing how children acquire the ability to generalize deferred imitation in stages: first across different test environments, and then later across different types or colors of stimuli.

The contribution of imitation to understanding other agents is examined in earlier chapters by Gallese, Hurley, Meltzoff, Goldman, and Gordon. By contrast, psychologists Michael Tomasello and Malinda Carpenter, like Rizzolatti, emphasize the contribution of action understanding to imitation. Here Tomasello and Carpenter review work in the past decade on the ways that imitative learning depends on intention reading.

In 1993, Tomasello, Kruger, and Ratner found no convincing evidence of imitative learning in nonhuman animals, and proposed that the understanding of behavior as goal directed or intentional distinguishes human social learning from social learning in other species. In this view, while human beings can either imitate observed means or choose other means to emulate observed goals, other animals do not distinguish means and goals in this way. Animals can copy movements without understanding their relevance to goals, or can learn about the affordances of objects by observing action on them. In neither case, the claim was, do other animals learn about the intentional, means-end structure of the observed action.

Subsequently, Whiten and colleagues obtained results with apes, using artificial fruit in a two-action paradigm, which were described earlier as widely influential in overcoming skepticism about imitation by apes. Tomasello and Carpenter comment here that such results can be interpreted in more than one way. Does a differential tendency to push or pull a rod to open the artificial fruit, in accordance with the model shown, reveal imitative learning with intentional structure or only emulation and affordance learning? They argue that other paradigms developed with children, which they review here, have made a clearer distinction between imitative learning and other forms of social learning (see also Meltzoff, vol. 2, ch. 1.5). It remains to be seen what results these methods will yield with other animals.

In these paradigms, the modeled action is unsuccessful or accidental. If the observer copies what was intended even though it was not shown, as opposed to only the observed movements or the observed though unintended result, that suggests the observer understands the intentional structure of the observed action. For example, an action modeled with an "Oops" indicating it was accidental is copied by 14- to 18-month-olds less than the same action without the "Oops." Eighteen-month-old infants (but not 12-month-olds) copy modeled actions equally whether they are successful or unsuccessful; they read the intended result into the model and produce the successful action even if they have only seen the unsuccessful model. While 14-month-olds copy an unusual means, such as touching the light box described earlier with their heads, they do so more often when the model's hands are free than when she is holding a blanket (Gergely et al., 2002). This suggests that the children infer that the model whose hands are free must have some purpose in adopting this unusual means, even if the purpose is obscure. Moreover, children learn more from an otherwise identical demonstration if they already have information about the model's prior intentions when they watch the demonstration.

Tomasello and Carpenter argue that in recent demonstrations of imitative learning in which the modeled behavior is the same and only the modeled intention varies across conditions, the ability to read intentions is needed to explain what is copied. Given the results from the various imitation paradigms, they regard it as most parsimonious to assume that children use their understanding of intentions to imitate. Further progress in understanding social learning in children and other animals can be made, they suggest, by paradigms that systematically factor the information at the social learner's disposal into information about the demonstrated behavior, its results, its context, and the demonstrator's intention.[28]

How then should we view the relationship between imitation and mind reading? On the one hand, Tomasello and Carpenter emphasize the dependence of full-fledged imitative learning, with an intentional, means-ends structure, on intention reading, and Rizzolatti similarly argues that action understanding precedes imitation. On the other hand, chapters by Hurley, Meltzoff, Goldman, and Gordon argue in various ways that imitation underlies early mind-reading abilities. Are these views in conflict?

Not necessarily, in our view. In order to appreciate their potential compatibility, however, it is important to distinguish various stages or levels in both imitation and mind reading and the ways these could build on one another dynamically in evolutionary and developmental processes. Recall the way Rizzolatti argues that action understanding precedes imitation in evolution: he distinguishes the mirroring of movements (in response priming) from the mirroring of goals (in emulation) and from genuine imitative learning with a flexible intentional structure relating observed means to observed results. He suggests that the capacity to copy observed results via mirror systems may underlie a phylogenetically early understanding of action in terms of goals and intentions, which in turn is needed for phylogenetically later imitative learning with intentional structure, in which the mirroring of means and of ends are linked flexibly in the larger mirror circuit that is characteristic of human beings. Recall also earlier suggestions that recognition of a fundamental self–other similarity via simulation (as in Gallese's primitive shared manifold, Hurley's layer three, Meltzoff's innate self–other equivalence, Gordon's constitutive mirroring) may developmentally precede the registration of a self–other distinction, and more generally precede the inferential abilities, on which more advanced mind reading

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[28] Recall Harris's suggested experiment with monkeys, described earlier.

depends, to identify and distinguish persons and to keep track of which mental states go with which persons. Very early imitation may express a fundamental self–other similarity, while the distinctive human capacity for imitative learning with its flexible means-ends structure in turn contributes to the development of the self–other distinction and of more advanced mind-reading skills.

Developmental psychologists Paul Harris and Stephen Want focus on the ability to imitate selectively, which they suggest may require a certain level of mind-reading ability. They compare the capacities of 2-year-old and 3-year-old children to learn from observing others correct their own errors in using tools. One series of experiments employs a transparent tube containing a toy that can be pushed out of the tube with a stick; however, if the stick is pushed through the tube in the wrong direction, the toy will be trapped inside.[29] Few 2-year-olds find the solution without demonstration. Some of them are then given a demonstration in which the model extracts the toy correctly, while others observe a model who first makes an incorrect attempt, says "Oops" to register his own mistake, and then goes on to extract the toy correctly. Children in both groups of 2-year-olds learn from the demonstration to use the stick to try to extract the toy, but in neither group do they learn how to do so correctly. They apply the stick in the two directions at random, and extract the toy about half the time. Similarly, 3-year-olds who observe the model are only able to extract the toy about half the time. However, a significantly higher level of success is achieved by 3-year-olds who observe the model correct his own error. (Just observing the incorrect demonstration without subsequent correction does not lead to success at either age.[30])

Harris and Want interpret these results in terms of different capacities for selective imitation. The 2-year-olds learn nonselectively from whatever demonstration they are given: correct, incorrect, or both. But the 3-year-old children have a capacity for selective imitation, which is revealed when they observe both the correct and incorrect variants and differentially select the correct variant. It is interesting that the older children learn more efficiently by observing a model's mistake and immediate self-correction than they do from their own string of trial-and-error attempts. The 3-year-old's greater capacity for selective imitation here may turn on the development of either sufficient intention-reading skills to understand the model's deliberate self-correction after a first unsuccessful attempt, or sufficient

[29] Similar results are obtained using a different apparatus.

[30] Note the parallels with Pepperberg's training of Alex.

understanding of the causal mechanics of the task. Harris and Want favor the former explanation and suggest a further experiment to address this issue.

They also sketch an intriguing possible connection between the development of selective imitation and the course of cultural evolution. In the upper Paleolithic period, an explosive development of complex tool forms began, after a very long period during which a standardized form of hand axe persisted more or less unchanged. What accounts for this relatively sudden change after such a long period of stasis? If imitation is the mechanism that gives rise to the ratchet effect described earlier, thus enabling culture to accumulate and evolve, could this advance in the development of human tool use be explained by the advent of human imitative learning? Perhaps the neural mirror systems for movements and for goals became linked at around this point into a larger mirror system, enabling characteristically human imitation with its flexible means-ends structure. However, Harris and Want doubt that the advent of imitation per se provides the needed explanation; the standard hand axes that persisted for so long already required a complex and challenging production process that was itself probably guided by imitative learning. Moreover, they argue that nonhuman primates display a capacity for imitative tool use and yet no ratchet effect occurs in their tool culture. Rather, Harris and Want suggest, the spark that set off cumulative progress in human tool use may have been a distinctively human shift from nonselective to selective imitation, not found in other primates, which speeded up the selective transmission of more effective tool variants from one generation to the next. On the other hand, recall that Whiten and colleagues report that chimps imitated selectively, while 3-year-old children did not, in a variant of Harris and Want's task! The jury is still out on how to explain these different results concerning selective imitation in children (see Whiten, vol. 1, ch. 11).

Neurologist Marcel Kinsbourne's hymn to imitation sounds themes from both preceding and following chapters in describing the ways in which human beings can find social entrainment more compelling than reason. The enactive encoding of objects in terms of their affordances for action is a pervasive general phenomenon that underlies imitation in particular: observed action affords imitation. But chasing predators is inadvisable; it is adaptive to inhibit overt imitation in many circumstances. Even infants imitate selectively; recall that they do not copy mechanical devices in the same way as they do people.

Yet the fact that patients with damage to frontal inhibitory areas imitate too widely suggests that overt imitation is just the disinhibited tip of the iceberg of continual covert imitation, which is itself just one aspect of enactive encoding. While covert imitation may function to assist the analysis of speech input through simulative synthesis,[31] Kinsbourne also suggests that it reflects a fundamental motivation of human beings, adults as well as children, to interact synchronously or entrain with one another, which is a mechanism of affiliation as well as of social perception and learning. He regards imitative entrainment as having potent persuasive effects, emotional as much as cognitive, on human beings.

Philosopher Susan Brison comments that Kinsbourne's view of the compelling social influence of imitative entrainment contrasts strikingly with the overrationalist dismissal of imitative influences that is often expressed when freedom of speech is invoked to argue against regulation of violent entertainment. She raises two important questions about what is in effect the ecology of responsibility. First, if a cultural environment entrains imitative violence, are the perpetrators of such violent acts nevertheless responsible for their acts? Second, should citizens take responsibility for doing something about the resulting violence? We can, she argues, answer *both* questions positively. Later chapters by Eldridge and by Huesmann take up related issues. Educationist Guy Claxton is struck by the importance for education of the pervasive although selective tendency to entrain; of the way the intentional stance arises out of the intentional dance, as he puts it. More generally, Kinsbourne's view of the powerful human tendency to entrain through imitation prompts questions about the broader social and cultural effects and functions of imitation. These are the focus of vol. 2, part II.

Volume 2, Part II Imitation and Culture

Social psychologist Ap Dijksterhuis agrees with Kinsbourne that imitation has important affiliative functions and is the default social behavior for human beings. The results he presents indicate that imitative behavior in human social interactions may be much more common than is generally recognized.

Dijksterhuis distinguishes two imitative pathways. First, he describes a "low road" to the imitation of specific observed behaviors, arguing that we are wired for such imitation by shared representations of our own acts and observed acts, such as those discussed in vol. 1, part I in connection with mirror neurons and ideomotor theory, and in vol. 2, part I in connection

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[31] See also Gordon (vol. 2, ch. 3), on simulative analysis by synthesis.

with innate self–other equivalences expressed in early imitation. However, his main focus here is on the less direct "high road" to the imitation of complex patterns of behavior. On the high road, imitation is mediated unconsciously by the activation of personality traits and social stereotypes, which lead observers automatically to assimilate their behavior to general patterns of observed behavior. Such imitation, he argues, acts as "social glue," with many beneficial social consequences; in many (though importantly, not all) cases it leads people to coordinate actions, to interact more smoothly, and to like each other.

Dijksterhuis describes an extensive series of experiments that provide striking evidence of heavy travel on the high road to imitation in everyday social life. In these experiments, normal adult participants are primed by exposure to stimuli associated with traits (such as hostility, rudeness, politeness) or with stereotypes (such as elderly persons, college professors, soccer hooligans). Hostility-primed participants deliver more intense "shocks" than control participants in subsequent, ostensibly unrelated experiments based on Milgram's (1963) classic experiments. Rudeness-primed participants spontaneously behave more rudely, and politeness-primed participants more politely, than control participants in subsequent, ostensibly unrelated interactions with experimenters. Youthful participants who are subliminally primed with words associated with the elderly, such as "gray," "bingo," or "sentimental," subsequently walk more slowly, perform worse on memory tasks, and express more conservative attitudes than age-matched control participants. College professor-primed participants perform better and soccer hooligan-primed participants perform worse than control participants on a subsequent, ostensibly unrelated general knowledge quiz. Such priming results are very robust. They hold across a wide range of verbal and visual primes and induced behavior, and when the primes are presented subliminally as well as when participants are conscious of them.[32] Either way, participants are unaware of any influence or correlation between the primes and their behavior.

As Dijksterhuis explains, these results show imitation in a broader sense than we have been considering up to now; traits and stereotypes elicit general patterns of behavior and attitudes, and influence the ways in which behavior is carried out, rather than eliciting specific novel behaviors. These broad imitative influences have been referred to as the *chameleon effect*

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[32] See also Bargh et al. (1996), Bargh (in press), Bargh and Chartrand (1999), Chartrand and Bargh (1996, 1999, 2002), Carver et al. (1983), Chen and Bargh (1997), Dijksterhuis and Bargh (2001), and Dijksterhuis and van Knippenberg (1998).

(Chartrand & Bargh, 1999). They are rapid, automatic, and unconscious, and do not depend on any conscious goal of the participant, making imitation the default social behavior for normal human adults. Just thinking about or perceiving a certain kind of action automatically increases, in ways participants are not aware of, the likelihood of engaging in that general type of behavior oneself. Nevertheless, these influences are often inhibited, for example, by goals that make conflicting demands; elderly-primed participants don't walk more slowly if they have an independent need to hurry. These influences are also inhibited when participants are focused on themselves. Again, overt imitation is the tip of the iceberg of underlying covert imitation.

Another leading researcher in this area, social psychologist John Bargh, has emphasized elsewhere how very hard it is for people to accept that these broad imitative tendencies apply to themselves, both because they are unconscious and automatic, so that people are not aware of them, and because such external influences threaten their conception of themselves as being in conscious control of their own behavior (Bargh, 1999). Participants are surprised by, and even tend to resist, the experimental findings. We might expect resistance to be especially strong where the high road to imitation would make antisocial behavior more likely, as in exposure to aggressive traits and stereotypes in violent entertainment, discussed by Eldridge, vol. 2, ch. 11 and Huesmann, vol. 2, ch. 12. Nevertheless, it seems plausible to suppose that the power of broad imitative influences on behavior is recognized and exploited by advertising campaigns that expose viewers to traits and stereotypes. As Bargh suggests, recognizing that we are subject to such automatic and unconscious imitative influences may help us to gain control of them and to assimilate behavior patterns more selectively.

In addition to being subject to automatic imitative influences, human beings often deliberately select a pattern of behavior to imitate because it is associated with certain traits and stereotypes, even if they do not actually partake of these traits or stereotypes. This can be benign; perhaps I can become virtuous, as Aristotle suggested, by behaving like a virtuous person. But like automatic imitation, deliberate selective imitation does not always operate benignly. For example, a group of cooperators may develop shared behaviors by means of which members identify one another as cooperators and exclude noncooperators from free riding. Noncooperators may then selectively imitate such behaviors in order to induce cooperative behavior from group members, and then fail to return cooperative behavior, thus deceptively obtaining the benefits of cooperation without paying the costs.

So-called "*greenbeard genes*" could produce genetically determined analogues of such imitative free riding (see Dawkins, 1982, p. 149). However, the evolution of a general capacity for selective imitation would make it possible to obtain the advantages of free riding without the need to evolve genes for specific behaviors (see Hurley, in press).

Sociologist Diego Gambetta examines the deceptive uses of selective imitation to impersonate members of a group or category to which the mimic does not belong. Adopting the term used in biology, he refers to such deceptive impersonation as *mimicry*, which he analyzes in terms of the relations among three roles: the mimic, the model, and the dupe. (Compare the quite different sense of "mimicry" in Call & Carpenter, 2002, p. 214, and Tomasello et al., 1993: copying modeled behavior without understanding its goals.) In models, an unobservable property is correlated with observable signature behaviors. The mimic imitates[33] the model's observable signature behaviors in order to mimic the model's unobservable property; that is, in order to deceive the dupe into treating the mimic as if he possessed the model's unobservable property as well as its observable behavior. The model or dupe in turn may develop defenses against mimicry. Gambetta provides a rich and often amusing set of examples of the relentless semiotic warfare among mimic, model, and dupe as they search for new ways to "outwit" one another, whether via genetic signs or intentional signals. The conditions under which mimicry is possible can be analyzed by means of signaling theory, which specifies equilibrium conditions under which truth is transmitted even when the signalers have an interest in deception, but Gambetta enriches this abstract analysis in two ways. First, he provides a set of illustrated semiotic distinctions: *cues* are costless to display and often mimic-proof; *marks* are lifestyle by-products that are often costly to mimic; *symbolic signs* are often cheap to display, of low evidential value, and vulnerable to mimicry. Second, he distinguishes various triangular relationships among mimic, model, and dupe. For example, is mimic pitted against dupe, via model, or pitted against model, via dupe? Gambetta calls for a systematic interdisciplinary extension of the study of mimicry.

Lawyer Harry Litman provides an example of Gambetta's concerns in the contemporary crime of identity theft. Commenting also on the research surveyed by Dijksterhuis, Litman notes that its potential public policy implications are immense, most obviously concerning the protection of media violence on freedom of speech grounds. However, in his view fur-

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[33] Although mimicry does not always rely on imitation; for example, it can rely on lying instead.

ther work is needed on the magnitude, selectivity, evolutionary role, and neural basis of high-road imitative effects, especially when the implications for policy about media violence are in question.

Sociologist John Eldridge takes up the question of why disagreement persists about the imitative influences of media violence. The issue has been highly politicized by libertarian, moral right, and feminist agendas and distorted by misleading reporting; some have questioned whether media violence can be identified and its effects researched objectively. Eldridge acknowledges the many studies showing a correlation of exposure to media violence and actual violence, as well as longitudinal studies concluding that causation runs from media violence to actual violence, such as those by Rowell Huesmann, described in vol. 2, ch. 12.

But Eldridge presses the point that causal claims rest on decisions about how the causal relata are identified, and he raises general issues about how images of violence are contextualized and given meaning so as to lead to one response rather than another. Eldridge finds it less fruitful to focus on the imitation of particular episodes of media violence than on the powerful role of the media today, including media violence, in the processes of socialization and transmission of values. For example, he describes a study in which 10-year-olds express a view of killing in the film *Pulp Fiction* as "cool." Yet he also emphasizes the different interpretations given to images of violence, taking images of war as an example. Are they viewed as news, expressions of patriotism, manipulative propaganda, spectacle, history, fictional entertainment, art? The influence of such images can depend significantly on the way they are interpreted. In his view, media violence contributes, along with other influences and subject to many contextual variables, to the vocabulary of motives by which we understand, excuse, and justify conduct.

George Comstock, co-author of a major meta-analysis linking media violence with actual violence (Paik and Comstock, 1994), agrees with many of Eldridge's points about interpretation and context, but is concerned that they may obscure important empirical issues about the imitation and emulation of violence. These issues arise even if, with Eldridge, we focus on broad patterns of behavior mediated by assimilation of stereotypes or values from the media (as in Dijksterhuis' high road to imitation) instead of on the copying of specific behaviors. Comstock argues that the combined weight of many studies makes it "irrefutably clear" that young people exposed to more media violence are more likely to behave aggressively; that there is a strong case for causation, not merely correlation; that the "reverse hypothesis" that aggressiveness leads to viewing of media violence is not supported by the evidence; that effect sizes are significant and comparable to those found in major public health risks; and that the influence of media violence extends to illegal and seriously harmful behavior.

Psychologist Rowell Huesmann concurs that the evidence is compelling that exposure to media violence increases the probability that children will behave aggressively. Huesmann usefully distinguishes short-term processes, which include priming, excitation transfer, and immediate imitation, from long-term influences that operate through observational learning (of schemas for attributing hostile intentions, of scripts linking situations to aggressive responses, and of norms for evaluating such scripts) and desensitization. While the long-term influences are cognitively mediated and lead to broad patterns of behavior, repeated short-term effects contribute to establishing long-term patterns of aggression. Huesmann presents an integrated view of empirical support for the causal influence of media violence on actual aggression from various mutually supporting paradigms. These include well-controlled experiments, robustly replicable correlational studies from various countries, and longitudinal studies and regression analyses showing that exposure to media violence during childhood predicts actual aggression years later, but not vice versa (when other possible explanations are controlled for, including initial aggressiveness, class, education, and so on).

Since 80% of those doing research on media violence conclude from the evidence that this form of violence is causing aggression, why, Huesmann asks, do a minority deny this causal link, and why does public understanding lag so far behind the evidence? Powerful vested interests are at stake; we dislike any suggestion of censorship; and, as social psychologists have emphasized, our conception of ourselves as autonomous is threatened by evidence of imitative influences in general, let alone when they are influences to aggression. But Huesmann suggests that the most powerful explanation is that the general importance of imitation in socialization and the molding of human behavior patterns has not yet been widely appreciated. In particular, he suggests, recent scientific work on the mechanisms and functions of imitation, such as the work reported in these two volumes, has not yet been digested, either by relevant disciplines or by the public. As Hurley comments, the risks associated with media violence may be better and more widely understood when what is being learned about imitation in general has been more widely assimilated and has been applied to the imitation of violence in particular.

Philosopher Jesse Prinz examines the failure of moral emotions to develop in psychopaths and the role of imitation in the normal development of moral motivations. Normally, he argues, moral judgments are intrinsically bound to moral emotions, and hence are intrinsically motivating. This link results from a process of moral development in which emotional mirroring and imitation play critical roles. But in psychopathy, emotional and hence moral development fails.

Psychopaths are often intelligent and can recognize that certain behaviors are conventionally regarded as wrong, but they fail to distinguish actions that would be wrong even if there were no rule against them (such as hitting other students) from actions that are merely against the rules (such as not wearing the correct uniform to school). They show deficits in nonmoral emotions, such as fear and sadness in nonmoral contexts, as well as deficits in moral emotions, such as empathy with others in distress. They are impulsive and find it difficult to inhibit an initial response or default plan of action. Prinz understands this constellation of features in terms of a deficit in the behavioral inhibition system (see Gray, 1987) that underlies many aspects of emotion and motivation. Psychopathic deficits in inhibitory emotions such as sadness and fear, Prinz suggests, may be symptoms of this underlying deficit. A sadness deficit may in turn contribute to lack of empathy with others' sadness, and remove one of the components of more complex emotions such as guilt and shame.

Prinz goes on to argue for the importance of broadly imitative processes in four stages of normal moral development. Moral responsiveness begins with emotional contagion and vicarious distress; young children "catch" emotions from others by imitating observed facial expressions and in other ways.[34] Imitative learning contributes in turn to the development of more active prosocial responses to other's distress, such as consoling; the acquisition of sensitivity to normative rules; and finally the acquisition of moral emotions and the distinguishing of moral from other norms. Moral development can be impaired by bad role models in these imitative processes, as well as by emotional deficits such as those found in psychopaths.

Prinz's account of moral development resembles Adam Smith's eighteenth-century theory of sympathy at certain points, especially with respect to emotional contagion. Smith hypothesizes that when I observe another in a situation that would induce a certain feeling in me, I automatically experience a weaker version of that feeling. Robert Sugden observes the way current work on emotional mirroring, its neural basis and

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[34] See the discussion of emotional mirroring and its neural basis in Rizzolatti (vol. 1, ch. 1), Iacoboni (vol. 1, ch. 2), Gallese (vol. 1, ch. 3), and Decety and Chaminade (vol. 1, ch. 4).

its developmental role, supports Smith's theory. Smith also postulates that human beings are fundamentally motivated to bring their feelings and responses into correspondence with those of others—thus in effect agreeing with Kinsbourne that people love to entrain. Commenting on Prinz's chapter, Huesmann concurs on the importance of emotional contagion in moral development, but also emphasizes the imitative aspect of the cognitive processes by which we learn to evaluate morally the scripts available to govern behavior (which may themselves have been imitatively generated, in his view), and to reject scripts that are morally unacceptable.

Psychologist Merlin Donald views human imitative skills as part of the broader human capacity for *mimesis*: purposeful analog motoric communication that reenacts and creatively modifies complex episodes and behaviors as continuous wholes, without parsing into chunks represented by discrete symbols.[35] He argues that basic mimetic capacities evolved as primarily motoric adaptations in hominids about two million years ago and remain just out of reach for most primates. Mimesis enabled not just imitation but also the rehearsal and refinement of skills, the public motoric display of perceived or remembered episodes, social coordination and ritual, nonlinguistic gesture and pantomime, and reciprocal emotional display or mirroring.

Human mimetic communication preceded symbolic language and provided the fundamental support for the cultural interactions and conformity to norms that eventually led to language. Symbolic language was scaffolded on mimesis, Donald claims; it emerged from stabilized networks in which human beings with mimetic skills and analog brains interacted. Moreover, despite the immense historical overlay of linguistic culture, the human mind and its cultures are still fundamentally mimetic. Mimetic, analog styles of representation operate below the cognitive surface, affecting the way we use linguistically structured symbols and providing the foundation of our mental communities.

Morten Christiansen stresses that even if Donald is right about mimetic culture preceding and scaffolding language, more needs to be said to explain the commonalities of structure across the world's languages. While the usual question is, Why is the human brain so well suited for learning language?, we need to ask, Why is language so well suited to being learned by the human brain? Christiansen argues that natural language has itself adapted to strong selectional pressures provided by specific constraints on

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[35] Compare Byrne (vol. 1, ch. 9) on behavior parsing by gorillas and Arbib (vol. 1, ch. 8.2) on the decompositional structure of imitation and its relationship to syntactic structure.

human learning and processing capacities, in particular, the capacities for processing sequential and hierarchical structures. That is, linguistic universals are not themselves genetically specified, but rather reflect the cultural evolution of language to fit universal but language-independent features of human cognition, and thus to be learnable. Moreover, the pressures operating on language to adapt to human learning capacities are significantly stronger than those operating on humans to be able to use language. Despite the differences among them, Donald, Christiansen, Byrne, Iacoboni, and Arbib agree in suggesting that social learning of the structure of complex actions may provide an essential evolutionary foundation for linguistic capacities.

As Susan Blackmore explains, "mimetic" in Donald's sense should not be confused with "memetic" in the sense of meme theory, as first proposed by Richard Dawkins and developed by herself (Blackmore, 1999), Daniel Dennett (1995), and others. According to meme theory, memes are analogous to genes in that both are replicators that evolve through a process of imperfect copying under selective pressure. Memes are understood to be whatever is copied by imitation, the mechanism that makes memetic evolution possible. So while imitation is just one aspect of mimesis in Donald's sense, it is fundamental to meme theory. While memes need not be representational, mimesis requires intentional, representational action. Donald views imitation as a relatively uncreative aspect of mimesis, while Blackmore argues that copying errors, recombination, and selection among variants makes memetic evolution creative in the same way that genetic evolution is. And while genetic adaptations may explain the emergence of basic mimetic capacities, including the capacity for imitation itself, meme theory explains culture in terms of the comparative reproductive success of memes themselves rather than the comparative reproductive success of genes.

What is the relationship between imitation and rationality? Modern human cultures tend to assume, as well as aspire to, rationality, despite experimental evidence of systematic human irrationality. The assumption that human beings make rationally consistent choices, as if they were maximizing along some single dimension of expected utility, is especially prevalent in economics. Biologists have also modeled animal behavior resulting from blind processes of natural selection as if it were the rational solution to maximizing problems. The gene-meme analogy thus leads to the question, Can a supposed tendency for human beings to act as if they were rational be shown to result from processes of memetic selection? Economist Robert Sugden answers "no." He argues, against an argument made by Ken Binmore (1994), that there is no reason to suppose that the memes that are most successful at being imitated will yield behavior conforming to rational choice theory.

Sugden's central point is that as-if rational behavior by replicators does not necessarily entail as-if rational behavior by the actors who carry those replicators. To make this point, he provides three related models of replicator population dynamics. Replicator types, whether genetic or memetic, replicate at a certain rate and have effects, via the choices made by the actors who carry them, on their own replication rates. For a replicator (as opposed to the actor who carries it) to behave as if it were rational means that it "acts" in such a way that it survives in a stable equilibrium. The three models make different assumptions about the causal loop by which replicators determine choices by the actor who carries them, and such choices in turn determinate rates of replication by replicators. The question then is, Will the as-if rationality of replicators lead the *actors* who carry the replicators to act as if they were rational?

Under unrealistically simplifying assumptions about the causal loop, it will do so: where each replicator type is the cause of one and only one action type, and where replicators reproduce asexually by producing exact copies of themselves. In this first model, decision probabilities exactly reflect the dynamics of the replicator population, and the actors as well as the replicators behave as if they were rational. But under more realistic assumptions, this does not hold. Sugden's second model shows that as-if rationality by genetic replicators does not induce as-if rationality by actors where reproduction is sexual, where each actor has genes from two parents and passes on at random only one of its pair of genes to its offspring, so that actions are determined by a combination of genes and decision probabilities no longer mirror the population of genes.

Nor do actors inherit as-if rationality from memetic replicators that reproduce asexually, but through selective imitation of other agents. In Sugden's third model, when actors meet, one actor compares the consequences of her own meme and the other actor's meme for a particular decision problem and decides accordingly whether to adopt the other actor's meme: whether to imitate. But these pairwise comparisons do not guarantee that the decision probabilities across the population of actors will respect transitivity; the decision probabilities may cycle in a way that is irrational at the level of actors, although they may be explicable at the level of memetic replicators.[36]

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[36] Many readers will no doubt be reminded here of the rational individual preferences and irrationally cycling collective preferences of social choice theory; see Arrow (1963).

As economist Paul Seabright and philosopher Mark Greenberg both emphasize, Sugden shows that rational behavior is not *guaranteed* to develop by genetic or memetic evolution, but leaves quite open whether it may *in fact* have developed by such means, which is a further, empirical question. Sugden's concern is to show that purely a priori approaches to this question are misguided. Just as the theory of biological evolution depends on an empirical understanding of actual genetic mechanisms, so we need to know "messy" facts about the causal loops governing memes and about their human transmitters, in order to know the consequences of memetic selection for the rationality of behavior.

Anthropologist Francisco Gil-White also calls for more empirical study of influences on the transmission of memes. He considers the common characterization of memes as selfish replicators to be mistaken. Nevertheless, he defends the usefulness of understanding cultural change in terms of Darwinian processes operating on memes, which are understood as elements of culture transmitted nongenetically that show inheritance, mutation, and selection. He explains that strict replication is not required by a Darwinian account of memetic evolution and cumulative adaptation, and responds to the objections that memes lack well-defined boundaries and that they change too rapidly for selection to determine cultural evolution. Nor does a Darwinian account of memetic evolution depend only on exact imitation as a copying mechanism; it can countenance other complex cognitive mechanisms of transmission, such as the emulation of a model's inferred goal based on observing a statistical cloud of the model's performances, even if these are unsuccessful. Gil-White emphasizes that the transmission of memes can depend, not just on the information content of the meme, but also on a range of noncontent-related influences described in classic work by Robert Boyd and Peter Richerson (1985), such as the meme's frequency in relation to other memes (*conformity bias*) and its association with high-status persons (*prestige bias*). While Harris and Want suggest in vol. 2, ch. 6 that selective imitation may explain cultural progress, Gil-White stresses the way noncontent biases on meme transmission can explain cultural differences. He sees memetic accounts of cultural change in terms of noncontent biases as rivals to "selfish-meme" accounts inspired by Richard Dawkins's selfish-gene theory. Finally, he criticizes Susan Blackmore's arguments that memetic evolution can drive genetic evolution. Blackmore in response defends her conceptions of memes as "selfish" and of memetic drive. She argues that Gil-White misrepresents meme theory's conception of replication and that meme theory can accommodate noncontent biases.

Mark Greenberg objects that Gil-White's defense of memetic evolution against the rapid-change objection assumes perfect selection: that everyone selects the most attractive variant of a particular type of behavior to copy, thus agreeing in their evaluations of such behavior. But in fact people may differ widely in their goals and hence their evaluations of others' behavior, and so select quite different examples to imitate. Moreover, human goal-seeking can result in radical departures from existing models rather than cumulative change.

Greenberg argues that the selfish-meme theory has the potential to challenge the commonsense goal-based account, but that its success will depend on its doing more explanatory work than competing goal-based accounts. For example, the development and spread of a technological innovation might naturally be understood as a result of deliberate, goal-directed thought and action: research, development, production, marketing, and rational consumer choice. The proliferation of an innovation may indeed reflect the differential imitation and survival of a meme for that innovation, yet human goals appear to explain *why* that meme is selectively imitated and hence spreads. (Greenberg's point here again recalls the suggestion by Harris and Want that *selective* imitation drove progress in tool use.) More generally, even when cultural changes do reflect the accumulation of variation under selective pressure, human goals may explain the selecting and hence the changes. Meme theory needs to show when and why the prima facie plausible goal-based account is inadequate and the deeper or more comprehensive explanation is that some memes are more conducive to their own replication than others are.

Greenberg draws an illuminating threefold distinction among ways in which memes might be selected. First, memes can be deliberately selected because of the relationship of their content to human goals: the commonsense account. Second, memes can be good at getting themselves copied by virtue of their content-related effects but regardless of whether they serve deliberate human goals (say, by exploiting other features of human psychology or society): the selfish-meme theory. Third, memes can be selected by mechanisms that are indifferent to their content, as in conformity or prestige biases: the noncontent bias theory. Noncontent bias accounts, in Greenberg's view, do not undermine content-based selfish-meme accounts. The fundamental issue is not between content-based and noncontent-based accounts of selection. Rather, it is whether either content-based selfish-meme theory or noncontent bias theory, or both in alliance, can do more explanatory work than the content-based, goal-directed, commonsense account.

Psychologist Nick Chater highlights another aspect of the explanatory competition between Darwinian memetics and commonsense, goal-based accounts of cultural change: speed. He distinguishes a Mendelian view of memetics, which he finds promising, from a Darwinian view, about which he is more skeptical than Greenberg. While Mendelian memetics explains cultural change in terms of the differential spread of memes, Darwinian memetics is more ambitious; it aims to explain cultural complexity as the result of blind selection among memes. As a result, he argues, Darwinian memetics faces a serious problem: Blind selection is slow and will be overtaken by fast intentional selection in the production of cultural complexity. Darwinian accounts of the emergence of biological complexity assume that variation is random, not directed, and that selectional forces operate by means of the reproductive success of whole organisms, not directly at the level of individual genes. But neither assumption holds for cultural transmission. We often create deliberate variation and imitate creatively, guided by our goals; we intentionally select particular aspects of models to imitate and decide not to imitate other aspects. Cultural complexity, unlike biological complexity, is largely produced by design; by sighted, not blind, watchmakers.

In response to the related challenges that Greenberg and Chater pose for meme theory, Blackmore agrees that goals are indeed relevant to memetic evolution, but they are just one of many factors contributing to selection processes. Selfish-meme accounts of religious practices do more explanatory work than goal-based accounts, she suggests, since the relevant goals were exploited and redesigned by religious memes.

Viewed in the overall context of these volumes, these last chapters come full circle by emphasizing the role of human goals in guiding deliberate selective imitation and hence cultural evolution. By what cognitive processes, deliberate or otherwise, do human beings acquire and pursue their goals? Other intelligent social animals can acquire goals by emulation, but few if any can learn imitatively novel means by which to achieve their goals. Other social animals do not engage, at least in the way that humans do, in mind reading—which arguably depends on the capacity for imitation and which certainly serves many human goals, along with other forms of simulative thought. However, human beings have a default tendency to imitate, automatically and unconsciously, in ways that their deliberate pursuit of goals can override but not explain. Do the distinctive human capacity and tendency to imitate at some level enable the effective, flexible pursuit of goals, or do goals guide selective human imitation—or both—in a dynamic process? To understand how culture emerges from biology, we should put the cultural roles of imitation into biological and psychological context. The cognitive neuroscience and the evolutionary and developmental psychology of imitation should inform our views of the roles and functions of imitation in human culture.

Why Imitation Matters

In light of the contributions from a variety of disciplinary perspectives that we have surveyed, the importance of imitation can be described in both substantive and methodological terms. Here we briefly sketch how the study of imitation illuminates substantive issues about the links between perception and action and between self and other; the modularity of mind; the relationships among various levels of description of minds in society; the relationship between genetic endowment and social environment in forming human minds; the relationships between cultural evolution, in which imitation is arguably the primary copying mechanism, and biological evolution, which gave rise to the capacity for imitation in the first place. We conclude by suggesting that the study of imitation illustrates promising methodologies for interactive collaboration among the cognitive and social sciences and philosophy.

The study of imitation sheds light on two relationships that are central to understanding minds in general and human minds in particular: the relationship between perception and action and the relationship between self and other. The following paragraph sketches our view of how it does so, drawing on suggestions in various chapters. While there is plenty of room for disagreement about the details, it is hard to doubt the relevance of imitation to these issues.

Hypotheses about the control, imitative, and simulative functions of the mirror system, and evidence from imitation studies for ideomotor and common coding theories, suggest that perception and action share a fundamental information space that is preserved as higher cognitive capacities and that distinctions are built on it (see Gallese, vol. 1, ch. 3; Decety and Chaminade, vol. 1, ch. 4; Prinz, vol. 1, ch. 5; Hurley, vol. 1, ch. 7; and Meltzoff, vol. 2, ch. 1). The distinction between results and the means to those results, on which goal-directed, perceptually guided intentional action as well as imitative learning depend, emerges as a flexible articulation of this shared processing (see Rizzolatti, vol. 1, ch. 1). However, perception remains fundamentally enactive, in a way that challenges orthodox views of perception and action as separate and of perception as motivationally inert (see Kinsbourne, vol. 2, ch. 7; see also and cf. Noë, in press). The intersubjectivity characteristic of human beings, the basis for their innate capacity to understand and empathize with one another, is enabled as a specialization of such enactive perception. Perceiving your action enactively, in a way that immediately engages my own potential similar action, thus enables me to understand, or to imitate, your action. Shared processing of the actions of other and self is a special aspect of the shared processing of perception and action. The problem of "knowledge" of other minds looks quite different from this perspective. It is not so much that intersubjective information bridges an informational gap between self and other as that the self–other distinction is imposed on the fundamental information space that self and other share. As Gordon puts it, the first person is multiplied—though care is needed over whether this multiplication is understood at the level of subpersonal information, at the personal level, or both (see and cf. Gallese, vol. 1, ch. 3; W. Prinz, vol. 1, ch. 5; Hurley, vol. 1, ch. 7; Meltzoff, vol. 2, ch. 1; and Gordon, vol. 2, ch. 3). Simulation theories of mind reading can be right about shared processing for self and other with respect to this fundamental intersubjectivity, even if more advanced aspects of mind reading require theorizing in ways enabled by language.

Imitation is also prime territory in which to investigate issues about the modularity of mind and the relationships among different levels of description: neural, functional, personal, social, and cultural. Does the study of imitation support views of cognition as emerging from layers of dynamic perceptual-motor skills scaffolded by social and cultural environments (horizontal modularity), rather than as embodied in a central module that interfaces between perception and action (vertical modularity; see Hurley, 1998, 2001; Brooks, 1999)? What does the common coding of perception and action in imitation imply about the modularity of mind? How do different levels of description of imitation constrain one another? How, for example, would shared subpersonal processing for self and other be reflected in personal-level understanding of others? What do neural mirror systems imply about imitation and mind reading? Why do some creatures have neural mirror systems but not imitative capacities, and what more is needed for imitation? What do hypotheses about the functional subpersonal architecture that enables imitation imply about neural structures and function (or vice versa)? About the development and nature of our capacities as persons to understand other persons? Do empathy and mind reading at the personal level depend on simulation? Is simulation, in effect, offline imitation? Is simulation a personal-level rival to theorizing, or a subpersonal mechanism, or both? Does cultural evolution depend primarily on blind, automatic mirroring mechanisms or on deliberative, goal-driven, selective imitation?

The study of imitation can contribute to our understanding of broad theoretical issues, such as those between nativists and empiricists about the relative contributions of genetic and environmental influences to psychology and language. These issues arise at various levels in the study of imitation. Why does a special capacity to learn imitatively from social environments evolve genetically—and why so rarely? What does imitation reveal about the relationship between human nature and other animals? Is the correspondence between perception and action that imitation exploits innate, as Meltzoff suggests, or is it acquired in cultural environments, as Heyes suggests? Does the location of mirror neurons in Broca's area suggest that imitative learning plays more of a role in language acquisition than nativists about language acquisition allow? Does imitation structure linguistic competence in some way as well as prompting performance (assuming that a competence/performance distinction is viable)? Do the recombinant ends-means and sequential-hierarchical structures and the self–other parity found in imitative action provide a basis for syntactic structure and shared meanings in linguistic action? If so, should we understand this foundation in evolutionary or developmental terms, or both? If not, what is the relationship between language and imitation? (See Iacoboni, Arbib, Byrne, Pepperberg, Pickering, Donald, Christiansen.)

More generally, imitation is a critical locus for understanding the ecology of human cognition and norms: the dynamic interactions between cognitive processes and sociocultural processes. Once the capacity for imitation has evolved, does it give rise to a new medium of evolution—culture—that can drive genetic evolution, or does genetic evolution remain in the driver's seat? Or do life and culture, brain and language, coevolve? Is automatic or selective imitation the primary engine of cultural evolution? (See Donald, Christiansen, Sugden, Gil-White, Greenberg, and Chater.) Are innate or cultural deficits primarily responsible for autism; for psychopathy; for violent aggression? Can individual responsibility itself be understood, compatibly with an innate human tendency to imitate, in partly ecological terms? (See Donald, Jesse Prinz, Eldridge, Huesmann, and Brison.) As we have seen, the study of imitation connects with practical issues; for example, it may have clinical applications in the treatment of autism (see Pepperberg, Jones), and policy implications in relation to media violence (see Huesmann, Comstock, Litman, and Hurley) and education (see Claxton). How should we respond to the irony of imitation: that the capacity for imitation appears to be a distinctive feature of human nature and may well be part of the basis for other distinctive features of human nature, such as mind reading and language, which together set us apart from other animals? Yet at the same time our innate, automatic tendencies to imitate can also threaten our conception of ourselves as autonomous and deliberative in ways that no other animals are.

Finally, the study of imitation illustrates a promising topic-based, interdisciplinary methodology. We have seen that imitation has important roles in human cognition and society. To seek a fundamental understanding of these, we do best to bring together the discoveries and theories of the various disciplines that study imitation, so that they can constrain, inform, and cross-fertilize one another—though of course we must remain aware of how specific aims and contexts differ across disciplines (see, e.g., Rizzolatti, vol. 1, ch. 1 and Byrne, vol. 1, ch. 9). In particular, these two volumes illustrate the fruitful interaction of techniques across disciplines: the interaction of single-cell brain recording; brain imaging work[37]; behavioral experiments; fieldwork; clinical work; and formal, conceptual, and theoretical arguments. Many new experiments as well as theoretical developments are suggested in these volumes as a result of interdisciplinary thinking.

These volumes also illustrate that there is work for philosophy to do that is often overlooked within a prevalent conception of philosophy as a strictly a priori discipline that addresses conceptual issues and is sharply separated from scientific inquiry about empirical matters. We do not subscribe to that division, but rather to the view that important conceptual and empirical issues are often densely and seamlessly intermingled, as they are in the study of imitation. As many scientists are aware, philosophical questions often grow organically out of scientific work, as again they do from work on imitation: questions that are at once philosophical and empirical and that can be addressed fruitfully by philosophy as well as by the sciences. We do not suggest that such questions should displace philosophy's historically derived traditional questions, but rather that they provide additional areas to which philosophical argument can contribute. Indeed, "natural philosophy" was long understood to include physics as well as metaphysics, logic, and ethics. We propose to revive and revise the term "natural philosophy" to describe the kind of empirically embedded philosophical work illustrated in these volumes.

Progress on some topics of fundamental and broad importance may demand topic-based research that cuts across disciplines, which, unfortu-

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[37] See the discussion by Iacoboni (vol. 1, ch. 2), Decety (vol. 1, ch. 4), and Kinsbourne (vol. 1, ch. 8.5) on the interaction of brain imaging and other techniques.

nately, contemporary institutional and disciplinary constraints often fail to facilitate. We hope that these volumes will encourage institutions to build opportunities for topic-based interdisciplinary research into their normal infrastructure and operating assumptions.

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I Mechanisms of Imitation

1 The Mirror Neuron System and Imitation

Giacomo Rizzolatti

1.1 Introduction

"Every one knows what attention is." This famous sentence by William James (1890, p. 403) appears to be appropriate also for imitation. Everyone knows what imitation is. Yet, as soon as imitation is more closely examined, this concept loses its simplicity; it appears to include different behaviors, some learned, some innate.

In this chapter, unless specified otherwise, I adopt Thorndike's definition of imitation. Imitation is learning to do an act from seeing it done (Thorndike, 1898). This definition includes two basic ideas: (1) imitation implies learning; and (2) during imitation the observer transforms an observed action into an executed action that is similar or even identical to the observed one.

How does imitation occur? The response to this question is obviously not easy. In the first place, why should an individual copy an action made by another individual? In everyday life, copying an action is typically useless and frequently dangerous. If an animal observing a conspecific eating some food imitates its movements, it will never get food. It will only aimlessly move its mouth. Imitation implies an understanding of what another individual is doing as well as the capacity to use this knowledge only in particular conditions.

Second, what information must the observer extract from an acting conspecific in order to imitate his behavior? Is it sufficient to understand the goal of the observed actions or must its details also be coded? Finally, there is the so-called "translation" problem. Sensory and motor systems are classically considered to be separate systems. Thus, how can the description of a visual event become a muscle excitation that faithfully replicates the observed event?

In this chapter, the following theoretical positions are defended:

1. Imitation is composed of two strictly related cognitive phenomena. The first is the capacity to make sense of others' actions. The second is the capacity, once the action is understood, to replicate it. According to the task and external contingencies, the imitated action can be structured differently. In some cases the observer replicates the goal of the observed action; in others the goal *and* the means used for achieving the goal are replicated.
2. The fundamental neurophysiological mechanism that underlies understanding of an action is a direct matching of the observed action with the motor representation of that action. This matching is made by the mirror neuron system. The matching of the observed action with its motor representation is a necessary prerequisite for imitation.
3. The matching mechanism by itself is not sufficient. It must be complemented by the activity of other mechanisms that modify and organize the mirror neuron system.

Here I summarize the properties of mirror neurons in monkeys, describe the properties of the mirror neuron system in humans, and finish by discussing the mechanisms that are necessary to achieve imitation.

1.2 The Monkey Mirror Neuron System: Motor and Visual Properties of F5 Neurons

Mirror neurons were originally discovered in area F5 of the monkey premotor cortex (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996a). This is a motor area that controls hand and mouth movements. A fundamental characteristic of this area is that many of its neurons discharge during specific goal-directed action (Rizzolatti et al., 1988). These neurons become active regardless of the effector (the right hand or the left hand or the mouth) used to achieve a specific goal (e.g., grasping an object). Conversely, they do not fire when a monkey uses the same effectors, but for another purpose (e.g., pushing objects away).

According to the action effective in triggering them, F5 neurons have been subdivided into various classes. Among them, the most represented are grasping, holding, tearing, and manipulating neurons.

A second fundamental characteristic of area F5 is that many of its neurons specify how a goal can be achieved. For example, the majority of grasping neurons discharge only if grasping is made using a particular type of prehension, such as a precision grip, finger prehension, and, more rarely, whole-hand prehension.

About 20% of F5 neurons respond to visual stimuli (Rizzolatti et al., 1988). One class of these visuomotor neurons is made up of *canonical neurons*, which discharge when a monkey sees an object that is congruent with the type of grip coded by the neuron (Murata et al., 1997). Visuomotor neurons in a second class do not discharge in response to the presentation of 3-D objects. The visual stimuli effective in triggering them are actions in which the experimenter (or a monkey) interacts with objects. Neurons with these properties are called mirror neurons (Gallese et al., 1996; Rizzolatti et al., 1996a).

Typically, in order to be triggered F5 mirror neurons require an interaction between hand and object. The sight of the object alone or of an agent mimicking an action is ineffective. The object's significance for the animal has no influence on mirror neuron response. Grasping a piece of food or a geometric solid produces responses of the same intensity.

A functional property of mirror neurons that is important for the issue of imitation is the relationship between their visual and motor properties. Most mirror neurons (93%) show a clear congruence between the visual actions they respond to and the motor response they code. According to the type of congruence they exhibit, mirror neurons were subdivided into strictly congruent and broadly congruent neurons (Gallese et al., 1996).

We labeled as strictly congruent those mirror neurons in which the effective observed and effective executed actions correspond both in terms of goal (e.g., grasping) and means, that is, the way the action is executed (e.g., precision grip). They represent about 30% of F5 mirror neurons.

We labeled as broadly congruent those mirror neurons that in order to be triggered do not require the observation of exactly the same action they code for motorically. Some of them discharge during the execution of a particular type of action (e.g., grasping) when executed using a particular grip type (e.g., precision grip). However, they respond to the observation of grasping made by another individual, regardless of the type of grip used (figure 1.1). Other broadly congruent neurons discharge in association with a single motor action (e.g., holding), but also respond to the observation of two actions (e.g., grasping and holding). Broadly congruent neurons are the largest class of mirror neurons (about 60%).

From this short review of the basic properties of F5 neurons, it appears that this area stores *potential* actions. The activation of F5 neurons does not necessarily determine an action; it evokes its representation. If other contingencies are met, this potential action becomes a *real* motor action (see Rizzolatti & Luppino, 2001). The potential actions associated with F5 neurons can be activated endogenously or exogenously. Exogenous (visual)

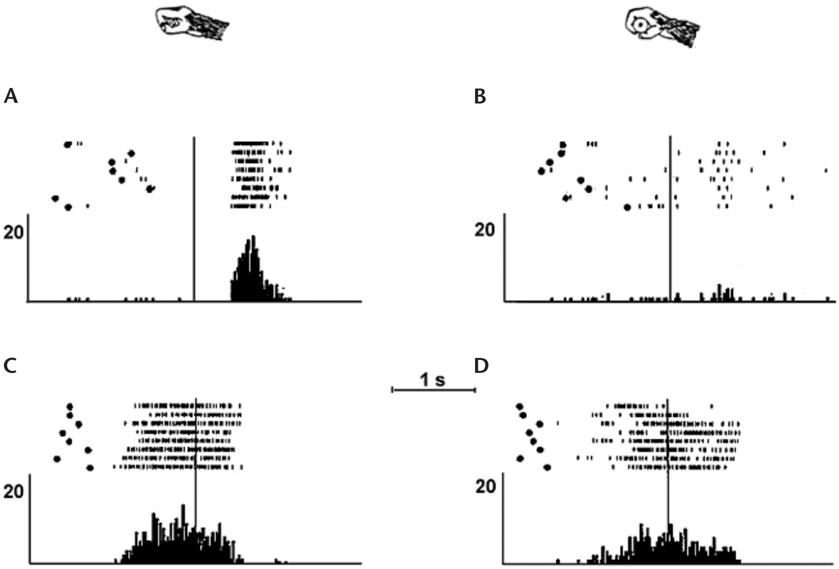

Figure 1.1

Example of a broadly congruent mirror neuron. (*A*) The monkey grasps a piece of food with a precision grip. (*B*) The monkey grasps a piece of food with whole-hand prehension. (*C*) The monkey observes an experimenter grasping a piece of food with a precision grip. (*D*) The monkey observes an experimenter grasping a piece of food with whole-hand prehension. In (*A*) and (*B*) the rasters are aligned with the moment in which the door of a testing box was opened (vertical line) and the monkey was allowed to grasp the objects. In (*C*) and (*D*) the rasters are aligned with the moment in which the experimenter touched the food (vertical line across trials). In the case of the monkey's active movements, the neuron showed a strong specificity for a precision grip. The filled circles indicate the beginning of the trials. Histogram bin width: 20 ms. Ordinates, spikes per bin; abscissas, time. (Modified from Gallese et al., 1996.)

activation is caused by the observation of objects (canonical neurons) or by the observation of actions made by others (mirror neurons).

1.3 Action Coding in the Temporal and Parietal Lobes of the Monkey

Neurons responding to the observation of actions made by others are not located only in area F5. In a brilliant series of studies, Perrett and his coworkers (Perrett et al., 1989; see for review Jellema & Perrett, 2002; Jellema et al., 2002) showed that neurons selectively responding to biological actions are present in the region of the superior temporal sulcus (STS). Actions effective in eliciting STS neuron responses are walking, turning the head, bending the torso, moving the arms, and facial movements, as well as gaze direction. A small set of neurons discharge during the observation of goal-directed hand movements (Perrett et al., 1990b). The motor properties of STS neurons have not been specifically investigated. Motor-related activity, however, if present, should involve only a limited number of STS neurons.

Another cortical area where there are neurons that respond to action observation is area PF (Fogassi et al., 1998; Gallese et al., 2002). This area forms the rostral part of the inferior parietal lobule. PF receives input from STS and sends output to area F5. Conversely, F5 sends output to PF, which in turn sends projections to STS. Information is flowing, therefore, not only from STS to F5, but also from F5 to STS. Direct connections between STS and F5 have not been described.

Neurons in area PF are functionally heterogeneous. Most of them (about 90%) respond to sensory stimuli (Hyvarinen, 1982; Leinonen & Nyman, 1979; Fogassi et al., 1998; Gallese et al., 2002). About 50% of them also discharge in association with a monkey's active movements.

PF neurons responding to sensory stimuli can be subdivided into three categories: somatosensory neurons (33%); visual neurons (11%); and bimodal neurons, which respond to somatosensory and visual stimuli (56%). Among the neurons with visual responses (visual neurons and bimodal neurons), 41% respond to the observations of actions made by another individual. The effective actions most represented are grasping, holding, manipulating, and bimanual interactions. One third of PF neurons triggered by action observation do not appear to have motor-related activity. The other two-thirds discharge also during a monkey's movement and, in most cases, show the visuomotor congruence typical of mirror neurons (PF mirror neurons) (Gallese et al., 2002).

From these findings the following picture emerges. Visually described actions are first stored in STS. In this area many neurons "resonate" in response to the sight of specific actions. STS action description is then transferred to PF. In PF, some neurons are exclusively visual, but most of them also discharge during action execution.

If one considers that the repertoire of actions that each individual possesses is restricted in comparison with the richness and variety of visual representations of observed motor actions, the following tentative hypothesis about the organization of the STS-PF-F5 circuit can be advanced. Each PF neuron receives visual descriptions of those actions that have the same meaning, e.g., grasping in different ways or by different persons. The neurons that receive this information are bidirectionally connected with the F5 neurons that code for grasping as a motor action. Thus the circuit on the one side "concentrates" the different visual descriptions of the same action on a restricted number of neurons, and on the other "labels" these neurons with a motor meaning. This convergence creates the basis for action understanding, regardless of the precise pictorial aspect of the action. I discuss later how this mechanism may also be involved in imitation.

1.4 Action Understanding: The Functional Role of the Mirror Neuron System

Since the discovery of mirror neurons, it has been proposed that they are involved in understanding actions. The core of this proposal is that an observed action acquires meaning for the observer when it activates motor schemas whose outcomes are known to the observer (see Rizzolatti et al., 2001).

There is an obvious objection to this proposal. Is motor activation really necessary to understand actions? In principle, an action could be understood in purely visual terms. Indeed, the data by Perrett and co-workers (see ch. 1.3) indicate that "prototypes" describing actions are present in STS. In addition, in humans, a rich description of body parts and body actions is present, not just in the STS region (see Allison et al., 2000), but also in the occipital cortex (Downing et al., 2001; Malach et al., 2002).

There is, however, a fundamental requirement that a description of actions must satisfy in order to provide meaning for the individual: It must link the external information to something that the individual knows. The visual system, like all sensory systems, is (by definition) a system that receives information. It does not generate it. In contrast, the motor system generates behavior and, on the basis of its consequences, is able also to "validate" the behavior produced. Thus, while the visual description of actions in STS is very useful for coding actions in a compressed way, this high-order visual information needs an additional mechanism to give it a meaning. F5 mirror neurons can effect this transformation. When the motor templates represented by mirror neurons resonate, the meaning of the observed action becomes transparent, because, when other contingencies are met, the activation of the same templates produces action.

The activation of representations of motor action is not the only way in which a visually described action may become meaningful. The observation that a certain visual event leads to consequences that the observer understands is another possibility. Note, however, that if the consequences of the observed actions do not directly concern the observer (such as a threatening gesture and its consequences), this type of understanding is different from that provided by motor mapping. It is a logical understanding, not a direct personal comprehension of what the other is doing.

An association between STS visual templates and subcortical centers also may give significance to an event. STS, besides sending information to PF, is part of a circuit that includes the amygdala and other centers related to emotions (Amaral et al., 1992). Activation of this circuit could give a personal significance to visual stimuli similar to that due to the activation of PF and F5 neurons. This, of course, assumes that there is a mirror neuron system for "hot," emotionally laden actions that is similar to that for the "cold actions" discussed earlier. Preliminary evidence suggests that this is the case (Wicker et al., 2003; see also Iacoboni, vol. 1, ch. 2).[1]

1.5 New Evidence of a Role for F5 Mirror Neurons in Action Understanding

The idea that the mirror neuron system is involved in action understanding can be tested by placing a monkey in situations in which the monkey is able to understand the meaning of an action, but the experimental sensory conditions are different from those that typically trigger mirror neurons. If mirror neurons are involved in action understanding, their activity should reflect the action meaning and not the sensory contingencies leading to action understanding.

A possible way to test this prediction is to present the monkey with auditory stimuli that evoke the idea of an action. This experiment was recently performed (Kohler et al., 2002). Activity in F5 mirror neurons was recorded while the monkey was observing a "noisy" action (e.g., ripping a piece of paper), or was presented with the same noise without seeing the action. The results showed that most mirror neurons that discharge on presentation of actions accompanied by sounds also discharge in response to the sound alone (audiovisual mirror neurons). Further testing showed that a large number of audiovisual mirror neurons respond selectively to a specific sound of an action. These results strongly support the notion that the discharge of F5 neurons correlates with the understanding of an action. The stimuli leading to action understanding are irrelevant. They could be visual or acoustical. Once the meaning of the action is specified, the neuron fires.

Another way to test whether action understanding triggers F5 mirror neurons is to prevent the monkey from seeing the action (and from

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[1] For discussions relevant to this section, see J. Prinz (vol. 2, ch. 13, p. 274ff), and the comments by Huesmann (vol. 2, ch. 19.6, p. 386).

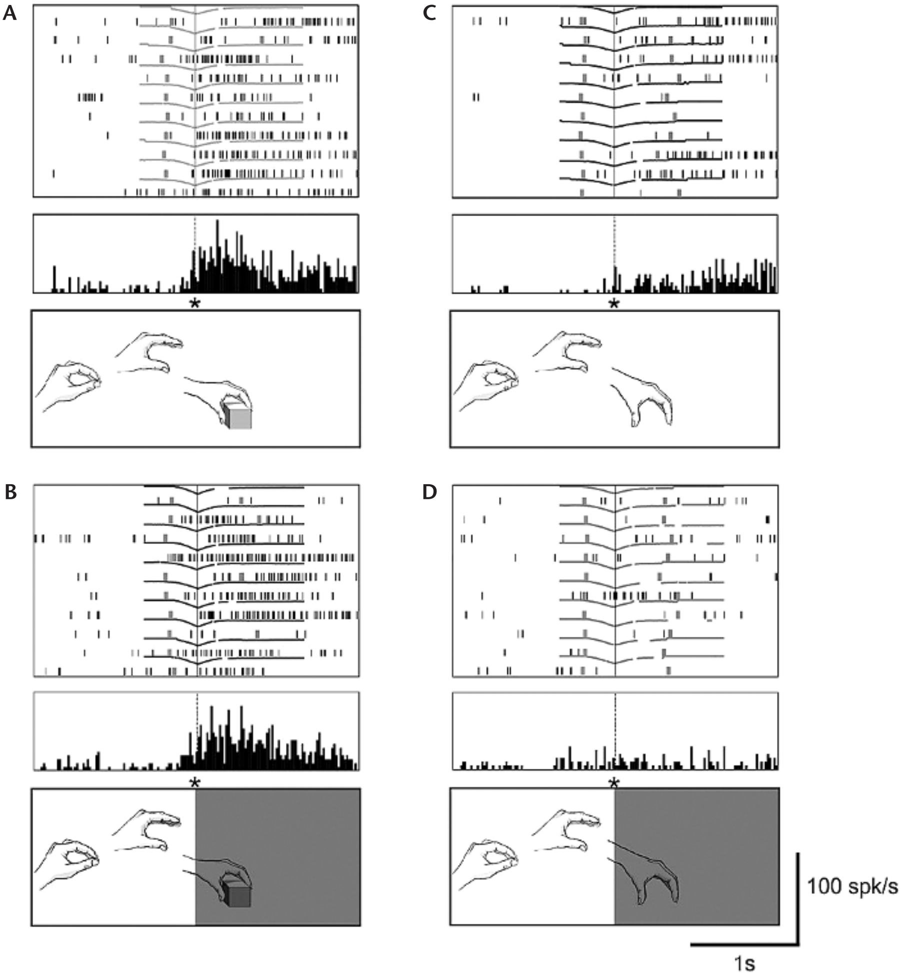

Figure 1.2
Example of a neuron responding to action observation in full vision and in a hidden condition. The lower part of each panel schematically illustrates the experimenter's action as observed from the monkey's vantage point. In panels *B* and *D* the gray square inside the black frame represents an opaque sliding screen that prevented the monkey from seeing the action the experimenter performed behind it. The asterisk indicates the location of a stationary marker attached to the frame. In hidden conditions the experimenter's hand started to disappear from the monkey's vision when it crossed this marker.

In each panel above the illustration of the experimenter's hand, the raster displays and histograms of ten consecutive trials recorded are shown. Above each raster, the continuous line represents the kinematics of the experimenter's hand movements hearing its sound), but to provide it with clues to what the action may be. If mirror neurons are involved in action understanding, they should also discharge in this condition.

An experiment testing this hypothesis was recently carried out by Umiltà et al. (2001). The experimental paradigm consisted of two basic conditions (figure 1.2). In one, the monkey was shown a fully visible action directed toward an object (''full vision'' condition). In the other, the monkey saw the same action, but with its final critical part hidden (''hidden'' condition). Before each trial, the experimenter placed a piece of food behind the screen so that the monkey knew that there was an object behind it. Only those mirror neurons were studied that discharged at the observation of the final part of a grasping movement and/or holding.

Figure 1.2 shows the main result of the experiment. The neuron illustrated in the figure responded to the observation of grasping and holding (A, full vision). The neuron also discharged when the stimulus triggering features (a hand approaching the stimulus and subsequently holding it) were hidden from the monkey's vision (B, hidden condition). As is the case for most mirror neurons, the observation of a mimed action did not activate the neuron (C, full vision and D, hidden condition). Note that from a physical point of view, B and D are identical. It was therefore the understanding of the meaning of the observed actions that determined the discharge in the hidden condition.

In total, more than half of the tested neurons discharged in the hidden condition. Out of them ($n = 19$), 7 did not show any difference between the hidden and full vision conditions, while 9 responded more strongly in the full vision condition. Of the remaining 3, the response was either more pronounced in the hidden condition than in full vision (1 neuron) or showed a temporal shift in response intensity.

In conclusion, both experiments in which the stimulus conditions were altered showed that F5 mirror neuron activation correlates with action understanding rather than with the stimulus properties leading to it. This finding strongly supports the notion that F5 activity plays a fundamental role in this function.

Figure 1.2
(continued)
expressed as the distance between the hand of the experimenter and the stationary marker over time. The rasters and histograms are aligned with the moment when the experimenter's hand was closest to the fixed marker (vertical line). Histogram bin width = 20 ms. The ordinates are in spikes per second. (Modified from Umiltà et al., 2001.)

1.6 The Mirror System in Humans

There is rich evidence that a mirror system exists also in humans. Evidence for this comes from electroencephalography (EEG), magnetoencephalography (MEG), transcranial magnetic stimulation (TMS), and brain imaging studies (e.g., Fadiga et al., 1995; Rizzolatti et al., 1996b; Grafton et al., 1996; Decety et al., 1997; Hari et al., 1998; Cochin et al., 1999). Many of these studies have been reviewed recently (Rizzolatti et al., 2001). Here only those particularly relevant for imitation are examined.

1.6.1 Transcranial Magnetic Stimulation Studies

The rationale of TMS studies of the mirror neuron system is the following. If there is a system endowed with mirror properties, the observation of an action performed by another individual should increase the motor-evoked potentials (MEPs) recorded from the observer's muscles involved in producing that action.

Fadiga et al. (1995) demonstrated that this is the case. Normal volunteers were required to observe an experimenter grasping different objects (transitive hand movements) or performing meaningless arm gestures in the air (intransitive arm gestures). As control conditions, detection of the dimming of a small spot of light or the presentation of 3-D objects was used. The results showed that observation of both transitive and intransitive actions produced an increase in the motor-evoked potentials recorded from the observers' hand and arm muscles. The increase was found in those muscles that the subjects would use to produce the movements observed.

Subsequent experiments confirmed the selectivity of the muscle excitation and described various cortical and spinal cord excitability changes caused by the observation of actions made by others (Baldissera et al., 2001; Gangitano et al., 2001; Maeda et al., 2002). Of these studies, the last two are of particular interest for imitation.

Gangitano et al. (2001) recorded MEPs from the hand muscles of normal subjects while they were observing grasping movements made by another individual. The MEPs were recorded at different intervals following onset of the movement. The results showed that cortical motor excitability faithfully followed the phases of the observed grasping movement (figure 1.3). This finding indicates that in humans the mirror neuron system codes for the temporal aspects of the observed movements and not only the meaning of the observed action.

Maeda et al. (2002) also recorded MEPs from two hand muscles of normal volunteers. The recordings were made while they observed video clips of

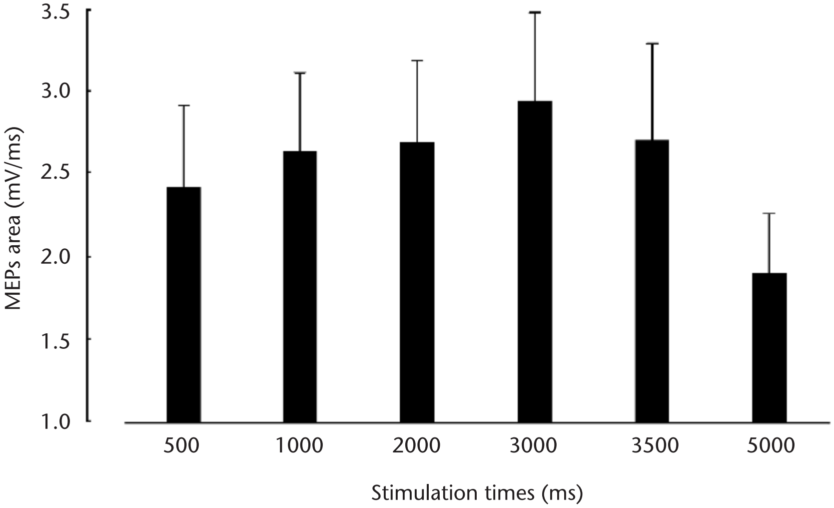

Figure 1.3
Averaged values of motor-evoked potentials (MEPs) of a hand muscle (first dorsal interosseus) collected at different times during the observation of a hand approaching a ball and grasping it. 500 ms, hand at the starting position (time value refers to the onset of the video clip showing the action); 3000 ms, hand maximum aperture. (Modified from Gangitano et al., 2001.)

different finger movements, such as thumb abduction or adduction. The finger movements were presented in two hand orientations: as if the actor were sitting next to the observer (hand "away" position) and as if the actor were in front of the observer (hand "toward" position). The results showed that the degree of cortical motor modulation depended on the orientation of the hand. Modulation was greater when the observed movement was performed in the hand away position (i.e., when the actor and the observer were in the same position) than in the hand toward position.

Summing up, TMS studies have shown two important properties of human mirror systems that have not been observed in the monkey. First, intransitive meaningless movements produce mirror neuron activation (Fadiga et al., 1995; Strafella & Paus, 2000; Maeda et al., 2002). Second, the correlation between the time course of the observed movements and the MEPs facilitation suggests a mirror mechanism that also codes for the movements forming an action. I previously referred (see Rizzolatti et al., 2002) to the movement-related mirror mechanism as the "low-level resonance mechanism," contrasting it with the "high-level resonance mechanism" of F5 where the coded element is the action. These properties of the human mirror neuron system, which may explain the great human capacity for imitation, are discussed in ch. 1.10.

1.6.2 Brain Imaging Studies

Early brain imaging studies showed that the observation of hand actions activates (besides various occipital visual areas) the STS region, the inferior parietal lobe, and the ventral premotor cortex, including Broca's area (see Rizzolatti et al., 2001). The finding of activation of Broca's area during observation of hand action was rather unexpected. Although comparative cytoarchitectonic studies indicate that the *pars orbicularis* of Broca's area (area 44) is the human homologue of area F5 (see Petrides & Pandya, 1994), the traditional view is that area 44 is the speech motor area.

In recent years, however, rich evidence has been accumulating that, in addition to speech representation, area 44 contains, similarly to monkey area F5, a hand motor representation (Krams et al., 1998; Binkofski et al., 1999a; Iacoboni et al., 1999; Gerardin et al., 2000; Ehrsson et al., 2000; Schubotz & Von Cramon, 2001). The hand motor representation, albeit greatly overlapping with that of mouth, is situated dorsally to the latter, sometimes invading the adjacent ventral area 6, where proximal arm movements are located. It is interesting to note that precision grip is richly represented in area 44 (Ehrsson et al., 2000). The same overrepresentation of precision grip is found in the monkey area F5 (Rizzolatti et al., 1988).

This activation of area 44 gave rise to some speculation about a possible exclusive role for this area in functions mediated by the mirror neuron system, with the explicitly stated doubt that in humans, verbal mediation rather than the mirror neuron system plays a fundamental role in these functions (see Heyes, 2001a). New experiments on the functional organization of the mirror system have shown that this view is wrong. Buccino et al. (2001) examined the general organization of the mirror neuron system using as stimuli mouth, hand, and foot actions. Transitive actions (directed toward an object) and intransitive actions were used. The following stimuli were presented: biting an apple or chewing; grasping a cup, grasping an apple or miming these actions; kicking a ball, and pushing a brake or miming these actions. Observation of an action was contrasted with the observation of a static face, hand, and foot, respectively.

The observation of object-related mouth movements resulted in activation of areas 6 and 44 bilaterally. In addition, two activation foci were present in the parietal lobe. The rostral focus was located in area PF (BA 40), while the caudal one was (most likely) in area PG (BA 39). The observation of intransitive actions produced activation of the same premotor areas as the observation of transitive actions, but there was no parietal lobe activation.

Observation of object-related hand and arm movements resulted in two areas of activation in the premotor cortex, one corresponding to area 44 and the other more dorsal in ventral area 6. Considering the motor organization of this region, it is likely that the former activation was caused by observation of grasping hand movements, while that of area 6 was caused by observation of reaching. As for mouth movements, there were two activation foci in the parietal lobe. The rostral focus was still in PF, but was more posteriorly located than the focus observed during mouth actions, while the caudal focus was essentially in the same location as that for mouth actions. During the observation of intransitive movements, the premotor activations were present, but not the parietal ones.

Finally, the observation of object-related foot actions resulted in activation of a dorsal sector of area 6 and activation of the posterior parietal lobe, in part overlapping with that seen during mouth and hand actions (BA 39), in part extending more dorsally. Nonobject-related foot actions produced the area 6 activations, but not the parietal ones.

The results of this study are important for several reasons. First, they demonstrate that the mirror system includes a large part of premotor cortex and the inferior parietal lobule. It is not limited to Broca's area. Second, they show that the activation map obtained during observation of actions made with different effectors is similar to the motor map (the so-called "homunculus") obtained with electrical stimulation of the same region. Finally, they allow one to rule out the idea advanced by some authors (see Grèzes & Decety, 2001; see also Heyes, 2001a) that the activation of area 44 is due to internal verbalization. Verbalization cannot be present during the observation of hand movements and magically disappear during the observation of foot movements.

In conclusion, the human mirror system is widespread and centered on the inferior parietal lobule and the premotor cortex, including area 44. The next section examines how this system is involved in imitation.

1.7 The Mirror Neuron System and Imitation

Imitation (as defined in ch. 1.1) is based on two distinct but related mechanisms: the capacity to understand actions done by others and the capacity to replicate those actions. The data reviewed in the previous sections strongly suggest that the mirror neuron system plays a fundamental role in understanding actions peformed by others. In this section I examine how this system is also involved in replicating the observed action.

Before doing this, however, it is important to stress the different ways in which the term "imitation" is used in psychological and in ethological studies. In psychological studies, "imitation" refers to the behavior of subjects instructed to replicate an action that is already in their motor repertoire. The aim is to discover the rules that the subjects use in copying others' behavior and to compare them with the rules used in acting on the basis of other biological and nonbiological stimuli (e.g., Brass et al., 2000; Bekkering & Wohlschläger, 2002; W. Prinz, 2002). In ethological studies, the stress is on learning. Imitation is the capacity to acquire a motor behavior previously not present in the observer's motor repertoire (see R. Byrne, 1995, 2002c; Tomasello & Call, 1997; Visalberghi & Fragaszy, 2002). Particular emphasis is often given here to the precise motor details of the imitated action (Tomasello & Call, 1997).

1.8 Imitation of Actions Present in the Observer's Repertoire: Brain Imaging Experiments

An important role in the renewal of interest in imitation in psychology has been played by the reconsideration of the concept of ideomotor compatibility (R. Lotze, 1852; James, 1890; Greenwald, 1970) by Prinz and his colleagues (see W. Prinz, 2002). According to these authors, stimuli and responses are represented in the cognitive system as events and coded in a commensurable format. Thus the perception of a stimulus event that shares features with a similar motor event tends to induce it (W. Prinz, 2002). The greater the similarity between the stimulus event and the motor event, the stronger will be the induction of the observed action.

These theoretical ideas and the finding that mirror neurons directly match the observed actions in their corresponding motor representations prompted brain imaging experiments aimed at finding the neural substrate that is specifically activated during imitation (Iacoboni et al., 1999, 2001; Nishitani & Hari, 2000).

Using functional magnetic resonance imaging (fMRI), Iacoboni et al. (1999) studied normal human subjects under two basic conditions: "observation-only" and "observation-execution." In the observation-only condition, the subjects were shown a moving finger, a cross on a stationary finger, or a cross on an empty background. The instruction was to observe the stimuli. In the observation-execution condition, the same stimuli were presented, but this time the instruction was to lift the right finger as fast as possible in response to them.

The fundamental comparison of the study was the one between the trials of the observation-execution condition in which the volunteers made the movement in response to an observed action (''imitation'') and the trials of the same condition in which the movement was triggered by the cross projected on a finger or an empty background. The results showed that there were four areas in which the activity was stronger during imitation trials than during other trials: left area 44, the right anterior parietal region, the right parietal operculum, and the right STS region (see for this last activation, Iacoboni et al., 2001).

In all trials of the observation-execution condition, the motor action (finger lifting) made by the subject was identical. The fact that activation of area 44 (an area also active in the observation-only condition) was stronger during imitation trials than during the other two observation-execution trials strongly suggests that a direct mapping between the observed and the executed act occurs in this area. Area 44, therefore, appears to contain a mirror mechanism.

Remarkably similar results were obtained by Nishitani and Hari (2000) by using the event-related neuromagnetic technique. This technique is inferior to fMRI in terms of spatial resolution, but allows one to obtain an excellent time resolution. In their experiment, Nishitani and Hari asked normal human volunteers to grasp a manipulandum, or to observe the same movement performed by an experimenter, or to observe and replicate the observed action. The results showed that during an active grasping condition, there was an early activation in the left inferior frontal cortex (area 44), with a response peak appearing approximately 250 ms before the touching of the target. This activation was followed within 100–200 ms by activation of the left precentral motor area and 150–250 ms later by activation of the right one. During imitation, the pattern and sequence of frontal activation were similar to those found during execution, but activation of area 44 was preceded by an occipital activation that was due to visual stimulation present in the imitation condition.

As far as the other activations described by Iacoboni et al. (1999) are concerned, the parietal activation could reflect a mirror mechanism similar to that proposed for area 44. This interpretation, however, is in contrast with the finding that superior parietal lobule activation is typically not present in experiments in which the subjects are instructed to observe actions only in order to understand them (see Buccino et al., 2001).

Furthermore, in the monkey, the superior parietal lobule, in contrast to the inferior one, does not receive input from STS, where visual templates of biological actions are coded (G. Luppino and M. Matelli, personal communication).

A possible alternative interpretation may be that during imitation the activation of motor representations of the intended actions produces, through backward projections, sensory copies of the intended actions. In the monkey, the superior parietal lobule and especially its rostral part (area PE) contains neurons that are active during proprioceptive as well as during active arm movements (Mountcastle et al., 1975; Kalaska et al., 1983; Lacquaniti et al., 1995). These properties suggest that the observed superior parietal activation may represent a kinesthetic copy of the intended movements. This interpretation fits well with positron emission tomography (PET) data by Decety and his co-workers (Decety et al., 1997; Grèzes et al., 1998), who also showed an increase in superior parietal activations when the subjects' task was to memorize actions in order to repeat them.

An interpretation in terms of sensory copies of the intended action may also explain the activations observed by Iacoboni et al. (1999) in the parietal operculum. It is known from monkey studies that there are several sensory areas located in this sector of the parietal lobe, among them areas PV and SII (Robinson & Burton, 1980a,b; Krubitzer et al., 1995). Brain imaging data have shown a similar organization in the human brain (Disbrow et al., 2000). Thus, by analogy with the interpretation of the parietal activation, one may hypothesize that the observed activation represents a tactile copy of the intended action. Interestingly enough, the pure observation of hand manipulation actions decreases signals evoked in the SII region by median nerve stimulation (Avikainen et al., 2002). In accord with these findings, the experiments of Iacoboni et al. (1999) found no activation in the parietal operculum during the observation-only condition.

The activation in STS is particularly intriguing. This activation, which is located in a caudal part of the STS region, rostral to and slightly dorsal to the motion area V5/MT, was close to significance only in the experiment by Iacoboni et al. (1999). Considering, however, the theoretical importance of a visual copy of the intended action, this activation was further investigated in a new experiment in which, as in the previous experiment, volunteers observed ("observation-only") or executed ("observation-execution") a finger movement with their right hand. The hand whose movement they observed was this time either the right or the left one and not the left hand only, as in the previous experiment. In half of the trials, the stimulus was a finger movement, in half a small cross presented on the finger (which was still). The hand of the subjects was hidden from their vision (Iacoboni et al., 2001).

The most interesting result of this experiment was the difference in activation of STS during observation (observation only) versus imitation (observation-execution) of the finger movements, according to which hand was *observed*. During observation, the strongest activation was caused by the movement of the hand *anatomically* corresponding to that used by the subjects in the experiment (i.e., the right hand). In contrast, during imitation, the strongest activation was seen in the condition in which the hand *spatially* corresponding to that of the subjects triggered the movement (figure 1.4). In other words, during observation the anatomical congruence was favored, while when imitation was required, the space common to the acting hand and to the observed hand was favored.

This reversal of activation intensity in STS during imitation is consistent with behavioral data showing that when an individual has to imitate the action of another individual facing him, he tends to imitate the observed action in spatial coordinates. This tendency can be easily demonstrated by touching one's own cheek and telling a person, "You have something here on your cheek." Invariably the addressed person touches the cheek of his/her own that is spatially congruent with that indicated by the speaker, and not the one anatomically congruent. Experimental evidence for this mirror-image imitation was provided by Shofield (1976a,b) and more recently by Bekkering et al. (2000). For an in-depth discussion of the effect, see Gattis et al. (2002).

From the neurophysiological point of view, it is likely that the reversal in activation from the anatomically congruent to the spatially congruent effector during imitation is caused by an efferent discharge coming from PF and priming the STS hand prototypes that are spatially congruent with the observed ones. This is most likely an adaptive behavior determined by the experience that there is an advantage in sharing space when two individuals face one another. Thus, the hand prototypes spatially congruent with the hand action to be imitated prevail over the prototypes representing the hand anatomically congruent to the observed one.

Taken together, these experiments strongly support the idea that the mirror system plays a central role in the imitation of actions that are already in the motor repertoire of the individuals. The mirror system matches the observed action with motor responses stored in the premotor cortex and allows a fast, efficient response to that action. In addition, these experiments suggest that sensory copies of actions to be imitated are formed

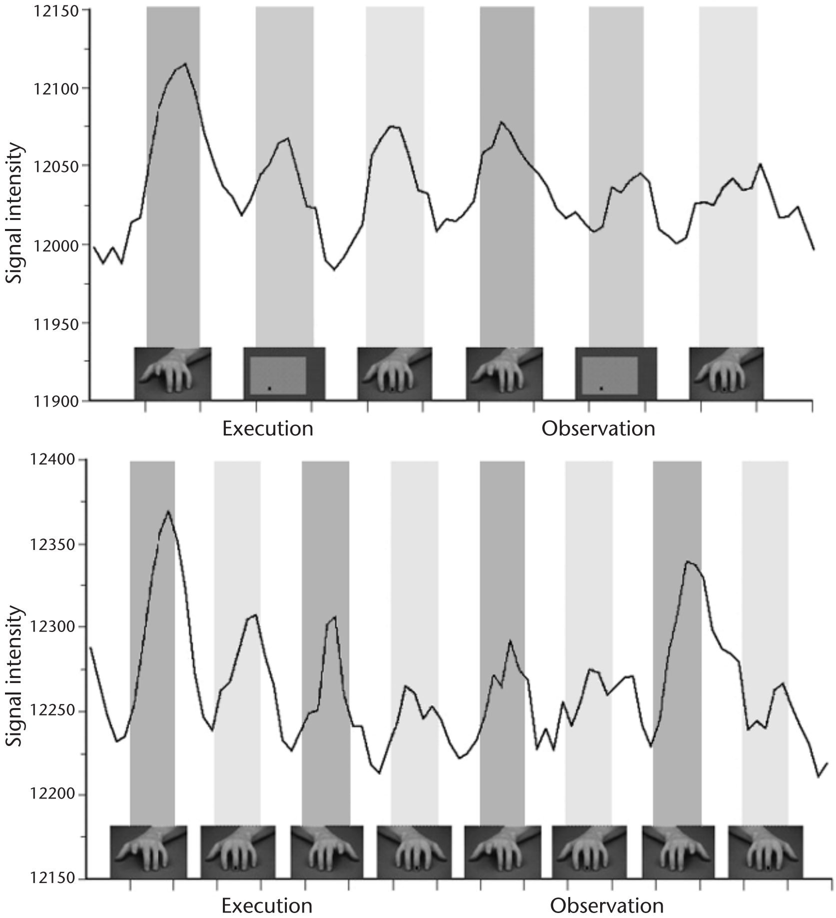

Figure 1.4
Time series of the active superior temporal sulcus (STS) site during a finger movement (lifting the right index finger—execution) and during observation of a similar finger movement made by another individual (observation). The finger movement in execution was triggered by the observation of finger lifting by another individual or by the presentation of a black cross on a finger. The small pictures correspond to the type of stimulus presented. Nine rest periods that were alternated with the eight active task periods are presented. See the text for other explanations. (Modified from Iacoboni et al., 2001.)

in various areas. This important theoretical point, however, requires further experiments in order to be definitively proved.

1.9 Imitation of Actions Not Present in the Observer's Repertoire: Brain Imaging Experiments

Unlike psychologists, ethologists typically stress the learning aspects of imitation. Many consider "true" imitation to require the precise repetition of an observed action previously not present in the observer's motor repertoire; the learning of actions with effects on the environment that are similar to the observed ones is not sufficient (A. Spence, 1937; Galef, 1988; Tomasello, 1990; R. Byrne & Tomasello, 1995). This view in large part relates to the need to exclude from imitation motor behaviors apparently learned by observation of action but in fact triggered by the meaning of the stimulus (A. Spence, 1937) or by its affordances (Tomasello, 1990).

Two different ways of learning a new motor behavior should be distinguished. One is substitution for the motor pattern spontaneously used by the observer in response to a given stimulus of another motor pattern, more adequate to reach the intended goal, on the basis of observation of the behavior of another individual. Examples could include the correct way to hold a tennis racket or to place a finger on a guitar's neck (action adjustment). The second way is learning, by observation, a new motor sequence that is useful to reach a certain goal (sequence learning). The ability to open a box only if a certain action sequence is followed could be an example of this second type of imitation learning (see also the artificial fruit of Whiten and Custance, 1996).

There are no experiments that I am aware of that have studied these two types of motor behavior from the perspective of mirror neurons. So in this section I discuss the issue of acquisition of new motor behaviors following observation of actions made by others mostly in terms of possible mechanisms that may explain them rather than on the basis of empirical studies.

The neurophysiological network that should intervene in action is that formed by STS, PF, and F5. As discussed earlier, this circuit stores many visually described actions in its visual node, STS. STS neurons send information to PF, where there are neurons that receive, in addition to STS input, backward connections from F5. The way an individual interacts with an object before learning is established by F5 canonical neurons that specify which type of movement (e.g., a specific type of grip) has to be used on the basis of the object's affordances (see Jeannerod et al., 1995). When the observer sees that another grip is more efficient than the one previously used to reach the goal of the action, this new grip is coded in STS. The learning process consists of the production of a motor pattern that activates, via backward connections, those PF neurons that receive the sensory copy of the desired action from STS. The comparison between the visual aspect of the performed action and the sensory copy of it will allow a modification of the internal motor pattern until this pattern produces an action similar to the observed one.

This model is basically an internal forward model (see Wolpert et al., 1995; Wolpert, 1997; Kawato, 1999; Arbib & Rizzolatti, 1999). Its main biological constraints are, on the motor side, the motor repertoire present in PF and F5 and, on the sensory side, the variety of action prototypes coded in STS and their plasticity. The presence in humans of a rich representation of intransitive motor acts, shown by TMS studies, renders the human mirror neuron system much more apt for imitation than the analogous monkey system, where the poor representation of intransitive actions (or even its absence) and the apparent poverty (on the basis of available evidence) of mirror neurons coding for precise details of actions present serious limits to the capacity for imitation. Without the storage of intransitive actions to complement basic object-related actions and precise copies of actions, the capacity of the monkey system to imitate the behavior of others should be rather limited.

Logically, the mechanism that is the basis of learning a sequence by imitation ought to be different. Here, unlike the case of action adjustment, the essential achievement is not the substitution of an action determined by an object's affordances with a more effective action, but rather the capacity to replicate a series of actions previously never executed.

An interesting hypothesis to explain how this type of imitation may occur has been recently advanced by Byrne (see R. Byrne, 2002c and chapter 9). According to Byrne, sequence learning by imitation is based on two operations. The first is the capacity to segment the perceived action into smaller units and to match them to "motor acts" already present in the motor repertoire of the observer. Mirror neurons are the elements that perform this matching.

The other essential operation ("string-parsing") consists of extracting the statistical regularities that characterize an action's sequence. This operation imposes high-order organization on the observed action sequence and, if successful, mirrors the original planning structure that produced the behavior. On the basis of neurophysiological data indicating a role for the mesial cortical area in sequence learning and execution (see Hikosaka et al., 1995, 2000; Tanji, 1996; Tanji et al., 1996; Shima & Tanji, 2000), Byrne proposed that these areas also play a role in string parsing. An additional possible neural substrate for this operation is the basal ganglia, which also appears to play a role in sequence learning.

Obviously, at present the proposed mechanisms for action adjustment and for sequential learning by imitation are both merely hypothetical. However, they suggest a series of brain imaging experiments that may be easily performed using the available technology.

1.10 Concluding Remarks

A point central to this chapter's attempt to give imitation a neurophysiological basis is that an understanding of actions preceded imitation in evolution. The mirror system evolved as a system whose main aim was to match sensory information to personal motor knowledge of action meaning. This system became progressively richer and more complex and, in humans, came to include intransitive actions and detailed specifications of how an observed action is executed. This evolved mirror system became the basis for reproducing actions performed by others; that is, for imitation.

A possible criticism of this view is that some actions produce imitation without any evidence that they have been understood. There are several examples of this type of behavior. In many species of animals, for instance, the observation of a movement made by one individual is a signal for the rest of the group to start a similar movement (e.g., the behavior of shorebirds studied by Thorpe, 1963). Imitation of this type, that is, imitation without understanding the meaning of an action, is present in humans. A well-known example is the capacity of newborns, first described by Meltzoff and Moore (1977), to imitate buccal gestures. Other examples are laughing, yawning, crying, and, as shown by Dimberg et al. (2000), involuntary mimicking of facial expressions. It is likely that the main purpose of these behaviors is to create a link between individuals by facilitating affiliative behaviors and inhibiting aggressive behaviors.

Is such imitation without understanding also dependent on mirror neurons? In the absence of empirical data, a response to this question can be, obviously, only hypothetical. It is tempting, however, to think that the same mechanism underlies these behaviors and action understanding. At this point an obvious conceptual difficulty arises. It is difficult to accept that relatively simple behaviors such the escape behavior of shorebirds mentioned earlier developed after action understanding and requires this understanding as its prerequisite. The interpretation given by Thorpe (1963, see also Tinbergen, 1953) in terms of releasing signals appears to be more parsimonious and convincing. A possible solution of this paradox might lie in the distinction between high-level and low-level resonance mechanisms (Rizzolatti et al., 2002).[2]

According to this proposal, there are neurons endowed with motor properties (motor neurons in a broad sense) that resonate when an appropriate stimulus is presented. The effect of this resonance is radically different according to the role that these neurons play in motor control. If they are close to the effectors, their low-level resonance elicits an actual motor action, with little if any cognitive effects. In contrast, if the neurons represent the action internally without necessarily causing motor effects (e.g., F5 mirror neurons), their high-level resonance would produce mostly cognitive rather than motor phenomena, such as action understanding.

This view, although hypothetical, has some interesting consequences. First, it allows one to give a unitary explanation of the different types of imitative behaviors, those accompanied by action understanding and those without it. Second, assuming that a mirror mechanism underlies both these phenomena, the unitary interpretation avoids the paradoxical notion that a cognitive function such as action understanding preceded in evolution capacities that can be explained without invoking high-level cognitive processes. Third, but not least, it provides clear, testable hypotheses about the mechanisms underlying imitation.[3]

Acknowledgments

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[2] For a relevant discussion see Hurley (vol. 1, ch. 7, p. 184).

[3] See the comments on this chapter by Rawlins (vol. 1, ch. 8.1, p. 195).

2 Understanding Others: Imitation, Language, and Empathy

Marco Iacoboni

2.1 Introduction

The study of the neural basis of imitation is in its first stage. Until a few years ago, the only available information on the neural underpinnings of imitative behavior was restricted to lesion data from neurological patients. Although extremely valuable, the information obtained from neurological observations is limited, mostly because the lesions causing the imitative deficits are naturally occurring ones and do not have the precise anatomical boundaries that allow a detailed study of the brain–behavior relationship. Two main factors have limited the neuroscience of imitation. First, there is little consensus on a definition of imitation (R. Byrne & Russon, 1998; Heyes, 2002). This lack of consensus has reduced the enthusiasm of neuroscientists for investigating the neural basis of imitative behavior. Second, even though some neuroimaging techniques have been around for about a quarter of a century, brain mappers initially had the tendency to stay away from complex phenomena, and imitation has been definitely perceived by them as a complex phenomenon. These two factors have led to the paradoxical situation of the late 1990s, when there were tens of peer-reviewed imaging studies on, say, saccades, and not even one on imitation!

A series of reports on experiments investigating the neural basis of imitation, however, has been published recently (see, for instance, Decety and Chaminade, vol. 1, ch. 4). This trend seems to result from two main causes. First, there is a recent tendency in the neuroimaging world to study complex phenomena, such as theory of mind (C. Frith & Frith, 1999) or even "social"-like interactions (Montague et al., 2002; Rilling et al., 2002). Second, macaque single-cell observations published in the early 1990s have provided good neuronal models of functional properties that are relevant to imitation (di Pellegrino et al., 1992; Gallese et al., 1996). This is particularly important because the mainstream imaging techniques generally rely on indirect measures of neuronal activity, such as blood flow. The existence of neurophysiological data that can help constrain the interpretation of the imaging data is generally considered extremely valuable.

In this chapter I summarize the most meaningful data obtained so far on the neural underpinnings of imitation. The plan is to relate these findings to a neural and functional model of imitation and its relations with two other functional domains, language and empathy. The approach I use here envisions brain mapping techniques as investigative techniques with explanatory power. Typically, brain mapping is perceived as some kind of sophisticated phrenology. Detailed aspects of cognitive functions are mapped onto precise neural structures. Obviously, the map obtained looks a lot more sophisticated than the phrenological maps of the nineteenth century. However, the explanatory power of this approach remains limited with regard to testing models. What I advocate here is an approach that combines imaging data with functional information obtained from single-cell observations. With this approach, it is possible to test information-processing models of imitation and its relations with other domains.

2.2 Minimal Neural Architecture for Imitation

2.2.1 An Action Recognition System in the Macaque Brain

Two European laboratories, David Perrett's and Giacomo Rizzolatti's, have systematically studied the properties of temporal, parietal, and frontal neural systems of the macaque brain that seem relevant to action representation and potentially to imitation. Following the leads that resulted from the studies of Charles Gross on the complex visual properties of inferior temporal neurons, Perrett and his collaborators have studied neurons in the superior temporal sulcus (STS) that respond to moving biological stimuli, such as hands, faces, and bodies (Perrett et al., 1989, 1990a; Perrett & Emery, 1994). These neurons seem to respond to moving bodies and body parts only when the body or body part is engaged in goal-oriented actions. For instance, some of these neurons respond to the sight of a hand reaching and grasping an object. The same neuron will not fire at the sight of the hand reaching toward the object but not grasping it. The modulation of activity in STS neurons is independent of low-level visual features. In fact, a point-light version of the same action, that is, a hand reaching and grasping an object, is enough to activate a neuronal response in these STS cells (Jellema et al., 2002). In other words, what these STS neurons code is the sight of a meaningful interaction between an object and an intentional agent.

The properties of STS neurons are limited exclusively, at least so far, to the visual domain, in that no neuronal responses in STS seem associated with motor behavior. In contrast, Giacomo Rizzolatti and his collaborators have described frontal and parietal neurons with motor properties (in that they are active when a monkey performs a movement) that also have visual responses similar to the ones observed in STS by Perrett (di Pellegrino et al., 1992; Gallese et al., 1996). These neurons have been described for the first time in a region of the inferior frontal cortex called area F5, according to an anatomical nomenclature that is becoming increasingly used (Matelli et al., 1985). In area F5 there exist two types of neurons with identical motor properties and quite different visual properties. The two types of neurons are called *canonical* and *mirror*. Both types fire when a monkey executes goal-directed actions, such as grasping, holding, tearing, and manipulating. Some of these neurons fire for a precision grip, as when a monkey grasps small objects like a raisin, and some other neurons fire for a whole-hand grasp, as when a monkey grasps larger objects, such as an apple. When it comes to their visual properties, canonical neurons that fire when a monkey grasps a small object with a precision grip also respond to the sight of small objects that can be grasped with a precision grip, but not to the sight of larger objects graspable with, say, a whole-hand grip. Note that these visual responses also occur when a monkey does not reach and grasp the object; the simple sight of the object is sufficient to activate canonical neurons. In other words, canonical neurons seem to be coding the affordance of an object, the pragmatic aspect of how to grab it, rather than its semantic content.

In contrast, mirror neurons do not fire at the sight of an object, but will fire at the sight of a whole action. So, say that there is a neuron in F5 that fires when a monkey grasps an object. That same neuron, if it is a mirror neuron, will fire at the sight of another individual grasping an object, but will not fire at the sight of the object alone and will not fire at the sight of a pantomime of a grasp in the absence of the object. In other words, these neurons seem to be matching the execution and the observation of an action. The functional properties of these neurons suggest that they may implement a simple, noninferential mechanism of action recognition based on neural identity. This mechanism may be a building block for imitative behavior.

A posterior parietal area of the macaque, area PF, situated in the rostral sector of the inferior parietal lobule, contains mirror neurons with functional properties that are substantially identical to the ones described in F5 (Rizzolatti et al., 2001). Area PF and area F5 are anatomically connected with robust projections (Rizzolatti et al., 1998). This pattern of cortico-cortical connectivity leads us to believe that F5 and PF belong to an integrated circuit for action recognition. Furthermore, STS, the region where Perrett has discovered the neurons with the complex visual properties described earlier, is connected with the posterior parietal cortex (Seltzer & Pandya, 1994). Thus these three cortical regions of the macaque brain, STS in the superior temporal cortex, area F5 in the inferior frontal cortex, and area PF in the posterior parietal cortex, seem to have functional properties and connectivity patterns that may instantiate a whole circuit for coding actions. The question that I address in the next section is whether there is a similar circuit for recognition of actions and possibly imitation in the human brain.

2.2.2 Minimal Human Neural Architecture for Imitation

The first attempts to demonstrate an action recognition system in the human brain similar to the one in the macaque brain were made using positron emission tomography (PET) and, as activation tasks, execution and observation of grasping (Grafton et al., 1996; Rizzolatti et al., 1996b). The idea behind these studies was the following. If there is a human action recognition system that is similar to the one described in macaques, motor areas in the human brain belonging to this system should be active during both execution and observation of grasping. Ideally, there should also be some anatomical correspondence between the human and the macaque areas. The early PET attempts were not entirely successful, even though some aspects of the empirical findings were encouraging. The two broadly defined regions of superior temporal cortex and inferior frontal cortex were indeed activated during both observation and execution of action. The areas activated within inferior frontal and superior temporal cortex during execution of grasping, however, did not spatially match the areas activated within inferior frontal and superior temporal cortex during observation of grasping. Furthermore, the posterior parietal cortex was found to be activated only during execution of grasping (Rizzolatti et al., 1996b). However, a second study comparing observation of grasping with imagination of this action did report activation of posterior parietal cortex during observation (Grafton et al., 1996). The reason the results of these first studies were successful only in part is probably due to technical limitations of the 2-D PET methodology used.

The second important feature of the action recognition system described in the macaque is that it is driven by goal-directed actions. To test whether human brain areas of the grasping circuit show a similar feature, we per-

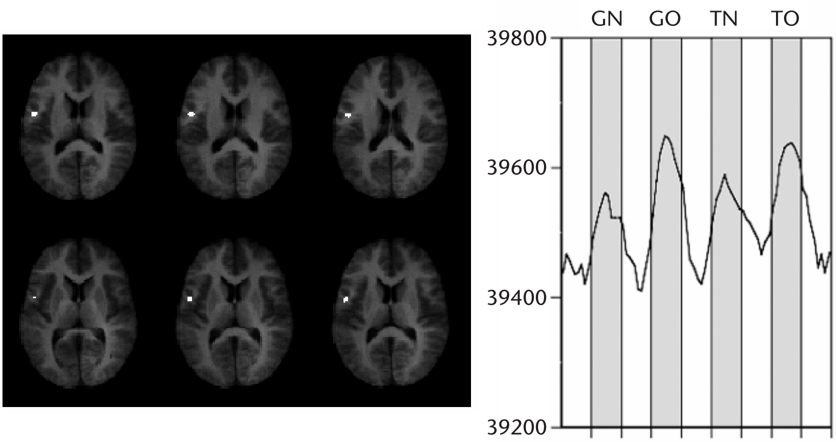

Figure 2.1
Activity in the human inferior frontal cortex (putative Brodmann area 44, in white in left panel) in object-directed and pantomimed actions. The dark gray bands correspond to task periods, whereas the white bands correspond to resting periods. Greater activity is observed for grasping (GO) and touching (TO) an object, compared with a pantomime of grasping (GN) and touching (TN).

formed a functional magnetic resonance imaging (fMRI) experiment in which subjects either performed an object-directed action (grasping or touching an object) or simply pantomimed the action without actually interacting with the object. The prediction is that a hand–object interaction should yield greater activity in regions coding goal-oriented behavior. Consistently with the macaque single-cell data, we found that the inferior frontal cortex had this pattern of activity (figure 2.1).

The early studies on grasping, however, had a conceptual limitation. Even though continuity is important, so that it makes sense to see some features of the action recognition system of the macaque in the human brain, one must also factor in the changes that the evolutionary process might have produced. Thus, to keep focusing on grasping seemed to us a mistake. Imitation seemed a much more promising paradigm to use. In fact, the action recognition system of the macaque has the property of being active both when the monkey performs an action and when it observes an action. These neural properties make this system an ideal candidate for being involved in or at least facilitating imitation. It is true that the imitative abilities of monkeys are limited, but even if one wants to apply the most stringent definition of imitation and thus conclude that monkeys

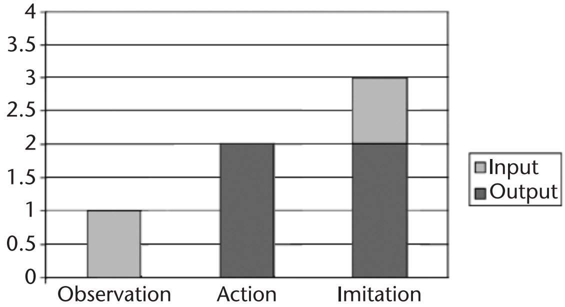

Figure 2.2
The predicted activity for mirror areas during imitation is approximately the sum of the activity observed during observation of an action and during execution of an action.

do not imitate at all, one can also conceivably argue that the action recognition system made monkeys "imitation-ready." Thus it is plausible to predict an involvement of this system in imitation. The way we conceptualized it is captured in figure 2.2. The idea behind this conception is simply that during imitation there is both observation and execution of an action. Thus, one can predict that areas endowed with mirror properties would show an activity pattern similar to the one graphed in the figure, with activity during imitation corresponding roughly to the sum of the activity during observation and execution of action. With the use of fMRI, we found two areas with these properties (Iacoboni et al., 1999). The first area was located in the *pars opercularis* of the inferior frontal gyrus, in inferior frontal cortex, and the second one was located rostrally in the posterior parietal cortex. Thus there was a convincing anatomical correspondence between the areas identified in the human brain as having mirror properties and the macaque mirror areas.

We initially proposed some sort of "division of labor" between the frontal and the posterior parietal mirror areas, so that frontal mirror areas would code the goal of the imitated action and the posterior parietal mirror areas would code somatosensory information relevant to the imitated action. This division of labor was based on considerations inspired by single-cell (Sakata et al., 1973; Mountcastle et al., 1975; Kalaska et al., 1983; Lacquaniti et al., 1995) and neuroimaging data (Decety et al., 1997; Grèzes et al., 1998). Empirical support for this proposed division of labor has been provided recently by an imaging study from our group. The study shows a modulation of activity in inferior frontal mirror areas during imitation of goal-oriented action, with greater activity during goal-oriented imitation than nongoal-oriented imitation (Koski et al., 2002).

To go back to the first experiment on imitation (Iacoboni et al., 1999), the third region identified by single-cell studies in the macaque as relevant to action recognition, STS, demonstrated a somewhat unexpected pattern of activity. As expected, there was greater activity in STS for action observation than for control visual tasks and for imitation compared with control motor tasks. However, there was also greater activity in STS for imitation than for action observation. This was a somewhat unexpected finding because the observed action was the same during imitation and during action observation. If STS simply encodes the visual description of actions, its activity should be the same during imitation and action observation. Two possible explanations of this finding are as follows: First, the increased activity during imitation may simply reflect increased attention to the visual stimulus because the subjects are supposed to imitate it. Alternatively, the increased STS activity may be due to efferent copies of motor commands originating from the frontoparietal mirror areas. These efferent copies would allow a prediction of the sensory consequences of the planned imitative action that would be compared with the description of the observed action provided by STS. If a good match is obtained, then the planned imitative action can be performed.

To test these contrasting hypotheses, we performed a second fMRI study of imitation in which the subjects were asked to imitate in two different configurations, *specular* (as in a mirror) and *anatomical*. During specular imitation, the subjects moved their right hands to imitate a left-hand action. During anatomical imitation, the subjects moved their right hands to imitate a right-hand action. It turns out that the specular form of imitation is the most common or spontaneous form of imitation early in human development (Wapner & Cirillo, 1968), and it tends to yield a better performance also in adults (Ishikura & Inomata, 1995). Thus we predicted that the specular form of imitation should produce greater activity in mirror areas if they are critical cortical areas for imitation. In fact, in the pars opercularis of the inferior frontal gyrus (the human homologue of F5), we found a reliably greater activity for specular imitation than for anatomical imitation (Koski et al., 2003).

This differential activity in the inferior frontal cortex during the two forms of imitation allowed us to test the two contrasting hypotheses about STS, the *attentional* versus the *predictive* hypothesis. If the increased activity in STS during imitation is due to attentional factors, the two forms of imitation, specular and anatomical, should yield similarly increased STS activity compared with action observation. The anatomical form of imitation, being less natural than the specular one, might yield greater activity as a result of increased attentional demands. In contrast, if the increased activity in STS is due to efferent copies of motor commands with predictive value allowing control of the imitative output, then the STS activity should be similar to the activity in the mirror inferior frontal area, with greater activity for specular imitation than for anatomical imitation. Also, given that efferent copies of motor commands are not produced during action observation, STS activity should not be greater during observation without imitation of a left-hand action than during observation without imitation of a right-hand action. The results shown in figure 2.3 support the predictive hypothesis, with greater activity during specular imitation than

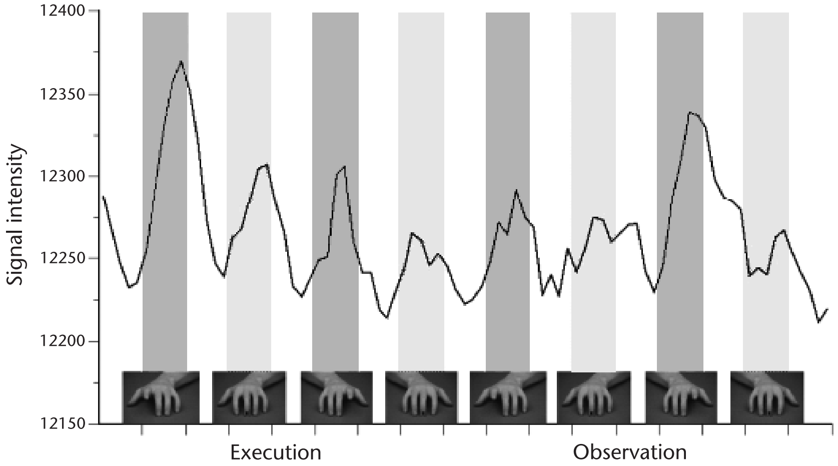

Figure 2.3

Time series of STS activity during imitation and observation of hand movements. The dark bands correspond to task periods and the white bands correspond to resting periods. From left to right, the first four tasks are motor tasks, the last four are observation-only tasks. The hands with the finger lifted up represent task periods when the subjects were shown finger movements. The hands with the cross on the finger represent task periods when the subjects were shown a static hand with a cue on one of the fingers. Thus, the first and third task periods here correspond to *mirror* and *anatomical* imitation, respectively. There is reliably greater activity in STS for *mirror* than for *anatomical* imitation. With regard to observation tasks, observed left-hand actions do not yield greater STS activity, suggesting that the effect observed during imitation is due to efferent copies of motor commands. (Reprinted from Iacoboni et al., 2001.)

during anatomical imitation, but not during left-hand versus right-hand action observation (Iacoboni et al., 2001). This suggests that the increased activity in STS during imitation is due to efferent copies of motor commands that originate in frontoparietal mirror areas and are sent back to STS for monitoring purposes.

To summarize, the information flow within the three areas (superior temporal, posterior parietal, inferior frontal) that form what we call the *minimal neural architecture* for imitation would be as follows:

- The superior temporal cortex provides posterior parietal mirror neurons with a visual description of the observed action to be imitated.[1]
- The posterior parietal mirror neurons provide additional somatosensory information regarding the action to be imitated and this information is sent to inferior frontal mirror neurons.
- Inferior frontal mirror neurons code the goal of the action to be imitated.
- Efferent copies of motor commands providing the predicted sensory consequences of the planned imitative actions are sent back to STS.[2]
- A matching process occurs in STS between the visual description of the action and the predicted sensory consequences of the planned imitative actions. If there is a good match, the imitative action is initiated; if there is a large error signal, the imitative motor plan is corrected until convergence is reached between the superior temporal description of the action and the description of the sensory consequences of the planned action.

This model predicts two things. First of all, the role of STS is extremely important when the action to be imitated is a novel action that is not in the motor repertoire of the imitator. Second, if there is such a robust shuffling of information between STS and frontoparietal mirror areas with regard to imitation, then the body maps of these cortices should have similar organizational principles. The first prediction has never been tested, as far as I know. The second prediction has been tested by us with fMRI. Given that at a premotor and posterior parietal level it is possible to observe a somatotopic representation of body parts, we predicted the topography of body parts in STS. Several laboratories had previously reported human STS

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1. A favored information flow from superior temporal to posterior parietal cortex rather than to inferior frontal cortex is postulated on the basis of more robust projections from superior temporal to posterior parietal cortex compared with the inferior frontal cortex.

2. Elsewhere we called these efferent copies reafferent (Iacoboni et al., 2001) to emphasize the information flow going from STS to frontoparietal mirror areas and back to STS.

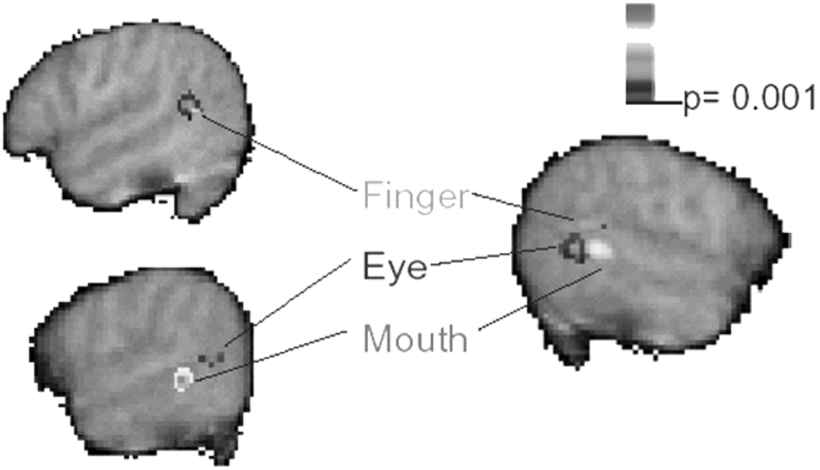

Figure 2.4
Topography of representation of body parts in human STS.

responses to biological motion, but owing to differences in methodology, it was difficult to extrapolate a map of body parts in STS from the published data. We thus performed another fMRI experiment in which the subjects observed hand actions, mouth movements, and eye movements (Dubeau et al., 2001). An orderly topography of body parts was observed in STS, as shown in figure 2.4. Such a topography has been subsequently confirmed by independent observations in our laboratory in separate studies using faces or hands as visual stimuli.

2.2.3 Functional Properties of the Minimal Neural Architecture for Imitation

The temporo-parieto-frontal circuit we delineated in ch. 2.2.2 seems to have relatively well-defined functional properties. Combining information from single-unit and brain imaging data, we have described a plausible information-processing flow that goes from STS to frontoparietal mirror areas, back to STS and then back to frontoparietal areas for the initiation of the imitative movement. In this section we extend the discussion on the functional properties of this model.

The functional properties of the minimal neural architecture for imitation can be mapped onto the functional architecture of modular pairs of forward and inverse models, a computational architecture developed in the motor control literature (Wolpert & Kawato, 1998; Kawato, 1999). Inverse models are important for motor control, whereas forward models are important for motor learning. An inverse model retrieves the motor plan necessary to reach a desired sensory state. The input of the inverse model is the desired sensory state and its output is the motor plan necessary to reach that state. In our case, the imitator desires to imitate the action of the actor, and an inverse model is created by STS inputting the visual description of the observed action into frontoparietal mirror areas that produce the output of the inverse model, the motor command necessary to imitate the actor. An efferent copy of the motor command (from frontoparietal mirror areas) is fed into STS to create a forward model that allows prediction of the sensory consequences of the planned imitative action. A forward model is a mimic (ironically so, this is imitation after all . . .) of the motor system, and if the prediction is confirmed by reafferent feedback, then the pair of forward and inverse models is reinforced by a "responsibility signal" (Haruno et al., 2001) that assigns "high" responsibility for imitating a given action to that specific forward-inverse model pair.

Several questions are left unanswered by this scenario. For instance, how does the pairing of STS input and frontoparietal output that determines inverse modeling occur?[3] Remember that STS neurons are driven by hand–object interactions and show visual invariance; that is, under widely different visual circumstances the same neuron will fire at the sight of the same kind of action. The F5 neurons also respond to the sight of a relatively large class of actions under different visual conditions. With regard to their motor properties, however, these neurons are often tuned to a specific action. Thus it is possible that the inverse-forward model pairing is initially facilitated because a large variety of visual stimuli nonselectively activate STS and F5. This nonselective visual activation, however, can be efficiently mapped only onto a few specific motor outputs coded in F5. When an inefficient motor output is selected, it will generate a large error signal in its forward model and will be assigned "low" responsibility for that specific visual input. When an efficient motor output is finally selected, a small error signal will be generated, and when the prediction of the forward model is confirmed by reafferent feedback, the pair of forward and inverse models will be given high responsibility for that action.

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[3] The same question is addressed by Cecilia Heyes in vol. 1, ch. 6, p. 158. She calls it the "correspondence problem." The solution that she proposes addresses a level of explanation somewhat different from the one we are addressing here. However, what she proposes is not only very plausible, but also is compatible with the functional architecture presented here.

Another question that is worth posing is the following. Within each region (STS, human inferior frontal or macaque F5, human posterior parietal or macaque PF), are the areas receiving inputs and producing outputs the same or different? In other words, how does the functional architecture of inverse and forward models map onto neural structures and above all onto mirror neurons? We recently performed a meta-analysis of some fifty fMRI datasets obtained from normal volunteers performing imitation and observation of hand actions (Molnar-Szakacs et al., 2002). We have observed that in the dorsal sector of pars opercularis of the inferior frontal gyrus (the human homologue of F5) there is an area that is active during both action observation and imitation, whereas in the ventral sector of pars opercularis of the inferior frontal gyrus, there is an area that is active during imitation but not during action observation.

One way of looking at these findings is that the dorsal sector represents the mirror sector of pars opercularis, whereas the ventral sector is simply a premotor area. Another way of looking at them, however, is that the dorsal sector of pars opercularis receives the STS input of the visual description of the observed action and produces the motor plan that forms the output of the inverse model, whereas the ventral sector of pars opercularis produces the efferent copy of the motor command to be sent back to STS and used by the forward model to predict the sensory consequences of the imitative action.

In STS, the meta-analysis that we performed shows that the areas active during imitation and action observation overlap completely. This suggests that the same STS area produces the visual description of the action used as input by the inverse model and receives the efferent copy of the motor command used by the forward model.

2.3 A Way to Language

2.3.1 The Essential Role of Broca's Area in Imitation of Finger Movements

Some neuroanatomical considerations suggest that area F5 of the macaque brain is the evolutionary precursor of Brodmann area 44 (BA 44) of the human brain (von Bonin & Bailey, 1947; Petrides & Pandya, 1994; Rizzolatti & Arbib, 1998). Brodmann area 44 is a cytoarchitectonic area that probabilistically maps onto pars opercularis of the inferior frontal cortex (Mazziotta et al., 2001a,b), an area that we have seen is strongly implicated in imitation and belongs to what we call the minimal neural architecture for imitation. BA 44 is part of Broca's area (some authors assign Broca's area to BA 44 only), the most important cortical region for language processing in the human brain. The simultaneous involvement of BA 44 in language and imitation, and the evolutionary anatomical considerations that I address later, suggest functional links between imitation and language. A discussion of these possible links is the focus of this section.

In the macaque frontal lobe, there is a major sulcus that divides the anterior granular prefrontal cortex from the posterior agranular motor and premotor cortex. This sulcus is called the arcuate sulcus since its shape resembles an arc. It has been suggested that the evolutionary process has transformed the dorsal sector of the arcuate sulcus of the macaque brain into the superior frontal sulcus of the human brain. The same process would have transformed the ventral sector of the arcuate sulcus into the inferior frontal sulcus of the human brain. Area F5 is ventral to the arcuate sulcus, and its human homologue would also be located ventrally with respect to the inferior frontal sulcus. Thus one would expect to find the human homologue of area F5 in the inferior frontal gyrus. And one would most likely find it relatively posteriorly located, sitting just in front of the premotor cortex represented in the precentral gyrus, given that F5 is a rostral premotor area. If one then considers the cytoarchitecture of F5, which is devoid of a granular layer, one would expect the human homologue of F5 to be an agranular cortical area.

If one considers all these points, the most likely candidate as a human homologue of F5 is BA 44 (Rizzolatti & Arbib, 1998; Geyer et al., 2000). In fact, BA 44 is the rostralmost agranular cortical field in the inferior frontal gyrus and is located right anteriorly to the ventralmost sector of the precentral gyrus. If BA 44 were the human homologue of macaque F5, then one would expect that from a physiological standpoint these two areas should share some features. In terms of motor representation of body parts, F5 in the macaque contains a representation for hand movement and one for mouth movements. Thus one would expect motor representation for the hand and the mouth in BA 44 also. In fact, several imaging studies have reported activation in BA 44 for motor tasks that engage the hand (Krams et al., 1998; Binkofski et al., 1999b; Iacoboni et al., 1999; Ehrsson et al., 2000) and the mouth (Fox et al., 2001). This also means that in an imaging experiment on, say, imitation of foot movements, one should not expect to observe activation of BA 44 if this activation reflects the motor aspect of BA 44 and not its linguistic (supposedly disembodied) one.

The activation studies that we have performed on imitation of hand movements have demonstrated that a sector of pars opercularis is activated during imitation and observation of hand actions. Its activity is also modulated by the type of imitation (specular versus anatomical) and by goal-oriented imitation. Our meta-analysis of hand imitation (Molnar-Szakacs et al., 2002) points to the dorsal sector of pars opercularis as the sector of Broca's area with these characteristics. Also, a meta-analysis of language tasks (Chein et al., 2002) suggests that the dorsal sector of pars opercularis is a critical language region. The convergence of the empirical data is impressive and suggests shared neural structures for imitation and language. It could be objected, however, that the activation observed in Broca's area during imitation is simply due to some kind of silent and perhaps unconscious verbalization (Heyes, 2001a). This objection does not really explain why there should be more verbalization in some imitative conditions but not in others. It also does not explain why the observation of hand movements activates Broca's area but the observation of foot movements does not. At any rate, the silent verbalization hypothesis cannot be dismissed too lightly.

To test whether the involvement of Broca's area in imitation is due to silent verbalization or to mirror activity for hand or mouth movements, we used repetitive transcranial magnetic stimulation (rTMS). This technique allows one to create a kind of temporary, transient lesion in the brain area stimulated (Walsh & Cowey, 2000). We stimulated the pars opercularis of the inferior frontal gyrus during imitation of hand actions and during a control visuomotor task. We also stimulated a control site. If activation of Broca's area in imaging studies of imitation is due only to an epiphenomenal silent verbalization, then producing a transient lesion in pars opercularis should not affect the imitative performance. If, in contrast, Broca's area is essential to imitation, then producing a transient lesion in pars opercularis should have an effect on imitation. And if this effect reflects impairment in functional processes that are specific to imitation and to BA 44, then performance in the control task should be unaffected by stimulation of pars opercularis, and performance in the imitation tasks should be unaffected by stimulation of the control site. The results we obtained in a recent rTMS study performed in our laboratory (Heiser et al., 2003) are consistent with the hypothesis of an essential role for Broca's area, namely BA 44, in imitation (figure 2.5).

The possibility remains that the effect we observed is language mediated, so that one has to name a finger movement in order to imitate it. However, this is quite unlikely if one looks at human development. In fact, infants can imitate much earlier than they can talk (Meltzoff & Moore, 1977). If Broca's area has an essential role in imitation, then it must be concluded that this area is not exclusively dedicated to language processing. It also

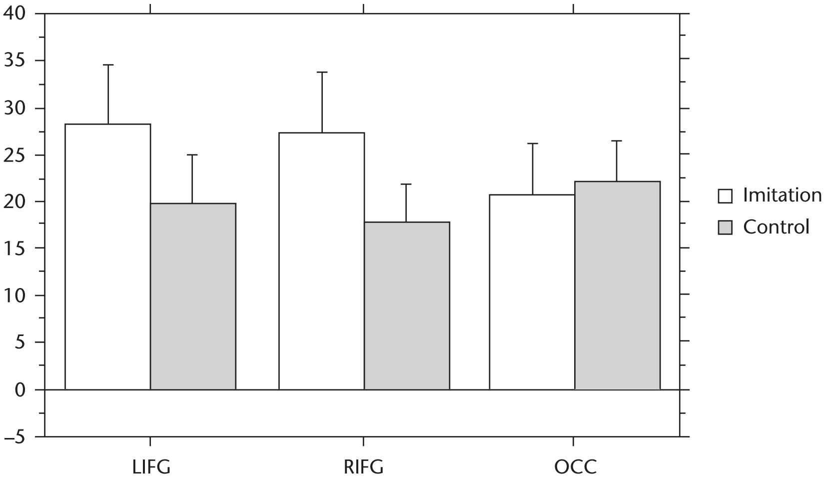

Figure 2.5
Percent errors in imitation (white bars) and control task (gray bars). LIFG, left inferior frontal gyrus (pars opercularis); RIFG, right inferior frontal gyrus (pars opercularis); OCC, control site in occipital cortex. There is a reliable increase in the error rate for rTMS over the left and right pars opercularis during imitation only.

suggests an evolutionary continuity between action recognition, imitation, and language.

2.3.2 Warping Chimp Brains onto Human Brains

The three areas that form what we call the minimal neural architecture for imitation are all located around a major sulcus of the human brain, the Sylvian fissure. The cortex around the Sylvian fissure is called perisylvian and it is known to be extremely important for language. It is possible that the circuit for action recognition in the monkey has evolved to support imitation and subsequently language in humans. From a relatively simple neural mechanism of matching observation and execution of an action (mirror neurons), more complex functional properties were built and more complex behaviors were supported. If this hypothetical scenario has some plausibility, one should observe across species morphometric changes localized around the Sylvian fissure.

The laboratory of Karl Zilles has warped magnetic resonance images of chimpanzees' brains into those of human brains. The process of warping the brain of one species into that of another can be quantified by mapping the local field deformations determined by the warping algorithm. By doing so, one can obtain a map of the local changes caused by the evolutionary process in the primate brain. What emerges is that the greatest changes can be observed around the Sylvian fissure, thus supporting the hypothesis that the action recognition system of the macaque is the evolutionary precursor of the neural systems associated with language in the human brain.

From a functional standpoint, the mirror system meets the criterion of the "parity assumption" between a sender and a receiver of a message proposed by Alvin Liberman and his motor theory of speech perception (Liberman & Mattingly, 1985; Liberman & Whalen, 2000). In this theory, what counts for the sender must count for the receiver. Hence, a common code for language perception and language production is necessary. Evidence in favor of such a code in the domain of language has been recently provided by a TMS study in which subjects listened to speech. It was found that the listeners' tongue muscles were much more excited by a single TMS pulse delivered over the motor cortex when they were listening to words that required strong tongue movements to pronounce (Fadiga et al., 2002). This evidence is clearly compatible with the motor theory of speech perception, according to which it is the activation of the articulatory motor gesture that enables the perception of the speech sounds.

Another empirical link between speech perception and the action recognition system of the macaque has been recently provided by single-unit data. It has been shown that mirror neurons in the macaque area F5 fire, not only at the sight of an action, but also at the sound of an action (i.e., breaking a peanut) in the dark (Kohler et al., 2002). These data suggest two things. First, mirror neurons have the auditory access necessary to implement speech perception. Second, they enable a multimodal representation of action that is not linked to the visual channel only. This may facilitate the learning of speech sounds via imitation.

However, the question that is typically raised here is, How does one go from a relatively simple action recognition system to the complex symbolic levels reached by human language? In the next section, rather than trying to answer the question, I look at the plausibility of the question itself and discuss language, not in the abstract forms often studied by mainstream linguistics, but in its daily, embodied form: conversation.

2.3.3 What We Talk about When We Talk about Language

Traditionally, linguists have approached language by trying to extrapolate the most formal and abstract aspects of it. As shown in figure 2.6 (left side), one can form sentences following what has been called a tree structure. The

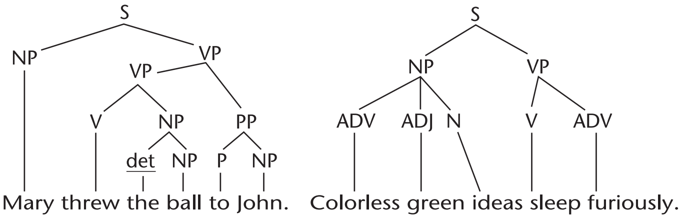

Figure 2.6

main idea behind it is that certain lexemes "govern" or "bind" some other lexemes. Thus, every grammatical sentence (S, top of the tree) consists at least of a noun phrase (NP) and a verb phrase (VP). NP and VP in turn break down into various "branches." An NP may consist of a determiner and an adjective and a noun, as for instance in the case "the funny guy." A VP may consist of a verb (threw) and an NP (the ball) and a prepositional phrase (to John) that can be further decomposed.

The benchmark test of this approach is shown in figure 2.6 (right side). The sentence is completely nonsensical and doesn't refer to real things, yet it still follows grammatical rules. This has been taken as evidence in favor of a universal grammar that can be processed similarly by all brains (Chomsky, 1981, 1986a,b, 1990, 1997, 1999). So the question here would be, How can such a formalized structure emerge from a relatively primitive action recognition system? A type of answer (very vague, admittedly) to this question that is provided by others elsewhere (Rizzolatti & Arbib, 1998) is that "gestures may be a primitive form of grammar." The problem with both question and answer is that they accept a view of language as a phenomenon that can be essentially reduced to formal constructs such as grammar.

The real question to ask is, How do people talk? Figure 2.7 shows a transcription of typical naturally occurring everyday speech. As can be seen, not only do violations of grammar (in italics) occur throughout the speech, but most importantly, this segment of speech is full of phenomena (indicated by question marks that show sound stretches, hesitation markers, false starts, self-repairs, prosodic emphasis, and manipulation of timing and word rhythm) that are meaningful to both speaker and hearer. These phenomena are not even part of what is studied by traditional linguists. However, Conversation Analysis (CA) has provided a corpus of robust empirical data that describe these phenomena well (Heritage, 1989; Goodwin & Heritage, 1990; Heritage & Roth, 1995; Goodwin, 2000; Goodwin & Goodwin, 2000).

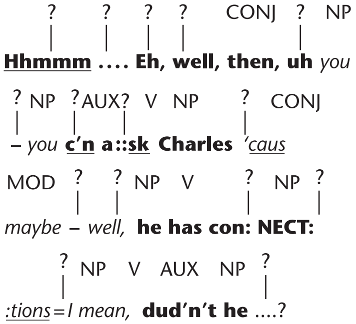

Figure 2.7

A salient feature of typical conversations that is ignored by traditional linguists is turn-taking. The average transition space from one speaker to another is less than 0.2 seconds, and longer pauses are immediately perceived as violations of temporal norms, even by young children. What enables such fast transitions is the hearer's tracking through the stream of the other's speech the appearance of fairly invariant, transiently appearing opportunities for taking a turn—which are not exclusively grammatical but rhythmic and pitch contour-intonational as well. CA data show that the fast transition that typically occurs between sentences is so familiar to both parties as a legitimate point for the other speaker to come in that elaborate strategies in rhythm, intonation, and even grammar have to be adopted by the original speaker in order to obtain a multisentence turn in conversation.

What comes out of CA's acknowledgment of language as an embodied practice is that such motoric processes as eye-gaze, body torque, rhythm attunement, and simultaneous gestures are part of a social interaction (rather than a "software program" as classic cognitivism advocates) that is critically dependent on the motor system's facility for temporal orientation and organization of sequence and, I propose, is also dependent on (and plausibly even deriving from) the action recognition or mirror system.

Thus, rather than trying to mimic a traditional grammatical structure in the domain of manual communication (the approach of Rizzolatti and Arbib, 1998), what I advocate here is to consider carefully the incontrovertibly motor elements that are at work in conversation and that human beings must still rely on to choreograph their interactions with each other. The processing of all those motor elements that give meaning to conversations requires a fast functional architecture that is not dissimilar to the one needed in motor control. Here is where forward and inverse modeling and the action recognition system, in which mirror neurons can coordinate activity between individuals with a simple matching mechanism, have a real computational advantage over classical cognitive architectures.

2.4 Feeling the Emotions of Others

2.4.1 Empathy and Imitation

Empathy allows the sharing of experiences, needs, and goals across individuals, thus playing a fundamental role in social cognition. The functional aspects and corresponding neural mechanisms of empathy, however, are poorly understood. When Theodore Lipps introduced the concept of empathy (*Einfühlung*), he theorized a critical role for the mechanism of *inner imitation* of the actions of others in generating empathy (as cited in Gallese, 2001). In support of Lipps's idea, empathic individuals exhibit nonconscious mimicry of the postures, mannerisms, and facial expressions of others (the *chameleon effect*) to a greater extent than nonempathic individuals (Chartrand & Bargh, 1999). Thus empathy may occur via a mechanism for representing action that modulates and shapes our understanding of the emotional states of other individuals.

Separate neural systems for emotions and action representation, however, do exist in the primate brain. The limbic system is critical for processing emotion and behavior, and the temporo-parieto-frontal circuit I described earlier (the minimal neural architecture for imitation) is critical for representing action. Anatomical data suggest that a sector of the insular lobe, the dysgranular field, is connected with the limbic system as well as with posterior parietal, inferior frontal, and superior temporal cortex (Augustine, 1996). This connectivity pattern makes the insula a candidate for relaying information about the representation of actions to limbic areas that process emotional content.

2.4.2 The Minimal Neural Architecture for Imitation and the Limbic System: A Role for the Insular Lobe

To test this hypothesis, we performed two experiments—a brain imaging experiment with normal volunteers and a neuropsychological study with both neurological patients and normal controls. In the brain imaging study (Carr et al., 2003) we used fMRI while the subjects were either observing or imitating emotional facial expressions. A modulation of the action representation circuit onto limbic areas via the insula predicts greater activity in the whole network during imitation, compared with observation of emotion. In fact, mirror areas would be more active during imitation than during observation because of the simultaneous encoding of the sensory input and planning of the motor output. Within mirror areas, the inferior frontal cortex seems particularly important here, given that an understanding of goals is an important component of empathy. The insula would be more active during imitation because its role as a relay would increase, compared with mere observation. Finally, limbic areas would also increase their activity because of the increased motor activity. Moreover, if mediation by representations of action is really critical to empathy and the understanding of the emotions of others, then even the mere observation of emotional facial expressions should activate brain regions of motor significance. Thus observation and imitation of emotions should yield substantially similar patterns of activated brain areas, with greater activity in premotor cortex, especially inferior frontal cortex, and in superior temporal cortex, insula, and limbic areas during imitation.

The results of the fMRI study confirmed our hypothesis. There was a substantially similar network of activated areas for both imitation and observation of emotion. Among the areas activated during both imitation and observation, the premotor face area, the dorsal sector of pars opercularis of the inferior frontal gyrus, the superior temporal sulcus, the insula, and the amygdala had greater activity during imitation than during observation of emotion.

The peak of activation in primary motor cortex during imitation of facial emotional expressions that we observed in our study corresponds extremely well with the location of the primary motor mouth area as determined by a meta-analysis of published PET studies, by a meta-analysis of original data in thirty subjects studied with PET, and by a consensus probabilistic description of the location of the primary motor mouth area obtained by merging the results of the two previously described meta-analyses (Fox et al., 2001). This confirms the robustness and reliability of the data, in spite of the presence of facial motion during imitation. This is because, even though motion artifacts were present at the individual level, the group analysis got rid of them since each subject had different kinds of motion artifacts and they were thus eliminated when all the data were considered. In keeping with this, the data also clearly show peaks of activity in the pre-SMA face area and the face area of the posterior portion of the rostral cingulate zone (RCZp) that correspond extremely well with the pre-SMA and RCZp face locations as determined by a separate meta-analysis of PET studies that focused on motor areas in the medial wall of the frontal lobe (Picard & Strick, 1996).

Thus, our dataset clearly represents the first fMRI demonstration of human primary motor and rostral cingulate face areas. With regard to premotor regions, the peaks that we observed correspond well with premotor mouth peaks as described by studies in which action was observed. In fact, robust premotor responses during the observation of facial emotional expressions were found, which is in line with the hypothesis that action representation mediates the recognition of emotions in others even during simple observation.

The activity in pars opercularis shows two separate foci during imitation, a ventral and a dorsal peak, but only the dorsal peak remained activated, albeit at significantly lower intensity, during observation of emotion. This pattern, with very similar peaks of activation, was also observed in our fMRI meta-analysis of imitation and observation of hand actions previously described (Molnar-Szakacs et al., 2002). In the monkey, F5 neurons coding arm and mouth movements are not spatially segregated, and our human imaging data are consistent with this observation. Furthermore, the imaging data on imitating facial emotion converge with the data on hand imitation in suggesting that the mirror sector of the human inferior frontal gyrus is located in the dorsal part of pars opercularis.

The anterior sector of the insula was active during both imitation and observation of emotion, but more so during imitation, fulfilling one of the predictions of the hypothesis that action representation mediates empathy. This is in line with two kinds of evidence available on this sector of the insular lobe. First, the anterior insula seems to receive slow-conducting unmyelinated fibers that respond to a light, caresslike touch and may be important for emotional and affiliative behavior between individuals (Olausson et al., 2002). Second, imaging data suggest that the anterior insular sector is important for the monitoring of agency (Farrer & Frith, 2002), the sense of ownership of actions, which is a fundamental aspect of action representation. This confirms a strong input into the anterior insular sector from areas of motor significance.

The increased activity in the amygdala during imitation compared with observation of emotional facial expression reflects the modulatory role of the action representation circuit in limbic activity. It has been long hypothesized (Darwin was the first in 1871; Ekman, 1973, 1999; Buck, 1980) that facial muscular activity influences people's affective responses. This is the first demonstration, however, that activity in the amygdala, a critical structure in emotional behaviors and in the recognition of facial emotional expressions of others, increases while subjects imitate the facial emotional expressions of others, compared with mere observation.

To further test the hypothesized mediation of limbic activity by action representation via the insula, we also studied the ability to recognize emotions in two groups of ischemic stroke patients and in a control group. We studied patients with insular lesions only and compared them with patients who had lesions outside the insula. If empathy occurs via modulation, implemented in the insula, of limbic activity by action representation, then an insular lesion should impair such a mechanism. This predicts a greater deficit in recognizing emotion in patients with insular lesions than in patients with lesions outside the insula. This is because the insula would be an obligated path through which the modulation of action representation networks must be channeled to reach limbic structures such as the amygdala. This prediction was confirmed by the empirical data. Although both groups of patients were significantly impaired compared with normals, the deficit in recognition of emotion was significantly greater in insular patients than in stroke patients with lesions outside the insula. The deficit in recognition of emotion in noninsular patients may be due either to nonspecific effects of the lesions or to some effects on the action representation network produced by the lesions. The additional evidence from the data obtained in neurological patients is extremely important because activation studies cannot fully determine if an activated area is essential to the task or behavior studied. Recently, repetitive TMS has been used to create transient lesions in normal subjects to test how essential a given activated area is, as in our rTMS study on imitation in Broca's area described earlier. Repetitive TMS, however, cannot reach deep structures such as the insula. Hence the clinical data are essential here.

Some preliminary neurological evidence in support of both the anatomical and functional proposal described here has also been described in a patient with a subcortical lesion encompassing the anterior sector of the insula. This patient had both the inability to detect disgust as presented in many different ways, from nonverbal emotional sounds to prosody to facial expressions, and the inability to experience disgust himself (Calder et al., 2000).

All in all, we understand the feelings of others via a mechanism of action representation that shapes emotional content, such that our empathic resonance is grounded in the experience of our acting body and the emotions associated with specific movements. As Lipps noted, when I observe a circus performer on a hanging wire, I feel I am inside him (as cited in Gallese, 2001). In order to empathize, we rely on mediation by the representation of the actions associated with the emotions we are witnessing and on a brain network that includes structures supporting communication between action representation circuits and circuits dedicated to emotional processing.[4]

2.5 Conclusion

The temporo-parieto-frontal circuit described here is the first available neural model of imitation in primates. The anatomical location and the functional properties that this circuit exhibits confirm a key role for imitation in learning and communication. This may not appear as big news to behavioral scientists who have studied imitation for years and have observed how imitative abilities are tied to social learning. The novelty, however, resides in the fact that our research program shows how the functional properties of a relatively well-developed large-scale neural circuit can now inform us about the functional characteristics of behavioral domains that remained for a long time impenetrable to a neuroscientific investigation. This information, in turn, can be used to test more general questions in the behavioral sciences; for instance, the innateness or learnability of some functions, or the approach human beings take to mentalizing.[5]

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4. For a discussion relevant to this section, see vol. 2, ch. 13 by Jesse Prinz and the comments by Huesmann in vol. 2, ch. 19.6, p. 386. ED.

5. See comments on this chapter by Arbib, vol. 1, ch. 8.2, p. 200, by Blackmore, ch. 8.3, p. 203. ED.

3 "Being Like Me": Self–Other Identity, Mirror Neurons, and Empathy

Vittorio Gallese

3.1 Introduction

We readily ascribe intelligence to other animals while being simultaneously inclined to think that—cognitively speaking—humans "do it better." We are and we feel we are different from other animals, even from our closest relatives among nonhuman primates, the apes. There are indeed many differences between humans and other primates. One of the most crucial is thought to be the capacity to "read" the mind of others, which many ascribe only to humans.

In daily life we are constantly exposed to the actions of other individuals inhabiting our social world. We are not only able to experience their behavior, understand its content, and predict its consequences, we can do more than that; we can also attribute intentions to other individuals. We can immediately recognize whether their behavior is the result of a purposeful and deliberate attitude or the unpredicted consequence of some accidental event that is totally unrelated to their will. As maintained by so-called "folk psychology," we are able to understand the behavior of others in terms of their mental states. This view prefigures a distinction between species that are confined to behavior reading and our species, which makes use of a different level of explanation: mind reading.

However, it is by no means obvious that behavior reading and mind reading constitute two autonomous, encapsulated realms. It is even less obvious that in understanding the intentions of others we employ a cognitive strategy totally unrelated to predicting the consequences of their observed behavior. Whenever we face situations in which exposure to others' behavior requires a response by us, be it active or simply attentive, we seldom engage ourselves in an explicit, deliberate interpretative act. Our understanding of a situation most of the time is immediate, automatic, and almost reflexlike. Therefore it seems preposterous to claim that our capacity to reflect on the real intentions determining others' behavior is all there is to understanding it.

Mind reading, whatever it might be, is at best only one part of our mental space. This space is multidimensional; it is as many-sided as the dimensions that characterize our mental life and as the many possible ways to live our lives and to look at them. We can put ourselves on a scale and check our body weight. Or we can think about what someone else shouldn't have thought about us. In both instances we do not experience any identity shift. We do not feel *different* when we are checking our body weight and when we entertain counterfactual third-person metarepresentations. This is quite rightly so, in that what does change is not the individual organism. What changes is the type of *relational specification* by which each organism (a biological system) engages itself during the various possible kinds of interaction with the world outside. Relational specifications constitute the almost infinite levels at which we may decide to *act upon* the world. And there are almost infinite levels at which *others* may do the same. We can take a swim, plant a tree, get a doctoral degree, or think about Ulysses, while simultaneously knowing in an implicit and unmediated way that others do the same and think the same, or that they do not. All these levels of interaction, when ascribed to others, pertain to different beings, different persons whom, nevertheless, we feel, recognize, and represent as similar to us.

Beside—and likely before—the ascription of any intentional content to others, we entertain a series of implicit certitudes about the content-bearing individuals we are confronted with. These implicit certitudes constitute the intersubjective relation and concern the sense of oneness, of identification with the other that makes sit possible to ascribe *any* content, whatever it might be, to the individual we are interacting with.

We could certainly hold a solipsistic view and claim that just because all individuals are the same, in defining cognition we should not waste our time with speculations on the relevance of others' minds. Solipsism recommends instead a focus on the *single* individual's mind. This should secure enough knowledge to define what a mind is and how it works. Following this perspective, the mechanisms enabling the epistemic relations between the rational agent and the world are of no relevance for the determination of representational content and for the understanding of what that content is and what it stands for (see Fodor, 1998).

But I will not adopt the solipsistic view. In this chapter I analyze from a neuroscientific perspective the constituents of the implicit certitudes enabling intersubjective relations, and what might be the neural mechanisms underpinning them. *Pace* solipsism, I propose that our cognitive stance toward life is but one expression of the many and diversified modes in which we interact with the world. From the very beginning of our lives, intersubjective relations constitute a major part of our daily interactions with the world. I will posit that intersubjective relations play a *major* and *constitutive* role in shaping our cognitive capacities and in providing the shared database required to establish meaningful bonds with other individuals.

After having identified the peculiar perspective inspiring the present proposal, let us have a closer look at social behavior. The pervasive social habits of primates are most likely the result of a very long evolutionary path in that these habits are patently not peculiar to primates. They are indeed diffused across species spaced as far apart in evolutionary time as humans and ants. Social interactions play different roles according to different modalities in different species. Nevertheless, transverse to and at the basis of all social species and all social cultures, of whatever complexity, is the capacity for identification with the individuals within those species and cultures. When I speak of self–other identity in this context, I mean the identification of the self with another individual as "like me" in some way (which can, but need not, involve mental identification). As humans, we implicitly know that all human beings have four limbs, walk in a certain way, act in peculiar ways, etc. If we share the same culture, we will, for example, all tattoo our body in a peculiar striped fashion, or wear the same school necktie at reunions, or be against the death sentence, etc.

Identity, as we have seen, is articulated on many different levels of complexity. Identity can be subjected to increasingly complex tests in which different species might score differently, but it is nevertheless the membership fee all individuals have to pay in order to self-guarantee the sense of belonging to a larger community of other organisms. Identity is so important within a group of social individuals because it enables them to predict more accurately the consequences of others' future behavior. This capacity in turn contributes to optimizing the employment of cognitive resources by reducing the meaning space to be mapped. Identity contextualizes content by reducing the number of possible information units the brain is required to process.

Several developmental psychology studies have shown that the identity-based capacity to predict others' behavior is a very early endowment of human beings. In infants the establishment of relations with others is accompanied by the registration of behavioral invariance. This in turn translates into the implicit procedural memory of the organism (on this point and for a discussion of the relevant literature, see Stern, 1985). This experience-driven process of constant remodeling of the system is one of the building blocks of cognitive development, and it capitalizes upon coherence, regularity, and predictability. Self–other identity underlies all these features, henceforth its high social adaptive value.

Anytime we meet someone, we do not just perceive that someone to be, broadly speaking, similar to us. We are implicitly aware of this similarity because we literally embody it. Meltzoff & Brooks (2001) have convincingly suggested that the "like me" analogy between infant and caregiver is *the* starting point for the development of (social) cognition. This analogical process proceeds in a bidirectional way. Infants use the observed behavior of their human companions as a mirror to gain more knowledge about themselves. But the same process also works the other way around; it enables infants to know about the others.

The posited important role of self–other identity relations in determining the cognitive development of our mind provides a strong motive to investigate from a neuroscientific perspective the functional mechanisms (and their neural underpinnings) at the basis of self–other identity. This is the main issue addressed in this chapter. Later on I discuss the neuroscientific results in relation to the notion of empathy, which, after several decades of almost complete oblivion, has forcefully reappeared in the contemporary debate on human cognition. After a brief historical review, I provide an enlarged account of empathy defined by means of a new conceptual tool: the *shared manifold* of intersubjectivity. I conclude by proposing that it is by means of this shared manifold that other human beings can be recognized to be similar to us. This identity relation will bootstrap imitation, interindividual communication, and mind reading.

3.2 "Being Like Me": A Neuroscientific Approach to the Self–Other Identity

One of the major contributions to a new understanding of human social cognition during recent decades has come from research in developmental psychology. As infants, for years we all heavily rely on interactions with our caregivers and with other individuals to learn how to cope with the world. Developmental psychology has provided an enormous amount of data that have literally revolutionized our way of looking at newborns and infants as cognitive agents. These results have shown, among other things, that at the very beginning of our life we almost immediately interact with others by *reproducing* some of their behaviors. The seminal study by Meltzoff and Moore (1977) and the subsequent research field it opened (see

Meltzoff & Moore, 1997; Meltzoff, 2002a,b; and Meltzoff, vol. 2, ch. 1), showed that newborns as young as 18 hours are capable of reproducing mouth and face movements displayed by the adult they are facing. The particular part of their body replies, although not as a mere reflex (see Meltzoff & Moore, 1977, 1994), to movements displayed by the equivalent body part of someone else. More precisely, this means that newborns set into motion, and in the correct way, a part of their body they have no visual access to, but which nevertheless acts to match an observed behavior. To put it very crudely, visual information is transformed into motor information.

This apparently innate mechanism has been labeled active intermodal mapping (AIM; see Meltzoff & Moore, 1997). Intermodal mapping defines a "supramodal act space" (Meltzoff, 2002a), which provides representational frames not limited to any particular mode of interaction, be it visual, auditory, or motor. Modes of interaction as diverse as seeing, hearing, or doing something *must* therefore share some peculiar feature that makes the process of equivalence carried out by AIM possible.

The issue then consists in clarifying the nature of this peculiar feature and the possible underlying mechanisms. My best candidate for a shared feature is the relational character intrinsic to any interaction between a biological system and the environment. Our environment is composed of a variety of lifeless though not refractory forms of matter and a variety of living things, whose peculiar character is more and more discerned by the infant's immature eye. Individuals confront many possible kinds of external objects and, because of their peculiar status as biological systems, are constrained in their modes of interaction. Any interaction requires a control system implementing a control strategy. Interestingly enough, control strategies share with modes of interaction a *relational* character. As modes of interaction, control strategies are essentially relational in that they *model* the interaction between organism and environment, to better control it.

However, a model is a form of representation. This step allows a relation of interdependence, if not even superposition, to be established between control of behavior and the representation to be established (see Gallese, 2000b). This relation holds for both organism–object and organism–organism modes of interaction. This relation is established at the very onset of our life, when no subjective representation can yet be entertained by us, because there is not yet a *conscious subject* of experience. The absence of a subject does not preclude, however, the presence of a primitive *self–other space*, a paradoxical form of intersubjectivity without subjects. The infant shares this space with lifeless objects as well as with living others, which are internalized by the infant because they are a projection of the control strategies governing the interactions they are part of. Both lifeless objects and living others are represented as the materialization of their implicit objectual character within these interactions. The physical space occupied by inanimate objects and bodies of the adult others is connected to the body of the infant to compose a blended, shared space.

What is the role and fate of this peculiar shared informational space in the course of cognitive development? This issue is worth scrutiny. The shared blended space enables the social bootstrapping of cognitive and affective development. Once the crucial bonds with the world of others are established, this space carries over to the adult conceptual faculty of socially mapping sameness and difference (''I am a *different subject*''). The more mature capacity to segregate the modes of interaction, together with the capacity to carve out of the blended space the subject and the object of the interaction, does not annihilate the shared space.

The shared space provides an incredibly powerful tool for detecting and incorporating coherence, regularity, and predictability in the course of an individual's interactions with his or her environment. The shared space is progressively joined by perspectival spaces defined by the establishment of capacities to distinguish the self from others while self-control is developing. Within each of these perspectival spaces information can be further segregated in discrete channels (visual, somatosensory, etc.), making our perceptual view of the world more finely grained. The concurrent development of language probably contributes to further separating out of single characters or modalities of experience from the original multimodal perceptual world, but the shared intersubjective space does not disappear. It progressively acquires a different role: to provide our self with the capacity simultaneously to entertain self–other identity and difference. Within intersubjective relations, the other is a living oxymoron, being just a *different self*.

My proposal is that the ''selfness'' quality we readily attribute to others, the inner feeling of ''being like me'' triggered by our encounter with others, is the result of this preserved blended intersubjective space. Self–other physical and epistemic interactions are shaped and conditioned by the same body and environmental constraints. This common relational character is underpinned at the level of the brain by neural networks that compress the redundant ''who did it,'' ''who is it'' specifications, and realize a thinner content state, which specifies what kind of interaction or state is at stake. This thinner content is shared just because, as we have learned from developmental psychology, the shareable characters of experience and action are the earliest constituents of our life.

Before presenting empirical evidence to support my hypothesis, it is necessary to clarify the conditions under which the neuroscientific level of description would appear reasonably apt to support it. The following conditions should do the job;

1. evidence of a neural representational format that can achieve sameness of content in spite of the specific quality of the mode of presentation of its referents;
2. indifference of the representational format to the peculiar perspective spaces from which referents project their content; in other words, indifference to self–other distinctions;
3. persistence of the same representational format into adulthood.

In the next sections I review neuroscientific evidence from our laboratory that appears to be in a good position to satisfy all three conditions.

3.3 Interactions and Their Models

The most rostral sector of the ventral premotor cortex of the macaque monkey controls hand and mouth movements (Rizzolatti et al., 1981, 1988; Kurata & Tanji, 1986; Hepp-Reymond, 1994). This sector, which has specific histochemical and cytoarchitectonic features, has been termed area F5 (Matelli et al., 1985). A fundamental functional property of area F5 is that most of its neurons do not discharge in association with elementary movements, but are active during *actions* such as grasping, tearing, holding, or manipulating objects (Rizzolatti et al., 1988).

What is coded is the relation, in motor terms, between the organism and the external object of the interaction. Furthermore, this relation is of a very special kind: a relation projected to an expected success. A hand reaches for an object, it grasps it, and does things with it. F5 neurons become active only if a particular type of interaction (e.g., hand–object, mouth–object, or both) is executed until the relation leads to a different state of the organism (e.g., to take possession of a piece of food, to throw an object away, to break it, to bring it to the mouth, to bite it). Particularly interesting in this respect are grasping-related neurons that fire any time a monkey *successfully* grasps an object, regardless of the effector employed, be it any of its two hands, the mouth, or both (Rizzolatti et al., 1988; see also Rizzolatti et al., 2000).

The independence between the nature of the effector involved and the end state that the same effector attains constitutes an *abstract* kind of representation. The firing of these neurons instantiates the same content (the new end state the organism will attain), even if it is differently mediated. In accord with information theory, a thinner content state has been reached by compressing redundant information about which effector or which dynamic parameters should be involved in the interaction. This compression process is not cognitive per se. It is just an information compression process. Nevertheless, by employing an intentional language, we could describe this neural mechanism in terms of goal representation (see Rizzolatti, 1988; Gentilucci & Rizzolatti, 1990).

Beyond purely motor neurons, which constitute the overall majority of all F5 neurons, area F5 also contains two classes of visuomotor neurons. Neurons of both classes have motor properties that are indistinguishable from those of the earlier-described purely motor neurons, while they have peculiar visual properties. The first class is made up of neurons that respond to the presentation of objects of particular size and shape in the absence of any detectable action aimed at them, either by a monkey or an experimenter. The monkey sees a particular object and the neuron fires. These neurons have been labeled canonical neurons (Rizzolatti et al., 1988, 2000; Rizzolatti & Fadiga, 1998).

The second category is made up of neurons that discharge when the monkey *observes* an action made by another individual and when it *executes* the same or a similar action. We labeled them mirror neurons (Gallese et al., 1996; Rizzolatti et al., 1996a; see Rizzolatti, vol. 1, ch. 1, and also Rizzolatti et al., 2001).

Let us first have a closer look at canonical neurons. Most grasping actions are executed under visual guidance. A relationship therefore has to be established between the features of objects and the particular motor specifications they might engender *if* the organism is aiming at them. The appearance of a graspable object in the visual space must somehow set in motion the retrieval of the appropriate mode of interaction required by the intended type of hand–object relation. Suppose we discover neurons that not only code for the motor acts they are supposed to control but also respond to the visual features that trigger them. We would then have a representational format for sameness of content (the successful end state of the hand–object interaction) regardless of the referent, be it the effector or the target object.

Indeed, canonical neurons respond to the visual presentation of objects of different sizes and shapes in the absence of any detectable movement by the monkey (Rizzolatti et al., 1988, 2000; Jeannerod et al., 1995; Murata et al., 1997). Very often a strict congruence has been observed between the type of grip that activated a neuron and the size and shape of the object that triggered the same neuron's response during mere observation of the object. But there is more; in the observation modality, a considerable percentage of neurons display an equally strong response to objects that although differing in shape, nevertheless all "afford" the same type of grip.

A possible interpretation of these findings is that canonical neurons instantiate a *multimodal* representation of organism–object relations. This representation is originally "motor" because it is triggered and driven by motor-control constraints. It is no coincidence that canonical neurons are part of the premotor cortex. However, the representation they instantiate loses its intrinsic motor quality once it blends with the information fed by visual and auditory (see section 3.4) channels. What is represented is not only (or perhaps not anymore) a motor plan; it becomes a multimodal semantic node.

The human brain is not different in this respect. Brain imaging studies in humans have shown an unexpected correlation between categorical perception of tools and the activation of premotor brain sectors (for review, see Martin & Chao, 2001; Malach et al., 2002; see also Gallese, 2003a). The experiments on monkeys described earlier shed light on the neural mechanism as the basis for these results in humans, which further corroborates the hypothesis proposed here.

These results are important because they emphasize that the intentional character, the "aboutness" of the representational format of our mind, is deeply rooted in the essentially relational character of body action, which in turn suggests the essentially *intertwined character* of action, perception, and cognition (see Hurley, 1998; Gallese, 2000b).

Representational content, and thus a *fortiori* conceptual content, cannot be fully explained without considering it as the result of the ongoing modeling process of an organism. The intrinsic need of any organism to control its dynamic interaction with the environment also constrains the way these interactions need to be modeled and hence represented. The same *sensorimotor* circuits that control the ongoing interactions of an organism with its environment also map objects and events in that environment, thus defining and shaping their representational content. Our representation of the world is a model of the world that must incorporate our idiosyncratic way of interacting with it. As will become clearer in the next section, this feature is not unique to organism–object interactions but also applies to interpersonal relations.

3.4 Self–Other Identity and Shared Multimodal Content

Let us return to neurophysiological data on monkeys from our laboratory. As briefly mentioned in section 3.3, the second class of F5 visuomotor neurons is made up of mirror neurons. They discharge both when a monkey makes a specific action and when it observes another individual making a similar action (Gallese et al., 1996; Rizzolatti et al., 1996a).

This evidence demonstrates that in *adult* individuals, both monkeys and humans (see Rizzolatti, vol. 1, ch. 1), a mirror matching neural mechanism can represent content *independently of the self–other distinction*, thus satisfying the last two criteria I posited to be necessary to ground my working hypothesis empirically. The first criterion, namely, sameness of content regardless of how the referents are presented, has not yet been addressed. In a recent study we investigated whether there are neurons in the monkey premotor cortex that discharge when the monkey makes a specific hand action and also when it *hears* the corresponding action-related sounds. The results showed that the monkey premotor cortex contains neurons that discharge when the monkey *executes* an action, *sees*, or just *hears* the same action performed by another agent. We have labeled these neurons audiovisual mirror neurons (Kohler et al., 2001, 2002). They respond to the sound of actions and discriminate between the sounds of different *transitive* manual or oral actions that are compatible with the monkey's natural behavioral repertoire. Audiovisual mirror neurons, however, do not respond to other similarly interesting sounds, such as arousing noises, or monkeys' and other animals' vocalizations. The actions whose sounds evoke the strongest responses when heard also trigger the strongest responses when they are observed or executed. The activity of this neural network does not significantly differ if events in the world, such as noisy actions, are specified at the motor, visual, or auditory level. Such a neural mechanism can represent the end state of the interaction independently from its different modes of presentation by sounds, visual images, or willed, deliberate acts of the body. All modes of presentation of the event are blended within a circumscribed, informationally thinner level of semantic reference.

Furthermore, and most important for our quest for a neural correlate of intersubjective identity, sameness of content is shared with different organisms. This shared semantic content is the product of modeling the observed *behavior* as an *action* with the help of a matching equivalence between what is observed or heard and what is executed.

Mirror neurons, like canonical neurons, instantiate a *multimodal* representation of organism–object relations. In the case of canonical neurons, these relations imply an interacting actor; thus they typically pertain to an actor-centered frame of reference. The object is relevant for someone who will do things with it, even if only potentially. However, mirror neurons also do something different. They map this multimodal representation across different spaces inhabited by different actors. These spaces are blended within a unified common intersubjective space, which paradoxically does not segregate any subject. This space is *"we" centric*.

It is worth mentioning that in both monkeys and humans, the mirror system has been discovered and studied in adult individuals (see Rizzolatti, vol. 1, ch. 1). This means that in humans, and even more so in monkeys, the shared space coexists with but does not determine self-awareness and self-identity. The shared intentional space underpinned by the mirror matching mechanism is not meant to distinguish the agent from the observer. As organisms we are equipped with plenty of systems, from proprioception to the expectancy created by the inception of any activity, that are able to distinguish the self from the other. Rather, the shared space instantiated by mirror neurons blends the interacting individuals within a shared implicit semantic content.

The self–other identity preexists and further parallels the self–other dichotomy. As convincingly shown by developmental psychology, the "being like me" analogy relies heavily on action and imitation of action, but is not confined to the domain of action. It is a global dimension that encompasses all aspects defining a life form, from its distinctive body to its distinctive affect. This global dimension covers a broad range of implicit certitudes we entertain about other individuals.

In the following sections I discuss many different forms of interaction, all contributing to the composition of the global experiential dimension we share with others. I will try to recompose all these multidimensional articulations of the self–other relationships within an integrated neuroscientific framework by introducing a new conceptual tool: the shared manifold of intersubjectivity.

3.5 Self–Other Identity and Empathy

Self–other identity goes beyond the domain of action. It incorporates sensations, affect, and emotions. The affective dimension of interindividual relations attracted the early interest of philosophers because it was recognized as a distinctive feature of human beings. In the eighteenth century, Scottish moral philosophers identified our capacity to interpret the feeling of others in terms of "sympathy" (see A. Smith, 1759/1976). But it was during the second half of the nineteenth century that these issues acquired a multidisciplinary character when they were tackled in parallel by philosophers and the scholars of a new discipline, psychology.

"Empathy" is a later English translation (see Titchener, 1909) of the German word "*Einfühlung*." It is commonly held that *Einfühlung* was originally introduced into the vocabulary of the psychology of aesthetic experience by Theodore Lipps (1903a) to denote the relationship between a work of art and the observer, who imaginatively projects herself into the contemplated object.

However, the origin of the term is actually older. As pointed out by Prigman (1995), Robert Vischer introduced the term in 1873 to account for our capacity to symbolize the inanimate objects of nature and art. Vischer was strongly influenced by the ideas of R. Lotze, who already in 1858 proposed a mechanism by means of which humans are capable of understanding inanimate objects and other species of animals by "placing ourselves into them" ("*sich mitlebend . . . versetzen*").

Lipps (1903b), who wrote extensively on empathy, extended the concept of *Einfühlung* to the domain of intersubjectivity, which he characterized in terms of *inner imitation* of the perceived movements of others. When I am watching an acrobat walking on a suspended wire, Lipps (1903b) notes, "I feel myself so inside of him" ("*Ich Fühle mich so in ihm*"). We can see here a first suggested relation between imitation (though "inner" imitation, in Lipps's words) and the capacity to understand others by ascribing to them feelings, emotions, and thoughts.

Phenomenology has further developed the notion of *Einfühlung*. A crucial point in Husserl's thought is the relevance he attributes to intersubjectivity in the constitution of our cognitive world. Husserl's rejection of solipsism is clearly epitomized in his fifth *Cartesian Meditation* (1953/1977, English translation), and even more in the posthumously published *Ideen II* (1989, English translation), in which he emphasizes the role of others in making our world "objective." It is through a "shared experience" of the world, provided by the presence of other individuals, that objectivity can be constituted. Interestingly enough, according to Husserl, the bodies of self and others are the primary instruments of our capacity to share experiences with others. What makes the behavior of other agents intelligible is the fact that their body is experienced, not as material object (*Körper*), but as something alive (*Leib*), something analogous to our own acting body as we experience it.

From birth onward the *Lebenswelt*, the world inhabited by living things, constitutes the playground of our interactions. Empathy is deeply grounded in the experience of our lived-in body, and it is this experience that enables us directly to recognize others, not as bodies endowed with a mind, but as *persons* like us. Persons are rational individuals. What we now discover is how a rationality assumption—we consider others to be persons like us, therefore rational beings—can be grounded in bodily experience. According to Husserl, there can be no perception without awareness of the acting body. It should be added that the awareness of our acting body cannot be detached from the mechanisms presiding over control of actions (see also Gallese, 2000a,b).

The relationship between action and intersubjective empathic relations becomes even more evident in the works of Edith Stein and Merleau-Ponty. In her book *On the Problem of Empathy* (1912/1964, English translation), Stein, a former pupil of Husserl, explains that the concept of empathy is not confined to a simple grasp of the other's feelings or emotions. Empathy has a more basic connotation. The other is experienced as another being like oneself through an appreciation of *similarity*. An important component of this similarity resides in the common experience of action. As Stein points out, if the size of my hand were given at a fixed scale, as something predetermined, it would become very hard to empathize with any other types of hand that did not match these predetermined physical specifications. However, we can easily recognize children's hands and monkeys' hands as such despite their different visual appearances. Furthermore, we can recognize hands as such even when all the visual details are not available, even despite shifts in our point of view, and even when no specification of visual shape is provided. Even if all we can see are moving light-dot displays of people's behavior, we are not only able to recognize a walking person, but also to discriminate whether it is ourselves or someone else we are watching (see Cutting & Kozlowski, 1977). Since in normal conditions we never look at ourselves when we are walking, this recognition process can be much better accounted for by a mechanism in which the observed moving stimuli activate the observer's motor schema for walking, than solely by means of a purely visual process. This seems to suggest that our grasping of the meaning of the world doesn't *exclusively* rely on its visual representation, but is strongly influenced by action-related sensorimotor processes.

Merleau-Ponty in the *Phenomenology of Perception* writes:

> The communication or comprehension of gestures come[s] about through the reciprocity of my intentions and the gestures of others, of my gestures and intentions discernible in the conduct of other people. It is as if the other person's intention inhabited my body and mine his. (1945, English translation 1962, p. 185)

Self and other relate to each other because they both represent opposite extensions of the same correlative and reversible system *self–other*. The observer and the observed are part of a dynamic system governed by reversibility rules.

The shared intersubjective space in which we live from birth continues long afterward to constitute a substantial part of our semantic space. When we observe other individuals acting, facing their full range of expressive power (the way they act, the emotions and feelings they display), a meaningful embodied link among individuals is automatically established.

The discovery of mirror neurons in adult individuals shows that the very same neural substrate is activated when some of these expressive acts are both executed and perceived. Thus, we have a subpersonally instantiated common space. It relies on the neural circuits involved in the control of actions.

The hypothesis I am putting forward here is that a similar mechanism could underpin our capacity to share feelings and emotions with others. My proposal is that sensations and emotions displayed by others can also be empathized with, and therefore implicitly understood, through a mirror matching mechanism.[1]

3.6 The Shared Manifold Hypothesis

Throughout this chapter I have argued that the establishment of a self–other identity is a driving force in the cognitive development of more articulated and sophisticated forms of intersubjective relations. I have also focused on the mechanism that enables this identity to be created. I suggest that the concept of empathy should be extended to accommodate and account for all the different aspects of expressive behavior that enable us to establish a meaningful link between others and ourselves. This enlarged notion of empathy opens up the possibility of unifying under the same account the multiple aspects and possible levels of description of intersubjective relations.

As we have seen, when we enter into relations with others, there is a multiplicity of states that we share with them. We share emotions, our body schema, somatic sensations such as pain, etc. A comprehensive account of the richness of content we share with others should rest upon a conceptual tool that can be applied to all of these different levels of de-

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[1] For discussions relevant to this section, see vol. 2, ch. 13 by Jesse Prinz and the comments by Huesmann, vol. 2, ch. 19.6, p. 386.

scription, while simultaneously providing their functional and subpersonal characterization.

I introduce the *shared manifold* of intersubjectivity as this conceptual tool (see Gallese, 2001, 2003b). I posit that it is by means of this shared manifold that we recognize other human beings as similar to us. It is just because of this shared manifold that intersubjective communication, social imitation, and mind reading become possible. The shared manifold can be operationalized at three different levels: a phenomenological level, a functional level, and a subpersonal level.

The *phenomenological level* is the level responsible for the sense of similarity, of being individuals within a larger social community of persons like us, which we experience any time we are confronted with other human beings. It could be defined also as the *empathic* level, provided that empathy is characterized in the enlarged way I advocate here. Actions, emotions, and sensations experienced by others become meaningful to us because we can share them with others.

The *functional level* can be characterized in terms of *"as if"* modes of interaction that enable models of a self–other identity to be created. The same functional logic is at work during control of one's own actions and in understanding others' actions. Both are models of interaction that map their referents onto the same functional nodes and share a relational character. At the functional level of description of the shared manifold, its relational character produces the self–other identity by enabling the system to detect coherence, regularity, and predictability independently from their source.

The *subpersonal level* is characterized by the activity of a series of mirror matching neural circuits. The activity of these neural circuits is in turn tightly coupled with multilevel changes within body states. We have seen that mirror neurons instantiate a multimodal intentional shared space. My hypothesis is that analogous neural networks might be at work generating multimodal emotional and sensitive shared spaces—the shared spaces that allow us to appreciate, experience, and implicitly understand the emotions and the sensations we assume that others experience (see Goldman & Gallese, 2000; Gallese, 2001, 2003b). No systematic attempt has been produced so far to validate or falsify this hypothesis experimentally. Yet there are clues that my hypothesis might be not so ill founded.

Preliminary evidence suggests that in humans a mirror matching mechanism is at work in pain-related neurons. Hutchison et al. (1999) studied pain-related neurons in the human cingulate cortex. Cingulotomy procedures for the treatment of psychiatric disease provided an opportunity to examine prior to excision whether neurons in the anterior cingulate cortex of locally anesthetized but awake patients responded to painful stimuli. It was noticed that a neuron that responded to noxious mechanical stimulation applied to the patient's hand also responded when the patient watched pinpricks being applied to the examiner's fingers. Both applied and observed painful stimuli elicited the same response in the same neuron.

Calder et al. (2000) showed that a stroke patient who suffered damage to the insula and the putamen was selectively impaired in detecting disgust in many different modalities, such as facial signals, nonverbal emotional sounds, and emotional prosody. The same patient was also selectively impaired in subjectively experiencing disgust and therefore in reacting appropriately to it. Once the capacity to experience and express a given emotion is lost, the same emotion cannot be easily represented and detected in others.

Emotions constitute one of the earliest ways to acquire knowledge about the situation of the living organism and to comprehend it in the light of its relations with others. This points to a strong interaction between emotion and action. We dislike things that we seldom touch, look at, or smell. We do not "translate" these things into motor schemas suitable for interacting with them (most likely "tagged" with positive emotions), but rather into aversive motor schemas (most likely "tagged" with negative emotional connotations). The coordinated activity of sensorimotor and affective neural systems results in the simplification and automatization of the behavioral responses that living organisms need to produce in order to survive.

The strict coupling between affect and sensorimotor integration is demonstrated in a study by Adolphs et al. (2000) in which these authors reviewed more than a hundred brain-damaged patients. Among other results, this study shows that patients who have suffered damage to sensorimotor cortices score worse than others when asked to rate or name facial emotions displayed by human faces.

Iacoboni and co-workers (Carr et al., 2001; see also Iacoboni, vol. 1, ch. 2) in a recent functional magnetic resonance imaging (fMRI) study on healthy participants showed that both observation and imitation of facial emotions activate the same restricted group of brain structures that includes the premotor cortex, the insula, and the amygdala. It is possible to speculate that such a double activation pattern during observation and imitation of emotions could be due to the activity of a neural mirror matching mechanism.

My hypothesis also predicts the existence of somatosensory mirror neurons that give us the capacity, when observing other bodies, to map different body locations onto equivalent locations on our own body. New experiments on both monkeys and humans to test this hypothesis are just getting started in our laboratory.

It should be added that the shared manifold of intersubjectivity does not require that we experience others the same way we experience ourselves. Rather, the shared manifold enables and bootstraps mutual intelligibility. Self–other identity is not all there is to intersubjectivity. As pointed out by Husserl (1973), if this were the case, others could not be experienced as others (see also D. Zahavi, 2001). On the contrary, the *alterity* of the other grounds the objective character of reality. The quality and content of our own self-experience of the external world are constrained by the presence of other subjects who are intelligible while preserving their character as other. This alterity, as we have seen, is present also at the subpersonal level instantiated by the different neural networks coming into play when *I* act versus when *others* act.

3.7 Conclusions

There is preliminary evidence that the same neural structures that are active during sensations and emotions are also active when the same sensations and emotions are detected in others. It appears therefore that a whole range of different mirror matching mechanisms may be present in our brain. This mechanism, originally discovered and described in the domain of actions, is most likely a basic organizational feature of our brain.

One of the mechanisms enabling emotional feelings to emerge is the activation of neural "*as if* body loops" (Damasio, 1999). These automatic, implicit, and nonreflexive simulation mechanisms, bypassing the body proper through the internal activation of sensory body maps, create a representation of emotion-driven, body-related changes. It is likely that the activation of these "*as if* body loops" can not only be internally driven but can also be triggered by observation of other individuals (see Adolphs, 1999; Goldman & Gallese, 2000; Gallese, 2001).

The discovery of mirror neurons in the premotor cortex of monkeys and humans has unveiled a neural matching mechanism that, in the light of more recent findings, appears to be present also in a variety of nonmotor-related human brain structures. Much of what we ascribe to the mind of others when witnessing their behavior depends on the "resonance mechanisms" (see Rizzolatti, vol. 1, ch. 1) that their behavior triggers in us. The detection of intentions that we ascribe to observed agents and that we assume to underpin their behavior is constrained by the necessity for an intersubjective link to be established. Early imitation is but one example of the intersubjective link in action. The shared manifold I have described here is a good candidate for determining and shaping this intersubjective link.[2]

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2. See the comments on this chapter by Jones, in vol. 1, ch. 8.4, p. 205; see also ch. 7 by Hurley in vol. 1 and ch. 3 by Gordon in vol. 2. ED.

4 The Neurophysiology of Imitation and Intersubjectivity

Jean Decety and Thierry Chaminade

4.1 Introduction

The purpose of this chapter is to marshal relevant findings from functional neuroimaging experiments on the relations between action and perception and on imitative behavior in humans in order to take a tentative step toward a better understanding of intersubjectivity. By "intersubjectivity," we mean the process by which mental activity (motives, intentions, feelings, emotions) is transferred between the self and others' minds (Trevarthen, 1999). This process exists, since we possess the ability to conceive as mentalistic agents not just the self but also others, even though we have access only to their surface behavior. Subjectively private mental states are communicated via body movements (e.g., gaze, speech, facial expressions, or posture), which are the signs of intentionality.

We will argue that at a low level, intersubjective behavior and social cognition involve an automatic and unconscious motor resonance mechanism that relies on the physiological properties of the nervous system. There is substantial neurophysiological evidence, both in monkeys (Rizzolatti et al., 2001) and in humans (Blakemore & Decety, 2001), for a distributed set of brain areas (or clusters of neurons) that are active when actions are self-generated or observed. Although such a mechanism is necessary, we claim it is not sufficient to explain how the intentions behind bodily motions are understood, nor can it account for the sense of agency. Investigating imitation at the neural level can provide essential clues for understanding how the self and the others share intentions through social interactions. As several developmental psychologists have argued, imitation is a natural avenue to developing intersubjective transactions between the self and other selves (Meltzoff & Moore, 1995; Nadel & Butterworth, 1999; Tomasello, 1999; Trevarthen, 1979).

Developmental research has indeed shown that babies are born with the capacity and the motivation to imitate human gestures, but that they are also equipped with what Meltzoff and Moore (1998) have termed a ''like me'' mechanism or a sense of like meness. This mechanism gives human infants a way to discover that others are similar to themselves. Imitation of human actions is the first bridge between the infant and others, and it serves the dual function of differentiating the broad class of ''others'' into individuals and providing an early means of communicating with them. It is through mutually imitative games that infants progress from conceptions of others as entities with whom one can share actions to persons with whom one can share goals and intentions. In addition, a growing body of research demonstrates that early on, infants develop a sense of themselves as situated, differentiated agents in an environment, as well as a sense of themselves as communicative and reciprocating social agents (Rochat & Striano, 2000).

Even though there exist precursors of intersubjective behavior in the animal kingdom—for instance, the contagion of emotions (for empathy) and motor mimicry (for imitation)—in this chapter we consider these issues only in light of research carried out in humans beings. Human social evolution has its roots in the natural history of the hominoid family, which diverged around 25 million years ago. It may be assumed that all behavior in primates, including our own species, derives from a combination of evolved tendencies, environmental modification, development, learning, and cognition (de Waal, 2001b). But continuity does not mean identity.[1] However, intersubjectivity has evolved to a special extent and has given rise to psychological processes described in terms of empathy, identification, or projection that are unique to humans, perhaps because of their relation to self-awareness. Imitation, like self-consciousness, may even be a distinctive aspect of human nature.

Self-consciousness could be regarded as just another adaptive trait, yet it has a great effect on our mental life. Not only are we capable of understanding and predicting our own and others' behavior, we have the ability to explain what our brain does and effortlessly make inferences about our own mental states and those of others. We have an idea of ourselves as

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[1] We take seriously the claim made by Povinelli and collaborators that evolution is real and that it produces diversity. Therefore it may be wrong to systematically assert that the parsimonious explanation of the behavioral similarities between humans and chimpanzees is the operation of equally similar psychological systems (see especially Povinelli & Bering, 2002).

agents; our awareness of causing an action is associated with a strong sense of self (S. Gallagher, 2000). Because we are self-conscious organisms, we explain our own behavior in terms of emotion, desires, intentions, and beliefs, and we assume that others also have similar mental states. In short, we have evolved from being behaviorists to being natural psychologists.

Humphrey (1980, 1982) long ago proposed that once self-consciousness had provided our species with a way of making introspective sense of our own behavior, then our own experiences and ways of understanding behavior would immediately and naturally be projected onto other people. Thus, humans come to understand the intentions of others through an introspective examination of their own mental states and processes—a kind of simulation of what it must be like to be in the "mental shoes" of the other person (Goldman, 2002; Harris, 2000; Gordon, 1986).

It is not satisfactory to talk about a set of areas activated when a specific action is performed without having a clear prior conception of both the processes involved and the expected brain responses.[2] Hence the search for understanding the functional architecture that implements intersubjectivity cannot proceed without careful definition of the relevant concepts (i.e., resonance, simulation, shared representations, imitation, and agency) that are used throughout this chapter. All of these concepts are rooted in the psychology and philosophy of mind and have come to be used only relatively recently in neuroscience.

The notion of *resonance* was introduced by Gibson (1966) as part of his ecological approach to perception, which assumes that: (1) perception serves an adaptive function and the external world must therefore provide information to guide biologically and socially functional behaviors; (2) this

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[2] As cognitive neuroscientists, we are well aware that powerful technologies such as positron emission tomography (PET), functional magnetic resonance imaging (fMRI), or magnetoencephalography (MEG) do not localize cognitive functions, but merely tell us where in the brain neurohemodynamic or electrically related activity takes place in relation to a given experimental paradigm. Having said that, we think that imaging techniques do contribute to revealing the functional architecture that instantiates the mechanisms involved in intersubjectivity. These neurophysiological data are especially worthy of consideration when they are integrated with data from other supplementary sources, such as developmental science, clinical neuropsychology, and psychopathology. In addition, the interpretation of neuroimaging data is probably more complex than behavioral data. One needs to be concerned not only with the nature of the task itself but also with the underlying physiology. For instance, it is not yet clear whether regional cerebral blood flow increases in PET or whether BOLD changes in fMRI reflect excitation or inhibition at the cellular level.

information is typically revealed in objective, physical, dynamic, multimodal events, as opposed to static, unimodal displays; (3) the information available in events specifies which events provided by environmental entities are opportunities for acting or being acted upon; (4) perception of these affordances depends upon the perceivers' attunements, that is, the particular stimulus invariants to which the perceiver attends. Resonance involves a simultaneous querying of many mechanisms at once and in parallel, just as a vibrating tuning fork can query many strings about their resonant frequencies at the same time. The idea requires both parallel processing, a radically modern idea in Gibson's time, and a group of mechanisms with which to resonate.

Later, Shepard (1984) proposed that as a result of biological evolution and individual learning, the organism is, at any given moment, tuned to resonate to the incoming patterns that correspond to the invariants that are significant for it. It is interesting that Shepard proposed that the external constraints that have been most invariant throughout evolution have become most deeply internalized, and even in the complete absence of external information, the system can be excited entirely from within (while dreaming, for example). Thus, unlike Gibson, Shepard makes explicit reference to internal representation.

Today, the concept of motor resonance is used in neuroscience as a metaphor to describe the behavior of a neuron that fires both when a monkey performs a given action (such as grasping a peanut) and when it watches another individual performing the same action (Rizzolatti et al., 2001), or when similar premotor areas are found to be activated during the execution of a given movement as well as during the observation of the same movement performed by another person (Fadiga et al., 1995).

The notion of *shared representations* is widely used in social psychology, especially in the field of communication. For successful communication to take place, the speaker and the listener have to attribute similar meanings to representations of the topic of communication. Communicators establish a shared representation of the topic of conversation in the communication process (Krauss & Fussell, 1991). Research in social sciences suggests that communication leads to internalization of shared representations. More generally, the meaning of a given object, action, or social situation may be common to several individuals and thus should activate the same neural network in their respective brains. These shared representations constitute the contents of a culture (Bruner, 1990). Within a culture, shared beliefs unify the cognitive and motivational processes.

The notion of shared representations can be applied not just across different individuals but also within individuals. It is central to several cognitive models of intentionality. For instance, Gopnik (1993) argued that the same representational form is used to encode an embedded intentional relation whether the latter involves the self as agent or another agent. Another influential cognitive developmental model proposes that the monitoring of first-person information (i.e., self-generated signals) and third-person information (i.e., signals from visual perception), both of which are crucial to the normal adult's understanding of social cognition and intersubjectivity, activate an internal intentional schema (Barresi & Moore, 1996). This schema has the capacity to coordinate first-person and third-person information and compute the attribution of action to the self or to the other.

Moreover, there is a long-standing position in psychology which assumes that perception and action share common coding mechanisms (e.g., Viviani, 2002). Notably, the common-coding hypothesis (W. Prinz, 1997a; Hommel et al., 2001; Knoblich & Flach, 2001) states that actions are coded in terms of the perceivable effects they should generate, and assumes that the representations of the intended effects of an action determine the production and perception of an action. Thus perceiving events produced by other individuals should activate the same representational structures that govern one's own planning and control of these actions. Recently the concept of such shared representations has been used to account for the demonstration that similar brain areas are activated during mental representation of one's own action, mental representation of another's action, and observation of another's action (Decety & Grèzes, 1999; Jeannerod, 1999; Grèzes & Decety, 2001; Decety, 2002a; Decety & Sommerville, 2003).

Imitation is an innate (i.e., present at birth and prior to the experience of learning a particular association between a stimulus and a response) capacity in the human species; it is both effortful and intentional (Meltzoff & Moore, 1999a; see Heyes, vol. 1, ch. 6 and Anisfeld, vol. 2, ch. 4, for a different view). There are evolutionary precursors of imitation in other species but, as argued by R. Byrne and Russon (1998), most of the cases currently claimed to be animal imitation should be rejected in favor of a simpler explanation, such as response facilitation. Conversely, some copying by great apes that has been discounted as emulation may warrant reevaluation as imitation. Here we use a narrow conception of imitation which requires the learning of a novel action and copying of both the goal of the action and the means used to achieve. In the studies described in this chapter, behaviors will be qualified as imitation if and only if they meet the following two criteria: the similarity of the goal and the means to achieve it and the novelty of each trial for the imitator.

4.2 Observing Actions Performed by Others

Although there is a large body of experimental data that have been interpreted in favor of the common coding of perception and action (W. Prinz, 1997a; Viviani, 2002), it is only in the past 15 years that neurophysiological evidence has started to accumulate (Decety & Grèzes, 1999). The discovery of mirror neurons in monkeys, which discharge during the execution of purposeful, goal-directed hand movements as well as when the monkey observes similar hand actions (Rizzolatti et al., 1996a; Rizzolatti, vol. 1, ch. 1), has encouraged the search for a comparable mechanism in humans.

Fadiga et al. (1995) recorded motor-evoked potentials elicited by transcranial magnetic stimulation (TMS) in subjects asked to observe grasping movements performed by an experimenter. At the end of the observation period, TMS was applied to the subject's motor cortex, and motor-evoked potentials were recorded from intrinsic and extrinsic hand muscles. The pattern of muscular response to this stimulus was found to be selectively increased in comparison with control conditions, demonstrating increased activity in the motor system during the observation of actions. This finding was confirmed by neuromagnetic measures made with magnetoencephalography (MEG) over the premotor cortex while the subjects observed another person manipulating an object (Hari et al., 1998). Similarities in electroencephalograph (EEG) signal desynchronization over the motor cortex were found to occur during both execution and observation of finger movements (Cochin et al., 1999). There are thus good arguments for low-level motor resonance phenomena, given that the motor cortex is activated during the observation of actions.

Several positron emission tomography (PET) studies have shown recruitment of premotor, parietal, and temporal activation during observation of actions. In the experiment by Rizzolatti et al. (1996b), the subjects were requested to observe the movements of an experimenter who grasped common objects. In another condition, the subjects had to reach and grasp the same object. Significant activation was detected in the left middle temporal gyrus and in the left inferior frontal gyrus. Another PET study conducted by the same group found activation in the SMA proper, the inferior parietal cortex, and the inferior frontal gyrus on the left side (Grafton et al., 1996). Recently, a functional magnetic resonance imaging (fMRI) study also demonstrated that observation of an action activates the premotor cortex in a somatotopic manner, which is reminiscent of the classical motor cortex homunculus (Buccino et al., 2001).

A series of studies performed by our group manipulated the cognitive strategy of subjects who were watching hand actions by instructing them to memorize the action either for later imitation or for recognition (Decety et al., 1997; Grèzes et al., 1998, 1999). When the subjects observed actions for later imitation compared with passive observation of the same actions, a specific hemodynamic increase was detected in the SMA, the middle frontal gyrus, the premotor cortex, and the superior and inferior parietal cortices in both hemispheres. A different pattern of brain activation was found when the subjects were observing the actions for recognition. In that case, the parahippocampal gyrus in the temporal lobe was activated. The intention to imitate thus has a top-down effect on the information processing involved in action observation. Observing the other in order to imitate tunes the regions involved in generation of action to a step beyond simple motor resonance, i.e., motor preparation. Note that in all of these studies, the right inferior parietal cortex was consistently found to be activated in conditions involving later imitation.

Altogether, these studies strongly support the view that action observation involves neural regions similar to those engaged during actual action production. Moreover, this motor resonance phenomenon seems to be selectively triggered by actions that belong to the motor repertoire of the subject watching them. J. Stevens et al. (2000) adapted the apparent motion paradigm, originally developed by Shiffrar and Freyd (1990), to present subjects in the PET scanner with a human model in different positions. Depending on the activation conditions, the subjects were shown either possible or impossible biomechanical paths of apparent motion. The left primary motor cortex and parietal lobule in both hemispheres were found to be selectively activated when the subjects perceived possible paths of human movement. No selective activation of these areas was found during conditions of impossible biomechanical movement paths. These results are consistent with the notion that we may understand the actions of others in terms of our own motor system (Shiffrar & Pinto, 2002; Viviani, 2002). It is also interesting that no premotor or inferior parietal activation was detected when individuals were presented with goal-directed movement in a virtual reality system (Decety et al., 1994). This may have been due to the poor resolution of the virtual reality system, which made it difficult for the subjects to perceive the movements as natural—that is, as produced by another biological agent—and hence to identify with the movements.

Such covert identification is critical. The capacity to identify with other conspecifics, considered a prerequisite to feeling sympathy and empathy (Hobson, 1989, 2002; Tomasello, 1999; Decety, 2002b), is a distinctive characteristic of human beings that other primates may not possess. Newborn human beings are innately highly attuned to other people and motivated to identify with others. From the earliest months of life, infants are engaged with other people and with the actions and feelings expressed through other people's bodies (Hobson, 2002; Rochat, 2002). Developmental studies have shown that children can infer intentions from movements when they are performed by people, but not by mechanical devices (Legerstee, 1991; Meltzoff, 1995). Consistent with these observations, experiments that examined motor priming effects on imitation resulting from observation of a biological (human) versus a nonbiological effector system (a robot) have shown only the former to induce such effects (Castiello et al., 2002).

To test the hypothesis that only the perception of naturalistic actions maps onto existing representations of action, Perani et al. (2001) presented subjects with object-grasping actions performed either by a real hand or by means of 3-D virtual reality or a 2-D television screen. The results showed common activation foci, in the left posterior parietal cortex and in the premotor cortex, for observation of real-hand actions and artificial ones, with a greater increase in signal for the real-hand condition. A striking finding was the selective involvement of the right inferior parietal cortex and the right superior temporal gyrus (STG) only in the condition of watching a real human hand grasping the objects.

Thus we propose in this chapter not only that the human system involved in the perception and understanding of actions performed by other selves might be based on a direct neural matching mechanism for perception and action, but also that it requires the capacity to both identify with other selves and to distinguish the self from other selves. We believe that such mechanisms are necessary to experience intersubjectivity and empathy. After all, as Hodges and Klein (2001) remind us, what makes humans special is their meta-ability—that is to say, their ability to go up a level and see the self and other as two distinct members in the category of agents.

4.3 Representing the Actions of Oneself versus Those of Others

One of the distinctive capacities of human beings resides in self-consciousness, which provides us with a way of consciously representing the intentions and actions of ourselves and others (Povinelli & Prince, 1998). Hence, we can ask human subjects to mentally simulate an action and simultaneously explore the underlying neural substrate thus activated. Psychophysics experiments have shown that temporal and cinematic properties of mentally represented actions mimic those of the real events represented (for a review see Viviani, 2002). For instance, in an experiment conducted by Parsons (1994), the subjects were shown pictures of either the left or the right hand in different orientations. In one condition, the task was to reproduce the position being shown by actual movement of the appropriate hand. In the second condition, no overt movement was required; the subjects simply had to tell whether the stimulus was a right or a left hand. In both conditions, the response times varied linearly as a function of the orientation of the hand and were highly correlated.

The similar constraints on actually performed and mentally simulated actions that act on internal representations may be hypothesized to reflect their neurophysiological instantiation. This idea is validated by several neuroimaging studies that have found activation sites in the SMA, premotor, primary motor, inferior frontal, and inferior parietal cortices lateralized to the left hemisphere, as well as the ipsilateral cerebellar cortex when subjects imagine right-hand-related actions (Decety et al., 1994; Lang et al., 1994; Stephan et al., 1995; Grafton et al., 1996; Roth et al., 1996; Porro et al., 1996; Parsons & Fox, 1998). Thus, consciously representing an action involves a pattern of brain activation that resembles that of an intentionally executed action because all of these areas are known to participate in action execution (Decety & Ingvar, 1990). There are differences, however, between actual and mentally represented actions in the SMA and in the cerebellum. It has been proposed that posterior cerebellar activation accounts for inhibition of movement during imagination (R. Lotze et al., 1999). This set of cortical areas, activated during both the generation and the mental simulation of one's own actions, can be described as sustaining the neural representation of actions and account for their functional equivalence.

Recently, Ruby and Decety (2001) asked subjects to imagine an action as being performed either by themselves (first-person perspective) or by another individual (third-person perspective). Both subjective perspectives were associated with common activated clusters in the SMA, the precentral gyrus, and the precuneus. First-person perspective-taking was specifically associated with increased activity in the left inferior parietal lobule and the left somatosensory cortex, whereas the third-person perspective recruited the right inferior parietal lobule, the posterior cingulate, and the frontopolar cortex.

A similar pattern of activation was discovered in a follow-up study that investigated perspective-taking at the conceptual level (Ruby & Decety, 2003). In this study, the participants, who were selected exclusively from among medical school students, were asked to judge the truthfulness of affirmative health-related sentences, from either their own perspective or that of laypersons. The left inferior parietal lobule was involved in a first-person perspective, while the frontopolar cortex and the right inferior parietal lobule were strongly activated when the subjects took the third-person perspective.

These results support the notion of shared representations of self and other, since common activated areas are found in both subjective perspectives, even at the conceptual level. However, the results also point out the crucial role of the inferior parietal cortex (and the frontopolar cortex) in distinguishing the perspective of the self from that of others, as well as the involvement of the inferior parietal cortex in intersubjectivity.

4.4 Reading Others' Intentions and Emotions

Developmental research indicates that the distinction between matching an observed motor program (the means of the model) and reproducing the correct use of an object (the goal) is deeply rooted in human cognition. For example, even 18-month-old children have no difficulty in distinguishing the surface behavior of people (what they actually do, the means) from another deeper level (what they intend to do, the goal) as demonstrated by Meltzoff (1995) using a reenactment procedure. This supports the idea that when observing someone's action, the underlying intention is equally or perhaps more important than the surface behavior itself (Baldwin & Baird, 2001).

A neuroimaging experiment was designed to differentiate the neural correlates of two implicit ways of retrieving an action, either by observation of its means or by referring to its goal (Chaminade et al., 2002). Although there is no clear-cut division in ecological situations (Whiten & Ham, 1992), the goal in this experiment was operationalized as the end state of manipulating the object and the means as the motor program used to achieve this relation. The actions consisted of sequentially moving Lego blocks from a starting position to a specific place in a Lego construction being built. The experimental conditions were derived from a factorial design in which the factors were (1) what was shown to the subjects during observation of the model, which, depending on the conditions, could be the whole action, only the means, or only the goal; and (2) the response performed by the subject, which could be to imitate, to observe, or to act freely. The results revealed partially overlapping clusters of increased regional cerebral blood flow (rCBF) in the right dorsolateral prefrontal area and in the cerebellum when the subjects imitated either the goal or the means. Moreover, specific activity was detected in the medial prefrontal cortex during the copying of the *means*, whereas copying the *goal* was associated with increased activity in the left premotor cortex.

Our results suggest that for normally functioning adults, imitating a gesture activates neural processing of the intention underlying the observed action. Activity in these frontal areas reflects the transformation of the partial information about an action given by the model into a complete action to be performed by the subject. The finding of the involvement of the right dorsolateral prefrontal cortex fits with its critical role in the preparation of forthcoming action based on stored information (Pochon et al., 2001). This region was more activated during the interaction that described the copying of the goal, which leads us to suggest that it stores the representation of the goal in short-term working memory. Therefore its activation during copying of the means suggests that this condition also activates a representation of the goal that is built online from the observed gesture (Miller, 2000). The right medial prefrontal cortex, which is known to play a critical role in reading others' intentions (Happé et al., 1999; Blakemore & Decety, 2001), was only found to be activated by the copying of the means, and may reflect the retrieval of the goal or intention of the actor from the observation of his or her gestures.

A powerful way to demonstrate the neural representation of the internal coupling between production, perception, and understanding postulated by the motor resonance theory as expressed by Shepard (1984) is to exploit the anticipatory effects of motor competence. Anticipatory adjustments are present in many language-related movements, such as speech, typing, and handwriting, and also in pointing (Viviani, 2002). This is particularly interesting because subjects are not conscious of these phenomena. For instance, in handwriting, anticipatory adjustments are used to predict the letter that is about be traced (Orliaguet et al., 1997).

We designed a neuroimaging study in which an extremely simplified depiction of human motion was presented to the subjects. All activation conditions included a black dot moving on a white screen showing different trajectories (Chaminade et al., 2001a). In two conditions, the trajectory corresponded to real computerized human-hand trajectories depicting either the cursive handwriting of the first *l* of the pairs "*ll*" and "*ln,*" or the first part of a two-phase movement pointing to a "large" and a "small" target. The cinematic characteristics of the second part (i.e., the second letter of the couple, or the second phase of the pointing movement) influence the characteristics of the first, and psychophysics studies demonstrated that the perception of the first part of the movement was sufficient for subjects to decide, in a forced-choice paradigm, the expected outcome of the action.

In the neuroimaging experiment, subjects were also presented with a forced choice for the expected outcome of the actions, and the results showed that although unaware of it, they did correctly anticipate the second part of the action. Two control conditions were also used. The first one controlled for the effect of anticipation in situations free of biological motion by depicting a ball bouncing on a spring with either high or low energy, and asking the subjects whether the ball would go "near" or "far." The second condition controlled for the visual input and motor output by depicting a ball going either to the top or the bottom of the screen, and asking the subjects to answer "top" or "down." When we subtracted these two controls from the two conditions of interest using a masking procedure, each condition was associated with specific areas activated in the superior parietal and premotor cortices, among other areas.

Thus, tasks involving anticipation from human motion involved frontoparietal circuits that are known to be fundamental elements in the control of action (Binkofski et al., 1999a). Moreover, writing anticipation resulted in activated clusters in the left frontal operculum, which is associated with language production, and in the left superior parietal lobule, which is associated with handwriting. Anticipation of pointing yielded activated foci in the left premotor cortex and in the right intraparietal sulcus, which are associated with performance of pointing. At a covert level (since the subjects were unaware of their performances), anticipating the motor event that will follow by observing someone else activates the brain areas that are involved when actually preparing and performing the same action. This experiment provides neurophysiological support for the psychophysical model, which suggests that visual perception of human motion is partly dependent on the motor capacities of the observer. Our results therefore strongly support the hypothesis that the neural motor system involved in the preparation and execution of action is also part of a simulation network that is used to interpret the perceived actions of others (Decety & Grèzes, 1999; Jeannerod, 1999).

Intersubjective behavior is rarely devoid of emotions and feelings. Empathy may be viewed as an other-oriented moral sentiment that fosters altruism (Sober & Wilson, 1998). This may be because an overt motivation for prosocial behavior is triggered when the self covertly (and automatically) resonates with the other (Decety, 2002b). We suggest that the perception of someone else's emotional state also relies on shared representations, since bodily expressions are an objective, measurable output of people's emotions.[3] This view was originally proposed by Adolphs et al. to account for impaired judgment of facial expressions in patients with lesions of the primary and secondary somatosensory cortices, insula, and anterior supramarginal gyrus in the right hemisphere. These authors conjectured that the reconstruction of knowledge about other people's emotional states might rely on a simulation of how the emotion would feel in the perceiver (Adolphs et al., 2000).

There is physiological evidence for this mechanism in the recognition of emotion from facial expression. For instance, viewing facial expressions triggers expressions on one's own face, measured with facial electromyography, even in the absence of conscious recognition of the stimulus (Dimberg et al., 2000). There is also a single-neuron recording experiment with neurological patients that has shown that the same neurons in the anterior cingulate cortex become active both when the patients feel pain and when they watch the noxious stimulus being applied to another individual (Hutchison et al., 1999).

Decety and Chaminade (2003) designed an experiment to test the hypothesis that sympathetic feelings occur when two individuals share similar feelings and concerns and, in the context of this study, when an observer (the experimental subject) resonates with a target person (the stimulus). Note that this hypothesis reflects the way, at a commonsense level, we can automatically interrelate with other people in everyday life; it is close to what Hodges and Wegner (1997) defined as automatic empathy, as opposed to controlled empathy, and what Nichols (2001) characterized as a "concern mechanism," which is considered to depend on a minimal capacity for mind reading and also on the affective system.

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[3] For relevant discussion see vol. 2, ch. 13, p. 274ff by Jesse Prinz and the comments by Huesmann, vol. 2, ch. 19.6, p. 386. ED.

Knowing that the emotions of empathy and sympathy most commonly arise when people directly perceive individuals in trouble or have a personal connection with them, we presented the subjects with dynamic stimuli that were created to elicit such feelings. For that purpose we asked semiprofessional actors to tell short stories whose narrative contents were either sad or neutral, as if they had personally experienced them. It was predicted that both the neural circuit for affective processing (namely, the amygdala and the adjacent cortices, the orbitofrontal cortex, and the insula) and the neural circuit underlying shared representations for observed and executed actions (parietal and premotor cortices) would be involved when the subject felt sympathy for the target person.

We further hypothesized that the feeling of sympathy would be disrupted or at least reduced if there was a mismatch between the narrative content of the stories and the emotional expression displayed by the actors (e.g., when a sad story was told with a happy expression). This situation may be considered, from the perspective of the viewers, as a sort of unexpected social situation, an inappropriate behavior that is less likely to produce shared feelings. We therefore predicted that neural responses in regions known to be involved in dealing with social conflict and negative affect, and accordingly, activity in the ventromedial prefrontal cortex and the superior frontal gyrus (Damasio, 1994; LeDoux, 1996), would be enhanced during the mismatch condition. In order to meet these experimental conditions, we asked the actors to tell the stories with either neutral, happy, or sad motor expressions of emotion. Their performances were videotaped and then edited to meet the constraints of a PET-activation experiment. The subjects were scanned while viewing these stimuli, and after each session they were asked to evaluate the mood of the person they had seen and how likable (in a broad sense corresponding to a feeling of sympathy) they found that person.

As predicted, in addition to a neurodynamic increase in the amygdala and adjacent cortices, cortical regions involved in the network for shared representations (namely, the dorsal premotor cortex, the pre-SMA, the central sulcus, and the inferior parietal lobule) were involved when the subjects felt sympathy with the persons who were telling sad stories. This was the experimental condition that was hypothesized to afford most concern toward others. Since the subjects performed no action during the conditions but merely watched video clips, we suggest that this network is recruited to simulate, at a covert level, the affective experiences of others (the storytellers). It is interesting to recall that according to several theorists, empathizing not only necessitates a sharing of affect, but a minimal distinction between the self and the other is also mandatory (Reik, 1948; C. Rogers, 1959; Kohut, 1971; Povinelli & Giambrone, 1999; Decety, 2002b). The results of the present study therefore lead us to speculate that when the subjects covertly simulated the narrative content of a sad story with the intention of rating their own affinity for the communicator (i.e., how likable they found the storyteller), the distinction between their induced emotional states and the affective experiences evoked by the narrative content of the story may depend on activity in the right inferior parietal lobule. Finally, the condition of a mismatch between a sad story and a happy expression of emotion by the communicators resulted in the lowest scores in the subjects' ratings of their feeling of sympathy and, as predicted, in increased activity in the ventromedial prefrontal cortex and superior frontal gyrus. The former is associated more with dealing with social conflicts (Damasio, 1994) and the latter with sensorimotor conflicts (Fink et al., 1999).

4.5 Reciprocal Imitation, Intersubjectivity, and Agency

Mutual imitation is acknowledged to play a central role in an infant's development of intersubjectivity and shared motivational states (Nadel & Baudonnière, 1982; Nadel et al., 1999; Hobson, 1989). Role-taking during early social interactions between infant and mother are frequent and considered a milestone in the linkage between their subjective experiences. Moreover, there is good evidence that reciprocal imitation plays a constitutive role in the early development of an implicit sense of the self as a social agent (Rochat, 1999).

In order to approach these issues at a neurophysiological level, two neuroimaging experiments were designed that involved reciprocal imitation. Each experiment compared subjects imitating with subjects being imitated; that is, the subjects were either presented with new actions they had to reproduce or were asked freely to perform actions that were reproduced online by another person. The two reciprocal imitation experiments differed in the type of action and the visual feedback given to the subjects. The assumption underlying these studies was that if we compare the reciprocal imitation conditions, that is, the self imitating the other versus being imitated by the other, the sense of the moving effectors belonging to the self (i.e., what Gallagher, 2000 called the "sense of ownership"), plus the visual and somatosensory inputs, are similar or coincide. What does differ between imitating and being imitated is the relationship between the effectors and input components, which can represent oneself either as the agent being imitated or as the imitator of the other's action. Note than in the two experiments, the behavior can be described as true imitation because the actions performed are new to the subjects in every trial, so that they are compelled to map their own actions onto the actions of the other.

The first reciprocal imitation experiment focused on mutual imitation of right-hand manipulations of an object in order to build simple constructions (Decety et al., 2002). In three conditions, the subjects manipulated the objects while watching an experimenter manipulating the same objects. The two main experimental conditions corresponded to the two situations of reciprocal imitation, in which the subjects either saw their self-triggered actions reproduced by the experimenter or had to imitate the experimenter's actions. Two other conditions in which the subjects and experimenter performed different actions and the subjects just observed the experimenter's actions were used as controls. Several key regions were involved in the two conditions of interest compared with the two control conditions; namely, the superior temporal sulcus, the inferior parietal lobule, and the medial prefrontal cortex. In the frontal lobe, activation was located in the medial prefrontal cortex, which is known to be engaged in mentalizing functions (Blakemore & Decety, 2001). Since confusion between the self and the other might occur in the two conditions of reciprocal imitation, it is interesting to find an activated cluster in this medial prefrontal region when the two conditions of imitation are compared with different actions in which such self–other confusion is not possible. When the two conditions are contrasted with each other, this region is involved, together with the pre-SMA, in the condition in which the subjects selected their own actions and saw these imitated by the other. The pre-SMA plays a functional role in temporal organization in internally guided movements (Tanji, 1994).

Another expected key region in this experiment was the inferior parietal lobule. When the two conditions of imitation were contrasted with the control condition in which the subjects acted differently from the experimenter, a lateralization of the activity in this region was found. The left inferior parietal lobule was activated when the subjects imitated the other, while the right homologous region was associated with being imitated by the other. Activation was also detected in the posterior part of the superior temporal gyrus, which is known to be involved in the visual perception of socially relevant body movements (Allison et al., 2000). This cluster was found in both hemispheres in both the conditions of imitating and being imitated, in contrast to the control condition. However, it was only present in the left hemisphere when the condition of being imitated was subtracted from the condition of imitating the other. This lateralization in the STG is an intriguing finding, and may participate in the neural basis involved in the distinction between first- and third-person information conveyed through the visual modality. We suggest that the right STG is involved in genuine visual analysis of the other's actions, while the left region is concerned with analysis of the other's actions in relation to the intention of the self. This part of the temporal cortex is an important component in a circuit involved in social cognition (which through direct and indirect connections receives input from the ventral and the dorsal visual streams, the amygdala, the orbitofrontal cortex, and the prefrontal cortices).

Since this latter temporal region is known to be associated with biologically relevant visual inputs, one could argue that our interpretation of these results in terms of the sense of agency should be limited to the specific case of imitation of manual manipulations of objects, and should not be extended to other situations in which the self is either in control of its actions or controlled by the other. To further examine the significance of the results of this first study while excluding visual reference to body parts, we performed a second neuroimaging experiment in which the subjects were shown a white screen on which two circles of different colors were moving smoothly (Chaminade & Decety, 2002). The subjects controlled one of these circles via a computer mouse and were told that another person was controlling the other circle. In the two conditions of reciprocal imitation, the subjects were moving their circles with the intention of either leading or following the other. In the first control condition, both subjects and the other acted freely with no imitation, and in a second control condition, the subjects merely observed the other's actions.

As expected on the basis of the results of the previous experiment, activity in the medial frontal and bilateral inferior parietal cortices was detected in the contrasts between the two reciprocal imitation conditions and the control conditions. In addition, no activity in the temporal lobe was found to be associated with the two reciprocal imitation conditions. Areas related to visual processing were activated for these two conditions within the right intraparietal sulcus, and bilaterally in the lateral occipital cortex when the subjects followed the circle controlled by the experimenter. These results demonstrate that the visual association areas that are recruited shift, in the absence of sight of the body, from body-recognition areas in the temporal lobe (Allison et al., 2000) to object-oriented areas in the lateral occipital cortex (Grill-Spector, 2001).

Another fulfilled prediction was that the lateralization of the inferior parietal cortex reflected the role played by the subjects in the imitative behavior. Left hemispheric activity was detected when they followed the experimenter, and right hemispheric activity when they saw the experimenter following their movements. The involvement of the inferior parietal cortex can no longer be explained by a visual reference to the body, and this supports our interpretation of a relation between the lateralization of activity in the inferior parietal lobule and the sense of agency (see figure 4.1).

This involvement of the inferior parietal cortex in the sense of agency is well supported by an impressive mass of converging evidence from neuropsychology (Kinsbourne, 2002) and other neuroimaging studies (Ruby & Decety, 2001; Farrer & Frith, 2002; Farrer et al., 2003), as well as from the abnormalities in attribution of intention found in schizophrenic patients experiencing passivity phenomena (S. Spence et al., 1997).

4.6 What Is So Special about the Human Inferior Parietal Cortex?

Imitation is a phylogenetically rare cognitive skill and is involved in cultural evolution. This may be the case because it is based on a rare cognitive computational ability, i.e., the intentional stance, and not just the widely present capacity for associating sensory inputs with one another and with motor outputs (Plotkin, 2002). In this chapter we have attempted to review recent functional neuroimaging studies that investigated the brain mechanisms involved in understanding actions performed by others, imitation, and in sharing mental states such as intentions and emotions. Although particular mental states can be regarded as private to their possessors, nevertheless, different individuals can share mental states of a given type by identifying with one another mentally. The similarity of activated areas (in the premotor and posterior parietal cortices) during observation of action, mental simulation, and imitation argues for a shared neural representation mechanism. However, the computational mechanisms involved in intersubjectivity cannot be reduced to this common mapping, either at the neurophysiological level or at the cognitive level. In humans, this system is interwoven with self-consciousness, as well as with the phenomenological experience of agency. Thus one highly relevant issue concerns how the self versus other distinction operates within these shared representations and which neural mechanisms are engaged in integrating and discriminating the representations activated from within and those activated by external agents.

Our functional neuroimaging studies on subjective perspective-taking, imitation, empathy, and agency, which were designed to explore both what is common to the intentional states of self and other and how they

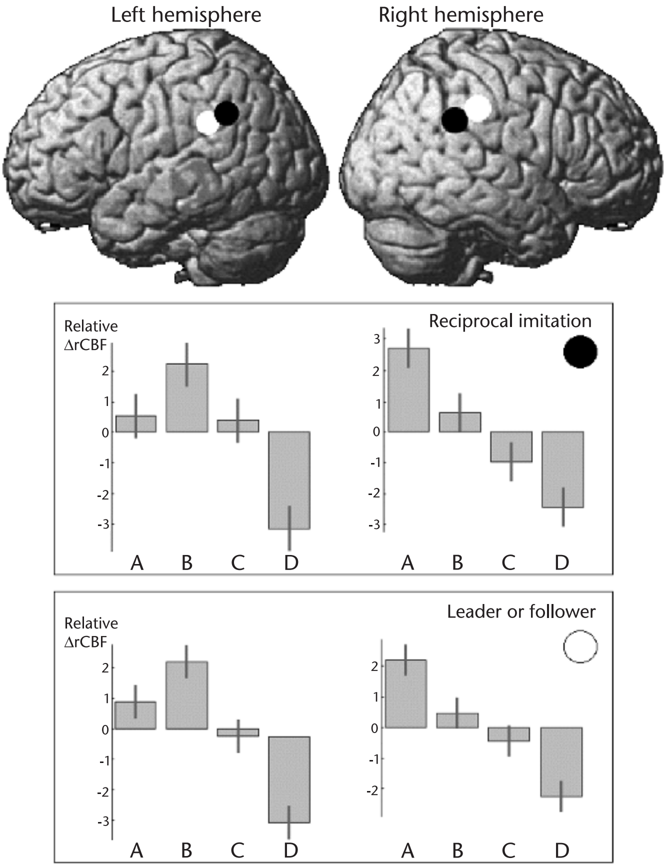

Figure 4.1

Hemodynamic activity in the inferior parietal lobule in an area in the vicinity of the posterior superior temporal sulcus during reciprocal imitation and leader versus follower experiments. The top histograms represent the relative signal change across the experimental conditions for the reciprocal imitation study by Decety et al. (2002). These are A, to be imitated; B, to imitate; C, different actions; and D, own actions. The bottom set is for the study by Chaminade et al. (2002). They are A, leading the other; B, following the other; C, acting differently; and D, observing the other's actions. Note the clear left versus right asymmetry. The right hemisphere is activated when subjects see the other imitating their actions, whereas the left hemisphere is activated when subjects imitate the actions performed by the other.

differ, have highlighted the central role of the inferior parietal cortex in intersubjective behavior, in conjunction with premotor and medial prefrontal areas in the right hemisphere. Our results also strongly suggest that the hemispheric laterality of hemodynamic activity is important and should be taken into account along with current clinical neurophysiological knowledge about the complex functions attributed to the parietal cortex in apraxia, body awareness, and more generally in higher-order representation of the body.

Other regions involved in imitation include the temporoparietal junction and the medial prefrontal cortex. The former region is activated by tasks that require processing the intention of a biological agent and are not confined to biological motion (Grèzes et al., 2001). It is also activated by speech and human sound movements (Griffiths et al., 1998). The latter region is also consistently activated in mentalizing tasks, that is, in attributing intentional states to oneself and to others (Blakemore & Decety, 2001; U. Frith, 2001), as well as in executive functioning, that is, in experiencing a cluster of high-order capacities, which includes selective attention, behavioral planning, and response inhibition (Siegal & Varley, 2002).

It is interesting that the prefrontal, inferior parietal, and temporoparietal areas have evolved tremendously in humans compared with nonhuman primates (see Passingham, 1998). The parietal cortex is roughly "after" vision and "before" motor control in the cortical information-processing hierarchy (Milner, 1998). The inferior parietal lobule is a heteromodal association cortex that receives input from the lateral and posterior thalamus, as well as visual, auditory, somaesthetic, and limbic input. It also has reciprocal connections to the prefrontal and temporal lobes (D. Eidelberg & Galaburda, 1984). Note that these anatomical studies were performed in rhesus monkeys, and we don't know much about the parietal connectivity in the human brain. It remains unclear whether the monkey's posterior parietal cortex performs functions similar to those in humans, especially those related to self-awareness. It is even claimed by some scholars (e.g., Milner, 1997), following Brodmann, that the human superior parietal lobe may be equivalent to the whole of the monkey posterior parietal lobe. If so, they are at least not fully equivalent. However, it should be mentioned that mirror neurons have also been discovered in the monkey parietal area (PF; see Gallese et al., 2002).

In our studies there was more activity in the left inferior parietal lobule when subjects imitated the other, and more activity in the right homologue region when they saw their actions being imitated by the other. We postulate that the left inferior parietal lobule computes the sensorimotor associations necessary to imitate an action demonstrated by the other, which is compatible with the literature on apraxia (e.g., Halsband, 1998), whereas the right inferior parietal lobule is involved in recognizing or detecting that the action performed by the other is similar to that initiated by the self.

There is plenty of evidence from clinical neuropsychology that the right inferior parietal cortex is important for body knowledge and self-awareness, and that lesions in this area can produce a variety of disorders related to body representation, such as anosognosia, asomatognosia, or somatoparaphrenia (Berlucchi & Aglioti, 1997). Of special interest are reports by Ramachandran and Rogers-Ramachandran (1996) of patients with right parietal lesions in whom the denial of hemiplegia can extend to the motor deficits of other patients, suggesting that the availability of an efficient body schema is necessary, not only for recognizing one's own actions, but also for understanding the actions of other individuals. It has been proposed by Heilman et al. (1998) that representation of the body must be continuously modified, updated by expectations (feedforward) and knowledge of results (feedback). Another similar formulation is that the central nervous system contains internal models that represent the current and predicted state of the motor system (Greenwald, 1970; Kawato, 1999; Berthoz, 2000). We speculate that the parietal cortex plays a major role in this mechanism through its connections with the cerebellum.

We would like to add to these accounts by proposing, in light of our neuroimaging experiments, and especially with reference to the conditions in which a subject sees his own action imitated by another individual, that the right inferior parietal lobule plays a key function (in conjunction with the right prefrontal cortex) in the unique human capacity to identify with others and thus to share subjectivities (Hobson, 1989; Meltzoff & Moore, 1998; Povinelli & Prince, 1998; Tomasello, 1999). This may well be a qualitative difference between human and nonhuman primates and not just a quantitative one. We parallel here the view developed by Povinelli and collaborators (2000) according to which the emergence of an integrated self–other representational system has occurred relatively recently (during the course of the last two million years of human evolution), and that the intimate psychological relation between the self and the other is one of the key psychological distinctions between human beings and their closest living relatives.

Finally, it is interesting to note that our abilities to represent our own thoughts and to represent another's thoughts are intimately tied together and may have similar origins within the brain (Happé et al., 1999; Keenan et al., 2000). Thus it makes sense that self-awareness, empathy, identification, and more generally intersubjective processes are largely dependent on right hemisphere resources (Decety & Sommerville, 2003).[4]

Acknowledgment

We thank Susan Hurley for her helpful comments.

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[4] See the comments on this chapter by Rawlins in vol. 1, ch. 8.1, p. 195 and by Kinsbourne in ch. 8.5, p. 210. ED.

5 An Ideomotor Approach to Imitation

Wolfgang Prinz

5.1 Introduction

When it comes to explaining human action, psychological theory has two major frameworks to offer: the *sensorimotor* and the *ideomotor* framework. In sensorimotor approaches, everything starts with stimulation, and actions come into being as consequences of that stimulation. Actions are considered responses to stimuli that precede them. Conversely, in ideomotor approaches, everything starts with intention, and actions come into being as the means for realizing those intentions. Actions are considered the means for certain ends that follow them.

Over the past decades, if not centuries, theorizing in the behavioral and brain sciences has been dominated by sensorimotor approaches, whereas ideomotor approaches have played only a marginal role (cf., e.g., Hommel et al., 2001; W. Prinz, 1997b, for possible reasons). In this chapter, I argue for the reanimation of ideomotor theory and the assigning to it a strong role in future theories of human action. More specifically, I will show that the ideomotor framework offers an attractive account of imitation and related behaviors. Part of this attractiveness comes from the fact that ideomotor approaches have ways to accommodate the operation of similarity between perception and action that sensorimotor approaches are lacking. Another reason is that ideomotor theory offers a broad approach that allows us to view imitation as a specific instantiation of a more general principle and to classify it among a larger family of socially modulated actions that all share the same representational background.

My argument has two parts. First I give a brief outline of the major tenets of ideomotor theory and their functional implications for imitation and related behaviors. This outline will eventually boil down to what I call the principle of *action modulation through perception*. This principle then serves as a methodological guide for the second part, in which I give an overview of some experimental paradigms we have recently devised to study certain patterns of action modulation in dyadic social settings, such as action imitation, action induction, or action coordination.

5.1.1 Ideomotor Theory

Imitation implies performing an act after and by virtue of seeing it done by someone else. Hence, some form of similarity between the act perceived in the other and the act performed by oneself is the defining feature that classifies an act as imitation. If it is true that similarity is at the heart of imitation, any theory of imitation must come up with an account of how similarity can be functional between the perceived act and the performed act. As has been pointed out elsewhere (e.g., Hommel et al., 2001; W. Prinz, 1990; W. Prinz & Meltzoff, 2002), the sensorimotor framework has no such account to offer. This is because in this framework perception and action are subserved by separate and incommensurate representational structures. On the perceptual side, representations stand for patterns of stimulation in sense organs and their derivatives; while on the action side, representations stand for motor commands and patterns of excitations in muscles. Obviously, these representations are incommensurate. Accordingly, although there may be ample room for *rule-based mappings* between representations for perception and action, there is no obvious room at all for *similarity-based matchings*.

This is different in ideomotor approaches. At first glance they do not seem to offer anything that could help us to understand imitation. This is because in its historical beginnings ideomotor theory was meant to account for intentional guidance of action only, not for perceptual guidance. However, in the meantime, the theory has become extended to cover both perceptual and intentional guidance. It is this modern, extended version of the theory that offers a new grasp on the issue of similarity.

The ground for the ideomotor framework was laid by R. Lotze (1852) and W. James (1890) in their discussion of voluntary action. According to the Lotze-James account, voluntary actions require that two conditions be met: (1) There must be an idea, or representation, of what is being willed (Lotze: *Vorstellung des Gewollten*), and (2) conflicting ideas must be absent or be removed (Lotze: *Hinwegräumung aller Hemmungen*). When these two conditions are fulfilled, the representations of the intended goal states have the power of generating the action directly, that is, without the need for any further volitional activity. Accordingly, cognitive representations are by their very nature impulsive. This is in principle true of all representations, but it is particularly true of representations that refer to movements and actions. The ideomotor principle of human action applies to these representations. "Every representation of a movement awakens in some degree the actual movement which is its object; and awakens it in a maximum degree whenever it is not kept from doing so by an antagonistic representation present simultaneously in the mind" (James, 1890, vol. II, p. 526).

How does the impulsive nature of cognition arise? Lotze and James both argue that it arises from previous learning. Whenever a motor act is performed, it goes along with a number of perceivable effects. Some are close to the action in the sense of being accompaniments of the act itself (kinesthetic sensations, etc.). Some others may be more remote consequences, such as the fact that a light goes on at a distance when one's fingers operate a light switch. Such regular connections between motor acts and perceivable bodily and environmental effects can then become functional in two different ways. One is *to expect certain effects, given certain acts*; that is, to predict an ongoing action's perceivable consequences. The other way is *to select a certain act, given an intention to achieve certain effects*; that is, to derive a goal-directed action from a predefined goal.[1] This latter relationship—which leads from intended effects to acts—forms the functional basis of the ideomotor principle: Any representation of an event of which we learn that it goes along with, or follows from, a particular action will afterward have the power to elicit the action that produces the event. This will apply not only to representations of body-related action effects (e.g., thinking of one's finger operating a light switch) but also to representations of more remote effects in the environment (e.g., thinking of the light going on).

This may be a nice principle, but it has so far only been concerned with how actions are prompted and guided through internally generated ideas. Yet, if it is true that thinking of an act (or its remote effects) has the power to prompt and instigate that act, this should be even more true in the case of perceiving that act, for instance as performed by someone else. An extension of the ideomotor principle along these lines was suggested by Greenwald (1970, 1972). Greenwald studied tasks in which certain responses were mapped to certain stimuli in such a way that the triggering stimuli could be same as, or similar to, feedback arising from their required responses. For instance, when a red stimulus light elicits a manual response that in turn triggers a red feedback flash, the triggering stimulus and the

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[1] The difference between these two perspectives corresponds to the difference between forward models and inverse models in motor control (see, e.g., Wolpert & Kawato, 1998). Forward models specify the sensory consequences of given motor acts, whereas inverse models specify the motor acts required to achieve given consequences.

feedback stimulus share the same color. In this case, the red stimulus light can take exactly the role of the movement-awakening thought or idea in the Lotze-James approach. It serves to prompt the respective manual response and it does so by its similarity with the perceivable effects (= feedback) associated with the action that it triggers (= manual response).

5.1.2 Similarity

With this extension, the Lotze-James-Greenwald approach offers itself as a straightforward framework for action imitation. It relies on the notion that the perception of an event that shares features with an event that one has learned accompanies or follows from one's own action will tend to induce that action. If this is so, the strength of the induction must depend on the degree of similarity, or overlap, between the stimulus event and the action-related event. In other words, perception may induce certain actions, depending on the similarity between percepts and acts.

The extended principle has two important functional implications: ideomotor mapping and common coding. The notion of ideomotor mapping refers to the learning requirements implied by this framework. In order for the principle to work, two requirements must be met. One is that the system must be capable of learning regular associations between actions and their (resident and remote) effects. This is the easy (and trivial) part. The other is less easy and certainly not trivial. Once established, these connections between actions and effects must also be capable of being activated and used in the reverse direction, that is, leading from representations of effects to initiation of actions (Elsner & Hommel, 2004; Elsner et al., 2002; Elsner & Hommel, 2001; Kunde, 2001; Kunde et al., 2004; Stock & Hoffmann, 2002).

The notion of *common coding* refers to the functional architecture implied by the extended principle. In the ideomotor framework action planning and action control are no longer separate from the perceptual representation of environmental events. Instead, a common representational domain for perception and action is invoked, with shared representational structures for perceiving events and planning actions (Hommel et al., 2001; MacKay, 1987; W. Prinz, 1984, 1990, 1997a). Since actions are represented through their perceivable effects, perception and action are no longer incommensurate—and this is why similarity can work.

5.1.3 Action Modulation Through Perception

I concentrate here on situations in which people watch other people's actions and/or their outcomes. For such situations, the ideomotor principle has a straightforward prediction to offer. The perception of particular actions and/or their outcomes in someone else should address those representational structures that are also involved in one's own planning and control of those actions. This leads us to the principle of *action modulation through perception*, according to which the planning and control of an ongoing action becomes modulated through concurrent action perception. Obviously, this modulation should be content specific in the sense that it should be dependent on the representational overlap between the actions that are being perceived and those that are being planned.

5.2 Experimental Evidence

The ideomotor principle can be read in two ways: as a summary of some implications of ideomotor theory or as a methodological guideline for designing tasks to study the social modulation of ongoing actions. In any case, its scope goes far beyond imitation proper. The principle should be applicable to all sorts of tasks in which people perform certain actions while they watch other people performing certain related actions. In this section I discuss evidence from three types of such tasks we have studied: interference between perception and action, action induction through perception, and action coordination in shared task environments.

5.2.1 Interference Paradigms

In interference paradigms we study people's performance when they plan certain intentional actions and at the same time watch someone else's related actions. I address two such paradigms: gesture initiation and gesture selection.

Gesture Initiation In this paradigm we studied how the initiation of a predetermined finger gesture is modulated by the concurrent perception of a related gesture (cf. Brass et al., 2001). The participants were presented with randomized sequences of two stimulus gestures. One showed an index finger, first in a static starting position and then at an unpredictable point in time moving upward. The other stimulus gesture showed the index finger in the same static starting position, but then moving downward at an unpredictable point in time. The participants' task was to respond as fast as possible with one of the same two gestures using their own index fingers. It is important to note, however, that response gestures were kept constant within blocks. In other words, in a given block, the participants would see a randomized sequence of up- and down-moving index fingers, but they were required to always initiate one and the same gesture (say, moving downward). Accordingly, within a given sequence of trials, the actions to be performed were prespecified throughout, and the identity of the triggering stimulus (moving up versus down) was completely irrelevant. The question was whether the irrelevant stimulus gesture would still modulate the actions to be performed.

Over a number of experiments we observed huge compatibility effects for both of the response gestures. Prespecified upward movements could be initiated much faster when they were triggered by upward-moving stimulus gestures, and downward movements were initiated faster when they were triggered by downward-moving stimuli. Technically speaking, this pattern of results implies a substantial stimulus-response compatibility effect (and, it is important to note, does so under conditions in which no selection of response is involved). We have to conclude that even such a seemingly simple operation as initiating a particular preselected gesture involves representational structures that are also involved in the perception of these gestures (Brass, 1999; Brass et al., 2001).

Gesture Selection In the gesture selection task devised by Stürmer (Stürmer et al., 2000), one of two hand movements could be presented as a stimulus gesture—either a hand spreading apart (with fingers extending) or a hand grasping (with fingers flexing). Again, both gestures would start from the same neutral initial posture. On each trial one of the two gestures was randomly selected for presentation and the participants were required to select one of the same two hand movements as the response gesture. However, the stimulus gesture presented was once more completely irrelevant for the selection of the response gesture. Instead, the relevant cue for gesture selection was provided by a color superimposed on the stimulus gesture. If the stimulus hand was red, the participants had to spread their hand apart, but if it was blue, they had to perform the grasping movement.

In this task, too, we observed strong stimulus-response compatibility effects. The speed at which a particular hand gesture could be selected was strongly modulated by the (irrelevant) hand gesture on which the (relevant) color cue was superimposed. The selection of response gestures was much faster when stimulus and response gestures corresponded to each other than in trials with no such correspondence.

In some experiments we manipulated the time of the color onset relative to the onset of the stimulus gesture itself, so that the participants would first see the stimulus gesture unfolding in neutral gray before the imperative color cue was superimposed after some time. With this manipulation we expected to see a gradual buildup of the compatibility effect over time. What we observed, instead, was a pronounced compatibility effect from the outset, that is, even in the condition in which the onset of the color cue coincided with the onset of the stimulus gesture. In a further experiment we presented stationary hand postures rather than dynamic gestures. Actually we chose the two postures representing the final end states of the gestures of spreading and grasping. Again, we expected weaker effects with postures than with gestures, based on the consideration that static stimulus postures exhibit less overlap with dynamic response gestures than dynamic stimulus gestures do. Again, however, we observed substantial compatibility effects from the outset (they were even somewhat larger than in the gesture experiments).

In sum, we may then draw two conclusions. One is that, like gesture initiation, gesture selection is strongly modulated by the concurrent perception of irrelevant stimulus gestures. This finding lends further support to the claim that perceiving and performing actions draw on overlapping, if not identical, representational resources. The second, more surprising conclusion is that end-state postures are particularly effective primes for triggering the gestures that lead to them. This is surprising since postures do not contain any dynamic information (unlike full-blown gestures, which provide both static and dynamic information). We take this to suggest that end states, or action goals, may play a prominent role in the mechanisms underlying the compatibility effect in gesture selection. It seems that perceiving the goal at which an action is directed leads to an even stronger modulation of concurrent performance than perceiving the movements through which this goal is achieved.

Goal-Directed Imitation A demonstration of conflict between movement- and goal-induced imitation has been provided by some recent studies with young children (Bekkering & Prinz, 2002; Bekkering & Wohlschläger, 2002; Gattis et al., 2002; Gleissner et al., 2000). In these experiments, 3- to 5-year-olds took part in a little game requiring the imitation of one out of four possible gestures: reaching for one's right ear with one's right or one's left arm and reaching for one's left ear with one's right or one's left arm. In two cases (left ear–right arm and right ear–left arm), the reaching arm had to cross the body midline, whereas no such crossing was involved in the other two cases. The children were nearly always correct in uncrossed tasks, but in crossed tasks a substantial number of imitation errors occurred. When a crossed gesture is demonstrated for imitation (say, left ear–right arm), two types of errors can be made: correct ear–wrong arm (effector error) or wrong ear–correct arm (goal error). Nearly all of the errors that actually occurred in these situations were effector errors; the children would copy the goal but choose a simpler movement to reach it. In a further study it was shown that this pattern is only exhibited when the gestures are really goal directed. In a control condition without goal attainment (i.e., where the same gestures were demonstrated without actually reaching for the ear), both types of errors were equally frequent (Gleissner et al., 2000).

Taken together, our interference studies provide an interesting lesson on what it actually means to perceive and perform an action. Not only must we conclude that action perception and production share common representational structures, but also that these shared structures contain more information than just the kinematics of the perceived or to-be-produced movement patterns. Instead, they seem to contain information about full-fledged, goal-directed actions, with goals (= ends) taking the functional lead over movements (= means). This is, of course, in full accord with ideomotor theory's central claim that actions are represented in terms of what they lead to.

5.2.2 Induction Paradigms

Further support for the prominent role of goals or goal-related intentions comes from induction paradigms. In induction paradigms we study how actions are spontaneously induced and/or modulated by the perception of other people's concurrent actions and their outcomes. In the literature, such spontaneous movements are often called ideomotor movements (W. Prinz, 1987). For instance, while watching, in a slapstick movie, an actor who walks along the edge of a plunging precipice, people are often unable to sit still and watch quietly. They will move their legs and their arms or displace their body weight to one side or another.

How is the pattern of induced body movements related to the pattern of the perceived events inducing them? Basically, two answers to this question have been suggested. The classical answer believes in stimulus-related, or *perceptual induction*, that is, in the working of similarity between the movements perceived and those produced. Perceptual induction occurs when people repeat through their induced movements what they see happening in the scene. Hence it considers ideomotor actions a special class of imitative actions—nonvoluntary imitation, so to speak. A competing answer is offered by goal-related, or *intentional induction*. Intentional induction occurs when people realize through their induced movements what they would like to see happening in the scene. Hence it considers ideomotor action a special class of goal-directed actions—futile instrumental activity, so to speak.[2]

In the following paragraphs I discuss evidence from two induction paradigms. In the first paradigm we studied the occurrence of unintended, spontaneous action while people watched the outcome of their own preceding actions. In the second paradigm we considered the spontaneous actions occurring while people watched the outcome of somebody else's concurrent action.

Own-Generated Actions We devised a paradigm that should allow us to study the relative contributions of perceptual and intentional induction to ideomotor action (Knuf, 1998; Knuf et al., 2001). The task was a computerized version of a simple bowling game in which the participants watched a ball moving toward a target on a screen, either hitting or missing it. At the beginning of a trial, the ball was shown at its starting position at the bottom of the screen, and the target position was shown at the top. Starting positions and target positions were always chosen so that the ball had to travel in either a northwestern or northeastern direction (leftward or rightward) in order to hit the target. The participants triggered the ball's computer-controlled travel and observed its course.

The ball's travel was divided into two periods, instrumental and induction. During the instrumental period (about 1 second) the participants could manipulate either the ball's or the target's horizontal position by

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[2] The discussion about the nature of ideomotor movements has a long history. Notably, a forerunner of the distinction between perceptual and intentional induction was proposed by the French chemist M. E. Chevreul. In his "Lettre à M. Ampère sur une classe particulière de mouvements musculaires," Chevreul drew a distinction between two possible cases of induced movements: "La tendance au mouvement déterminée en nous par la vue d'un corps en mouvement, se retrouve dans plusieurs cas, par exemple: (1) lorsque l'attention étant entièrement fixée sur un oiseau qui vole ..., *le corps du spectateur se dirige ... vers la ligne du mouvement*; (2) lorsqu'un joueur de boule ou de billard suivant de l'œil le mobile auquel il a imprimé le mouvement, *porte son corps dans la direction qu'il désire voir suivre à ce mobile*." "The tendency to move which is induced in us when we see a moving object can be observed in several cases, for example, (1) when one's attention is entirely fixed on a bird flying [...] *the observer's body will tend to move in line with the bird's flight direction*; (2) when a player of billiards or boule follows with his eyes the ball he has just pushed along, *he will direct his body into the direction in which he would like to see the ball rolling*." (Chevreul, 1833, p. 262; italics added).

corresponding joystick movements. In the ball condition, horizontal joystick movements would shift the ball to the left or the right (after which it would continue traveling in the same direction as before). In the target condition, the same horizontal joystick movements would shift the target to the left or the right. In both conditions these shifts were required for obtaining a chance to hit the target, since the initial directions of the motion were always chosen so that hits would never occur without such shifts.

We were interested in studying spontaneous joystick movements during the induction period (which followed the instrumental period and lasted for about 2 seconds). Would such movements occur at all and how would they be related to the happenings on the screen? Perceptual induction predicts the same pattern of joystick movements for both conditions; they should always point in the direction the ball moves (leftward or rightward).

Intentional induction predicts a more complex pattern. First, it leads one to expect that spontaneous joystick movements should only become induced on trials with upcoming misses, not on trials with upcoming hits. On upcoming hits, the participants should anticipate that the ball will eventually hit the target, so that no further instrumental activity is required to reach the goal. However, on upcoming misses, the participants should be able to anticipate that the ball will eventually miss the target—which should then induce movements performed in a (futile) attempt to affect the further course of events. The details of these attempts should depend on two factors: the object under previous instrumental control (ball or target) and the side on which the ball is expected to miss the target (left or right misses). In the ball condition (where the ball was previously under control), joystick movements should act to push the ball toward the target (i.e., rightward in the case of a left miss, and leftward in the case of a right miss). In the target condition (where the target was previously under control), joystick movements should act to push the target toward the ball (leftward in the case of a left miss and rightward in the case of a right miss).

The findings from our bowling game lent strong support to intentional induction but not to perceptual induction. First, it turned out that the direction of the ball's movement (leftward or rightward) did not induce corresponding joystick movements by itself. This rules out perceptual induction. Second, on trials with upcoming hits, induced movements were virtually absent. However, third, on trials with upcoming misses, we observed pronounced induced movements, whose directions were dependent on both the object under initial control (ball or target) and the side of the upcoming target miss (left or right), which is exactly in line with the pattern predicted by intentional induction. Once more these findings suggest that in this paradigm also, goal-based induction plays a stronger role than induction based on movements leading to those goals.

However, perceptual induction was not completely ineffective. For instance, when one studies movements that are induced in noninstrumental effectors, that is, effectors that are not instrumentally involved in initial joystick control (such as unintentional head or foot movements), one sees perceptual induction also. This seems to suggest that noninstrumental effectors tend to follow the direction of the ball's travel. However, at the same time, intentional induction was also effective in head and foot movements. Accordingly, the final picture will need to encompass both intentional and perceptual induction (for more detailed discussion, see Knuf et al., 2001).

Other-Generated Actions In this paradigm we studied spontaneous ideomotor movements in a situation in which participants observed the outcome of actions performed by someone else (De Maeght, 2001; De Maeght & Prinz, 2004). The participants observed the same task as before, that is, hits and misses in the bowling task. However, this time they did so in the understanding that they were watching the visible outcome of another alleged individual's performance.[3]

While observing the game, the participants were required to perform a tracking task that served as a means for recording spontaneously occurring induced movements. In their right hand they held a joystick that controlled a marker on the right margin of the screen. Their task required them to track the vertical position of the traveling ball with a marker (i.e., move the marker so that it always matched, as precisely as possible, the ball's height on the screen). However, in analyzing those tracking movements, we were not interested in performance on the (relevant) vertical dimension. Instead, we focused on the (irrelevant) horizontal dimension. If action

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[3] Not only does this paradigm come closer to the prototypical cases of ideomotor action, which all refer to action induced by watching someone else (W. Prinz, 1987), it also avoids a serious problem that cannot be circumvented with self-generated actions. When people perform spontaneous movements in response to watching the outcome of their own previous instrumental action, there is often no way to clearly discern true ideomotor movements (i.e., those induced by the actual stimulus pattern) from the aftereffects of previous instrumental actions (i.e., those induced by previously active intentions).

induction is also obtained under this condition, it should exhibit itself in spontaneous, unintentional drifts to the left or the right.[4]

Our first experiment had two parts. In the first part, the participants were required to play the bowling game themselves (player mode); in the second part, they were required to track the visible outcome of another (alleged) individual's performance on that game (observer mode). This experiment allowed us to assess the pattern of induced action in both the bowling and the tracking task. Actually, part one of the task was an exact replication of one of the experiments with self-generated actions—not only in terms of design but also of results. However, a different pattern of results emerged in part two. In the tracking task, perceptual induction was strong throughout, whereas intentional induction was clearly weaker (it was reliable in the ball condition but not in the target condition).

In a further experiment we studied participants in the tracking task (observer mode) who had not been involved in the bowling task (player mode) before. The results showed that for pure observers, action induction was in general much weaker than for observers who had acted as players before. However, the basic pattern of induced action was unaltered. Perceptual induction was weak throughout, which, in the ball condition, again went along with weak intentional induction. However, in the target condition, intentional induction was absent.

Finally we aimed at weakening the participants' belief in an intentional agent behind the observed bowling patterns. In this experiment we had the participants again play the bowling game before we studied them in the tracking task. This time, however, the instructions would make them believe that the hits and misses they observed were generated by a computer (rather than an alleged individual in an adjacent room). Even under these conditions, some indication of intentional induction survived (at least in the ball condition), whereas perceptual induction no longer occurred.

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4. The tracking task differs from the bowling task in two important respects. First, ideomotor movements arising in the observer mode will be free from the aftereffects of previous self-performed intentional actions. Therefore, intentional induction should be weaker in observers' tracking than in players' bowling. Second, since the tracking task requires tracking the ball, it requires attention to be focused on the ball's route. This is different from the bowling task, which requires (and allows) the subject to focus attention on the ball in the ball condition and on the target in the target condition. Therefore somewhat conflicting attentional demands may arise in the target condition of the tracking task, whereas no such conflict is entailed in the ball condition. This factor, too, may act to strengthen the inductive power arising from the ball.

In Sum At this point, we are far from seeing a full picture of action induction. Still, on the basis of the evidence collected so far, we may draw a few empirical generalizations. First, spontaneous induction of action through action perception is a widely occurring phenomenon and can be studied in controlled experimental settings. Second, there is clear evidence for both perceptual and intentional induction. Perceptual induction is stimulus triggered and goes bottom-up, whereas intentional induction is goal directed and goes top-down. Third, induction (both perceptual and intentional) is not an automatically occurring by-product of action perception. At best, it may be conditionally automatic in the sense indicated by Bargh (Bargh, 1989, 1997) and Hommel (2000). For instance, it is strongly modulated by context factors, such as (1) observing own- versus other-generated actions, (2) previous active involvement in the action observed, and (3) attribution of observed outcomes to intentional agents, and so on. Fourth and finally, it has become clear that action induction is not just a matter of imitation. Perceptual induction is imitative, but intentional induction is not. Instead, it makes people act as if they were able to correct what they see happening, rather than just repeating it.

5.2.3 Coordination Paradigms

In coordination paradigms we study the social modulation of action in tasks requiring a division of labor and coordination of action between two participants. More specifically, we study how the planning of intentional action in one participant gets modulated by his or her perception of the other participant's complementary actions (Sebanz et al., 2003).

In order to study such effects, we devised a standard two-choice interference task (figure 5.1a). In this task, a color cue served as the relevant imperative signal (i.e., red or green). The color cue specified which response key to press (i.e., left or right). In addition to the relevant color cue, an irrelevant spatial cue was presented that would also point to either the left or the right. In one experiment this cue was provided by two pointing gestures of a hand, in another experiment by two arrows. Over a given sequence of trials, the four possible combinations of color cues and spatial cues were presented at equal frequencies and in random order. As a result, there were two types of trials, compatible and incompatible. In compatible trials, the irrelevant spatial cue was compatible with the response required by the relevant color cue (left-left or right-right), whereas in incompatible trials, the two were incompatible (left-right or right-left).

Not surprisingly, a marked interference effect was obtained. The responses were much faster and errors were less frequent in compatible than

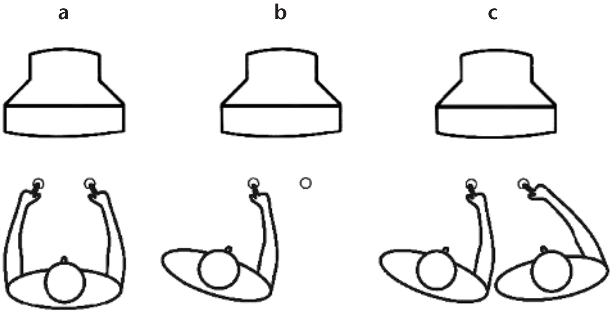

Figure 5.1

Schematic illustration of the two-choice interference task. (a) Standard version, (b) partial version, (c) shared version. (See the text for further explanation.)

in incompatible trials (and as results for a third condition with a neutral spatial cue indicate, this difference seemed to imply both facilitation in the compatible case and inhibition in the incompatible case).

This is the standard, two-choice version of the task. Consider next what one might call a partial version (figure 5.1b). By this I refer to a so-called "Go/NoGo" task in which the participants were required to respond to stimuli with one of the two colors (Go) and not to respond to the other color (NoGo). In this version, the participants were seated either to the left or the right in front of the computer screen so that the spatial cue was either pointing toward them or away from them. Accordingly, on both Go and NoGo trials, one can still distinguish between compatible and incompatible trials (although the reaction times are only available for Go trials, of course). This time, however, no interference effect was observed on Go trials. We take this result to suggest that action induction due to the (irrelevant) spatial cue requires that the *relationship* between the two stimulus cues (leftward as opposed to rightward pointing) be matched by the same *relationship* between the two responses (leftward as opposed to rightward responding).[5]

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[5] In other words, for the spatial compatibility effect to occur, mere overlap of features between stimuli and responses (left pointing-left responding, etc.) is not enough. What is required instead is dimensional overlap between stimulus sets and response sets; that is, a match between the dimensions for characterizing differences among stimuli and differences among responses (i.e., leftward versus rightward pointing and leftward versus rightward responding); cf. Reeve and Proctor (1990), Kornblum et al. (1990), and Kornblum & Stevens (2002).

After these preliminaries, we now come to the shared version of the task (figure 5.1c). What can we expect when we arrange the task so that two partial responders are sitting next to each other in front of the screen (one to the left and the other to the right), and one is in charge of red, the other in charge of green stimuli? Note that this arrangement implies, for each participant, exactly the same Go/NoGo task as before. Still, the shared task differs from the partial task in the social microcontext provided. In the shared condition, each of the two participants acts as a contributor to a common, shared task to which the other participant sitting next to him or her is contributing as well. Obviously, there are two options here. One is that each individual acts on his or her own, as in the partial task. The other is that each of them forms a joint action plan for the shared task in which the other's actions are functionally equivalent to one's own actions. If that were the case, the interference effect that was absent in the partial task should be back in the shared task. In the shared task, the opposition between one's own left position and the other's right position should reestablish the left-right dimension on the response side.

Remarkably, this is exactly what our results show. Therefore we may conclude that in a shared task environment, where a simple rule for the division of labor is agreed upon, two individuals coordinate their activities so that they act like the two hands of one person. Accordingly, in the shared task, action performance gets modulated by action perception in a complementary way; people treat the others' actions like their own actions. To be sure, by no means do they imitate them. They do not do what the others do. Rather, they do what their share of the task requires, but they take the other's actions into account.

It is important to note that further experiments have shown that the interference effect is not obtained when one participant is acting as a partial responder whereas the other sitting next to him or her is not acting at all. In other words, it seems that the mere presence of another individual is not sufficient to produce the effect. Rather, the spatial interference effect requires that one believe that the other person shares the task.

5.3 Conclusions

At this point the results of our studies on action modulation through perception suggest the following major conclusions:

- Ideomotor principle and imitation Action imitation may arise as a by-product of action perception. People tend to perform those actions they see (or would like to see) being performed by others.

- **Ideomotor principle and action modulation** Action perception modulates action planning in a number of ways (of which imitation is but one). Action modulation occurs automatically, but its details depend on task requirements and social context (i.e., conditional automaticity).
- **Common coding for perception and action** Perception and action share a common representational basis. Action perception and action planning are subserved by common representational resources.
- **Actions, action effects, and goals** Actions are represented in terms of what they lead to (i.e., their perceptual effects). Learning leads from actions to anticipations of perceptual effects. Conversely, planning leads from intended effects to actions.[6]

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[6] See the comments on this chapter by Arbib, vol. 1, ch. 8.6, p. 215, and by Donald, vol. 1, ch. 8.7, p. 217. ED.

6 Imitation by Association

Cecilia Heyes

6.1 Introduction

In a small class, a fun-loving student is reading aloud the essay she finished at 4 a.m. Glancing up at the professor, she sees his eyebrows rise sharply from silent concentration to a look of dubious surprise. Another student immediately copies the gesture, showing ingratiatingly that he too has spotted the error. The reader knits her brows in a query.

Imitative movements have a great deal in common with nonimitative movements. Both the ingratiating and the fun-loving student were reacting to the same observed body movement, and both reactions depended on a host of processes that mediated the detection and encoding of the distal stimulus and the selection and control of the motor response. Furthermore, in this example, performance of the imitative and nonimitative movements was based on the attribution of mental states. Both students understood the professor to be expressing doubt and disapproval, and both intended their reactions to communicate how much (or how little) they understood.

The obvious difference between imitative and nonimitative movements is that in the former case but not the latter there is a relationship of similarity, a match, between the observed movement, the stimulus, and the reactive movement, the response. This relational property provides a minimal definition of imitation; it distinguishes imitation from other contingent reactions to observed body movements.

If a fundamental feature of imitation is contingent behavioral similarity, research on imitation has the task of explaining the causes and consequences of this similarity. Investigating consequences, contributors to these volumes consider whether the practice of imitation (rather than that of producing dissimilar or nonimitative reactions to body movements) is a requirement for cumulative cultural evolution (Tomasello & Carpenter, vol. 2, ch. 5; Donald, vol. 2, ch. 14; and Gil-White, vol. 2, ch. 16), whether it promotes mutual understanding (Gallese, vol. 1, ch. 3; Pepperberg, vol. 1, ch. 10; Meltzoff, vol. 2, ch. 1; Goldman, vol. 2, ch. 2; and Kinsbourne, vol. 2, ch. 7) and what its effects are on economic behavior (Sugden, vol. 2, ch. 15) and interpersonal aggression (Eldridge, vol. 2, ch. 11; Huesmann, vol. 2, ch. 12; and J. Prinz, vol. 2, ch. 13). Addressing causes, researchers are investigating which neural systems are involved in the production of imitative reactions (Rizzolatti, vol. 1, ch. 1; Iacoboni, vol. 1, ch. 2; and Decety & Chaminade, vol. 1, ch. 4), whether common representational structures are involved in detecting a model's movement and producing an imitative movement (Prinz, vol. 1, ch. 5 and Dijksterhuis, vol. 2, ch. 9), and how features of a model's performance are analyzed and selected for imitative production (Byrne, vol. 1, ch. 9; Whiten et al., vol. 1, ch. 11; Anisfeld, vol. 2, ch. 4; and Harris & Want, vol. 2, ch. 6).

This chapter is about the causes rather than the consequences of imitation. It addresses the "correspondence problem" (Alissandrakis et al., 2002a; Nehaniv and Dautenhahn, 2002a), a question posed only by the phenomenon of imitation. How is sensory input from another individual's movements translated into matching motor output? The chapter begins by outlining the *associative sequence learning* (ASL) model, which offers a simple account of the kind of information-processing mechanisms responsible for this translation, and their origins in experience (Heyes & Ray, 2000; Heyes, 2001a; Hoppitt & Laland, 2002). Subsequent sections compare the ASL model with other hypotheses about the causes of imitation and identify evidence that does or would help to resolve key issues.

6.2 Associative Sequence Learning

The ASL model offers an account of the information-processing mechanisms involved in imitation of both familiar and novel movements, of movements that were and were not previously part of the observer's repertoire. Cases of both kinds are described here as imitation, but only the latter constitute imitation learning.

6.2.1 Imitation

The ingratiating student provides an example of the imitation of a familiar movement. He had, presumably, raised his eyebrows many times before he saw the professor doing so; he did not learn in this episode *how* to raise his eyebrows. Nonetheless, there was something inside him providing the

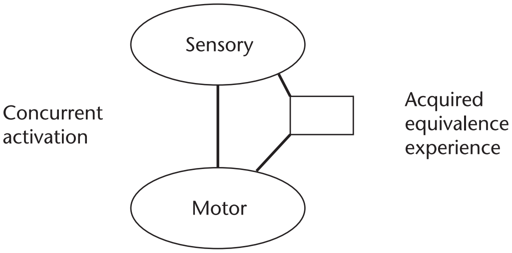

Figure 6.1
Direct and indirect vertical associations.

potential to react to the sight of the professor's movement with a matching movement, and the source of this potential is far from obvious. Note that the professor's and the ingratiating student's movements looked the same from a third-party perspective (e.g., to the fun-loving student), but not to the imitator himself. Watching the model, he saw arcs rising above dark blobs in the upper part of an oval face, but raising his own eyebrows yielded little, if any, distinctive visual input; the movement was felt rather than seen. Any solution to the correspondence problem must be able to explain cases like this, in which the imitated movement is "perceptually opaque," as well as those, such as imitation of finger movements, in which it is "perceptually transparent" (Heyes & Ray, 2000).

The ASL model suggests that both when the movement is transparent and when it is opaque, imitation is made possible by a vertical association between a mental picture of the movement performed by the model, and a mental image of what it feels like to perform the same movement, i.e., a movement that is perceived as the same from a third-party perspective. In other words, imitation is made possible by an excitatory link between a sensory representation of the observed movement (encoding properties of the movement detected via the distal senses) and a motor representation (encoding somatosensory properties and motor commands) (see figure 6.1). When such a link exists, excitation of the sensory (typically visual) representation, by observation or recollection of the represented movement, will lead to excitation of the motor representation.[1] If the link or association is

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[1] Vertical associations are likely to be bidirectional, allowing the sensory representation to activate the motor representation, as in imitation, but also enabling the motor representation to activate the sensory representation, as in some cases of internal mental practice or motor imagery.

sufficiently strong, excitation of the motor representation will result in the activation of muscles involved in execution of the represented movement (e.g., Strafella & Paus, 2000; Stürmer et al., 2000), but it may or may not lead to overt performance of the movement. Typically, at least in healthy human adults, activation of the motor representation can be inhibited so that performance of imitative movements, like that of nonimitative movements, can be brought under intentional control.

Where do these vertical associations come from? The ASL model suggests that whereas a few vertical associations may be innate, the majority are formed through experience that provokes concurrent activation of sensory and motor representations of the same movement. This experience may consist of concurrent observation and execution of the same movement, leading to a "direct" vertical association, or it may involve exposure to a common stimulus in conjunction with, on some occasions, observation of the movement, and on other occasions with its execution.[2] For example, a child may hear the sound of a word such as "frown," sometimes when she is frowning and at other times when she sees another person frowning. As a consequence of this "acquired equivalence" experience (Hall, 1996), sensory and motor representations of frowning will each become linked to a representation of the sound of the word. This "indirect" vertical association enables activation of the sensory representation to be propagated to the motor representation via the word representation, and to the extent that it allows the sound of the word concurrently to activate sensory and motor representations of frowning, to the formation of a direct vertical association between them (Rumiati & Tessari, 2002; Tessari & Rumiati, 2002).

The ASL model assumes that nonmatching vertical associations, links between a sensory representation of one movement and a motor representation of another, providing the basis for systematically non- or counter-imitative behavior, can be formed in the same way as matching vertical associations, links between sensory and motor representations of the same movement. It suggests that if a system contains more matching than nonmatching vertical associations, this discrepancy is due primarily to the environment in which the system has developed.

The human information-processing system typically develops in an environment that favors the formation of matching vertical associations in

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[2] Although concurrent activation or "contiguity" is emphasized here for clarity of exposition, the ASL model assumes, in line with contemporary theories of associative learning (see Hall, 1994 for a review), that the formation of vertical associations depends on contingency in addition to contiguity.

a number of ways.[3] First, gross human anatomy is such that many movements of one's own distal appendages can be viewed in much the same way as those of another person. When I watch many of my own hand and finger movements, the appropriate motor representations are activated concurrently with sensory representations, arising from visual feedback, which are similar to the visual percepts that arise when I observe someone else performing the same movements. Second, the typical environment of human development contains optical mirrors and other reflecting surfaces—instruments that allow one's own facial and whole-body movements to be viewed from a third-party perspective—but not video playback devices that provide visual feedback from one movement during execution of another. Third, during early development, humans are surrounded by other humans who imitate them. Leaning over a cot, we coo when a baby is cooing, grimace when a baby is grimacing (Field et al., 1985; Papousek & Papousek, 1989). We do not react to cooing with grimacing or grimacing with cooing in a way that would promote the formation of nonmatching vertical associations. Finally, there is language. Generally speaking, the range of movements constituting the referents of each action word look more alike, from a third-party perspective, than those of other action words. Only if natural languages contained words like "frile," referring to you frowning and to me smiling, would the use of language promote the formation of nonmatching vertical associations.

6.2.2 Imitation Learning

The ASL model assumes that a novel behavior consists of familiar elements or "primitives" arranged in a novel sequence and that two kinds of processes are initiated when a novel behavior is observed (see figure 6.2). First, sensory representations of the sequence components are activated and "horizontal" links are formed between them. The model says little about these horizontal links (see Byrne, vol. 1, ch. 9, for discussion) because it assumes that they are not specific to imitation; that they are formed through the same processes of sequence learning regardless of whether the novel behavior is imitated, counterimitated, or merely stored to allow future recognition. However, to the extent that each sensory representation

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[3] I am grateful to Giacomo Rizzolatti for suggesting, in a question during my talk, that the challenge for the ASL model is not to show that humans have experience that would lead to matching vertical associations, but to explain why they have more experience of this kind than of the kind that would promote the formation of nonmatching vertical associations.

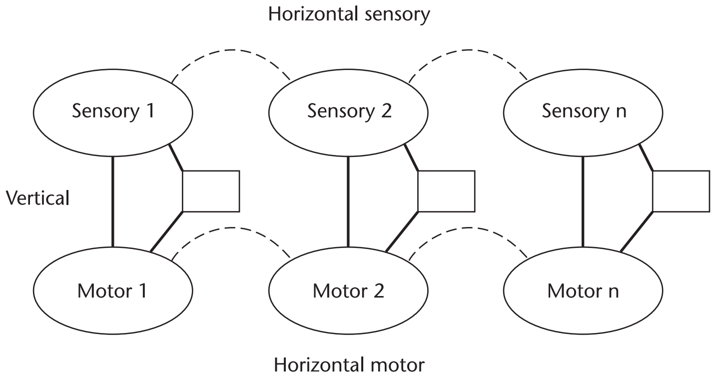

Figure 6.2
The associative sequence learning (ASL) model of imitation.

in the sequence is part of a matching vertical association, formation of the horizontal links between sensory representations will allow the second, imitation-specific process to occur. That is, successive activation of each sensory representation, by observation or recollection of the model's behavior, will provoke activation of matching motor representations in the same order, providing the potential for overt performance of a rough copy of the observed novel movement. Furthermore, repetitive activation of this sequence of motor representations allows them to become horizontally linked. This horizontal linkage of motor representations constitutes motor learning, produces a new motor primitive, and improves the potential fluidity of imitative movement. Thus, according to the ASL model, imitation learning occurs when matching vertical associations allow sensory input from another's behavior, rather than feedback from one's own, to provide the input for motor learning (Heyes, 2003).

6.3 Evolution and Development

The ASL model implies that the capacity to imitate and to engage in imitation learning does not depend on an innate module, a special-purpose cognitive mechanism shaped by natural selection (cf. Meltzoff & Moore, 1997; Decety & Chaminade, vol. 1, ch. 4). Rather, it suggests that the capacity to imitate depends on experience, that the effect of this experience is to reconfigure relatively general-purpose cognitive processes, and that this effect is mediated by associative learning; arguably the most general of all psychological processes. Thus it proposes that vertical associations are formed by the same processes that mediate Pavlovian and instrumental conditioning and that a repertoire of these vertical associations links together two sets of horizontal processes—one involved in learning sequences of distal stimuli and the other in motor learning. Vertical associations reconfigure these into a common system in the sense that they allow sensory input from the movements of others to drive motor learning.

6.3.1 Animals

Evidence that chimpanzees can imitate (e.g., Whiten, 1998 and Whiten et al., vol. 1, ch. 11) is consistent both with the ASL model and with a more nativist conception of imitation. It is plausible that chimpanzees have the opportunity to form some vertical associations and that an innate module for imitation is ape- or primate-specific, rather present in humans alone. Studies reporting that "enculturated" chimpanzees, those that have had extensive contact with humans, are better imitators than their wild-born and/or mother-reared conspecifics (Tomasello, 1996) suggest that experience plays a substantial role either in enhancing imitative performance or in generating imitative ability. A role of the latter kind is less compatible with a nativist perspective than with one that emphasizes ontogenetic processes, but these data certainly do not provide specific support for the ASL model. This model would imply that the active ingredients of human contact, the experiences that make a specific contribution to the development of imitative ability in chimpanzees, involve being imitated, being rewarded for imitation, exposure to mirrors, and hearing words or other signifiers—experiences providing the opportunity to form vertical associations. However, until we know the results of research comparing the imitative abilities of chimpanzees raised with different kinds of human contact, it will remain equally plausible that the active ingredient is, for example, engagement in joint attention behavior (Carpenter et al., 1995).

Because avian species are such distant relatives of hominids, research on imitation in birds has a more direct bearing on the question of whether human imitation is based on an innate module or on more species- and domain-general processes of learning. Recent work has provided evidence of imitation in birds that is at least as strong as the current evidence of imitation in chimpanzees. It suggests that pigeons, quail, starlings, and budgerigars can imitate simple movements such as thrusting the head upward or downward to remove a stopper from a food box (F. Campbell et al., 1999; Heyes & Saggerson, 2002), and operating a treadle with a foot or beak (e.g., Akins & Zentall, 1996). Furthermore, the most advanced research in this field indicates that like imitation in humans, motor imitation by birds can be deferred, and that it can be modulated by the perceived consequences of the model's behavior (Akins & Zentall 1998; Dorrance & Zentall, 2001). These data do not "disprove" the existence of an ape- or human-specific innate module for imitation, but they certainly imply that such a device is unnecessary to produce imitative behavior, and given the small brain and limited intellect of the average bird, make it plausible that in the right rearing environments, associative learning is sufficient to yield a capacity for imitation.[4]

The ASL model suggests that a capacity for associative learning is the basic psychological requirement for imitation, and this capacity is known to be present in a broad range of taxa. So why is there relatively little evidence of imitation in animals? Why apes and birds, and not monkeys and rats? One possible answer is that the ASL model is wrong; ape and avian imitation could be mediated by different, specialized processes that are products of convergent evolution. This view would be supported if as much high-quality research effort was devoted to imitation in monkeys and rats as in apes and birds, and if this effort revealed, not merely ambiguous findings (e.g., C. Mitchell et al., 1999; Visalberghi & Fragaszy, 1996), but that, given comparable opportunity to form vertical associations, they are less able to imitate. The ASL model predicts that given the right experience, many animals will be able to imitate. However, it also suggests that

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4. It may seem strange to emphasize birds' capacity for motor imitation, their ability to copy body movements, given that they have long been famous for their vocal imitation. There is no doubt that some birds have a remarkable capacity to imitate conspecific vocalizations and/or arbitrary human sounds (see, e.g., Pepperberg, vol. 1, ch. 10), and that this is important from a number of theoretical perspectives. However, in relation to the specific question of whether human imitation is based on general processes or on a dedicated innate module, avian vocal imitation is less informative than avian motor imitation. This is because vocalizations are relatively perceptually transparent; they give rise to similar sensory inputs when observed and executed; and therefore imitation of vocalizations could be achieved by an error-correction process that adjusts motor output until sensory feedback matches sensory input from the model (Mowrer, 1960). An error-correction process of this kind is insufficient to explain imitation of opaque movements (e.g., facial expressions) because when an opaque movement is imitated, the sensory feedback to the observer does not match the sensory input received from the model. Human imitative competence includes opaque movements, and therefore it is easier to argue that human imitation and avian vocal imitation are based on distinct psychological mechanisms than to show that human and avian motor imitation have independent roots (Thorndike, 1898).

humans acquire many of their vertical associations through cultural artifacts and practices, and therefore the model could be compromised by too much, as well as too little, imitation in animals.

6.3.2 Infants

An obvious implication of the ASL hypothesis is that the range and identity of the movements that a child, or indeed an adult, can imitate will depend on their experience, and specifically on the range of movements that they have either concurrently seen and done, or for which they have associates in common, such as verbal labels. To suppose that a few matching vertical associations are innate, rather than experience dependent, would not radically change the model, but it would not be viable if, as suggested by a substantial body of research from several laboratories, newborn human infants can imitate a broad range of face and hand gestures (see Meltzoff & Moore, 1997 for a review).

Having reanalyzed all published experimental data on imitation in neonates, Anisfeld (1991, 1996; Anisfeld, vol. 2, ch. 4; and Anisfeld et al., 2001) has concluded that the evidence is compelling for only one movement—tongue protrusion. For other candidates, such as mouth opening and lip protrusion, he argues that the data are inconclusive, either because there is a preponderance of negative findings or because the reported effects could be artifacts produced by imitation of tongue protrusion. Supporting and extending this view, recent studies have reported further evidence that neonatal imitation is confined to tongue protrusion (Couturier-Fagan, 1996), the failure to find imitation of tongue protrusion (Ullstadius, 1998), and results consistent with the idea that the tongue protrusion effect in early infancy is due either to an "innate releasing mechanism" or vertical association (Heimann & Ullstadius, 1999) or is not sufficiently specific to constitute imitation (Jones, vol. 1, ch. 12). The latter studies show that the frequency of tongue protrusion in very young infants increases not only when they have observed tongue protrusion but also when they are exposed under comparable conditions to flashing lights (Jones, 1996) or rousing music (Jones, 2002).

Many infancy researchers continue to believe that newborns can imitate a range of movements and that this provides decisive support for the idea that human imitation is based on an innate module. However, the "believers" seldom refer to the work of Anisfeld, Jones, and other skeptics, and have not yet addressed the specific questions their work has raised (e.g., Nadel & Butterworth, 1999; Heyes, 2000). Until there is open exchange on these issues, it will be difficult to draw any firm conclusions about neonatal imitation, and thereby to take an important step in resolving the question of whether imitation is mediated by a dedicated, innate module or by relatively domain- and taxon-general processes of learning.

6.4 Intentionality and Culture

It has been proposed that imitation is intrinsically "goal directed" (e.g., Gattis et al., 2002) or "intentional," and that it is this property that enables imitation to contribute to cumulative cultural evolution (Tomasello et al., 1993a). Depending on what is meant by goal and intention, the ASL model is compatible with both of these proposals.

6.4.1 Outcomes

The term "goal" is sometimes used to refer to an observable outcome or effect of a movement; to a state of the actor's body, or of an object, or a spatial configuration between the actor's body and an object, which obtains at the end of a whole movement or at the end of a component of a movement sequence. For example, a fist may be the outcome of a hand-closing movement, and gripping a glass may be the outcome of reaching toward a glass. If a goal is understood to be an outcome, then the ASL model is perfectly consistent with the suggestion that goals are an intrinsic part of the imitation process.

Intransitive movements, such as hand and facial gestures, have been used to illustrate the ASL model (e.g., Heyes & Ray, 2000) because when imitation is understood to consist of contingent, similar reactions to body movements, intransitive movements provide the clearest examples. With transitive (i.e., object-related) movements, such as dropping a ball in a cup, it is not always obvious that the model's body movement was part of the stimulus configuration to which the observer was reacting; he or she may have been reacting to the object's movement alone. However, the ASL model applies to imitation of both transitive and intransitive movements—to contingent, similar reactions to stimulus configurations that include body movements plus movements of an object, and to body movements alone—and assumes that in both cases a large proportion of what is encoded in sensory and motor representations is information about outcomes. Specifically, and in accordance with what has long been known about motor control, it assumes that the motor commands encoded in motor representations specify outcomes, not "muscle twitches" (D. Campbell, 1954).

6.4.2 Intentions

A goal can be more specifically characterized, not just as any outcome, but as an outcome toward which a movement is directed by an error-correction process, and in this case the outcome may be described as an intention and the movement as intentional. Thus, dropping a ball in a cup would be a goal if it followed adjustments to the actor's hand position made by a process sensitive to the distance between hand and cup, but this outcome would not be a goal if the ball just happened to land in the cup when the actor sneezed and lost his grip. The ASL model suggests that this kind of goal directedness is a property of many but not all cases of imitation, and that it has limited potential to explain the key feature of an imitative action—its similarity to that of the model.

Error-correction processes can contribute to the formation of matching vertical associations. For example, an error-correction process comparing visual feedback from an observer's own finger movements with a visual representation of a model's finger movement would terminate when the observer was performing the same movement as the model, i.e., when a sensory (visual) representation and motor representation of the same action were concurrently activated. However, this is only one of many routes to the formation of matching vertical associations. For example, mirror exposure, synchronous movement, and being imitated all allow concurrent activation of matching sensory and motor representations without the involvement of error-correction processes, and error correction is available only for perceptually transparent movements.

An error-correction process comparing visual feedback from opaque movements, such as facial gestures, with a visual representation of a modeled movement would not be able to reduce the discrepancy substantially, and when it had done the best it could, the executed movement would hardly resemble the one observed, i.e., the sensory representation would be activated concurrently with a nonmatching motor representation. Perhaps, as proposed by Meltzoff and Moore (1997), there are error-correction processes that compare movements, not in terms of their visual features, but in relation to some properties that even opaque movements have in common when they are observed and executed. This is an interesting possibility, but it is difficult to test without clear hypotheses about the ''common currency'', about the nature of the nonsensory or ''amodal'' properties used for comparison and the processes through which they are derived from sensory input.

In addition to enabling formation of some matching vertical associations, and thereby contributing to the potential to imitate, it is likely that error-correction processes are typically involved in translating this potential into imitative performance. Thus, when a motor representation is activated by a sensory representation via a vertical association, the observer may intend to perform the represented act. In other words, performance of the act may be regulated by an error-correction process that compares somatosensory information encoded in the motor representation with somatosensory feedback from movement, as well as visual information encoded in the sensory representation and visual feedback (Wolpert & Kawato, 1998). However, this is not a distinctive feature of imitation. Performance of many nonimitative and counterimitative movements is also goal directed or intentional in this sense, and like those other categories of movement, imitation is not always intentional. The occurrence of nonintentional imitation is indicated in healthy adult humans by the chameleon effect (Chartrand & Bargh, 1999; Dijksterhuis, vol. 2, ch. 9), and the phenomenon of perceptual induction (Knuf et al., 2001; W. Prinz, 2002), and in patients with frontal lesions by their utilization behavior (Lhermitte, 1983).

6.4.3 Higher-Order Intentions

In the third and most specific sense of goal to be considered here, imitation is intrinsically goal directed if it is mediated by higher-order intentions; if imitation invariably involves the observer making inferences about the outcome that the model intended to achieve through an action. In this sense the observer's goal is an outcome that is represented by the observer as being the same as the outcome intended by the model. Thus, imitative performance after watching a ball dropped in a cup would be guided by the intention, not merely to drop the ball in the cup, but to drop the ball in the cup *as intended by the model*.

It is not yet certain at what age it becomes possible for imitation to be guided by higher-order intentions (Heyes, 2001a; Huang et al., 2002; Meltzoff, 1995), but introspection alone leaves little doubt that once we reach adulthood, many of our imitative actions are guided in this way. In an aerobics class, or when being trained to operate a machine, one selectively imitates intended actions—the pirouette and the key press, not the jarring of the table or the sneeze. However, the ASL model does not distinguish imitative actions guided by higher-order intentions from other imitative behavior for two reasons. First, invoking higher-order intentions does not help to solve the correspondence problem, the explanatory challenge uniquely posed by imitation. My intention to imitate an intended action may on some occasions help to explain *why* I did the same thing as a model, but it does not explain *how* I was able to do it.

Second, the available evidence suggests that in nature there is no special relationship between imitation and higher-order intentionality; imitation often occurs without the attribution of intentions to the model (e.g., Dorrance & Zentall, 2002; Chartrand & Bargh, 1999; Dijksterhuis, vol. 2, ch. 9; Knuf et al., 2001), and when the model's intentions *are* represented, it seems that, as in the case of the fun-loving and ingratiating students, they are just as likely to lead to nonmatching action as to imitation.

Recent positron emission tomography (PET) studies have addressed these issues by comparing activation of the medial prefrontal cortex, an area implicated in the attribution of intentions to others (Shallice, 2001), during imitation and during the performance of carefully chosen control tasks (Decety & Chaminade, vol. 1, ch. 4). One of these studies (Chaminade et al., 2002) used video footage of a model's hand selecting and grasping a Lego block from an array and moving it to one of several locations on a board. On any given trial, the participants were allowed to observe the beginning of this sequence (the "means"), the end of the sequence (the "goal") or the whole sequence, before being required to select the same block and put it in the same place on their own board. The results showed that regional cerebral blood flow (rCBF) in the medial prefrontal cortex was greater during "means" trials than during "goal" trials. If we assume that activation of the medial prefrontal cortex is specific to higher-order intentionality, this effect implies that at least in the "means" condition, imitative performance was guided by the attribution of intentions to the model. However, the involvement of higher-order intentionality under these circumstances does not imply that imitation necessarily or even typically involves the attribution of intentions. At least two features of the experimental situation are likely to have promoted attribution of mental states. The participants were explicitly instructed to do the same thing as the model, and, on "means" trials, their view of the outcome of the model's movement was tantalizingly occluded.

In another PET study (Decety et al., 2002), rCBF in the medial prefrontal cortex was greater when the participants were imitating a model's hand moving objects around within an array (imitation) and when they were watching the hand of a person imitating their own spontaneous movements of the objects (being imitated), than when they simply received visual feedback from their own spontaneous movements of the objects (control). This result implicates the medial prefrontal cortex, and therefore higher-order intentionality, in the processing of contingent body movements, but it does not demonstrate a special relationship between the attribution of intention and matching contingent body movements, i.e., imitation. To test for such a relationship, it would be necessary to compare activation of the medial prefrontal area when participants are required to respond to each modeled movement with a matching movement (imitation) or with a nonmatching movement (counterimitation).

If it turns out that imitation does not typically involve higher-order intentionality and that the attribution of intentions is no more likely to give rise to imitative than to counterimitative action, there may still be good reasons to focus research attention on behavior that is both imitative and guided by higher-order intentionality—on the intersection between these two sets. Even if, as the ASL model implies, higher-order intentionality does not play an especially significant or distinctive role in the causation of imitative behavior, it remains plausible that fostering the development of higher-order intentionality (Iacoboni, vol. 1, ch. 2; Gallese, vol. 1, ch. 3; Meltzoff, vol. 2, ch. 1; and Goldman, vol. 2, ch. 2), and promoting cumulative cultural evolution (Tomasello et al., 1993a) are its most important effects, and behavior at this intersection is crucial for testing these hypotheses. The ASL model is not incompatible with these proposals but it has a different focus. It offers a solution to the correspondence problem, and in the process emphasizes, not what imitation can do for culture, but what culture can do for imitation (Heyes, 2001b).

6.5 Mirror Neurons and Representation

The ASL model assumes that vertical associations are formed through concurrent activation, a Hebbian principle that can be expressed, in neurological rather than psychological or functional terms, as "neurons that fire together, wire together." It is therefore unsurprising that the ASL model is compatible with the existence of mirror neurons (Rizzolatti, vol. 1, ch. 1), and, more generally, mirror tissue (e.g., Buccino et al., 2001). Broadly speaking, it suggests that mirror tissue is the neurological embodiment of vertical associations. Neurons that previously fired only during execution of an action become mirror neurons, which fire during observation as well as execution of an action through linkage with neurons that discharge only during observation of an action. A link of this kind is formed when the two neurons are activated at the same time, and this happens most commonly when the action is simultaneously observed and executed (Iacoboni, vol. 1, ch. 2).[5]

In this section, the foregoing functional interpretation of mirror neurons is compared with two alternatives. The first alternative suggests that mirror tissue mediates symbolic or amodal representation of action, and the second encourages us to interpret the function of mirror neurons in the context of an ideomotor theory of action.[6]

6.5.1 Inference versus Association

A vertical association consists of a sensory and a motor representation linked so that one can excite or activate the other. It does not include an abstract, symbolic, or amodal representation of action, a representation of a kind that could be said in any traditional sense to support inferences or confer meaning (cf. Bandura, 1986; Meltzoff & Moore, 1997). However, some neurological studies seem to indicate that mirror neuron activity mediates symbolic representation.

One study of this kind shows that some mirror neurons in the ventral premotor cortex of the monkey fire when the animal reaches for and grasps an object, when it observes the experimenter executing the same sequence, *and* when the final part of the experimenter's action, the grasp, is hidden from view by a screen (Rizzolatti, vol. 1, ch. 1; Umiltà et al., 2001). Discharge occurs in the latter condition only if, prior to the trial, the monkey saw the object at its usual location. This striking finding can be naturally and vividly described by saying that the neurons in question "infer" the experimenter's movement when it is occluded, but this description should not obscure the possibility that associative, rather than strictly inferential, processes are responsible. In Pavlovian conditioning, a response that was

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[5] Some mirror neurons fire not only when a monkey observes and executes a particular action but also when it observes the object toward which the action is typically directed (vol. 1, ch. 1 by Rizzolatti and ch. 2 by Iacoboni). Viewed from the ASL perspective, this suggests that "Hebbian" connections can be formed between sensory (visual) representations of objects and motor representations, as well as between sensory (visual) representations of observed actions and motor representations. The term "vertical association" refers primarily to connections of the latter kind because by definition it is these that play a specific, functional role in imitation.

[6] If mirror neurons are the neurological equivalent of matching vertical associations, one would expect the monkeys in which mirror neurons have been identified to be able to copy the specific actions for which their neurons have mirror properties. As far as I am aware, this hypothesis has not been tested.

once made only after the second of two stimuli comes to be elicited by the first. Applying this principle to mirror neurons, one would expect that after repeated observation of reaching toward an object, followed by grasping the object, the first stimulus, the sight of reaching, would be sufficient to make the neuron fire. However, if the first stimulus configuration was altered between training and testing by, for example, removal of the object from its usual location, generalization decrement would reduce the probability of conditioned responding.

Experiments implicating Broca's area (BA 44/45) in imitation (e.g., Iacoboni et al., 1999) may also seem to indicate that at the functional level, imitation is mediated by symbolic or amodal representations. This is because Broca's area is famous for its role in production of language, and we tend to think of language as a quintessentially symbolic system. However, three considerations make it clear that one cannot infer from Broca's activation that symbolic mediation is necessary for, or typical of, imitation. First, current evidence suggests that imitation is not always associated with activation in Broca's area (Grèzes & Decety, 2001). Second, Broca's area has nonlinguistic as well as linguistic functions (e.g., Iacoboni, vol. 1, ch. 2; Wise et al., 1998). Third, and most important, linguistic mediation does not necessarily imply symbolic mediation.

Even when Broca's area is involved in imitation because of its linguistic functions, when it reflects covert naming, it does not follow that a causal role in generating imitative behavior is being played by nonsensory, nonmotor representation of the meaning of the action. In language users, naming an action enables it to enter a conceptual network of the sort that confers meaning and supports inferences. However, naming is itself an act—a motor event that is sometimes detectable through the senses—and it is fully possible that when naming plays a role in imitation, it does so via its sensorimotor properties, not through the access it provides to the conceptual system. This possibility is represented in the ASL model by indirect vertical associations, links between representations of the sight and the feel of an act that are formed through experience in which each has been paired, on separate occasions, with exposure to a common stimulus such as a name.

Recent behavioral experiments using the serial reaction time task (Nissen & Bullemer, 1987) suggest that symbolic mediation is unnecessary, not only for imitation, but also for imitation learning. In these experiments (Heyes & Foster, 2002), observers watched a model performing a complex sequence of finger movements in response to an asterisk moving between boxes arranged in a horizontal line on a computer screen. The observers were subsequently required to perform the task themselves under three conditions: when the task was exactly the same as that performed by the model (basic transfer), when the screen stimuli were arranged vertically rather than horizontally (perceptual transfer), and when responses were made with the thumbs rather than the fingers (motor transfer). If the observers encoded what they saw symbolically, if they acquired abstract or amodally represented sequence knowledge by observation, they would be expected to perform well under each of these three conditions. In fact, however, when compared with controls who had not observed the model, the observers showed evidence of learning in the basic and perceptual transfer tests, but not in the motor transfer test. This implies that the observers' learning was effector specific, that it could not be transferred from fingers to thumbs, which is what one would expect if, via vertical associations, the sight of the model's finger movements excited motor representations of the same finger movements but did not give rise to symbolic processing.

6.5.2 Similarity versus Contiguity

The ideomotor framework (e.g., W. Prinz, 2002 and chapter 5) and the ASL model have a great deal in common. They are both compatible with William James's (1890) formulation of the ideomotor principle: "Every representation of a movement awakens in some degree the actual movement which is its object; and awakens it in a maximum degree whenever it is not kept from doing so by an antagonistic representation present simultaneously in the mind" (James, 1890, vol. II, p. 526). They both portray imitation as a product of more general psychological processes, rather than of a specialized module, and they are both consistent with recently discovered stimulus-response movement compatibility effects (e.g., Brass et al., 2001; Stürmer et al., 2000; W. Prinz, vol. 1, ch. 5). Finally, both models suggest that, in some sense, there is a common representational scheme underlying the perception and performance of action. However, whereas the ASL model claims that this commonality is acquired and based on contiguity, the ideomotor framework implies that it is intrinsic and based on similarity.

Thus, it would appear that the ASL model and the ideomotor framework differ with respect to two questions. First, is imitation mediated by one kind of representation or two? The ideomotor framework says that a single kind of representation of action has both sensory and motor properties, while the ASL model assumes that there are distinct sensory and motor representations, which become linked by vertical associations into a common representational scheme. Second, is imitation governed by similarity or by contiguity? The ideomotor framework suggests that observation of a movement, *x*, will activate or ''awaken'' performance of actions to the extent that they are similar to *x*, while the ASL model suggests that sight of *x* promotes the performance of other actions to the extent that they have in the past been performed contiguously with the sight of *x*.

The first of these contrasts may be more apparent than real. The ideomotor framework may be expressing the view that even if integration of sensory and motor processing is acquired rather than intrinsic (e.g., even if mirror neurons are vertical associations), the level of integration typically achieved in mature humans is so profound that it is no longer useful to distinguish sensory and motor representations. If so, the contrast between the ideomotor framework and the ASL model merely reflects their different preoccupations; the former with mature, human competence and the latter with learning and development in human and nonhuman animals. However, if the ''one representation or two'' question is empirical, experiments examining the role of experience in the development of mirror neurons and tissue and, more broadly, in the capacity to imitate, may help to resolve this issue in addition to the ''similarity versus contiguity'' question.

For example, the ASL model predicts that neurons in monkey area F5 will develop mirror properties only for actions that have been contiguously seen and done, or for which a common stimulus has been paired on some occasions with observation of the action and on other occasions with its execution. Furthermore, it predicts that ''countermirror'' properties could be acquired in the same way; that if a monkey repeatedly saw a precision grip before executing a power grip, neurons would emerge that fire both during observation of the first action and execution of the second. Translating this prediction to the functional level, the ASL model suggests that if a person repeatedly saw a hand-opening movement while performing a hand-closing movement, the sight of the hand opening would no longer facilitate the same response, and that after sufficient training it would facilitate the opposite response (Stürmer et al., 2000).

Countermirror and counterimitation effects of this kind would not be expected if similarity, rather than contiguity, is the fundamental principle of imitation. However, even if these effects were observed, similarity could still play an important role in imitation. We could infer that similarity was irrelevant only if equally strong imitation and counterimitation (or mirror and countermirror) effects emerged from equivalent amounts of training, and even the literature on associative learning, the context of the ASL model, provides reason to doubt that this would always be the case (Hall, 1994). Early associationists, such as Hume (1740/1984) and J. S. Mill (1843/1974), emphasized the importance of "resemblance," and although experimental psychologists have been able to find little evidence that the formation of associations depends on similarity rather than temporal contiguity, the results of a few studies suggest that when contiguity is carefully controlled, similar stimuli are more readily associated (e.g., Rescorla & Furrow, 1977; Lolordo & Jacobs, 1983). If analogous results were obtained in research on imitation—where, by hypothesis, the conditioned and unconditioned stimuli derive from observation and execution of an action—the ASL model would need to be modified to incorporate the principle of similarity. This would include acknowledgment that matching vertical associations are formed more readily than nonmatching vertical associations, and would bring the ASL model and the ideomotor framework even closer together.

6.6 Conclusion

The ASL model is empiricist in that it emphasizes the role of experience in producing the capacity to imitate, but it is neither behaviorist nor anti-evolutionary. Associative learning mechanisms are inferred, rather than directly observable, causes of behavior, and the model assumes both that they are products of natural selection and that they operate according to an evolutionary algorithm of variation and selective retention (D. Campbell, 1974; Heyes, 2003).

It has been argued in this chapter that the ASL model is consistent with current behavioral and neuroscientific data on imitation in human and nonhuman animals, and that it is compatible both with the idea that imitation is intrinsically outcome directed and with many of the central tenets of the ideomotor framework. It is at odds with claims that imitative action is necessarily intentional, or that it invariably involves the attribution of mental states, but these may well turn out to be definitional issues. More interesting from an empirical perspective are the contrasts between the ASL model, the ideomotor framework, and theories suggesting that imitation is mediated by amodal or symbolic representations. The resolution of these issues will not only require experimental research of the kind discussed here, but also clearer and more complete specification of the models themselves, enabling each to generate differential, testable predictions. The ASL model may well turn out to be quite wrong—its fallibility may be its greatest strength—but it will have fulfilled a function if it contributes to the development of a clear, detailed theory of imitation, with firm empirical support (Wimsatt, 1987).[7]

Acknowledgments

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[7] See comments on this chapter by Galef, vol. 1, ch. 8.8, p. 218, and by Whiten, ch. 8.9, p. 220. ED.

7 The Shared Circuits Hypothesis: A Unified Functional Architecture for Control, Imitation, and Simulation

Susan Hurley

7.1 Introduction

Various researchers at the currently buzzing intersection of work on motor control, imitation, and simulation have suggested that these processes are closely connected or even co-constituted (see and cf. Rizzolatti, vol. 1, ch. 1; Gallese, 2000b and vol. 1, ch. 3; and Iacoboni, vol. 1, ch. 2; Meltzoff, vol. 2, ch. 1, on the AIM hypothesis; C. Frith et al., 2000; Jeannerod, 1997, 2001; Grush, 1995 and forthcoming; Gerrans, forthcoming; Gordon, 2002; Oztop & Arbib, 2002; Proust, forthcoming; Wolpert et al., 2003; Wolpert & Kawato, 1998; Blakemore & Decety, 2001; Gallese & Goldman, 1998). There is something intuitively right and important here, yet the suggested relationships are often partial or expressed in one of several overlapping technical jargons that may be inaccessible to those in other disciplines who are interested in essentially the same issues. At this point it is worth exposing a set of related substantive issues fully and clearly, in a way that cuts across disciplinary boundaries. Accordingly, I here put forward in plain terms[1] one version of a unified framework that makes the relationships among the mechanisms that enable control, imitation, and simulation explicit. I call it the *shared circuits hypothesis*. It can be regarded as a relation of the *common coding hypothesis* about perception and action (W. Prinz, vol. 1, ch. 5), although it describes the commonality in terms of the dynamics rather than the coding of perception and action (see also Arbib on Prinz, vol. 1, ch. 8.6, p. 215). It is also closely related to Gallese's *shared manifold hypothesis* (vol. 1, ch. 3), though it situates elements of Gallese's views explicitly within an overall framework.

The shared circuits hypothesis is a midlevel hypothesis about subpersonal functional architecture, cast at a level of description between that

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[1] Though with links to technical terms noted.

of neural implementation and of the personal level of conscious perception and intentional action.[2] While it may be too early to claim definitive empirical support for this particular specification, it may nevertheless have heuristic value in sharpening up questions and predictions at both higher and lower levels, while avoiding over-simple or a priori projections between subpersonal and personal level descriptions. Related work in this area has not always kept clear track of distinctions between neural, functional subpersonal, and personal levels of description. While the boundaries between levels are not wholly opaque, it will conduce to clarity and progress to recognize distinctions between levels, and to frame issues about interlevel relations, more explicitly. Looking downward from the functional shared circuits architecture, we can ask whether there is evidence that particular neural circuits implement parts of it. Looking upward, we can ask what its behavioral and cognitive implications are, by comparison with quite different architectures. If information about self and other is processed subpersonally along the lines suggested by the shared circuits hypothesis, what implications if any might that have for the role and uses of such information at the personal level? For example, if intersubjective information is prior, at the subpersonal level, to information that differentiates self and other, does this have any implications about the basis of our personal-level knowledge of other minds? Unfulfilled predictions or incompatible neural circuitry could lead either away from the general idea of shared circuits for control, imitation, and simulation, or to a better specification of those shared circuits.

I draw attention as I proceed to some striking aspects of the shared circuits hypothesis. In particular, this hypothesis connects a shared information space for action and perception with a shared information space for self and other, while at the same time illustrating how the distinctions between self and other and between the imagined and the real can be imposed on these shared information spaces. In this model, information about persons arrives in the subpersonal version of the first person plural: without distinction or inference between self and other. Moreover, the shared circuits hypothesis illustrates a horizontally modular architecture: it avoids the common conception of perception and action as separate and peripheral to central cognition (see Hurley, 1998, 2001). Rather, it views perception and action as dynamically co-constituted and sees cognitively significant resources, such as the self/other and imagined/real distinctions,

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[2] Read "animal level" for "personal level" where appropriate; for a defense of this move, see Hurley, 2003.

and information for action understanding and planning, as emerging from the information space that perception and action share.

The shared circuits hypothesis is a theoretical model that describes a functional architecture in five major stages or—better—layers. (The allusion to Brooksian subsumption architecture is intentional—another expression of what I call "horizontal modularity"; see Brooks, 1999.) Some of these could be further expanded into different sublayers. Multiple instances of the shared circuits structure could be linked together into a network of such shared circuits, for hierarchical yet flexible control permitting the decomposition and recombination of elements. Further questions arise about how the specific layers might map onto phylogenetic or ontogetic stages. The order of the layers is intended to be logically intuitive and to reflect increasing complexity, but not necessarily to represent the order of evolution, development, or learning. In particular, the order of layers 1 and 2, and of layers 4 and 5, is heuristic, as I shall explain below. What is essential to the shared circuits model is the conception of progressing from local simulation, via the idea of a reversed forward model, to higher level simulation of global significance to the system, and from the shared space for perception and action to the shared intersubjective space and to self/other and imagined/real distinctions. But whether this theoretical model describes paths of evolution, development, and/or learning is a further question.

7.2 First Layer. Basic Adaptive Feedback Control with Inverse Model

The first layer constitutes a simple adaptive control system or servomechanism for general purpose motor control, which can usefully be compared to a thermostat. The elements of this layer are: (1) a target or reference signal (such as desired room temperature, in the case of the thermostat); (2) an input signal (actual room temperature, in the case of the thermostat), which is the joint result of (3) exogenous events in the environment (such as nightfall) and the output of the control system (such as the level of heat output); (4) a comparator, which determines whether the target and input signals match and the degree of any mismatch or error (for example, the room is still 5 degrees below the desired temperature); (5) output, which is determined by comparison between target and input signals (for example, heat output is turned up); (6) a feedback loop, by which output has effects on the succeeding input signal (for example, actual room temperature rises). (See figure 7.1.)

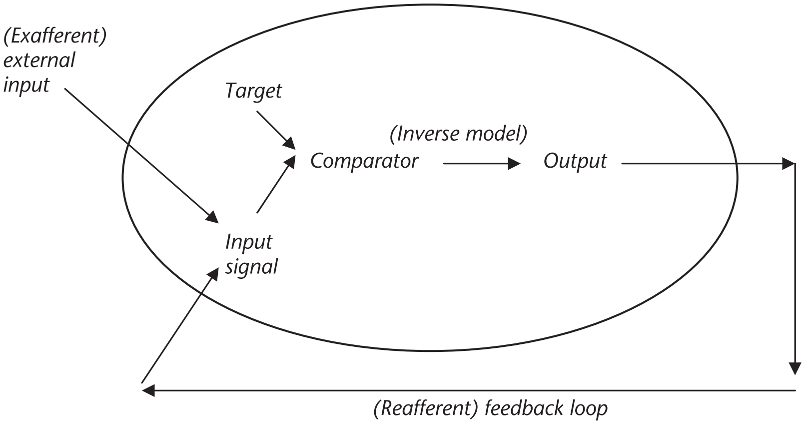

Figure 7.1
First layer: basic adaptive feedback control.

Some terminology and observations: the function that maps target signals onto output in the context of actual input signals is sometimes called an *inverse model*. In effect, it maps target to means, or specifies the means that will be used to approach the target, in given circumstances. The feedback loop at this layer is relatively slow, since it operates in real time (for example, the room takes a while to warm up after the heat has been turned up). In organisms, such feedback loops are often referred to as *reafferent feedback*: *reafference* is input to the system resulting from the organisms own activity, by contrast with *exafference*, input that results from exogenous events. Reafference, for example, includes visual and proprioceptive inputs resulting from movement of one's own hands, or movement through space, or manipulation of objects. Exafference captures inputs from events originating in the external environment, both inanimate and animate. It would include, for example, visual inputs resulting from movements by other creatures in a social group. This kind of system is *adaptive* because it adjusts itself to changing environmental conditions and compensates for exogenous disturbances: in the presence of different exogenous events, different output is needed to achieve the target. The control process is cyclical and dynamic; it does not have discrete steps or a nonarbitrary start or finish. Input is as much an effect as a cause of output. Information about inputs is not segregated from information about outputs; the dynamic relations among inputs and outputs are critical for control. This feature will be preserved as further layers are added; to the extent that perception and action

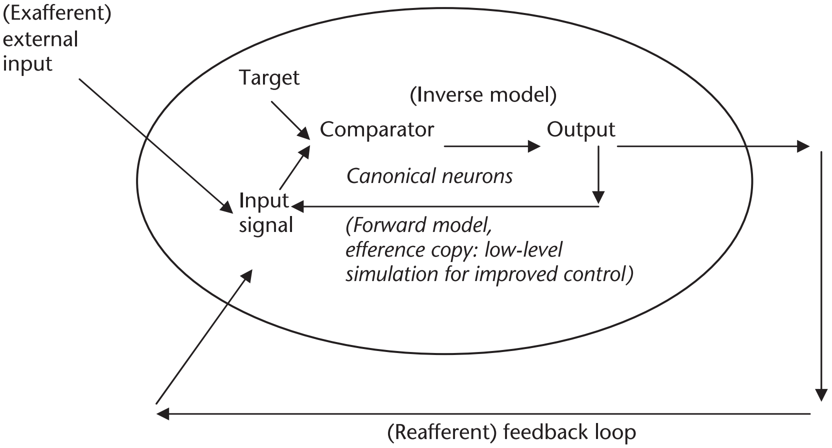

Figure 7.2
Second layer: simulation for improved control. Forward model added to basic adaptive feedback control.

arise out of a system with this basic feature, they share a fundamental information space (see Hurley, 2001, 1998).

7.3 Second Layer. Low-Level Simulation: Forward Model Added to Basic Adaptive Feedback Control

An inner loop is now added that maps the output signal back onto the input signal. In organisms this mapping is often understood in terms of *efference copy* (or *corollary discharge*); in engineering it is referred to as a *forward model*. Over time an association is established between copied output and subsequent input, so that efference copy comes to evoke the associated input signal. It can then operate as a forward model to predict the consequences of output on input. (See figure 7.2; new aspects are italicized.)

This process provides a general purpose improvement in the functioning of the motor control system, because the system does not need to wait on the real effects of output to produce reafferent feedback in real time. Rather, the system can bypass this relatively slow real-time process by learning and then anticipating the likely effects of output on input. In effect, efference copy produces a *simulation* of the expected effects of the system's output, which speeds up the control process and smoothes the appropriate behavioral trajectory. In the case of a significant mismatch between real and simulated input, a local switch can default back to real reafferent feedback while the forward model is further finetuned to improve its subsequent predictions (see Grush, forthcoming; Wolpert & Kawato, 1998; Haruno et al., 2001; Wolpert et al., 2003). This simulation is low-level in the sense that simulation can perform its speeding and smoothing functions without the system needing to monitor continuously or to access globally whether it is using actual or simulated feedback.

Recall that the order of the layers is heuristic and does not necessarily represent the order of evolution, development, or learning. For example, in the learning of particular tasks, layer 2's forward models may be acquired from feedback, enabling motor prediction, before layer 1's inverse model models are acquired, enabling motor control (Flanagan et al., 2003; here I am indebted to comments from Marco Iacoboni). One does not necessarily have to be pursuing a goal in order to learn to predict the sensory consequences of movement, even if it is natural to conceive of such prediction of feedback in an instrumental context.

Notice, however, that a system that includes reafference as well as efference copy has the resources to track the distinction between information about events in the world and information about goal-directed activity originating in the organism, that is, its behavior. When the train I am on pulls out of the station, I register movement relative to the train on the next platform, but this does not necessarily give me information about whether my train or the train on the next platform has begun to move. Comparison of efference copy with reafference gives an organism the resources to resolve the analogous subpersonal ambiguity, and hence provides information about the distinction between activity by the self and activity by the world ("self" here is neutral between persons and other animals). This is a familiar point (for discussion and references, see Hurley, 1998, pp. 140–141 and passim). Note that this information could provide part of the basis for the personal level distinction between action and perception, and that if so the distinction between action and perception emerges from shared processing resources, a shared subpersonal information space. Note also that information for the self/world and action/perception distinctions is prior to and more general than information for the self/other distinction (see layers 3 and 4 below). In this sense there are more and less fundamental layers of information about self.

At this point it would be predicted that cells or cell assemblies that mediate the association between efference copy and input signals might come to have both motor and sensory fields. Suppose an animal typically acts in a certain way on the perceived affordances of a certain kind of object: eating a certain kind of food in a certain way, for example. There will be associations between efference copy for the eating movements and a multimodal class of inputs characteristic of such objects and the eating of them. Any cells or cell groups that mediate this association might thus have both sensory and motor fields that between them capture the affordances of the objects in question. *Canonical neurons* are candidates for such sensorimotor affordance neurons (see Rizzolatti, vol. 1, ch. 1; Iacoboni, vol. 1, ch. 2; Gallese, vol. 1, ch. 3).

7.4 Third Layer. Reverse Forward Model for Priming, Emulation, and Imitation

Now consider how the system described so far would apply to visually transparent movements: movements that produce visual reafference, as when the creature watches his own hand movements. (The contrast here is with visually opaque movements, such as facial expressions: while they produce proprioceptive reafference, the creature cannot normally see his own facial expressions.) As the creature watches his own hand movements, an association is formed between efference copy and visual reafference from such movements. Here it would be predicted that cells that mediate this association might have matching sensory and motor fields. If the creature watches another perform hand movements of the same kind and he receives similar visual inputs, these will also activate his sensorimotor matching neurons with their motor fields. The sensory fields of such matching neurons cannot discriminate between his own actions of this kind and similar actions by others; the cells fire when he does something or observes someone else do the same thing. *Mirror neurons* are of course candidates for such matching sensorimotor neurons, and provide the neural underpinning for the kind of primitive blended intersubjective information space described by Gallese (vol. 1, ch. 3) in terms of a *shared manifold* and by Gordon (vol. 2, ch. 3) in terms of *constitutive mirroring*. Note the intimate relationship between the sharing of circuits for action and perception and for self and other: the blended intersubjective information space is a specification of and presupposes the generic blended sensorimotor information space.

Assume now that the sensorimotor matching association is bidirectional. Then, as well as efference copy simulating input signals, as in forward models described so far, input signals can also evoke efference or motor output. The forward model can, in effect, run in reverse (see and cf. Gallese

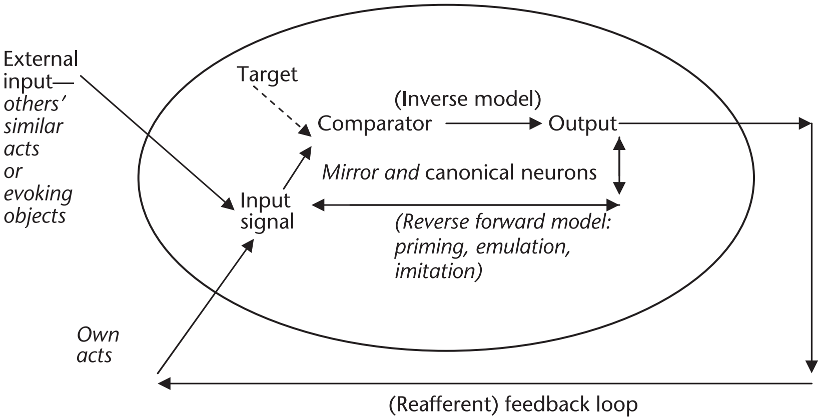

Figure 7.3
Third layer: reverse forward model for priming, emulation, imitation.

& Goldman, 1998; after I wrote this my attention was drawn to a similar idea in Blakemore & Decety, 2001). The predicted result would be motor copying at some level or levels. (See figure 7.3.) If a particular shared circuit controls details of movement (Rizzolatti's *low-level resonance*; vol. 1, ch. 1, pp. 65, 76), a predicted effect would be motor priming and copying of similar movement. If it controls the result of movement (Rizzolatti's *high-level resonance*, as in the monkeys in whom mirror neurons were discovered; vol. 1, ch. 1, p. 63) rather than the detailed movements that are the means to these results, a predicted effect would be emulation. If shared circuits for both motor means and results are themselves flexibly associated and work together, they could enable full-fledged imitation in which means as well as ends are copied (as revealed by the two-action methodology for identifying imitation; see vol. 1, chapters 9 through 12; see also Tomasello, 1999). Such full-fledged imitation would be predicted to be rarer than either response priming or emulation separately, since it would require circuits for both means and ends, appropriately linked together. And indeed it is rarer (see vol. 1, part II, on imitation in animals).

The distinction between an inverse model and a reverse forward model is functional; the neural paths that perform these functions might largely overlap. An inverse model functions instrumentally to bring about a goal by matching a target within a comparator system. A reverse forward model does not in itself have this instrumental function (see and cf. Peterson & Trapold, 1982). The priming of my own action by observing someone else's similar action is rather a by-product of the presence of the forward model, which functions at layer 2 to provide predictions that improve the functioning of the control system. However, this priming may in due course be exapted for other functions, such as those associated with imitation and simulation.

The neural mechanism by which such reverse functionality might be acquired is a matter of speculation. Perhaps co-firing associated with the operation of the forward model strengthens backprojecting connections thus unmasking backprojections (cf. Heyes, vol. 1, ch. 6, p. 170, on ''firing together and wiring together'').

Circuits with this reverse forward model aspect could function in a variety of useful ways. They could operate to generate behavioral building blocks or modules that could be strung together in program level imitation, of sequences (Byrne, vol. 1, ch. 9) or of hierarchical structures (Whiten et al., vol. 1, ch. 11). They could allow an infant to form three-way associations among observed behavior by its parents (who have survived to reproduce, so may have adaptive behaviors not all of which are heritable), observed circumstances in which its parents perform such behavior, and its own similar behavior. Such associations could drive contextual imitation: act like that, when the environment is like this (Byrne, vol. 1, ch. 9, p. 228).

Note that the sensorimotor affordance associations described in the second layer (mediated by canonical neurons?) could also be bilateral. If so, observation of an object that affords some type of action would be predicted to prime the type of action afforded (see and cf. Lhermitte's utilization syndrome patients; Lhermitte, 1983, 1986; Lhermitte et al., 1986).

So far, the reverse forward model account does not explain imitation of visually opaque acts. How can a correspondence be established between one's own acts and similar acts by others, when there is no reafference in the same modality as observations of others' acts? For example, a creature receives visual input when observing another's facial expressions, but normally only receives proprioceptive, not visual reafference from its own facial expressions. How then can an association be established between my seeing another's facial expression and my making a similar expression myself? One answer is that some such correspondences are innate (Meltzoff, vol. 2, ch. 1). Another is that they are acquired in a variety of ways, through experience with mirrors, or with being imitated (Heyes, vol. 1, ch. 6).

The shared circuits model is compatible with these suggestions; it has no commitments about whether opaque correspondences are innate, acquired, or both. It also naturally accommodates another suggestion: that *stimulus enhancement* can establish associations between one's own and others' similar acts for visually opaque actions. Suppose a social creature repeatedly visual observes others' actions of a certain type, and its attention is thereby drawn to the characteristic objects of such actions. Such stimulus enhancement repeatedly evokes in the observer an innate or otherwise acquired response to those objects. As a result, an association is formed between visual observations of others' actions and one's own similar action. This is not initially imitation or any kind of copying; the object independently evokes others' and one's own acts. But while the link is initially indirect, nevertheless an association between own and others' acts may be established. Cells that mediate this association may acquire mirror properties such that subsequently merely observing another's act comes to prime similar action by the observer. In this way mere stimulus enhancement may develop into copying, and an indirect stimulus enhancement link may develop into a direct sensorimotor matching link. This suggestion about how opaque correspondences could be established is similar to one Heyes makes (in vol. 1, ch. 6) about the mediating role of words, but it is more general, and applies to stimulus enhancement at large.[3]

7.5 Fourth Layer. Simulation for Action Understanding with Output Inhibition

Next consider the possibility that a creature might observe another's act, which primes a similar act in the usual way, yet its own action is inhibited so that the observed behavior is not actually copied. In effect, the output of the reversed forward model is taken off line prior to motor output. Since observing the other's act is still associated with motor priming even when copying is inhibited, such observation could be interpreted as providing the observer with a simulation of what it is like to perform that kind of act, or a kind of understanding of the action: doing *that* is like *this*. Simulation for action understanding is off-line copying. (Cf. Rizzolatti, vol. 1, ch. 1, on

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[3] Heyes's ASL model (Heyes, vol. 1, ch. 6) claims that visual and motor representations are linked according to the same Hebbian principles whether the movement is perceptually opaque or transparent. The only difference is that in the transparent but not in the opaque case, self observation will lead to the formation of links between movements that are the same from a third party perspective. What I am here regarding as stimulus enhancement could be regarded as acquired equivalence learning. The ASL model cites words as examples of the kind of stimuli that could act as the "third term" in acquired equivalence learning, but acknowledges that, as in most experiments on acquired equivalence in animals, the third term is often a nonlinguistic stimulus. Thanks here to Cecilia Heyes.

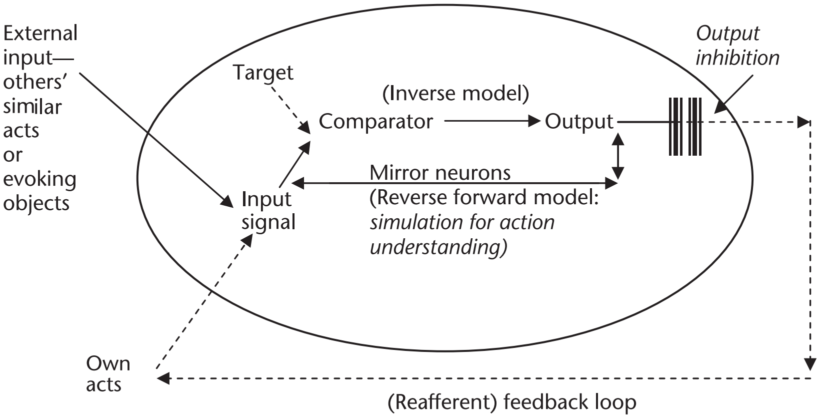

Figure 7.4

Fourth layer: simulation for action understanding with inhibition of output.

action understanding preceding imitation; the views are consistent if priming of a movement and emulation of a goal are distinguished from full-fledged imitation, even though all are forms of copying. See also Meltzoff, vol. 2, ch. 1.) Applied to emulation circuits that control the result of movement, the simulation would provide information about the goal to which the other's movement is directed. The ability to pick up the information that another's movement is directed toward a certain goal can be regarded as enabling an early stage in understanding other agents and hence other minds. (See figure 7.4.)

Although it uses the same circuit in reverse, simulation for action understanding can function at a higher level than the simulation for speeding and smoothing control described in the second layer (by "control" here, I refer to the overall function of the control system, not merely to that of the inverse model component). Recall that the basic functions of a forward model in a control system do not require the system to monitor continuously whether it is relying on actual reafference or on the forward model, even though it should be able to switch between them as needed. In other words, as long as the forward model works well and there is no significant mismatch in retrospect, the system does not need to know that it is using the forward model to improve control. The distinction between actual and simulated feedback does not have global significance for the system. By contrast, for simulation flexibly to subserve, as needed, understanding as opposed to copying an action, the system has to track the distinction between states in which the its output is inhibited and states in which it is not; this distinction *is* of global significance. Information about whether a movement is another's or one's own now overlays the primitive blended intersubjective manifold. Information about the distinction between self and other thus emerges. (Recall that the level of description of this information is subpersonal in this hypothesis; while this information is enabling, it is a further question how it is used at the personal level).

In particular, the shared intersubjective space is here prior to the self/other distinction, so that subpersonal information about persons in effect arrives in the first person plural, in a form that does not distinguish or infer between self and others. Subpersonal processing of information about other agents is more a matter of simulated recentering of first-personal or self-information processing than of inference from first person information to third person information. At the level of subpersonal information, the problem of ''knowledge'' of other minds is reconfigured: it is neither one of starting from information about the self and constructing a bridge across a gulf to information about other persons, nor one of starting from information about other persons and from the resources it provides somehow generating information about the self. The shared circuits hypothesis gives concrete if subpersonal form to the interdependence and parity of information about self and other minds.

Again, it is a further question how these subpersonal relations are reflected at the personal level. Do they give any support to a parallel priority of the first person plural at the personal level? How should ''priority'' indeed be understood in this question: as a question about development, or about the structure of mature understanding of other persons, and what is the relation between these? Can personal level understanding and knowledge of other minds be noninferentially based on or enabled by reliable subpersonal information? Is there any reason, conceptual or empirical, to believe that the problem of knowledge of other minds is similarly reconfigured at the personal level, so that it is neither one of starting from the first person perspective and constructing a bridge across a gulf to the third person, nor one of starting from the third person perspective and from the resources it provides somehow creating the first person perspective? Careful further thought is needed here. We should not simply help ourselves to an isomorphic projection from the subpersonal to the personal levels, but nor should we assume that the structure of subpersonal information processing has no implications for the personal level.

One way of responding to these issues is suggested by the affinities between the shared circuits hypothesis and Gordon's version of simulation theory (see especially 1995b, pp. 56, 58, 68; see also 2002; vol. 2, ch. 3). In

Gordon's felicitous phrase, constitutive mirroring *multiplies the first person*, through a process of making sense of observed behavior and the self's matching response together, under a common scheme of reasons, a process that assigns incoherent mental states to different persons (Gordon, vol. 2, ch. 3, p. 103). While the shared circuits model offers a subpersonal description in which first person plural information is prior to first person singular and third person singular information, Gordon's account of the multiplication of the first person under a scheme of reasons is more ambitious in linking subpersonal constitutive mirroring to personal level understanding of other minds.

Gordon appeals to *ascent routines* to explain how simulation can underwrite mind reading without depending on inference from the first to the third person, as other versions of simulation theory do (see Gordon, 1995a; vol. 2, ch. 3; compare Gallese & Goldman, 1998). When I use an ascent routine, I answer a meta-question about my own or another's mental states by looking at the world; ascent routines are as well suited in principle to answering questions about another's mental states as about one's own. For example, to answer a question about whether I believe *p*, I consider whether *p* is true; to answer a question about whether another believes *p*, I perform an egocentric shift and imaginatively recenter myself to the other's perspective, and then again consider whether *p* is true. Similarly, for questions about what I or another perceive or intend: I look out at the world and the reasons it provides, though in the case of others having first transformed myself imaginatively. Note that on this view, to answer questions about what I or others believe, perceive, or intend, someone must first have the ability to perceive and act in the world. There is here another parallel, between Gordon's conception of ascent routines and the first aspect of the shared circuits model I noted earlier: the way a shared intersubjective space is distilled out of and simulatively employs the shared perception/action information space.

7.6 Fifth Layer. Counterfactual Input Simulation for Deliberation and Planning

Finally, the system can be taken off-line on the input side as well as the output side. Counterfactual inputs of possible acts and affordances can be simulated and the resulting motor activations entertained and compared without commitment to action and its costs; circuits for means and ends can be linked and recombined flexibly. Simulation at both ends could provide information that would enable deliberation and planning, and

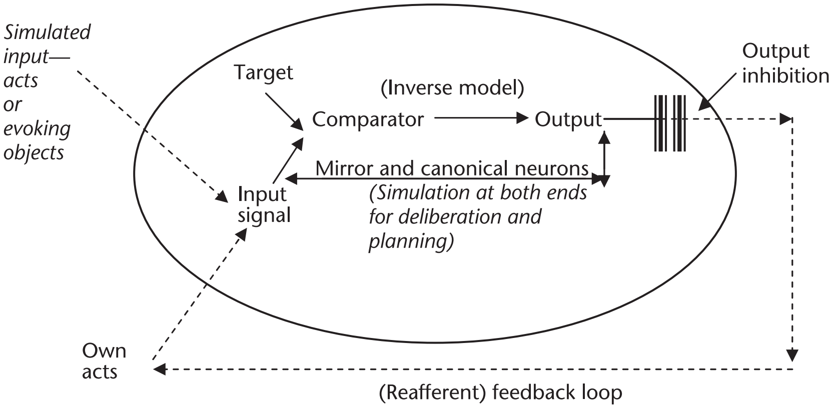

Figure 7.5
Fifth layer: counterfactual input simulation for deliberation and planning.

counterfactual and instrumental reasoning. For these functions, it would be essential for the system to keep track of whether it is simulating or not; the distinction between the imagined and the real thus emerges, close on the heels of the self/other distinction. (See figure 7.5.)

However, keep in mind that the order of the layers presented here is heuristic and does not necessarily represent the order of evolution, development, or learning; those are questions for further investigation. Layer 4's simulation and inhibition of output may accompany or follow rather than precede layer 5's simulation of input. That is, the shared circuits hypothesis does not specify the phylogentic or developmental priority between subpersonal information about self versus other and subpersonal information about the imagined versus the real. Rather, it provides generic, adaptable tools for framing more specific hypotheses.

7.7 Concluding Remarks

The five-layer shared circuits hypothesis I have sketched provides a unified subpersonal architecture for control, imitation, and simulation at a middle level of description: a functional level above that of neural implementation but below that of the normatively constrained and/or conscious personal level. It raises a variety of questions about how this functional architecture might map onto the neural and personal levels; the model may thus play a useful heuristic role even if it proves to be wrong in details (although care is needed to avoid over-simple interlevel projections and isomorphism assumptions). For example, looking down to the level of neural implementation, we can ask: where might the postulated comparators be located? (PF? STS? Compare Rizzolatti in vol. 1, ch. 1 and Iacoboni in vol. 1, ch. 2.) Are shared circuits for the results of action found in prefrontal areas while those for detailed movements are in parietal areas? Does the model bear any relationship to the distinction between ventral and dorsal processing streams? Does it cast any light on the presence and function of mirror neurons in Broca's area and their relation to linguistic capacities? I have sketched the dynamics of the shared circuits model in cybernetic terms, but if neural implementations can be found, their interactive behavior through time could be represented as the evolution of a phase space in the manner of dynamical systems theory, and its attractor structure investigated.

Looking up to the personal level, we can ask: What behavioral, cognitive and functional predictions does the model provide? Intentional agents achieve their goals by means that can be given successively finer specifications, related by an asymmetrical "do *x* by doing *y*" relation: for example, I turn on the light by flipping the switch by moving my fingers. If we envisage a series of spectra with control of the ultimate result or goal of action at one extreme, and control of detailed fine movements that are the means to the result at the other extreme, then the shared circuits model could apply at successive linked points along such spectra. Thus the means outputted to the target of one circuit could be the target of the next circuit. A network of such linked circuits would support hierarchical control while permitting the flexible decomposition and recombination of goals and means. What relationship might such recombinant flexibility have to the recombinant flexibility characteristic of language? What does the model suggest about the functional relationships among three distinctive human capacities: for imitation, mind reading, and language (cf. Rizzolatti & Arbib, 1998; Iacoboni, vol. 1, ch. 2; Arbib on Iacoboni, vol. 1, ch. 8.2, p. 200; Meltzoff, vol. 2, ch. 3)? What implications does it have for the issue of whether simulation approaches to mind reading require an inference from the first to the third person (cf. Gordon, ch. 3; Goldman, ch. 2; Meltzoff, ch. 1; all in vol. 2)? What constraints does the model suggest on the relationships among various personal level distinctions: between action and perception, between self and other, between reality and appearance? Can the model play any role in distinguishing conscious and unconscious mental states and processes (see and cf. Hesslow, 2002; Frith et al., 2000; Gray, forthcoming; Jeannerod, 1997)? How might it be extended to include the emotional mirroring postulated by various researchers (see vol. 1, chapters 1 through

4, by Rizzolatti, Iacoboni, Gallese, and Decety & Chaminade, respectively)? Might the layers of the model usefully be mapped onto evolutionary or developmental stages, in theorizing the imitative and mind reading abilities of other animals or children?

I conclude by summarizing the shared circuits hypothesis. Theories about the control, imitative, and simulative functions of the mirror system, and evidence from imitation studies for ideomotor and common coding theories, suggest that perception and action share a fundamental information space that is preserved as higher cognitive capacities and distinctions are built on it. The distinction between results and the means to those results, essential to goal-directed, perceptually guided intentional action as well as to imitative learning, emerges as a flexible articulation of this shared processing. But perception remains fundamentally enactive, in a way that challenges orthodox views of perception and action as separately constituted and of perception as motivationally inert (see and cf. Kinsbourne, vol. 2, ch. 7; Noë, in press; Hurley, 1998).

The intersubjectivity characteristic of human beings, their distinctive capacity to understand and empathize with one another, is enabled as a specialization of enactive perception: I perceive your action enactively, in a way that immediately engages my own potential similar action, thus enabling me to understand, or to imitate, your action. Shared processing of the actions of other and self is a special aspect of the shared processing of perception and action. In an enabling role, this subpersonal informational structure may have implications for the epistemology of other minds. Within this informational structure, it is not so much that intersubjectivity bridges a self/other gap as that the self/other distinction is imposed on the fundamental information space that self and other share. Simulation theories of mindreading can be right about shared processing for self and other with respect to this fundamental intersubjectivity, even if more advanced aspects of mindreading require theorizing, in ways enabled by language.

Three aspects of the shared circuits hypothesis are noteworthy. First, it connects a shared information space for action and perception (understood in terms of control processes) with a shared information space for self and other (enabling imitation, intersubjective identification, and action understanding). In effect, the shared intersubjective space is distilled out of the shared perception/action space. Second, it illustrates how the distinctions between perception and action, between self and other, and between the imagined and the real, which provide information that enables the mental lives of persons, can be imposed on these shared information spaces.[4] In particular, the shared intersubjective space is here prior to the self/other distinction, and information about persons arrives in the first person plural, in a form that does not register the self-other distinction. Processing information about other agents is more a matter of simulated recentering of the first person than of inference from the first person to the third person. At the subpersonal level, the problem of "knowledge" of other minds is reconfigured: it is neither one of starting from information about the self and constructing a bridge across a gulf to information about other persons, nor one of starting from information about other persons, and from the resources it provides somehow generating information about the self. The shared circuits hypothesis gives concrete form to the interdependence and parity of self understanding and understanding other minds. Finally, the shared circuits hypothesis thus illustrates what I call a *horizontally modular* architecture (Hurley, 1998, 2001): it avoids the common conception of perception and action as separate and peripheral to central cognition. Rather, perception and action are dynamically co-constituted, and cognitively significant resources, such as the distinctions between self and other and between the imagined and the real and information for action understanding and planning, emerge from the information space that perception and action share.[5]

Acknowledgments

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[4] In a way that converges with the broadly Kantian view that these two distinctions are intimately connected; cf. Strawson (1959, 1966).

[5] For discussion relevant to this chapter, see especially Gallese, vol. 1, ch. 3, and Gordon, vol. 2, ch. 3.

8 Commentary and Discussion on Mechanisms of Imitation

8.1 Reflections on Mirror Systems

J. N. P. Rawlins on Rizzolatti and on Decety and Chaminade

8.1.1 Imitation

Imitation requires a mapping between one's own behavior and the behavior of some other or others. This mapping may be necessary but not sufficient for a behavior to count as imitative, since definitions of imitation vary. Views differ on how precise the mapping and how novel the resulting behavior must be in order to count as true imitation. For example, Rizzolatti uses Thorndike's definition, "learning to do an act from seeing it done." Decety uses a more restrictive definition, which specifies that imitation must be intentional and effortful; moreover, the behavior that results must be novel and must share the goal of the observed behavior and use similar means to attain it. My purpose here is not to argue for one definition or another. Rather, I wish to consider the neural circuitry activated when monkeys or humans engage in action or observe the same action in others—the conditions under which this circuitry is effectively activated and the psychological functions it might serve—and to propose some new experimental approaches to these issues.

8.1.2 Why Should Monkeys Have Mirror Neurons?

The discovery of mirror neurons in the brains of monkeys demonstrates the existence of a link between vision and action. Mirror neurons are as powerfully activated when a monkey observes some action being performed by another individual as they are when the observer itself engages in the same action. But what are monkey mirror neurons for?

There are many examples of the behavior of one individual conforming to the behavior of another. Flocks of birds move together; people in conversation tend to adopt similar postures. These kinds of behavioral conformity can be observed informally, with no need for sophisticated experiment, and are widely attributed to response facilitation or priming. There is no need to assume that they must depend upon understanding the behavior of others, or result from some intentional or effortful component. However, they do require a mechanism by which a sensory input—typically a visual one—can appropriately drive the motor system. Could monkey mirror neurons provide such a mechanism?

Mirror neurons in monkey area F5 are activated by object-related hand or mouth movements; precision grip is also represented there. Such a system could have a role during development if infant monkeys learn to forage by observing what other foraging monkeys pick up and eat, and then doing the same themselves. I do not know if there is evidence for this kind of learning. However, as Rizzolatti indicates, for such a system to increase foraging efficiency, it would have to represent the right kind of objects to pick up and ingest. It would be counterproductive to copy hand and mouth movements without relating them to the kinds of objects that the observed actors actually manipulate.

In fact, in monkeys there is no evidence of such copying of mere movements, unrelated to goals (see Voelkl & Huber, 2000, on goal-related imitation of movements by marmosets). Moreover, there is reason to believe that monkey mirror neurons may respond only to goal-directed actions. For example, Rizzolatti describes mirror neurons that require the observer monkey to have seen the target object of the observed movement, even if the object is then hidden behind a screen. Under these conditions, a movement that does elicit a mirror response may be identical to a movement that does not, if the observer monkey has not seen the target object placed behind the screen. To activate such mirror neurons, the observer monkey must detect not just a movement but also a specific goal; so simple response priming does not appear to be the function of these neurons.

It may come as a relief to dancing instructors that the human mirror system can be entrained by nongoal-directed, intransitive movements as well as by goal-directed movements. Human beings are enthusiastic imitators, in multiple senses of the term. But as Decety convincingly argues, mirror systems offer neural mechanisms that could underpin a range of distinctively human processes, beyond imitation. If area F5, where mirror neurons were first observed, is really the monkey homologue of the human Broca's area, which plays a crucial role in our linguistic ability, then perhaps a system that originally conferred quite different evolutionary benefits now subserves our effortless acquisition of language.[1] Still, monkeys do not acquire language, so what advantages would a mirror system have for a monkey?

8.1.3 Are Monkeys Beginner Mind Readers? Is Mind Reading an Exclusively Human Preserve?

Rizzolatti attributes to the monkey mirror system a role in enabling monkeys to begin to understand the actions of others. Seeing the actions of another activates one's own mirroring motor system and thus allows the other's behavior to be matched to one's own repertoire and its consequences predicted, just as the consequences of one's own motor activity might be predicted by a forward model. However, there is at present no experimental evidence for such proto-"mind reading" in monkeys either.

The following experimental approach may yield fresh evidence on this issue. Single-unit recording experiments have found *place cells* in the rat hippocampus, which are active when the rat is located in particular places. Place cells in the monkey hippocampus have also been identified, but these are active when the monkey simply looks at a particular place; it need not be physically located at that place. Consider an experiment with two monkeys. Monkey A has a place cell that fires when the monkey looks at place x. We now arrange that monkey A can see monkey B, and that monkey B but not monkey A can see place x. Under these conditions, if place cells for place x are activated in monkey A's hippocampus just when monkey B is looking at place x *and* monkey A is watching monkey B, that would suggest that monkey A has inferred the place that monkey B is looking at. Such a result would seem to be evidence of elementary mind reading by monkeys. If such a result were obtained, its relationship to the monkey mirror system would be worth investigating.

Decety suggests that mind reading is a uniquely human ability. I know of no convincing counterevidence for this claim, but I would nonetheless like to speculate about the possibility that similar abilities could have evolved in other social animals. One particularly interesting group to consider might be social cetaceans, which use echolocation. Whereas primates generally have to be looking in the right direction to see what others in their social group are attending to, there is surely no such constraint in

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[1] In acquiring language, we effortlessly copy verbalizations we hear. If imitation must be effortful, as Decety requires, how would this effortless copying be better described?

whales. If one individual is using active sonar to interrogate some object of interest, the return echo will presumably be available to all the other individuals within range. Each individual is in a sense immersed in the current preoccupations of all the other animals in the group. This offers a wonderful potential handle for investigating the evolution and range of mind-reading abilities.

8.1.4 The Human Mirror System: Is Imitation Its Key Function?

Under what conditions are human mirror systems activated? Does this activity function primarily to drive imitation? Given the constraints on single-unit recording in the human brain, much of what we know is derived from functional imaging of regional blood flow changes. Although evidence from other methodologies is also available, none allows us to characterize the range of drivers to which particular mirror neurons may respond. Our conclusions are therefore derived from general changes in the activity of brain regions. We cannot at present know whether there are neurons within those regions whose activities are quite different from the group as a whole. Despite this limitation, some striking findings have been obtained, such as the finding Decety reports of a hemispheric difference in parietal activation between imitating and being imitated.

Functional imaging studies all require subtraction methods. The experimental condition is contrasted with a comparison condition intended to be identical in all but the crucial variable of interest. Just the same kind of formal relationship between experimental and control conditions exists in classical conditioning designs for the study of associative learning. When Pavlov's dogs learned that the sound of a bell was followed by the delivery of food, they started to salivate in response to the bell. An innate response to the delivery of food was now elicited by the *signal* of food. But how can we be certain that this new response really depends on having detected and learned the association that we so carefully arranged between the sound of the bell and the delivery of food? In Pavlovian conditioning we arrange a correlation between a signal and an outcome, and assume that the conditioned response to the signal that develops does so because that relationship has been learned. If we had arranged that the signal and the outcome were uncorrelated, and the same response to the signal had developed, then this could not be because the animal had learned the correlation. We would therefore assume that some mechanism other than Pavlovian conditioning was responsible for the change in behavior. Control procedures for associative learning experiments are designed to test the possibility that an apparently conditioned response in fact arises via some other, nonassociative route. For example, does the bell come to elicit drooling even if the bell did not reliably predict food?

There are two ways of settling that question. One is to arrange a negatively correlated comparison condition. In this case, food is never presented when the bell has just sounded. Animals exposed to this kind of contingency typically differ in their responses from those exposed to Pavlov's positively correlated condition. This control is not usually the preferred comparison, though, because it has become clear that animals learn the negative correlation—they expect that food will *not* be delivered when the bell sounds. Any difference in behavior between the positively correlated and negatively correlated groups might therefore stem from this inhibitory learning, rather than from the excitatory learning in the positively correlated group. As a result, the more generally accepted comparison condition is a "truly random" control condition, in which the bell and the food are each presented from time to time, but food is no more likely to be delivered after the bell sounds than when the bell has not sounded.[2]

The functional imaging paradigms used to study imitation and mirror systems have typically used comparison conditions that entail observation alone, or observation of an unrelated action. Imitation leads to more activation than either of these conditions. But just as in classical conditioning, unrelated comparison conditions may differ in important ways from negatively correlated ones. Moreover, in studying mirror systems, the negatively correlated control condition is, I suggest, more analytically informative than the unrelated comparison condition typically used.

If mirror systems are important for imitation as such, then they should not be activated when one must do the opposite of what the actor does—indeed, one might predict deactivation. If, on the other hand, they play a key role in understanding the actions of others, then they should be at least as powerfully activated in a paradigm in which an observer needs to do the opposite of an actor as in the standard imitation paradigm in which the observer needs to do the same as an actor. Imagine that we watch an actor assemble a complex puzzle that requires a strict sequence for assembly and disassembly. If we know that our job is going to be to assemble the puzzle ourselves, we clearly need to remember and subsequently reproduce the actor's sequence of actions. That will presumably powerfully activate the mirror system. But what if we know that our job will be to *dis*assemble

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[2] This comparison also has a potential drawback because there is reason to believe that animals may actively learn the lack of a relationship between the two stimuli—a learned irrelevance paradigm.

the construction? We now need not only to observe and identify what the actor does, but also to plan for ourselves the reversed sequence of actions we will need to use in order to attain our goal of achieving the status quo ante. This would not be imitation in Decety's sense, because it has a different goal and a different sequence of actions. Nonetheless, it is undoubtedly very different from seeing someone carry out actions that are unrelated to one's own task. I propose that such an experiment would be a more rigorous way to determine whether the mirror system functions primarily to drive imitation or the understanding of actions.

8.2 Action Recognition, Imitation, and Language Are Different

Michael Arbib on Iacoboni

Marco Iacoboni's chapter shows how study of the monkey mirror system has inspired a body of excellent work on human imitation using functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS). Since space is limited, I will just comment on section 2.3, which focuses on the key issue of the relationship between the action recognition system and the emergence of language. This will raise broader issues concerning the status of linguistic theory and the brain mechanisms that underlie the evolution of language.

Let us begin with the specific. In chapter 2 Iacoboni summarizes a previous discussion by myself and Rizzolatti as follows:

> How can such a formalized structure [of a parsing tree for grammar] emerge from a relatively primitive action recognition system? A type of answer ... (Rizzolatti and Arbib, 1998) [henceforth R&A] ... is that "gestures may be a primitive form of grammar." The problem with both question and answer is that they accept a view of language as a phenomenon that can be essentially reduced to formal constructs such as grammar. (Iacoboni, vol. 1, ch. 2, p. 93)

However, the apparently quoted phrase, "gestures may be a primitive form of grammar" occurs nowhere in R&A! Instead, these authors:

> examine whether or not a "prelinguistic grammar" can be assigned to the control and observation of actions. If this is so, the notion that evolution could yield a language system "atop" of the action system becomes much more plausible. (Rizzolatti & Arbib, 1998, p. 191)

I can see why some readers may have mistaken talk of a "prelinguistic grammar" for the claim that "gestures may be a primitive form of grammar," but (1) R&A's approach is semantic rather than syntactic, and (2) emphasizes differences as well as commonalities. R&A stated:

> We view the activity of "canonical" F5 neurons as part of the code for an imperative case structure, for example,
>
> Command: grasp-A(raisin)
>
> as an instance of grasp-A(object), where grasp-A is a specific kind of grasp, to be applied to the raisin. *Note that this case structure is an "action description," not a linguistic representation.*... [Again,] we might say that the firing of "mirror" F5 neurons is part of the code for a declarative case structure, for example,
>
> Declaration: grasp-A(Luigi, raisin)
>
> which is a special case of grasp-A(agent, object), where grasp-A is a specific kind of grasp, applied to the raisin (the object) by Luigi (the agent). *Again, this is an "action description," not a linguistic representation.* (Rizzolatti & Arbib, 1998, p. 192; italics added.)

In the case analysis by Fillmore (1966), the sentence "John hit Mary with his hand" is viewed as the "surface structure" for a case structure "hit (John, Mary, John's hand)," which is an instance of the case frame "hit (agent, recipient, instrument)," which makes explicit the roles of "John," "Mary," and "John's hand." However, being able to grasp a raisin is different from being able to say "I am grasping a raisin," and R&A are clear that the neural mechanisms that underlie the doing and the saying are different. However, the case structure lets us see a commonality in the underlying representations, thus helping us understand how a mirror system for grasping might provide an evolutionary core for the development of brain mechanisms that support language.

The key point of language is that it can provide sentence structures that can describe very different actions (and much, much more). The "case structure" of an animal's action is a human description of a limited capability; the "case structure" of a sentence exemplifies a human linguistic "frame" that the human can use to describe freely novel situations that have never arisen before.

I agree with Iacoboni that one must "factor in the changes that the evolutionary process might have produced," but am concerned when he says that even though "the imitative abilities of monkeys are limited,... one can also conceivably argue that the action recognition system made monkeys 'imitation-ready'" (vol. 1, ch. 2, pp. 81–82). In Arbib (2002), I introduced the term "language-ready" to indicate that early *Homo sapiens* might well have had brains like ours and yet not have had language—the brain was ready to learn language but the culture had not yet produced language to learn. However, all the evidence says that monkeys cannot learn to imitate in any major sense, no matter what opportunities are provided by the social and physical environment, while chimpanzees exhibit imitation, but in a form limited with respect to the human's. I thus find Iacoboni's use of "imitation-ready" to be unfortunate, and suggest that what I would call an imitation-ready brain (i.e., one that could master imitation given the right environment) did not evolve until well into the hominid line (or at least millions of years after the common ancestor of monkeys and great apes, if "simple" imitation is all that is of interest). Indeed, I hypothesize (Arbib, 2002, in press) that recognition of manual actions, imitation, and the ability to acquire and use language rest on a nested, evolutionary progression of brain mechanisms. I take seriously our ability to produce myriad novel sentences, seeing the openness of language as both grounding for and emerging from the ability to translate between cognitive structures and verbal structures within the framework of social communication.

In section 2.3.3 Iacoboni presents a transcription of "everyday speech" (figure 2.7) and stresses that

> not only do violations of grammar . . . occur . . . , but . . . this segment of speech is full of phenomena that are . . . not . . . studied by traditional linguists.
>
> A salient feature of typical conversations that is ignored by traditional linguists is *turn-taking* [which depends on] . . . the hearer's tracking . . . [of] transiently appearing *opportunities for taking a turn—which are not exclusively grammatical* but rhythmic and pitch contour-intonational as well. [vol. 1, ch. 2, pp. 93–94; my italics.]

Iacoboni is right to emphasize the importance of turn-taking, but I think that he is wrong to be so dismissive of the work of traditional linguists (who do include phonologists and not just grammarians, after all). In his figure 2.7, speech is not only labeled with "?" for "stuff" but also with syntactic markers for what the speaker and the hearer would recognize as the "real" message. Just as Newton made progress by first treating the sun, Earth, and moon as points, and then others developed the study of the tidal effects of the moon, so it makes sense to start with a model of the "perfect" speaker and then seek to understand why limitations of memory, delays in production, and changing rhetorical goals (competition of different thoughts for expression, new thoughts as one speaks, etc.) produce imperfect utterances. "Ums" and "ahs" are imperfections of language production, not its essence. I do take the point that the understanding of such elements will come from motoric concepts (such as signaling of delays in reaching a communicative goal) but still suggest that the motoric analysis should be complemented by a more idealized production model that is closer to traditional linguistics. However, when Iacoboni (vol. 1, ch. 2, pp. 94–95) urges us to "consider carefully the incontrovertibly motor elements that are at work in conversation [whose processing] . . . requires a fast functional architecture that is not dissimilar to the one needed in motor control," my concern is twofold. (1) I do not know of any studies in monkeys that relate neural processes to turn-taking. (2) Most species have a fast functional architecture for motor control, but only humans have language, so that the last statement ignores the very differences whose bridging across evolutionary time one needs to explain.

8.3 Evidence for Memetic Drive?

Susan Blackmore on Iacoboni

I was thrilled when I learned of Iacoboni's discovery that when a chimpanzee's brain is morphed onto a human brain, the areas of greatest expansion are those that are used in imitation. "Yes!" I thought. "This is exactly what I predicted on the basis of memetic theory. Whoopee—memetics is right!" But then I had to pause, because this is how to make the worst mistake in the book. Construct a wacky theory, derive a prediction from that theory, discover the prediction is correct and then (illegitimately) conclude that the theory must be true. So I would like to describe the prediction and consider whether these findings do have any implications for memetics.

Dawkins's (1976/1989) original idea in coining the term "meme" was to point out that when people imitate each other, they not only copy information, they must select what to copy, and their copies are not perfect. This is all that is required to apply the principles of universal Darwinism and, by definition, the information people copy is a replicator. Dawkins called that new replicator the meme.

One implication of the theory of memetics is that the capacity for imitation must inevitably let loose a new evolutionary process and, as Dawkins originally put it, "Once this new evolution begins, it will in no necessary sense be subservient to the old" (Dawkins, 1976/1989, pp. 193–194). He criticized his colleagues because "In the last analysis they wish always to go back to 'biological advantage'" to answer questions about human behavior (Dawkins, 1976/1989, p. 193). But if memes are replicators, then we must consider memetic advantage too. Humans must be the product of two replicators, not just one, and this should be obvious in the way they have evolved.

In exploring the implications of memetic advantage, I hypothesized that the interests of the memes might force the genes to take a direction different from that which they would have taken otherwise; they would be forced to follow the direction taken by memetic evolution. This is the coevolutionary process I called *memetic drive* (Blackmore, 1999, 2001).

Put simply, the hypothesis is this. Once human ancestors could imitate, memes appeared and began competing to be copied, their success depending on the type of meme and the preferences and abilities of the people doing the copying. Given that at least some of the memes would provide survival benefits, this means an advantage to genes for the ability to copy those memes. If better imitation requires a bigger brain, then this process alone will tend to increase brain size and improve the ability to imitate. As this ability increases, more memes will appear and their evolution will take off in various directions, perhaps including the creation of rituals, clothes, body decoration, or music, including behaviors that are of more advantage to those memes themselves than to the genes of the people copying them. If being able to display the latest memes provides status (which is a reasonable assumption), then it will pay everyone to copy the best imitators, and to mate with them. Either way, this creates an advantage for genes for the ability to copy the latest memes. In this way genes would be expected to track the direction taken by purely memetic evolution and thus we humans have ended up with brains that are not only much larger, but are specially designed to be good at music, ritual, art and, of course, language.

This hypothesis allows for some (admittedly rather general) predictions. In particular, if brain size has been meme driven, then within groups of similar species brain size should correlate with the ability to imitate. Of course there are few species capable of imitation, but this prediction holds for humming birds (Jarvis et al., 2000). Other aspects of the big brain hypothesis have been confirmed using simulations and mathematical modeling (Bull et al., 2000; Higgs, 2000). More specifically, I predicted that brain scans of people either initiating or imitating actions should reveal that "imitation is the harder part—and also that the evolutionarily newer parts of the brain should be especially implicated in carrying it out" (Blackmore, 2000b, p. 73). This implies that the parts of the brain that differ most between chimpanzees and humans should be those involved in imitation (assuming that present-day chimpanzees are closer to our common ancestor than humans are). Finally, if memetic drive is responsible for the evolution of language, then we should expect the language areas in the human brain to be derived from areas originally used for imitation.

This is what Iacoboni and his colleagues have demonstrated, thus confirming these predictions. In chapter 2 (vol. 1, p. 91) Iacoboni concludes that "from a relatively simple neural mechanism of matching the observation and execution of an action (mirror neurons), more complex functional properties were built and more complex behaviors were supported." The question now is, Why? The standard evolutionary view must be that it happened in the interests of the genes. Like Dawkins's colleagues, most people will presumably "wish always to go back to 'biological advantage'." But the wider alternative remains; that when it comes to human evolution there may be more than one replicator competing for survival.

There is nothing mysterious about memetics. Memes are not mystical entities floating about in a few theorists' minds. They are nothing more nor less than whatever it is that people copy when they imitate. So if you admit that people (imperfectly and selectively) copy each other, and you define a replicator as information that is copied with variation and selection, then you have to conclude that memes exist. All the doubt must be about whether memetics can ever prove itself useful as a science, and whether memes really have played the crucial role in human evolution that memetic theory suggests. Iacoboni's findings fit perfectly with the predictions made, but then, as he discusses in his chapter, there are many possible explanations for them. Memetics has made a start, but it has a great deal further to go if it is to prove its worth in understanding human evolution.

8.4 The Role of Mirror Neurons in Imitation

Susan Jones on Gallese

The mirror neuron was second only to imitation itself as the hardest working concept at the conference at Royaumont. Some participants spoke of the mirror neuron as though, all by itself, it could be a mechanism for imitation. More specifically, some seemed to have the idea (too briefly and therefore crudely expressed here) that mirror neurons might be capable of directly converting observed behavior into executed behavior. If this were true, then the problem of finding a plausible common mechanism for different imitative acts would be as good as solved. But in my view, how imitation actually happens is not much clearer since the discovery of mirror neurons than it was before.

The burden of these comments is that the role of mirror neurons in producing imitative behavior is not likely to be as a means of converting visual input about behavior into motor output of a copy of that behavior. Instead, I would put my money on Gallese's vision of mirror neurons as sources of the experience of common experience with other people, animals, or robots like ourselves.

Gallese has first-hand experience of mirror neurons, and has probably thought about their possible functions more than most. He proposes that mirror neurons are part of a mechanism for the automatic, subpersonal, nonpropositional recognition and understanding of the actions of others. This recognition and understanding of just the nature of others' behaviors might then feed into an understanding of the intentions and states behind those actions—in other words, it might produce empathy—and other forms of intersubjectivity. Then, to the degree that these experiences and the knowledge they yield are prerequisites for the ability to imitate, mirror neurons would be part of a mechanism for imitation.

Gallese does not suggest that mirror neurons function directly or even primarily to produce imitation, except perhaps in newborn human infants. This seems like appropriate caution, given what Gallese and Rizzolatti tell us in this volume about their single-cell recordings from mirror neurons in the monkey premotor cortex—and also, given what they do *not* tell us. They do not tell us about any data linking mirror neurons to imitation. This does not mean that mirror neurons are not involved in imitation—only that we don't yet know whether they are and if so, how.

We are told instead about data from monkeys on the responsiveness of mirror neurons to both the sight and the production of the act of reaching for and grasping an object. Given that the data are about reaches and grasps, the question becomes how what we know about the production of these actions can inform, first, speculation about the role of mirror neurons in producing the grasping action; and second, speculation about how imitative behavior is produced.

The first thing to note is that these reaching and grasping actions in the monkeys (and in the experimenters) are not imitative; and the responsiveness of mirror neurons to these actions does not give rise to imitation. Specifically, Gallese does *not* tell us that when the mirror neuron fires in response to either the sight or the sound of the grasping action, the monkey moves its own hand. Mirror neurons, then, are not transducers. They respond to both sensory input and motor events; they do not respond *to* sensory input *with* motor events. They do not automatically convert visual or auditory input into a motor response (at least, not in the adult; more about this qualification in a moment).

The idea that mirror neurons link observed actions directly to stored "motor plans" also seems wrong. For example, there has been a lot of work done on targeted reaching and its development (see, e.g., K. Newell & Molenaar, 1998; Rosenbaum et al., 1996). The data indicate that even such an apparently simple behavior is actually mind-numbingly complex in execution. That is because of the number of elements that have to be controlled when you (or Gallese's monkeys) reach toward an object. These include a host of different muscles (twenty-three on each side of your body can be involved in reaching) and different joints, acting from different starting points under highly variable conditions in the nervous system, in the muscles, in the forces produced by gravity interacting with posture, and so on. Because of the number of degrees of freedom in the conditions for reaching, it is thought that each reach is pretty much unique. The particular combination, sequence, and intensities of muscle movements in any one reach cannot be anticipated, even at the beginning of that particular reach. Instead, it seems most likely that reaches and other motor behaviors are dynamic and assembled online. That means that in every instance where someone reaches out and grasps an object, the action is assembled in that moment, is tailored to the contextual conditions of that moment, and is continuously monitored and adjusted even after it is launched. It is therefore very unlikely that the control of the huge number of different sequences that produce actual reaches is permanently represented in the central nervous system as "motor plans."

This is what reaching for objects looks like from the beginning (e.g., Thelen, 2001). Human infants do not reach at birth. In fact, they put in a lot of hard work before they succeed in reaching to grasp objects at about 5 months of age. Moreover, the developmental course of reaching is so different in different infants that it provides a strong argument against the idea of innate neural systems for reaching (Thelen, 2001; Thelen et al., 1993). Certainly, newborn infants do nothing to suggest that they come equipped with mirror neurons preprogrammed to play a role in reaching.

In short, the data so far suggest that any role played by mirror neurons in object-directed reaches and grasps is indirect and acquired in development. Mirror neurons are not transformers of visual input into motor output. And mirror neurons do not initiate the implementation of stored motor plans.

Our topic is not targeted reaching or grasping, but the much broader metabehavioral category of imitation. What, then, are the implications for the role of mirror neurons in enabling us to imitate any of a host of motor behaviors that we see, or hear, or feel, or imagine others performing? Gallese seems to be proposing two quite distinct roles—one for imitation in newborn infants and another for imitation beyond the newborn period.

Gallese suggests that perhaps imitation in newborn humans *is* the product of a transducerlike mirror neuron. Again, there are no data. We know nothing about the development of mirror neurons in monkeys, let alone in humans. This point is worth emphasizing. We do not know when or how monkeys develop the mirror neurons responsive to object grasping. And we certainly do not know that human newborns have mirror neurons that respond during tongue protrusions, which is the most commonly matched behavior in studies of newborn imitation.

The appeal of the idea that the newborns have mirror neurons is obvious. It has been argued for decades that imitation in the neonatal period is achieved via active intermodal mapping (Meltzoff & Moore, 1997, 1983a)—that is, the matching of mental representations in different modalities. But how this mapping might be accomplished has never been plausibly spelled out. Gallese suggests that the match is achieved by mirror neurons. In previous accounts of imitation in newborns, the proposed match was between two kinds of sensory information—visual and proprioceptive representations of tongue protrusion, for example. Now the proposal seems to be that mirror neurons both respond to visual input of an observed action and also initiate a motor behavior that replicates that same action. This idea resembles the classic reflex loop much more than the mirror neuron as observed in Gallese's own experiments.

The data on behavioral matching in newborns do not fit the hypothesis all that well. First, newborn infants in imitation experiments do not reproduce the adult model's behavior in a one-to-one fashion, as might be expected of a "visual in–motor out" device. Typically, they produce fewer tongue behaviors than they see, and these are clustered irregularly throughout the trial. If mirror neurons are mediating between the visual input and the motor output, what is the source of these long delays?

Until the discovery of mirror neurons, much was made of the fact that behavioral matching by newborns in many experiments *did* occur after a delay, as the delay was thought to indicate something more interesting than an automatic response that might be a fixed action pattern. For example, in Meltzoff and Moore's 1977 study (which Meltzoff re-presented at Royaumont[3]), the infants had pacifiers in their mouths as they watched an adult do tongue protrusions at a rate of 4 in 20 seconds, then had 2.5 minutes each to produce tongue protrusions in the absence of a model. Their graph indicates that the infants produced tongue protrusions at a rate of about 0.5 in 20 seconds (40+ tongue protrusions/(12 infants × 2.5 minutes)/3 segments per minute. The same graph indicates that the infants produced less than 1/10 of a mouth opening for every 4 mouth openings produced by the adult (Meltzoff & Moore, 1977). In later experiments (e.g.,

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[3] The conference with the same name as this volume, held at Royaumont Abbey, France, in May 2002. ED.

Meltzoff & Moore, 1983a), a model typically would produce 4 tongue protrusions in a 20-second period, then assume a still face for another 20 seconds—and it was while the model was *not* tongue protruding that the infant's tongue protrusions were most numerous.

A second potential problem for the idea that mirror neurons are the intervening mechanism between the adult model and the imitating newborn is the fact that the one behavior that infants reliably produce in imitation experiments—tongue protrusions (Anisfeld, 1996)—is also produced with equal enthusiasm when the stimulus is not an adult model doing tongue protrusions, but is instead some other arousing stimulus such as flashing colored lights (Jones, 1996) or music (Jones, 2001). Clearly, these tongue protrusions match nothing and are not produced by mirror neurons. It is possible that infants in very similar circumstances produce tongue protrusions in response to different arousing stimuli via different mechanisms, but it is certainly not parsimonious. An alternative is that tongue protrusions by newborns in response to all of these stimuli, the sight of adult tongue protrusions included, are by-products of arousal, and that newborn imitation itself might be a chimera.

One further consideration. I have said why, to me, the evidence says that the role of mirror neurons in producing behavior is neither simple nor direct. The mechanism for producing behaviors such as directed reaches and object grasps—with which mirror neurons are empirically (as opposed to speculatively) related—is almost certainly not a bunch of mirror neurons acting like a big reflex loop with a "stop-go" function added at some point in development. This is also a very unlikely description of a mechanism for imitation. Thus, if behavioral matching by newborns *did* turn out to be the product of a simple, direct, reflexlike, behavior-in/behavior-out mechanism with mirror neurons in the middle, it would mean that behavioral matching by newborns is not mechanistically related to imitation beyond the newborn period. In other words, if mirror neurons *are* the mechanism underlying behavioral matching by newborns, then behavioral matching by newborns goes nowhere developmentally and is consequently less interesting than we thought.

I like Gallese's core idea, which is that mirror neurons are the seat of our experiences of identification and empathy. This idea captures the one thing about mirror neurons that makes their functions potentially different from the functions of two separate but closely interacting populations of cells. The one thing about mirror neurons that is different is that these cells can fire for a specific instance of a broader category of actions—say, for a particular object grasp—but not "know" whether the action was mine or yours. What would such cells be good for if not to blur the lines between me and you and let us each know the other to be like ourself?

I am afraid, however, that this new idea is in danger of being lost in the rush to make the mirror neuron fit existing holes in our theories. We are such good synthesizers, and we get such aesthetic pleasure out of making the pieces fit, that we are understandably tempted to go far beyond the data. This has happened to a great extent with the mirror neuron. However, we should probably resist the temptation to assume that nature works as elegantly as it would if we designed it ourselves. Often it doesn't, and we are in the business of finding out what's true, not what would make a good and intellectually satisfying story.

8.5 Overlapping Brain States while Viewing and Doing

Marcel Kinsbourne on Decety and Chaminade

Decety and Chaminade introduce their broad goal as one of making "a tentative step toward a better understanding of intersubjectivity" (vol. 1, ch. 4, p. 119). With respect to the "intimate psychological relation between self and other (p. 139)," they arrive at the view that there is a unique human capacity to identify with others and thus share subjectivities. I focus here on the theoretical implications of some of the intriguing discoveries that have arisen from Decety's elegantly conceived research program.

8.5.1 Two-Way Traffic

According to Decety and Chaminade, "the discovery of mirror neurons ... has encouraged the search for a comparable mechanism in humans" (vol. 1, ch. 4, p. 124). Mirror neurons fire both when a particular action is perceived and when the animal itself executes this action. By "comparable mechanism," they refer to brain areas that activate on functional imaging both when an action is perceived and when it is performed. They do not claim that there are mirror neurons in these areas, and there is currently no way of knowing this. The statement is rhetorical, drawing an analogy between a cell population and a single cell type.

Distinct neural systems subserve knowledge of persons and of objects (Mitchell et al., 2002). Decety organizes his functional neuroimaging research in line with the presumed two-way traffic in the case of persons. He differentiates between knowing something about oneself and about others. He sets up comparable eliciting conditions, which differ in only one critical respect, along the lines of perceiving versus performing, self versus other. The conditions will generate a nearly identical activation profile in the cortical manifold. Those regions of activation that do not overlap both conditions are presumed to code for the critical difference between the conditions. In one study he can, for example, attribute the self versus other distinction to a corresponding left versus right hemisphere engagement. The strategy works seamlessly. How then should we understand the analogy with mirror neurons? Does it refer to a real functional parallel or is it mere metaphor? Do mirror neurons tie percept and action together or are they merely indifferent to the distinction between them?

8.5.2 The Spell of Mirror Neurons

Why have mirror neurons so captivated the imagination of neuroscientists? Perhaps it is because they run counter to a seemingly irresistible trend to atomization in neural brain models. The contest between the lumpers and the splitters in cognitive neuroscience is unequal. Focal brain lesion effects reveal which functions are dissociable, but functions that do not dissociate very well might be shown to do so in the future, when the patient with the strategically located lesion turns up. So case-by-case, instances of differentiation of functions increasingly preponderate over communality of functions. In contrast, demonstrating what is indissoluble, or fieldlike, or "resonant" (Shepard, 1984) in the brain's functioning generally has to await technology that is only minimally within our current reach. So "assembly" models of brain function, a collage somehow pasted together ("integrated"), predominate. Mirror neurons offer a tangible integration of perceived and performed action and better still, they do so by means of an experimentally accessible specialized single cell type. The opportunity is hard to resist. Based on this microscopic edifice, theories of the brain mechanism of "theory of mind," the nature of autism, cultural advance, etc., are copiously proposed.

8.5.3 Shared Representations

Did mirror neurons expressly evolve to unite percepts with actions or intentions for adaptive advantage? The fact that they respond during both perceiving and performing does not prove that they are instrumental in coordinating these two domains. Perhaps they evolved, not to represent both perception and production, but to represent neither in particular. They might simply exist within a sphere upon which both perception and performance draw, namely, representing the action in question, leaving it to other circuitry to represent the perception-production distinction.

The notion that a single representation serves alternative mental states, rather than that separate representations are secondarily shared or united, is strongly supported by the work of Decety and others that shows common coding of perception and action. Consider one of his designs in which three conditions are implemented: representing one's own action, another's action in imagination, and another's action directly observed. Instead of there being three distinct processes that activate distinct areas or even ''modules,'' the findings suggest that the three conditions utilize the same core neural representation of the action in question.

If self- and nonself-related representations have the same neural activity in common, rather than a specifically evolved connection, this might make the neural intertwining seem incidental rather than functionally critical. Shared representations, and also mirror neurons, would only incidentally tie percepts and actions together, being indifferent to which is being experienced at the time. If this is so, it does not invalidate the generally held belief that the communality of perception and action subserves the adaptively useful function of ''simulation.'' Simulation is variously nominated to be an instrument of perceptual recognition, mind reading, emotional affiliation, and empathy. Any or all of that could still be the case. The core neural organization in question would merely not have specifically evolved for any of the stated purposes. Instead, it would represent a preadaptation on which human natural selection capitalized when the above-listed complex cognitive processes evolved.

8.5.4 Selectivity in Imitation

What does it take to elicit an imitative response? In the case of a neuron, as far as we know, it requires a percept that is biologically and therefore motivationally relevant. The grasping hand elicits firing from the mirror neuron if it is grasping an object, but not if it is grasping thin air. In the case of a human and specifically an infant, the imitated motion derives from a person rather than a surrogate, such as a toy, robot, or other machinery. Nor are all human motions that are within sight automatically imitated overtly. The individual seems overtly to imitate only movements that are high on a hierarchy of relevance, firmly fixated in focal attention, and performed by other humans. Covert enactive encoding has broader boundary conditions, implicating specific movements as well as more abstractly conceived actions.

By what means is ''resonance'' in motor representations that correspond to perceived actions typically held covert, so as not to result in overt movement? If the perception and the production were represented in distinct neural machinery, then an inhibitory barrier between them could hold overt imitation in check. If the resonance arises from an early stage of unified representation, then an inhibitory barrier at the output side would be more likely. The fact that unwanted imitation occasionally breaks through in pathological cases, both neuropathology and psychopathology, somewhat favors downstream inhibition.

8.5.5 Interpretation of Functional Neuroimaging

Decety and Chaminade present fMRI evidence for differential local activations in relation to both perceptual-motor and socioemotional variables. Dramatic and convincing as this evidence is, it is of course subject to the well-known uncertainties that are common to the field of human functional neuroimaging and have not yet been resolved. Are the most activated areas those that are most critical to the process being studied? Are some inhibitory? As for areas that did not notably activate, we know that areas may participate in a function without producing activation maxima in PET or fMRI scans.

At present, the interpretation of functional images remains tentative, and calls for support from converging findings, particularly in lesion studies. A striking convergence between neuroimaging and lesion neuropsychology is offered by the finding of Decety et al. (2002) that a self-generated action and its observed counterpart exhibit mirror-image activations in opposite hemispheres. Although other areas were activated under both conditions, the left inferior parietal lobule was activated in the self-generated condition, and the opposite, the right inferior parietal lobule, in the other-generated condition. This dissociation is consistent with a proposed dissociation of function between the hemispheres, which attributes pursuing one's own action plan ("continue ongoing behavior") to the left hemisphere, and suspending it to monitor the (animate or inanimate) environment ("interrupt ongoing behavior") to the right hemisphere (Kinsbourne, 1989).

For lesion neuropsychology, the findings of Decety's research program are generally heuristic rather than confirmatory. His studies, and similar ones that he and Chaminade reference, suggest a host of functional localizations that have never been uncovered by traditional neuropsychological studies, although patients with focal brain lesions have been assiduously investigated for a century and a half. This exemplifies an edge for functional imaging over classical neuropsychology, but by the same token it also raises questions.

What focal lesion selectively renders a patient unable to distinguish between actions he performed spontaneously and ones by means of which he imitated another? This specific deficit has not been described in focal brain lesions. Perhaps that is because it has not been looked for. But then again, confusion between the self and another person would surely be expected to lead to some quite dramatic complaints and observations. Findings from classical lesion neuropsychology and from functional neuroimaging have not been systematically reconciled. Even consensual guidelines as to what lesion effects can be predicted from activation peaks in imaging, and vice versa, do not exist.

When functional brain imaging pinpoints an area that is particularly activated during a given activity, converging supportive evidence is required before firm conclusions can be drawn about the localization of the relevant function. When a lesion destroys this area, is performance impaired, as would be predicted based on the neuroimaging results? For converging validation, one can supplement lesion data with specifically planned and precise momentary inactivation of cortical territories by transcranial magnetic stimulation. Understanding what the activation maxima of functional images convey about how the brain works is a work in progress. Decety and colleagues constructively and imaginatively address the relationship between perception and action. Do they cast light on the brain's basis of intersubjectivity (Trevarthen & Aitken, 2001), a phenomenon that is regarded as a building block of socioemotional development?

Their stated objective was to further understanding of intersubjectivity. "Intersubjectivity is the process by which mental activity—including conscious awareness, motives and intentions, cognitions and emotions—is transferred between minds" (Trevarthen, 1999, pp. 415–417). Taking simulation theory for granted, they have conclusively identified at least part of the neural substrate that is activated both by self-action and the action of others. But more simply construed, they show how both acting and perceiving draw on some common and on some disparate neural circuitry. In my opinion, they have not yet promoted understanding of intersubjectivity, but they have in place a research design that can be adapted to that purpose. To verify that among the activated regions are some that interpret the perceived action in terms of motives, intentions, and so on, they might use a different, still more exacting experimental design in which in one condition the subject observes without making inferences ("interobjectivity" only) and in the other the subject observes the same activity, but makes intersubjective inferences. Subtracting the activation pattern of the first from that of the second might possibly reveal components of the inferential brain mechanism.

8.6 Action, Ideation, and Perception

Michael Arbib on W. Prinz

In chapter 5 Wolfgang Prinz rejects sensorimotor approaches in which actions come into being as a consequence of stimulation, in favor of ideomotor approaches, in which everything starts with intention, and actions come into being as the means for realizing those intentions. I would rather stress a cycle of perception-ideation-action that denies primacy to either approach (Neisser, 1976; Arbib, 1989). Since it is a cycle, it does not matter which term comes first. Our action may be in response to an unexpected noise as much as to an idea, while the action may lead to new sensory stimuli whose interpretation, and ensuing course of action, depends on our current internal state (of which the intention may be a small part).

Prinz claims that in the sensorimotor framework, perception and action are subserved by separate and incommensurate representational structures. He points out that on the perceptual side, representations stand for patterns of stimulation in sense organs and their derivatives, while on the action side, representations stand for motor commands and patterns of excitations in muscles. In general, perception does not register sensory stimulation, but instead interprets these as signals for "things in the world," and these "things" can include actions ("sensing" a movement and interpreting it in terms of its observed or inferred goal). This is as true for ideomotor theory as for its alternatives.

Indeed, Jordan and Rumelhart (1992) have shown how learning may create forward models that bring motor output and sensory input into congruence, and Arbib and Rizzolatti (1997) have outlined the relevance of such ideas in exploring the functionality of the mirror system. Moreover, I think Prinz himself supports the action-ideation-perception cycle when he later notes that "regular connections between motor acts and perceivable bodily and environmental effects ... become functional in two different ways. One is *to expect certain effects, given certain acts*; that is, to predict an ongoing action's perceivable consequences. The other way is *to select a certain act, given an intention to achieve certain effects*" (vol. 1, ch. 5, p. 143), and his first endnote discusses the distinction between forward models and inverse models in motor control.

Prinz presents the Lotze-James theory as requiring for an action to be voluntary that "two conditions be met: (1) There must be an idea, or representation, of what is being willed ... and (2) conflicting ideas must be absent or be removed" (p. 142). Unfortunately, this is circular, since it says no more than that an action is voluntary if it is willed! Will aside, it is also consistent even with involuntary behaviors within sensorimotor theory, for which I take prey capture by frogs and predator avoidance to be a paradigm case (Arbib, 1987). For example, a frog confronted with several flies builds a representation in its tectum that encodes for each fly the "idea" that it should be snapped at (condition 1); then a winner-take-all circuit may determine which fly is indeed snapped at (condition 2). I find it reasonable to believe that a complete theory of human action will include many cases of pairing of action and response that do not require invoking the idea of the triggering action (as when we swerve suddenly to avoid a collision, without consciously recognizing the actions of the other driver).

As Prinz notes, the defining feature of an imitative act is some form of similarity between the act perceived in the other and the act performed by oneself. Space does not permit me to comment on the elegant experiments that Prinz summarizes, save to suggest that they seem more consistent with an action-ideation-perception cycle than purely ideomotor approaches. Instead I want to stress the subtleties that arise in the imitation of new actions. Imagine (for those old enough to remember manual gearshifts) that you have learned to change among the forward gears of a car. You developed a generic skill (a parameterized set of actions) of using compliant motion to get the gearshift to a desired end position. But having mastered that, if you try to imitate someone changing into reverse gear, it is highly likely that the first few times there will be a grinding sound and the car may stall. The problem is that you "recognized" the action as if it were just the "forward-gear action" to move to a new position. It requires a new act of attention, and perhaps explicit instruction, to learn that an additional movement is involved, such as pressing down the head of the gearshift in a direction orthogonal to the overall trajectory to augment correctly the class of actions already in your repertoire.

Thus, what I want to add to the ideomotor story and the mirror neuron story is the fact that when we observe an action or try to understand or imitate an action, it is only in some cases that we can already have the complete idea of the action. In general we need not only the representation of what the action is like but also the representation of how it differs from the thing it is most like. Of course, if there is no significant difference, then we are back in ideomotor territory. But if we are in a situation where finding that difference and factoring it into our behavior is required, then in some sense the perception of the failings of an old idea is driving the creation of a new idea that will then result in a skilled action.

8.7 The Application of Ideomotor Theory to Imitation
Merlin Donald on W. Prinz

Wolfgang Prinz has presented several elegant demonstrations of strong coupling between percepts and actions that support an ideomotor approach to imitation. Although I have no problem with his experiments, I am not completely convinced of the applicability of his theoretical model to imitation. Or perhaps it would be more accurate to say that the model cannot be as simple, or as universal as he proposes, for several reasons.

First, it is worth reminding readers that the building blocks of the vertebrate motor system do not follow an ideomotor principle. Simple segmental reflexes, and even some of the more complex suprasegmental reflexes, are sensorimotor in nature, and ubiquitous, even in humans. They are present in the nervous systems of all vertebrates and form the evolutionary foundation for all voluntary action. For very good adaptive reasons, they are generally quite resistant to the kinds of perceptual influences Prinz describes. An example is the so-called "H-reflex," which balances movement patterns that engage antagonistic muscle groups. It adheres to what Prinz calls a sensorimotor principle, in that it is the output of a highly quantifiable, reliable, and linear set of responses to a specific stimulus. The same is true of most basic protective reflexes, such as sneezing and vomiting, even when they involve significant suprasegmental coordination. For many species, this is the only type of action available. Of course, higher vertebrates and human beings have additional kinds of movement control, but reflexes are nevertheless built into their motor systems. In some instances, these reflexes can be overcome by corticospinal influences, but in most cases they cannot. In every case, voluntary action systems evolved on the backbone of reflexes, adding certain modifications but not replacing them. While some classes of action are undoubtedly ideomotor in their governance, many are not, and thus the ideomotor principle is far from universal.

Second, the ideomotor principle does not apply to all classes of voluntary movement. Prinz seems to be claiming that ideomotor theory provides a universal principle that governs voluntary action, including imitation. In humans, it appears that way. But humans are special, and demonstrations in human subjects are not necessarily representative of a universal principle. An ideomotor theory of imitation will have serious difficulty explaining why imitation is so difficult for many species when they obviously have very good control of voluntary movement in some domains. Many primates have very precise control of voluntary movement in specific areas, such as visual-manual coordination, and yet lack precise imitative skills in those same areas. If their movements were governed entirely by ideomotor principles, then their imitative skills should reflect the precision of their actions and perceptions in various domains, but they do not. For example, apes can visually parse many subtle human gestures and respond to them appropriately, but they cannot reproduce those gestures, despite having sufficient motor control to do so.

The same criticism applies to the theory of "mirror" neurons. To a degree, mirror neurons behave as if they were components of ideomotor maps, and their existence seems to bolster the likelihood that ideomotor theory will prove useful in explaining some aspects of voluntary movement. However, the presence of mirror neurons does not guarantee the existence of imitative skills in a species. Monkeys have mirror neuron systems and learn to make excellent predictions about the consequences of their actions, but are nevertheless very poor at imitation. Imitation is different. Its explanation will not entail a simple extrapolation of a universal principle of movement control. In human evolution, the refinement of imitative skill has been linked to the emergence of mimetic gesture, role-playing, social transmission, and skilled rehearsal; in a word, to the intensification of social life, nonverbal communication, and group coordination.

8.8 How to Analyze Learning by Imitation
Bennett Galef on Heyes

For me, the most interesting feature of Heyes's associative-sequence learning model of imitation is not that it predicts that the ability to imitate will be experience dependent or that imitative learning is simply the production of novel sequences of familiar acts, controversial though those notions may be. Rather, my attention is captured by the assertion that the ability to imitate rests entirely on processes that are not unique to imitation itself. It is here that the contrast with theories, such as Meltzoff's active intermodal matching model (Meltzoff & Moore, 1999a), that postulate a dedicated, innate mechanism for imitation that transforms visual input into representations encoding modeled movements, is most pronounced.

The implications of Heyes's approach are quite profound. If, as Heyes proposes, imitation results from the formation of horizontal links among visual representations and vertical links between sensory and motor representations, such general processes may be better studied in nonimitative than in imitative situations, where they may be confounded. To the extent Heyes is correct, imitation becomes an epiphenomenon reflecting the activity of basic processes with functions other than support of imitative learning that can be studied without reference to imitation. For example, in Heyes's view, as I understand it, studies of the effects of practice on learning motor sequences would inform our understanding of imitation, much as studies of rhyming skills and sensitivity to phonemes inform our understanding of reading (Bradley & Bryant, 1983; Bryant et al., 1990). Imitation, like reading, can be viewed as an emergent property of mechanisms evolved for other purposes (Gould & Vrba, 1982).

The second point that I would like to make is that identifying the general substrate of imitation, whether behavioral or neuronanatomical, may be a hopeless task. As Heyes, and others, have indicated repeatedly, the most convincing evidence of imitative behavior in nonhuman animals is found in chimpanzees and birds (Heyes, 2002; vol. 1, ch. 6). Despite decades of effort by numerous investigators (e.g., Visalberghi & Fragaszy, 2002), there is only the most limited evidence of imitative learning in monkeys (Voelkl & Huber, 2000) and none in rodents (C. Mitchell et al., 1999). Birds imitate (e.g., Akins & Zentall, 1998; Moore, 1992), chimpanzees imitate, and humans imitate. Probably dolphins (Herman, 2002) and orangutans (Russon & Galdikas, 1993; van Schaik & Knott, 2001) imitate as well. This unusual phylogenetic pattern suggests that the behavioral phenomena we conventionally label as imitative are products of convergent evolution rather than of descent from a common ancestor (Moore, 1992). If so, there is no reason to expect the same behavioral or physiological substrates to underlie imitation in all imitative species.

Compare imitation by quails, chimps, and humans, as described in the literature. A quail may show an increased probability of using one of two simple responses, say pecking at and stepping on a treadle, after seeing a model use one method rather than the other to obtain food (e.g., Akins & Zentall, 1998). A chimp, after extensive training may learn, marginally, to follow a do-as-I-do command (e.g., Tomasello et al., 1993b) or, when manipulating a complex object, will sometimes copy a demonstrator's actions with greater or lesser fidelity (e.g., Whiten, vol. 1, ch. 11). A human adult can, without special training, closely imitate a near-infinite number of acts after seeing them but once.

Are such differences in performance quantitative or qualitative? We don't know. Still, we describe chimps, quails, and humans as "imitators," although quite different processes may support their imitative learning. Many models of imitation learning may be correct. Different models may simply describe substrates of imitation on different branches of the phylogenetic tree or at different points in development.

8.9 The Imitative Correspondence Problem: Solved or Sidestepped?
Andrew Whiten on Heyes

Among the interesting and important contributions to imitation research described in Cecilia Heyes's chapter, two stand out. First is the associative sequence learning (ASL) model for the fundamental causal processes underlying imitation, particularly for what Nehaniv and Dautenhahn (2002a) have called the correspondence problem. This problem—of how the sensory input generated in observing another's action becomes translated into motor output that will produce a recognizably similar action by the imitator—is arguably the central scientific puzzle in imitation research. So far the field has little to offer as a solution to how imitators manage this almost magical-appearing trick, so principled hypotheses such as that offered by Heyes deserve our critical attention.

Second, Heyes outlines a suite of experimental studies that, along with those by Zentall that she cites, appear at last to provide convincing evidence for imitation of a quite sophisticated character in birds. Given how elusive such demonstrations have proved in the course of a century's efforts (Whiten & Ham, 1992) this is an increasingly satisfying body of empirical results to have put before us.

The difficulties I perceive in the ASL model, however, seem to be sharpest when these two contributions are juxtaposed. For example, can the ASL model really explain the achievements of the budgerigars in Heyes and Saggerson's experiments when they copy use of a foot rather than the beak to solve the artificial foraging task set them?

The essence of the ASL model is that (1) ("vertical") associations are built up, by one or more special kinds of experience, between actions observed in others and corresponding actions by oneself; and (2) ("horizontal") associations among sequences of observed actions can be translated into corresponding sequences of actions performed by oneself. Accordingly, imitation can be learned "from scratch" by associative processes widely available in the animal kingdom.

Heyes outlines several possibilities for the special experiences necessary to build the vertical associations, or correspondences. Whether imitation can indeed be acquired by these associations remains to be empirically tested, but for several there appear to be inherent difficulties, especially once we move from the human case (which Heyes focuses on when outlining ASL) to those such as the budgerigar. The following paragraphs consider each hypothetical basis for association in turn (Heyes & Ray, 2000; Heyes, vol. 1, ch. 6).

1. Experiencing others (e.g., mother) imitating oneself The problem here is, what tells naïve learners when the actions they see in others are (or are not) correspondences of their own actions? Either they already need to have the correspondence problem solved to recognize these occasions or there must be an explicit external signal. Such signals are simply not known in human parent–infant interactions on the scale necessary, let alone in budgerigars. Moreover, there is evidence that recognition of being imitated emerges in childhood later than the ability to imitate per se (Suddendorf & Whiten, 2001).
2. Synchronous actions of self and other This seems to present exactly the same logical problem. What indicates when a synchrony is operative unless the correspondences are already recognizable?

The alternative—that during an imitator's formative experiences, matching is simply the most probable correlate between those of its own actions destined to exhibit correspondence, and the actions of others—seems no less implausible. For example, Custance et al. (1995) found a chimpanzee was able to match a human performing several different actions such as touching one's nose or touching the back of one's head, and Call (2001) showed similar kinds of copying in an orangutan. It seems unlikely that the apes' past experiences of performing these actions had most often occurred when others were doing the same thing, such that the correspondencies would have been learned through mere association.

3. Instructor feedback As implied in relation to point (1), this would presumably have to occur on an extensive and comprehensive scale to acquire imitative matching from scratch, which we do not see in either the case of a child or that of animals like the budgerigar.

In short, options (1)–(3) appear either to assume that the correspondence problem is already solved, so that the "matching" occasions can be recognized, or require a program of systematic signaling ("this is a match") on a scale for which there is no evidence, particularly for the nonhuman species. This leaves:

4. Mirror self-observation This route would not have been available for most of human evolution and is surely not relevant for the various species

of birds now shown to imitate (but see Suddendorf & Whiten, 2001, and Whiten, 2000, on an apparent correlation between the ability to acquire a "concept" of imitation, and mirror self-recognition).

5. Language providing a correspondence "bridge" For example, the term "frown" is used to label both one's own expression and that of others. But (even setting aside the controversial neonatal case) human imitation emerges before language, and this route will not help budgerigars.

6. Seeing and moving one's own appendages, generalized to others' appendages that look similar Of all the hypothesized experiential routes to imitation, this one does not suffer the inherent problems noted for the others, and to that extent has the most apparent plausibility. However, it seems to almost dismiss the imitative correspondence problem as a problem. It is saying that, for example, I know through experience what to do to make my hands appear to give a "thumbs-up"; and when I see someone else give a thumbs-up, it looks recognizably like my own action, so I can do it. This sounds superficially so easy that we have then to ask why imitation is so elusive in the animal kingdom, and why even in certain human cases such as autism (J. Williams et al., 2001) and apraxia (Goldenberg & Hermsdörfer, 2002) it is problematic, despite associative learning processes evidently being in place. Moreover, as Heyes recognizes, this route will not serve for actions of the self one cannot see, and the budgerigars' copying of beak use is just one of many such cases.

As noted earlier, the ASL model can be seen as having two parts: the vertical correspondence component and the horizontal sequential learning component. However, one could argue that only the first of these counts as a model of imitation as such; for once the correspondence problem is solved, the second component can be seen as the learning of perceived sequences of events *per se*, something we already know certain birds and mammals can do, quite apart from the imitative context (Shettleworth, 1998). The concerns expressed here can therefore be summarized by questioning whether ASL really offers a model of imitation, or instead too often sidesteps, or has to assume solved, the thorny correspondence problem, a criticism that can in a similar way be directed to Byrne's string-parsing model in chapter 9 (i.e., is it really a model of imitation or does it rely on the correspondence problem being already solved?). None of this is to argue that imitation cannot *develop* significantly through experience (to the contrary; Whiten, 2000), but rather that the hypothesis that imitation can be learned *from scratch* through basic associative processes faces some quite fundamental logical difficulties.

II Imitation in Animals

9 Detecting, Understanding, and Explaining Imitation by Animals

Richard W. Byrne

9.1 Introduction

Imitation is magical. That element of magic is what so fascinated comparative and developmental psychologists for much of the twentieth century, and explains the academic popularity of imitation today—in the face of a persisting lay view that imitation is a mere sham of intelligent behavior, a cheap trick. The magic is twofold. First, how can the imitator recognize that an action it performs is ''the same'' as that observed in another? The perspectives may be very different, with little visual or auditory similarity; it is magic. Second, how can a package of skills be ''transferred'' from one individual's repertoire to that of another? If this trick can be done, it offers a rich method for the transmission of useful procedures between individuals, and even across generations. But how might a complex of goals, rules, processes, and schemata be obtained from simply seeing an act done by another? It is magic.

Confronted with magic, the scientist has only two options. Either the observations must be mistaken or a nonmagical way must be found to accommodate the data—perhaps by taking a different viewpoint, perhaps by extending or changing theories. Imitation has seen both options applied in recent years. However, a major pitfall in bringing science to this particular magic has been the shifting use of definitions, as I will try to illustrate. There is a real danger, if ''imitation'' means different things in different contexts and to different researchers, that an *impossible* set of characteristics will be attached to it, making the poor scientist's task quite impossible. For this reason, no apology will be made for a sometimes fussy-seeming care in definition.

9.2 Imitation in the Comparative Psychology Tradition

Since Thorndike first drew psychologists' attention to the problems posed by imitation, and provided one of the simplest useful definitions, "learning an act by seeing it done" (Thorndike, 1898), comparative psychologists have sought an acid test of whether a species can or cannot imitate. Now they are confident they have found it: the two-action method. For comparative psychologists, this paradigm now forms the operational definition of imitation (B. Galef, personal communication). In the two-action method, separate groups of individuals are each allowed to watch a model, often a conspecific, solving the same task (B. Dawson & Foss, 1965; Heyes, 1993). Each model applies a different method, but all methods succeed. Then the individuals are tested on their own. If they each tend to match the method that was shown to them, the species is deemed to have shown imitation. By this criterion, a growing list of species are now claimed to show imitation, or "true imitation" as it is sometimes known by these researchers.

Although various workers define imitation in different ways, in reality all are using an operational definition (what the two-action method measures), so it is to the *method* that we must look. When we do, we find that what has been found varies from case to case; "true imitation" is not the same in different experiments. There are three main dimensions of variation: opacity, complexity, and learning.

9.2.1 Opacity

Consider the now well-known phenomenon of neonatal imitation, in which a baby, even when only minutes old, is shown a distinctive facial gesture such as tongue protrusion to one side, or mouth opening and shutting, and copies the act seen (Meltzoff, 1996; Meltzoff & Moore, 1977). Nothing new is being learned (the act may be "novel" in a trivial sense, since a neonate may not have yet done it, but these simple facial gestures are within the latent repertoire of newborn humans and were indeed chosen for that reason). No problem is being solved; the biological function of neonatal imitation is rather considered to be a social one. What is remarkable is the highly *opaque* nature of the translation, from visual inspection of an adult's face to the muscular movements needed to match the gesture. How does the infant do it? These data dramatically illustrate what has been called the correspondence problem, of knowing that two actions are the same when they have been experienced in very different ways. Explanations for this magic have varied from disbelief (Anisfeld, 1991 and vol. 2, ch. 4), through reconstrual of the behavior as less magical and explicable on existing theory (Heyes, 1993 and vol. 1, ch. 6; R. Mitchell, 1987), to development of a new theory, involving an innate, amodal system for one-to-one mapping among sense modalities (Meltzoff, 1990a and vol. 2, ch. 1).

But in other two-action experiments, the translation is not always so opaque. Closest to the neonatal human data are perhaps studies in which Japanese quail match a simple action, pecking or stepping up, seen as achieving a food reward (Dorrance & Zentall, 2001). A bird's eyes are close to its beak, so the visual and proprioceptive experience of pecking are very different from the sight of another bird's peck, and a quail cannot even see its own feet when it steps up, so visual-visual matching is problematic. Budgerigars can easily see their feet, but a case can still be made that matching actions of the beak must involve rather opaque translation (B. Dawson & Foss, 1965; Galef et al., 1986; Heyes, vol. 1, ch. 6). This is not the case when a primate learns to perform a task with its hands. A number of primate species have been shown to match a human's hand action (poking, twisting, etc.) applied to a box clasp that affords several different manipulations (Bugnyar & Huber, 1997; Custance et al., 1999; Stoinski et al., 2001; Voelkl & Huber, 2000; Whiten et al., 1996). However, recognizing an action as the same when done by oneself and by another is a good deal less magical when the action is done by a hand. Hands are uniquely shaped and highly familiar, so there is little ambiguity in how two hands are to be matched. The correspondence problem remains, but it is now a tractable one that an artificial intelligence engineer would feel confident in investigating by visual-visual mapping. It is not magic.

9.2.2 Complexity

When I watch a competent mechanic deal with a blockage in the carburetor of my car, I may be able to learn a new skill by observation and apply it myself when the car next fails. I will have acquired a novel and rather complex behavioral routine. This illustrates the second magical aspect of imitation—as a rich and powerful method of social learning. In the two-action method, there is usually no attempt to demonstrate learning of any *new* skills; the actions tested are familiar ones in the species' existing repertoire. The "true imitation" of most comparative psychologists, operationally defined by the two-action method, has little to do with learning a skill. Only one experiment of this type has aimed to test learning a sequence of actions (Whiten, 1998). Each of four chimpanzees, all of whom had rich experience of human living in a "language acquisition" program, learned the particular three-action sequence it was shown, although all sequences were equally effective in opening the box that contained food. However, it took several cycles of observation and testing before the learning reached statistical significance. Zoo gorillas, similarly tested, failed to show any such learning (Stoinski et al., 2001).

9.2.3 Learning

A useful distinction introduced by Janik and Slater (2000) in a review of vocal learning in animals is that between production learning, in which a new behavioral complex is acquired, and contextual learning, in which a familiar behavior is applied in novel circumstances. Contextual learning is illustrated by the predator-specific alarm calls of vervet monkeys (Struhsaker, 1967). Young monkeys start to produce these distinct calls without any particular experience. The call form seems to be tightly defined genetically, developing reliably in many environments. However, the referents to which the alarm calls are given do change during development. An infant may give an eagle alarm to a falling leaf, but later it will restrict the call to broad-winged soaring birds, and finally only to a serious predator, the martial eagle, *Stephanoaetus coronatus* (Seyfarth & Cheney, 1986).

Applying this distinction to imitation, it is clear that *production imitation* is generally neither sought nor found in the two-action method. However, *contextual imitation* occurs when the appropriate site or occasion on which to apply a familiar action is learned by observation. Contextual imitation may be a useful cognitive capacity for transmitting habits, through populations or over generations, even if any learning of new behavior patterns relies on simpler means than production imitation, such as trial-and-error learning.

However, in many cases when two-action experiments have been done, no effort has been made to distinguish an alternative possibility. This is a simple idea, although it has been given several names (R. Byrne, 1994; R. Byrne & Russon, 1998; Thorpe, 1956, 1963): response facilitation, priming, perceptual-motor resonance, and perhaps also contagion (although it would seem that Thorpe intended this to apply only to innate perceptual-motor linkages, rather than more generally).

Imagine a species with a highly restricted repertoire of, say, seventeen discrete behaviors and no capacity to build new ones. Confronted with a foraging problem, an individual applies actions from this repertoire, and those that are followed by advantageous consequences are more likely to be applied again in similar circumstances (trial-and-error learning). The actions are generated in an order that is determined by the activity level of whatever brain unit, or record, controls the corresponding action. But suppose now that when one of the seventeen actions is seen to be done by another individual, the activity level of the corresponding brain unit is temporarily increased. The action is ''primed''; that particular response has been ''facilitated.'' (This may or may not involve a serious correspondence problem, as discussed earlier.) Tested with the two-action method, because such observation changes the relative probabilities of trying one action rather than another, the species would automatically show the behavior held to demonstrate ''true imitation.'' Yet, to the extent that anything is learned, it would be by trial-and-error learning of when to reapply a successful action, rather than by observational learning.

What is needed to demonstrate observational learning in the two-action paradigm is a *delay before testing*, preferably filled with other activities. If the delay were long enough, one might presume that the activity levels of brain units would return to their resting levels, although nothing is known of the time course of this process, so it is not clear how long would be long enough. Better, if the critical actions were used for purposes irrelevant to the experimental task in the time before learning was tested, one could be confident that genuine contextual learning by imitation had occurred. Zentall's quails showed learning when first tested 30 minutes after they observed a model, and Heyes's budgerigars were tested up to 22 hours later, periods that were inevitably filled with other activities (although whether these activities employed the motor actions later tested is not certain), so contextual imitation is highly likely. In most experiments of the two-action paradigm, contextual imitation has yet to be demonstrated.

9.3 Learning Skills by Imitation in the Everyday Lives of Animals

This chapter is about learning skills, so we now set aside the fascinating issues attendant on the ''hard problem'' of perceptual-motor correspondence. The two-action method has successfully shown that young (and even newborn) human babies, Japanese quails, and budgerigars are all able to make such correspondences—or at least, the majority of researchers believe that is what the evidence means. Problems for the future include the generality of this capacity across species and whether it has any role in learning skills, or, as suggested by Byrne and Russon (1998), instead functions because mimicry is important in social recognition and social bonding.

We now focus on the second magical aspect of imitation, its potential for allowing the observational learning of complex skills. Here, the comparative psychology tradition, searching for "true imitation" as operationally defined by the two-action method, has little to say because in all the two-action experiments carried out with birds and newborn humans, the behaviors examined have been simple, familiar ones. This is no criticism; the issue has been perceptual opacity, not acquisition of skills. Unfortunately, the picture is no different in most two-action experiments with nonhuman primates, where the fidelity with which skills can be passed on has been the ostensible focus. Here, the actions have been manual—twisting a handle, pushing out a bolt, pulling a lever—so the correspondence between the act as done by the self and the other has been rather transparent. Moreover, no effort has been made to ensure that these actions were not part of the individual's preexisting repertoire before the experiment; usually, since simple actions were chosen for testing, they most likely were.

Acquisition of novelty has been examined in only two experimental paradigms, both with great apes. First, as noted earlier, the learning of novel, three-action sequences, each made up of simple manual actions, was examined in four chimpanzees and six gorillas (Stoinski et al., 2001; Whiten, 1998). The chimpanzees were kept in enriched conditions and might be argued to have been "enculturated" by humans, and they gradually learned the sequence; the gorillas were part of a zoo collection, and they did not. Second, imitation of novel actions has been reported in experiments in which great apes are first trained to "do as I do" for a reward, then tested with other manual and bodily gestures chosen to be unfamiliar to the subjects (Custance et al., 1995). Observers blind to the purpose of the experiment were shown video clips of an ape's behavior just after a gesture had been demonstrated to it, and could reliably detect which particular action, out of a small set of possible gestures, had been shown to the subject. However, the match between the actions of the ape and those of the human demonstrator was reported to be quite poor. This opens the door to an explanation other than imitation. Great apes, unlike most animals, have very large repertoires of manual action (e.g., the only published chimpanzee ethogram includes 515 separate behaviors, yet this categorizes the actions only at a very broad level rather than specifying the exact form of action, as is typical of ethograms for simpler species; Nishida et al., 1999). It is difficult to be sure, then, that the gestural copying reported in these experiments reflects observational learning of new behavior patterns, as the researchers believe, or whether instead rare actions in the preexistent repertoire are primed (made more salient) by seeing them demonstrated, so the individual is then likely to perform an action it otherwise seldom would.

Experimental evidence for observational learning of novel, complex actions by animals is therefore weak at present. Instead, we must turn to observational data for significant evidence of nonvocal production imitation in animals. Inevitably, observational evidence is more easily challenged than experimental evidence, and the skeptical approach of dismissing the observational data is still quite feasible. If animals do not acquire new, complex skills by observational learning, there is no need for a new theory. However, as my blocked carburetor example reminds us, humans *can* augment their repertoire of skills by observation, even if this has become less common in a modern, western environment where verbal instruction is preferred. As with stonemasonry in medieval Europe, in traditional societies today crafts are typically acquired by a combination of uninstructed observation and individual trial and error (Parker, 1996). It is hard to deny that humans have the capacity to acquire novel organizations of behavior by observational learning. Given this fact, it may be productive to examine nonhuman primates' behavior for signs that they too have some such capacity. Moreover, a cognitive theory is needed to explain the capacity, whichever species it is finally agreed can learn skills by imitation.

Observational evidence is most sturdy when animals acquire complex behaviors that are not part of their natural repertoire (Pepperberg, vol. 1, ch. 10, makes the same point for vocal learning). Great apes brought up or kept as pets by human caregivers seemingly readily acquire "human" behaviors. In careful analyses of rehabilitant orangutans, this has been shown to imply acquisition by imitation (Russon, 1996, 1999; Russon & Galdikas, 1993, 1995). With natural ape behaviors, alternative explanations are, however, harder to exclude. In particular, a complex performance might have been acquired by gradual, trial-and-error learning because it was the most *efficient* way to do the job, given the physical requirements of the task. In this view, while learning may be helped by many social influences—*social facilitation*, which increases the motivational disposition for performing that sort of task; *stimulus enhancement*, which focuses attention on particular places and objects; *response facilitation*, which changes the probability with which actions are tried out; and various sorts of *emulation* (R. Byrne, 1998a) that allow the individual to learn aspects of the task structure—production imitation is not one of them.

Attempts to avoid this criticism have pointed to various characteristics as unlikely to be products of socially guided, trial-and-error learning alone.

They include variation in behavioral style from site to site, improbable complexity, and insensitivity to affordances.

9.3.1 Site-to-Site Variation in Behavioral Style

Social traditions may exist as a result of mechanisms other than imitation and are known in many species (Roper, 1983). But if precisely the *same* task is done differently in different populations, it would seem that the persistence of the less efficient variants must reflect imitation (or, more improbably, teaching), since trial and error should operate as a ''hill climbing'' algorithm and force convergence on the most efficient method.

This has been argued to apply to wild chimpanzees, with respect to their style of eating insects with tools (Whiten et al., 2001). *Dorylus* ants are captured by dipping sticks into dense masses of insects. All the chimpanzee individuals in some populations use long sticks in a two-handed process (McGrew, 1974), but in others they rely on the apparently inefficient one-handed use of short sticks (Boesch & Boesch, 1990; Sugiyama et al., 1988). *Macrotermes* termites are extracted with fishing probes. In some populations, it is routine to resharpen the probes or use both ends, both of which are apparently efficient methods; but in other populations, blunted tools are discarded and wholly new ones made (McGrew et al., 1979).

Unfortunately, if the environment differs in some critical way among chimpanzee populations, a simpler explanation may be that the behavioral styles reflect adaptive solutions to slightly different environmental problems (Tomasello, 1990). It is nearly impossible to establish the identity of environments over the functionally relevant aspects of a complex task, most of which are not known.

Moreover, it might be expected that over an extended time, occasional innovations would produce just the same hill-climbing process as trial-and-error learning, even with a social habit that was acquired ontogenetically by imitation. This means that the idea of population differences in important skills must be regarded with considerable suspicion. Are we supposed to accept that these habits, believed to have important survival value to chimpanzees, are so new that there has been too little time for an optimal tradition to have been reached?

9.3.2 Improbable Complexity

Most everyday actions of animals are organizationally simple and readily understood as a result of innate dispositions and normal learning processes. If, in contrast, highly complex skills could be shown to be learned with great reliability and considerable standardization of form, then imitation (or teaching) would be suspected. This has been noted for plant feeding techniques in gorillas and chimpanzees (R. Byrne & Byrne, 1993; Corp & Byrne, 2002), for insect catching and nut-cracking with tools by chimpanzees (Boesch & Boesch, 1983; Goodall, 1986), and for an Israeli population of black rats that has learned a special technique for eating the cones of non-native pine trees (Terkel, 1994). It is not known in detail how these skills develop, but experimental work with the rats has shown that trial and error with social facilitation and stimulus enhancement is quite insufficient. Only by presenting a graded series of part-processed cones, working back from the solution, was it possible to teach naïve rats to strip cones efficiently. Given the partly nocturnal, arboreal behavior of black rats, it has not been possible to determine whether infant rats experience such graded learning sequences, either accidentally or as a consequence of deliberate maternal behavior, or whether they are able to observe adults processing the cones.

Gorilla infants certainly have ample opportunity to see what their mothers are doing to process difficult plants, at close range and over many months. Several different techniques are acquired that are appropriate for dealing with different plant challenges: spines, tiny hooks, stings, hard casing. Each technique is multistage, often involving bimanual coordination, with the two hands used in different roles to achieve a single result, and different digits in a single hand are used independently to allow partly processed material to be held while further plants are processed with both hands (R. Byrne et al., 2001a). Very strong individual hand preferences are found, which is often considered an adaptive response to complexity, and several tasks share population-level right-handedness (R. Byrne & Byrne, 1991).

"Complexity" is notoriously hard to measure in any valid way, but consistent ordering of sequences of five or more separate actions, chosen from a repertoire of more than seventy functionally different manual processes, suggests a level of complexity at least equivalent to that of many everyday human manual tasks (R. Byrne et al., 2001b). Idiosyncratic variation, both from trial to trial and from animal to animal, and even from mother to offspring, is found at lower hierarchical levels; they include grip types, which digits are involved, the extent of movement, and hand preference. However, the organization of the processing sequence, including bimanual coordination, hierarchical embedding of subprocesses as subroutines, and the main sequence, is remarkably standardized (R. Byrne & Byrne, 1993).

Reliable acquisition of the elaborate and highly structured organization of several different processes, by the age of 3 years in gorillas, has been argued to strongly suggest program-level imitation: copying the structural organization of a complex process by observation of another's behavior, regardless of how the exact details of the actions are performed (R. Byrne, 1993; R. Byrne & Russon, 1998). This argument depends on the fact that there are many alternative methods, some much more obvious to human observers. (I recommend that skeptics try this experiment: Give naïve human subjects the problem of eating a gorilla food, explaining the difficulties to them. Stinging nettles, for instance, have the most painful stings on the main stem and the petiole, the least on the leaf underside; the leaf blades are the most nutritious part. I predict that the unhappy subjects will not readily discover the method used by mountain gorillas, which minimizes the pain of consumption while maximizing intake.) The alternative methods are almost certainly less efficient than the precise technique used by gorillas, so in principle trial-and-error learning might eventually converge upon that technique. The case for imitative learning depends on the improbability of this happening, reliably for every mountain gorilla, in the 3-year period of skill development, and especially with plants (such as nettles and thistles) that discourage playful exploration because of the pain they induce.

9.3.3 Insensitivity to Affordances

The reliable acquisition of complex skills by individuals would be much less improbable if the physical constraints of the task and the animal's anatomy were severe, tightly channeling the process of learning. In the case of manual skills in great apes, this seems at first sight implausible; ape hands are highly flexible grasping effectors, and plants can be processed in many ways. But a stronger challenge to imitative learning comes from the idea that animals—or at least, nonhuman primates—may be exquisitely sensitive to quite subtle properties of physical objects, and that knowledge of these properties can guide relatively rapid learning. This is the idea of learning affordances (Tomasello, 1996, 1998). While there is at present little positive evidence that this concept offers a realistic account, the possibility is hard to refute without experimental manipulation.

One approximation to an experimental test is provided by the unfortunate circumstance that some populations of wild great apes have experienced high levels of encounters with human-set snares, which severely maim the hands of curious infants and young juveniles that explore them (Stokes et al., 1999). Nevertheless, some of these young victims survive to adulthood, learning to deal effectively with hard-to-process plants that normally require elaborate manual skills. Since maimed hands are radically different than those of able-bodied apes, very different affordances are presented to these animals. Thus, if the techniques for processing food are a consequence of the structure of hands and affordances of plants, the disabled apes should acquire idiosyncratic techniques that are adjusted to efficient utilization of the remaining capacities of their hands. However, they do not (R. Byrne & Stokes, 2002; Stokes & Byrne, 2001). Instead, they use the *same* techniques as able-bodied animals, working around each of the points at which their hands do not allow actions to be done in the normal way. Their modifications affect just those aspects of the skill that vary among the able-bodied: methods of gripping, the digits or hands used for a purpose, and so on. Since the apes that sustain these hand injuries are still at an age when many skills are developing, it has been argued that this insensitivity to affordances must reflect program-level imitation from the only model available, the able-bodied mother.

None of these arguments is completely watertight, and it may still be asserted that nonhuman apes simply cannot learn complex novel skills by imitation. The human capacity to do so may, after all, be derived in some unspecified way from linguistic competence. But what if we take the challenge of accepting that nonlinguistic apes can use program-level imitation in developing skills? Are we facing magic? Or can a plausible mechanistic theory be sketched that is capable of explaining this facility?

9.4 A Mechanistic Theory of Learning Skills by Observation

Acquiring a complex, novel skill can be viewed as a process of building a new organization out of old components, which may themselves be quite elaborate processes or very elementary actions (R. Byrne & Russon, 1998; A. Newell & Simon, 1972). Depending on the existing repertoire of actions, putting together the same skill may therefore be a simple or a highly complicated matter. Moreover, the ability to do so will usually be strongly influenced by knowledge of the mechanical properties of the objects involved—their affordances—and thus dependent on previous, perhaps "playful" exploration. And several social influences, including stimulus enhancement (K. Spence, 1937), response facilitation (R. Byrne, 1994), and indirect learning of affordances by emulation (Tomasello, 1990; Whiten & Ham, 1992), will inevitably affect the power of trial and error to build new organizations of skill. All these factors will potentially affect even "imitative" learning of a complex skill.

For behavioral organization to be copied from another's behavior, it must first be detected. The process I propose to account for this is one of *behavior* *parsing*. Parsing cannot be directly applied to skilled action, since such action does not consist of visible units; it is fluid movement, without natural joins between separate elements. The first thing we need is a system that can recognize elements in this fluid movement and so reduce it to a string of components. For these components to be of any use as building blocks for assembling a new skill, each must correspond to an action already in the repertoire of the observer. Detection of an element is in itself not a trivial process, but a neural system exists that already meets the requirements for this process: the mirror neurons of area F5 in the premotor area of macaque monkeys (Gallese et al., 1996; Gallese & Goldman, 1998; Rizzolatti et al., 2002; Rizzolatti et al., 1996b). Contrary to conventional wisdom, monkeys are not great imitators (Visalberghi & Fragaszy, 1990); mirror neurons are unlikely to have evolved originally as part of an imitative learning system, but rather as part of social comprehension, allowing subtle dispositions and objectives of social companions to be discerned. However, mirror neurons can in principle convert a stream of fluid action into a string of elements, each of which is already part of the repertoire of the observer. (Note that the observer's prior knowledge will determine the length of this string. If the observer can already perform major parts of the process, matching will be high level and the string short.) If this string can be learned or remembered in some way, then it can be imitated (see Heyes & Ray, 2000; Heyes, vol. 1, ch. 6).

The resulting *action-level* imitation would treat the whole string as a unit, a linear, chainlike structure. Action-level imitation inevitably lacks the power, efficiency, and flexibility that we associate with human planning, in which hierarchical structures can be manipulated (see Dawkins, 1976; Lashley, 1951). Suppose that, rather than direct copying of linear strings of actions, the strings themselves are input to a parsing process. Is there sufficient information in the surface form of skilled behavior to reveal the underlying organization? If only one "look" were allowed, a single pass through an elaborate process, the answer would certainly be "no." Organization is not there for the seeing; it can only be extracted from the statistical properties of many observations. How, then, might the underlying organization, the "deep structure" of action, be detected merely from observing the surface form? Are any clues available?

According to the behavior parsing model (BP), there are numerous clues (R. Byrne, 1999, 2002a). Crucially, parsing must focus on essential elements rather than on coincidental or idiosyncratic variants that occur from time to time. Every execution of a motor action is slightly different, but some aspects must remain constant across successful attempts at the same goal. ("Goal" is a mentalistic description, but in fact for the feeding activities of great apes mentioned earlier, and for many complex manual skills acquired by young children, consummatory activity makes the end state of an observed action readily discernible.) If numerous sequences with the same end state can be compared, the elements they have in common define the *necessary steps* of the process, and reveal their characteristic *ordering*, if there is one. (Whether these elements are themselves actions, or states of the environment produced by actions, is an empirical question that does not affect the power of the model; see Byrne, 1999. Common sense suggests that it is often easier to see transformations of objects than the manual movements that effected them, suggesting that actions upon objects should be particularly easy to learn by imitation.) As well as the sequence of important steps in the course of a successful execution, the same hypothetical process of string comparison can reveal bimanual coordination, where this is so crucial that it recurs on nearly every sequence, because it creates correlated activity of the two hands. The BP model predicts that great apes, including humans, should be acute at mentally "summating" numerous sequences of action so that correlations and exceptions are rendered obvious. Such an ability would suggest a dedicated neural system that operates unconsciously and automatically.

Most skilled action, of humans or apes, seems to have a modular structure in which some strings of actions are tightly bound together, whereas at other points the linkage is weak. This organization is highly functional since it allows the tightly bound modules to function as units—to be recruited as a whole into other tasks or substituted by other modules that achieve the same local ends. But can *modularity* be "seen" by a mechanistic process? The BP model includes several ways in which this could be done. First, the *interruption* between modules should be relatively harmless, allowing the smooth resumption of processing afterward; in contrast, interruption within a module would force "beginning again" at the start of the module. Thus, by paying attention to the points of smooth resumption, module breaks are revealed. More generally, the distribution of pauses in execution should show clustering at module boundaries rather than within modules. If young apes are sensitive to these most classic data of cognitive psychology, then they will be able to separate action into modules.

As the whole process becomes less opaque and mysterious, as a result of both parsing and independent trial-and-error exploration, other sources of information about modular organization become available. These include *substitutions* of one module for another (for instance, if an animal occasionally processes an arboreal plant, making bimanual processing infeasible); *omissions* of a module when it is unnecessary (for instance, if a handful of leaf material is unusually free of dead material, no cleaning is needed before consumption); and *local repetitions* of a module that vary in number, revealing the unity of the elements in the repeated substring (for instance, if stripping leaves generates insufficient material for a full handful, stripping may be repeated once or several times, provided the animal has the individual digit control to allow the already-acquired material to be retained in one hand).

Moreover, the same variation in repeated substrings is a potent clue to hierarchical organization. When one or more modules is used as a subroutine within the main process, repetition inevitably occurs and thus indicates that there must be some criterion for deciding whether to iterate the module. Similarly, *substitution* of one module for another under different circumstances, and recognition of *already familiar* substrings within an unfamiliar sequence, are indications of the flexible and efficient processing that use of a hierarchical organization can give (Dawkins, 1976).

By the standards of artificial intelligence, the BP model is underspecified; it needs to be determined exactly how strings of elements are dissected out for parsing in the first place, and whether the whole process could operate efficiently with no information on the affordances of objects. It seems highly likely that real young apes, human or otherwise, would bring to the task considerable task-specific knowledge from their prior exploration of the world—the effects of simple manual actions and the opportunities for changing objects—making the learning process more efficient. Nevertheless, the BP model provides clear methods by which the structural organization of a complex, novel process can be learned partly by program-level imitation. When this happens, the finer details of action—hand movements, grips, laterality, and so forth—may be acquired in other ways, such as individual exploration, or also by program-level imitation at lower levels in the hierarchy of behavior.

9.5 But Is It Imitation?

In recent years, several new terms have been added to the lexicon of those grappling with the conceptual and practical issues raised by imitation. Program-level imitation clearly goes beyond processes by which trial-and-error learning can be aided by social circumstances (stimulus enhancement, response facilitation, etc.), and which can be modeled simply as priming of brain records. Equally, however, the BP model offers no explanation of the opaque correspondence problem. To those who restrict the term "imitation" to processes that can overcome the opaque correspondence problem, program-level imitation is not really imitation. Indeed, although novel *organizations* of behavior can be imitated by BP mechanisms, it may be that the movement patterns used in the copying are rather different than those of the individual copied, since these fine details may be most efficiently acquired by individual exploration. Is this really "imitation" at all? If not, what else might it be?

To capture the difference between imitation-for-a-purpose, in goal-directed copying, and mere parody that cannot be put to use, the term *mimicry* has been introduced—meaning "imitation for its own sake" (Tomasello et al., 1993a). The BP model does not require the intentions of the imitated individual to be first discerned by the copier, so at first sight it might seem appropriate to label the outcome mimicry. However, intentions attributed to the individual copied are *second*-order intentions (Dennett, 1983), whereas Tomasello's discussion concerns *first*-order intentions, such as desires and beliefs of the imitator. Since we cannot tell that an infant human, chimpanzee, or gorilla does not have first-order intentions when it engages in such activity, insisting on the term "mimicry" is unhelpful. (Attempts to dismiss as mimicry the copying of rather complex everyday human actions, shown by many human-raised great apes, because the copying appears pointless to us, have likewise been met with the comment that human researchers cannot know what rewards or amuses a human-reared ape, and thus cannot legitimately assume purposelessness; Russon, 1996.) Moreover, it is highly functional in biological terms for an infant to copy any action of its mother or other close associate that they perform repeatedly, especially if signs of satisfaction or any consummatory activity are associated with the action.

In any process of learning a complex skill, prior knowledge of the physical properties of the environment, and to what extent they can be modified, is likely to be crucial. Tomasello (e.g. 1994) has suggested that great apes may sometimes be able to learn these things by observing others ("emulation"), but cannot learn their actions by observation ("imitation"). In early versions of Tomasello's theory (see R. Byrne, 1998a for details), what was learned by emulation was seen simply as the final result of an action (called *goal emulation* by Whiten and Ham, 1992), and this certainly cannot apply to program-level imitation, where the goal of eating edible items needs no learning. Understood as *affordance learning by observation*, emulation potentially has much greater power. Since the BP model is indifferent as to whether the input consists of strings of actions, or strings of an object's states (each produced by an action, which itself may be hard to see clearly), it might be claimed to be a sort of repeated emulation process. However, the cardinal point of emulation seems to be that cause-and-effect learning enables enhanced problem solving without copying behavior. In the BP model, there is no reliance whatsoever on understanding cause and effect, and indeed program-level imitation may copy actions whose means of effect remain obscure. In contrast, an important aspect of behavior *is* copied—its organization—without necessarily including slavish replication of details. In some ways, then, program-level imitation is the reverse of emulation. Also note that the plausibility of emulation as a null hypothesis for young great apes has been questioned (R. Byrne, 2002b), since young children prove able to imitate long before they can emulate (Want & Harris, 2002).

Rather than using any of these categories of quasi-imitative process, it may be more helpful to view program-level imitation as a spinoff from a much more fundamental process—a part of high-level *perception*. Just as possession of a mirror neuron system enables simple elements of goal-directed action to be "seen" directly, so complex actions, treated as strings of such elements, can be parsed to extract organization from the inevitable statistical regularities present in any behavior produced by a planning process. This chapter has focused on one consequence of that process, the ability to use the observed organization to build complex skills new to the observer more efficiently than pure trial and error would ever allow. However, the BP process itself may have wider uses than program-level imitation. "Seeing" through the surface form of behavior, to the deep structure of the observed individual's plans, is an important part of interpreting that individual's action. Program-level imitation may therefore be seen as a handy index of an individual's ability to represent the complex actions of others.

A mechanical process that can extract from the statistics of observable behavior (and probably a good background knowledge of the local environment of action) the high-level organization of effective, organized action is but a short step from being able to "see" intentions and cause and effect. Both in everyday life and in the underlying physics of forces, the abstract idea of *causation* is closely related to the visible facts of contact and correlation. Likewise, the efficient result of complex, directed action is very close to its *intention*. Behavior parsing may be a necessary precursor to "seeing" the plans and purposes of others and how their behavior works to achieve these purposes.

9.6 A Possible Evolutionary Scenario

Viewing imitation in this way, as an outcome of behavior parsing, leads to a possible explanation of the evolutionary origin of more humanlike comprehension of objects and agents in great apes (R. Byrne, 1997). Unlike monkeys, great ape individuals have shown in a number of ways that they are able to represent and take advantage of the knowledge, ignorance, or intentions of others. Yet great apes do not live in more complex societies than monkeys do (except for the fact that their greater understanding must inevitably make their societies richer in perceived complexity), so that theories that link all intellectual advance in the primate lineage to social pressures have no explanation.

Great apes do, however, confront a much greater feeding challenge than monkeys. Their large size, combined with locomotor adaptations for arboreal feeding while hanging below branches, means that their long-distance travel is significantly less efficient than that of monkeys. Moreover, compared with Old World monkeys, apes' guts are less well adapted to cope with coarse leaves and unripe fruit, despite their absolutely greater size. Yet great apes occur sympatrically with Old World monkeys in almost all forests where they live, and they largely eat the same range of foods: fruit, leaves, and a wide range of minor items such as fungus, insects, and bark. If monkeys are better adapted for exploiting this diet in every way, then it seems mysterious that any ape species survive at all.

Suppose, however, that the response to the severe ecological challenge of feeding competition from monkeys was an adaptation in apes that allowed *effective acquisition* and *social transmission* of complex feeding skills—skills that permitted more efficient feeding than the straightforward picking, peeling, and stripping of monkeys, and hence allowed access to otherwise unavailable food sources. Suppose further that this adaptation included behavior parsing as a basis for quick and reliable learning of any skills that painstaking trial and error had caused to enter a local population, allowing the development of traditions that transcended one generation.

In this conjecture, behavior parsing is not only a necessary part of the process of discerning others' purposes and how their behavior can be copied to achieve these purposes ourselves, but was an evolutionary stepping stone on the way to the modern human ability to attribute cause and intention. If so, much that is "special" about human thinking has its evolutionary origins in dealing efficiently with tricky plant problems.[1]

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[1] See the comments on this chapter by Zentall, vol. 1, ch. 12.1, p. 285, and by Elsner ch. 12.2, p. 287. ED.

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10 Insights into Vocal Imitation in African Grey Parrots (*Psittacus erithacus*)

Irene M. Pepperberg

10.1 Introduction

The study of animal imitation, like that of animal cognition, animal–human communication, or numerical competence, generates considerable debate and as many definitions of the behavior as there are researchers in the discipline, and generally focuses on primates. Outside of the ornithological literature on song acquisition, avian vocal imitation is often ignored or considered a special, irrelevant case of imitative behavior (e.g., Shettleworth, 1998) because the imitated actions are perceived and produced within the auditory, not the visual, channel and their rationale may be difficult to determine. Avian allospecific vocal learning, however, is one of the few cases in which the copied behavior is, in accord with Thorpe's (1963) definition, completely novel—replication of an otherwise improbable act—and thus less likely to be confounded with social facilitation, stimulus enhancement, or other forms of nonimitative socially mediated learning (Fritz & Kotrschal, 1999). Here I examine replication of human speech by African Grey parrots, explain why I believe it is both referential and true imitation, show how various forms of input (e.g., my model/rival training) affect such learning, use my data to support the suggestion that imitation most likely occurs at multiple levels of complexity (see R. Byrne & Russon, 1998), and examine neurological issues involving imitation in a nonprimate, nonmammalian species.

10.2 Vocal Learning as an Imitative Act

Vocal imitation, even in a sense less strict than Thorpe's, is uncommon. Even vocal *learning* occurs in few nonhuman species (Lachlan & Slater, 1999) and its occurrence is rarely truly imitative. The acquisition of conspecific songs or calls by oscine birds, for example, does not necessarily qualify as imitation. Its development in the absence of a model is abnormal (e.g., Marler, 1970), but oscines are generally predisposed toward conspecific learning (Petrinovich, 1985); thus the modeled act is not improbable (Thorpe, 1963). Also, the resultant behavior is not usually identical to the model's behavior (Kroodsma, 1996). True vocal imitation can be claimed only when subjects engage in goal-directed learning and use of allospecific utterances, a task that involves building some representation of an alien communication code (e.g., bottlenosed dolphins, *Tursiops truncatus*, reproducing computer-generated whistles for specific rewards, McCowan & Reiss, 1997; white-crowned sparrows, *Zonotrichia leucophyrs*, learning song sparrow, *Melospiza melodia*, song, Baptista & Catchpole, 1989; African Grey parrots, *Psittacus erithacus*, using English labels as intentional requests, Pepperberg, 1988a).

Even when avian vocal learning is considered imitation, few researchers examine levels of behavioral complexity or data suggesting that successful imitation depends on the form of input (cf. Fragaszy & Visalberghi, 2001). Considerable data exist on input and levels of avian allospecific acquisition (see Baptista & Gaunt, 1994; Pepperberg, 1985, 1991b) and on oscine neural learning pathways (e.g., deVoogd et al., 1993; Jarvis & Mello, 2000), but not with respect to true imitation. If, as I maintain, vocal imitation involves acquiring *exceptional* vocalizations (Pepperberg, 1985, 1986a,b), that is, communication characterized by vocal learning unlikely to occur during normal development and that is used functionally after learning, such as acquisition of referential allospecific forms, then issues of complexity, input and output, and neural bases (e.g., mirror neurons) are critical for understanding avian imitation. With a somewhat unusual species—one known for its mimicry—the African Grey parrot (*Psittacus erithacus*), I study how input affects learning, how these parrots precisely reproduce human speech, and their referential use of such sounds. Because their vocalizations are often requests, such imitation, although involving auditory and vocal channels, is as goal directed as that in studies involving physical actions (see Akins & Zentall, 1996; Fritz et al., 1999). Not being a neurobiologist, I merely speculate on the bases for such behavior.

10.3 Reproduction of Human Speech by African Grey Parrots

To the human ear, an African Grey parrot's speech closely matches that of its trainers. Some researchers (e.g., Greenewalt, 1968; Lieberman, 1991), however, argue that birds cannot inherently produce human speech sounds and that birds' "speech" is an artifact of human perception (see following discussion). But might physical characteristics of avian speech match those of humans? If so, and if these characteristics are those that scientists use to describe human speech, such data would support the contention that vocal learning in Grey parrots is an imitative act. Consequently, a student and I compared acoustic and articulatory data for human and psittacine vowels and consonants.

10.3.1 Phonological Analyses

Using standard phonetic and statistical techniques, we analyzed spectrograms and videotapes of speech samples from a human-raised, male Grey parrot, Alex, who had spent the last 14 of his 15 years interacting with humans, including training on cognitive concepts and English labels. We compared Alex's and my vocalizations because I was Alex's principal trainer, and observers claim his utterances closely resemble mine. The analyses were complicated and here I summarize only our most relevant findings (for details, see Patterson & Pepperberg, 1994, 1998; Pepperberg, 2002).

F_0 Analyses We measured fundamental frequencies, F_0 (source vibration at the avian syrinx; syringeal constriction at the tracheal base functionally resembles that of human vocal folds in phonation; Gaunt & Gaunt, 1985; Scanlan, 1988). Some researchers propose that an oscine bird (e.g., a mynah, *Gracula reliogsa*) uses each half of the syrinx independently to produce two different sinusoidal pure tones whose interaction produces "formant frequencies of the original human speech sound that the bird is mimicking. . . . We perceive these nonspeech signals as speech because they have energy at the formant frequencies" (Lieberman, 1984, p. 156).[1] F_0 analyses, however, show that Alex, like humans and unlike most songbirds (Greenewalt, 1968; D. Miller, 1977), uses one set of articulators to produce speech (Patterson & Pepperberg, 1994). He has one F_0 and his absolute values are in the general range of those of an adult human (124–276 Hz; Peterson & Barney, 1952).

F_1 and F_2 Analyses Accurate perception of human speech involves processing formants (F_x): resonant frequencies of the human mouth opening

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[1] Mynahs do not independently use two halves of their syrinx to produce formants from F_0s as Lieberman (1984) suggests, but their mechanism differs from that of Grey parrots (Klatt & Stefanski, 1974). Budgerigars produce human vowels by amplitude modulation (as Lieberman suggests), but because their syrinx cannot produce two independent sounds, they produce the modulation via a different, as yet undetected, mechanism (Banta Lavenex, 1999).

(F_1) and oral cavity (F_2) that could also represent specific parrot vocal tract areas; sometimes F_3 is necessary (Borden & Harris, 1984; Lieberman, 1984). A formant is not a harmonic of F_0; harmonics, if present, appear as odd multiples of F_0. F_1 and F_2 variations may differentiate vowels for classes of human speakers. We compared Alex's and my F_xs and tested whether Alex's formants predict his vowels. Differences and similarities exist between our data. For both F_1 and F_2, his range is less than mine and lacks my low-frequency values. For most vowels, his F_1, which in humans roughly corresponds to tongue height, differs considerably from mine and, unlike mine, varies little across vowels; his tongue height varies little. Our F_2s, which in humans correspond to front-to-back tongue position, are similar. Like mine, his vowels are somewhat distinguishable by F_2; his front-to-back position varies considerably. Thus, as for humans, his formants correlate with specific resonances of the vocal tract area (Remez et al., 1987; Warren et al., 1996). His F_3s, which in humans indicate whether speech-producing constrictions occur toward the front or back of the vocal tract, were rarely observed or were nearly indistinguishable from F_2. All his vowels cluster in the high to low midrange but his /i,I,E,ae/ and /U,ə,a/ respectively cluster as "front" and "back" vowels. /u/ is a back vowel for most standard American English speakers; for Alex and me it is a diphthong. It has two parts, /u_1/ and /u_2/. Mine are front vowels; Alex's are front and back vowels, respectively.

Comparisons of Psittacine and Human Stop Consonants Traditional acoustic analyses for stops (consonants with blocked air flow) generally applied to Alex. We examined voice-onset timing (time, in humans, between the lips opening to release air and the start of vibration by the sound source), number of bursts (bursts result from the release of air pressure built up by lip closure), and stop loci (high-energy peaks associated with voiceless aspirated portions of stops). We measured formant frequency in the first 10 ms of voicing following a stop, average formant frequency during the steady-state portion of a vowel following a stop, and time from the beginning of voicing to when formants assume a steady-state pattern.

Similarities and differences exist for our stops (Patterson & Pepperberg, 1998). The similarities involve statistically distinct acoustic characteristics and separation of stops into voicing and place of constriction subsets. The differences involve specific subset divisions and likely mechanisms for /b,p/ production. Compared with my subsets, his /b/ is an outlier; his /p/ clusters nearer /d,g/ than /t,k/. Alex must produce bilabial /b,p/ without lips; he seems to compensate with mechanisms (esophageal involvement) not normally used by humans (Patterson & Pepperberg, 1998).

10.3.2 Evidence for Physical Imitation

Our research suggests that Alex's fidelity of vowel and stop imitation is most likely limited only by differences in human and avian vocal tracts (e.g., lack of lips). His vocalizations all resemble human samples; characteristics that describe human speech and processes used to produce human speech generally work for him (Patterson & Pepperberg, 1994, 1998). F_0 data specifically show that Alex, like humans, produces true resonances, not sinusoids at appropriate formant frequencies. Such data support an interpretion of Alex's speech acts as physical imitation. Also, he must learn to manipulate various vocal tract areas to produce human speech; some researchers call such behavior gestural learning. The process may take considerable time and practice; Alex's patterns evolve slowly toward human speech unless new labels involve previously acquired phonemes (Pepperberg, 1999).

Three other aspects of Alex's speech resemble young children's speech and suggest purposeful imitation. First, Greys also use sound play (phonetic "babbling" and recombination; Pepperberg et al., 1991) to derive new speech patterns from existing ones. After acquiring "gray," for example, Alex produced "grape," "grate," "grain," "chain," and "cane," which we eventually mapped to appropriate referents (Pepperberg, 1990b). Second, his recombinations suggest that he abstracts rules pertaining to the beginnings and endings of utterances. In over 22,000 vocalizations, we never observed backward combinations (e.g., "percup" instead of "cupper" or "copper"; Pepperberg et al., 1991). His behavior suggests that he parses human sound streams and acoustically represents labels in humanlike ways, and has similar phonetic categories (Patterson & Pepperberg, 1994, 1998). Third, he may exhibit anticipatory co-articulation. He may separate specific phonemes from speech flow *and* produce these sounds to facilitate production of upcoming phonemes (e.g., /k/ varies significantly between "key" and "corn"; Patterson & Pepperberg, 1998). Such behavior observed in conjunction with sound play is often used as evidence for top-down processing (Ladefoged, 1982).

10.4 Referential Use of Learned Vocalizations

Crucial to my argument for Alex's imitation is that his speech is *referential*. Purposeless duplication of an act (e.g., rote reproduction of human speech) lacks cognitive complexity and is "mere" mimicry. But if an act is performed because the imitator understands its purpose—to reach a goal, be it an object or intentional communication, that is otherwise impossible to obtain—then the imitation is intentional and complex, most likely indicating cognitive processing. Moreover, to use imitated speech referentially, Alex must discriminate among, appropriately categorize, and treat as meaningful even minor human sound differences; he must know that "want pea" and "want tea" elicit different responses in trainers.

Alex exhibits such processing. He can label more than 50 exemplars, 7 colors, 5 shapes, quantities to 6, 3 categories (color, shape, material), and uses "no," "come here," "wanna go *x*" and "want *y*" (*x* and *y* are appropriate location or item labels). He combines labels to identify, request, comment upon, or refuse about a hundred items and to alter his environment (Pepperberg, 1990a). He processes queries about category, relative size, quantity, and the presence or absence of similarity or difference in attributes; shows label comprehension; and semantically separates labeling and requesting (Pepperberg, 1983, 1987a,b,c, 1988a,b, 1990b, 1992; Pepperberg & Brezinsky, 1991). Given an array of, for example, different numbers of intermingled red and blue balls and blocks, he can quantify any subarray (Pepperberg, 1994a). His responses are not paired associations; he answers multiple questions about the same objects. He easily adds new exemplars to his categories of color, shape, material or object labels, and new categories to his repertoire (e.g., number). Previous studies on mimetic birds, using standard conditioning techniques, failed to produce such learning (Pepperberg, 1999). Why did Alex—a creature with a walnut-sized brain, and one so different from that of humans, nonhuman primates, mammals, and even songbirds—succeed?

10.5 Effects of Input on Vocal Learning in Grey Parrots

Alex was taught via the model/rival (M/R) procedure, which differs considerably from standard animal training techniques (Pepperberg, 1999). Was the technique responsible for his success? To find out, my students and I compared this technique with other procedures. Here I describe this system, contrast it with less successful forms, and discuss our findings.

10.5.1 Description of the Different Training Techniques

M/R Technique Basic model/rival (M/R) training, adapted from Todt (1975), involves three-way interactions among two humans and one bird. M/R training introduces labels and concepts and helps shape pronunciation; it demonstrates targeted vocal behavior through *social interaction*. A parrot observes two humans handling one or more objects in which it has shown interest, then watches the humans interact. The trainer presents an object or objects to the other human and queries the other human about the selection (e.g., "What's here?" "What color?"), rewarding correct answers with praise and the object (or objects). The second human is a model for the parrot's responses and the bird's rival for the trainer's attention. This person is also used to illustrate the consequences of errors; incorrect responses (such as those the bird might make) are punished by scolding and temporarily removing the object (or objects). The model is asked to try again or to talk more clearly if its response was (deliberately) incorrect or garbled, thereby showing the bird "corrective feedback" (see Goldstein, 1984; Vanayan et al., 1985). The human pair demonstrate *referential* and *functional* use of labels, respectively, by providing a one-to-one correspondence between label and object and modeling label use as a means to obtain the object (Pepperberg, 1981, 1990a,c). The bird is also queried and initially rewarded for approximating correct responses. As training progresses, the reward criteria tighten, adjusting training to the parrot's level. The model/rival and the trainer also reverse roles, showing how either can use the communicative process to request information or effect environmental change. Without experiencing this role reversal, birds exhibit two behavior patterns that are inconsistent with interactive, referential communication. They neither transfer responses to anyone other than the human who posed questions during training, nor learn both parts of the interaction (Todt, 1975).

M/R training intentionally uses *intrinsic* reinforcers. To ensure the correlation of the labels or concepts to be learned with their appropriate referents, the birds' rewards are the specific object to which the uttered label or concept refers. Earlier unsuccessful avian–human communication attempts used *extrinsic* rewards (Pepperberg, 1999); for example, one food that neither related to, nor varied with, the label or concept being taught. Extrinsic rewards delay acquisition by confounding the label of the targeted exemplar or concept with the food. My birds never receive extrinsic rewards.

After using M/R input successfully, my students and I tested how changing the system might affect learning, not only with respect to sound reproduction, but also comprehension and appropriate use (i.e., actions requiring cognitive processing). We varied the major aspects of input in M/R training—reference, context or function, and interaction—and a related aspect, modeling. Reference is considered to be an utterance's meaning—the relationship between labels and the objects to which they refer—and is exemplified by our use of referential rewards. Determining the referent—and whether one true referent exists—often requires cognitive processing by the receiver (W. Smith, 1991). To determine the referent for signal *a*, the receiver cannot simply process the signal and remember and interpret it as being associated with situation *x*, but rather must choose, based on additional information, among different aspects of situation *x*. The more explicit the referent, the more easily the signal is learned. Context or function involves the particular situation and effects of an utterance's use; our initial use of a label as a request gives the bird a reason to learn the unique and unfamiliar set of sounds. Both cognitive processes and motivation are important for extracting a signal's function from many possibilities in a given situation; explicit functionality assists learning. Social interaction indicates which environmental components of the modeled act should be noted, assists in determining their relative importance and order, emphasizes common attributes—and thus possible underlying rules—of diverse actions, and allows input to be continuously adjusted to the learner's level. Interaction and modeling engage a subject directly, provide contextual explanations of reasons for, and demonstrate consequences of, actions. All such aspects are crucial to successful imitation and require cognitive abilities.

To vary training with respect to these factors and to test their relative importance, I contrasted M/R tutoring with sessions using different forms of input involving human interaction, videotapes, and audiotapes. Most of these studies had to await additional subjects. Alex might have failed to learn simply because protocol changes had been made, not because of the quality of the changes; new subjects would not be influenced by prior experience. We thus performed one M/R variant experiment with Alex and seven sets of experiments with three naive Greys—Kyaaro, Alo, and Griffin (Pepperberg, 1999; Pepperberg et al., 2000). In each study, the labels were counterbalanced across training conditions and were always labels that could be produced by Grey parrots.

Eliminating Aspects of Training In Alex's "M/R-variant 1" (Pepperberg, 1994b), two humans modeled a sequence derived from Korean counting labels, *il ee bam ba oo yuk chil gal*, but without reference to either specific items or Alex's existing English number labels (Pepperberg, 1994a, 1997). He saw only a line of pictured numerals; no sound was attached to a particular numeral. The labels were chosen as part of another study on serial learning (Silverstone, 1989) and to differ maximally from English. The training lacked functional meaning and all but minimal referentiality, but maintained joint attention among bird, humans, and pictured numbers (known to facilitate label acquisition by children; Baldwin, 1991). The trainers maintained role reversal, included Alex in interactions, and rewarded him with vocal praise and the opportunity to request favored items ("I want *x*"; Pepperberg, 1987a); errors elicited scolding and time-outs.

The first set of experiments with the juvenile parrots compared simultaneous exposure of Alo and Kyaaro to labels in three conditions. Socially isolated in condition I, they heard audiotapes of Alex's sessions; input was nonreferential, not contextually applicable, and noninteractive. Socially isolated in condition II, they saw videos of Alex's sessions; input was referential, minimally contextually applicable, and noninteractive. Condition III involved standard M/R training. Condition I paralleled early allospecific song-acquisition studies (e.g., Marler, 1970); condition II involved still-unresolved issues about avian vision and video (i.e., whether the flickering of a cathode ray tube and its lack of ultraviolet, which birds can see, affect their ability to attend to or recognize video as representing reality; see Ikebuchi & Okanoya, 1999; Pepperberg & Wilkes, 2004). Each bird received training in all three conditions.

Experiments two through five tested video learning in more detail. Because interactive co-viewers can increase video learning in children (M. Rice et al., 1990), in experiment two a co-viewer provided social approbation for viewing and pointed to the screen while making comments like "Look what Alex has!" but did not repeat targeted labels, ask questions, or relate content to other training. The birds' attempts at a label could receive only vocal praise. Social interaction was limited; referentiality and functionality matched earlier video sessions (Pepperberg et al., 1998). Because the extent of co-viewer interaction might affect video learning in children (St. Peters et al., 1989), in experiment three our co-viewer uttered targeted labels and asked questions (Pepperberg et al., 1999). Because the absence of a reward might deter video learning, in experiment four an isolated parrot watched videos while a student in another room monitored its utterances through headphones and could deliver rewards remotely (Pepperberg et al., 1998). Experiment five used live videos from Alex's sessions because the birds might have habituated to the single video previously used per label (although each tape depicted many different responses and interactions among Alex and the trainers; Pepperberg et al., 1999). We are replicating video studies with a liquid crystal monitor to see if the flickering of the cathode ray tube rather than our experimental manipulations affects learning (Pepperberg & Wilkes, 2004).

Experiments six and seven examined the role of bird–trainer joint attention. For children, label acquisition occurs when adult–child duos focus jointly on objects being labeled (e.g., D. Baldwin, 1995). In experiment six, a single trainer had no visual or physical contact with parrot or object.

She faced away from the bird and talked about an object placed within reach of the bird, emphasizing its label (“Look, a shiny *key*!”, “Do you want *key*?” etc.—phrases framing the label, allowing repeated label use without causing habituation; Pepperberg, 1981). A bird’s attempts to utter the targeted label could receive only vocal praise, thus eliminating considerable functionality and social interaction (Pepperberg & McLaughlin, 1996). In experiment seven, we retained bird–trainer–object joint attention, but eliminated aspects of modeling by having only a single student label objects and query the bird (Pepperberg et al., 2000).

10.5.2 Results

In sum, the birds failed to acquire referential use of targeted labels in any non-M/R condition, but succeeded in concurrent M/R sessions on other labels (Pepperberg, 1999). For Grey parrots, at least, purposeful imitation requires input involving two humans who demonstrate the referentiality and functionality of a targeted label, socially interact with each other and the bird, exchange roles of questioner and respondent, portray effects of errors, provide corrective feedback, and adjust training as a subject learns. Success also requires cognitive processing by the parrot to evaluate the input. Without such input and processing, even supposedly mimetic birds fail to learn entirely or acquire limited associations rather than full referential use of labels; that is, they cannot transfer label use from training to testing and from training exemplars to other instances of a relevant object or concept; or they reproduce a label but do not comprehend what they produce (Pepperberg, 1994b; Pepperberg et al., 1998, 1999; Todt, 1975).

Thus three birds—Kyaaro, Alo, and Griffin—failed to learn referential labels in any video session; the first two failed to learn from audiotapes (Griffin did not receive audio training), and Kyo and Griffin did not utter labels in experiments six and seven. In contrast, all birds appropriately identified items (e.g., cork, paper, wood, wool) targeted in basic M/R sessions. Tapes of solitary sounds produced by the birds revealed that they practiced only M/R-trained labels (Pepperberg et al., 1991; Pepperberg, 1994b; Pepperberg & McLaughlin, 1996). Of interest is that Griffin clearly produced targeted labels after two or three M/R sessions subsequent to experiment seven. We suspect he actually acquired labels in that experiment, but did not use them until he observed their use modeled. (Note: birds that were switched to M/R training after fifty video sessions needed about twenty sessions before they produced labels.)

In M/R variant-1, Alex learned the modeled label string, but the results differed from those of M/R studies in two important ways. First, acquisition took an unusual 9 months (Pepperberg, 1981, 1994b; Silverstone, 1989). Second, and most striking, was that he could not immediately use, nor subsequently learn to use, these labels referentially, that is, for either serial labeling or quantity. Even after we modeled one-to-one correspondences between eight objects and the label string, he could not refer to smaller quantities using elements in the string (e.g., say "il ee bam ba" when shown four items and told "say number"); he had learned an unanalyzed phrase (Pepperberg, 1994b). Given his previous M/R-based success (e.g., Pepperberg, 1990b, 1992, 1994a), the current failure was most likely a consequence of training, not a cognitive deficit (Pepperberg, 1994b).

The M/R technique also encompasses other elements of input (e.g., quality of input, identity of model, trainer role reversal; Pepperberg, 1991a,b) that we did not initially vary. Subsequent work (Pepperberg et al., 2000; Pepperberg & Wilcox, 2000) studied these forms and their cognitive correlates, and reaffirmed that standard M/R training, with all its elements of input, is the more effective protocol for referential learning.

10.6 Implications for Studies of Imitation

The results of the work reported here highlight issues relevant to imitation studies in all creatures, with implications for general learning theory. Training that produces mere mimicry does not result in the acquisition of purposeful "improbable acts" (Thorpe, 1963), implying that mimicry and imitation involve different learning mechanisms and possibly cognitive processes. Imitation requires specialized input; generating imitation and determining the level of imitation in a given species with a known range of cognitive capacity and learning ability may depend upon environmental and tutoring conditions. Japanese quail (*Coturnix japonica*), for example, learn from an observer more often when they are hungry than when they are satiated (Dorrance & Zentall, 2001), which supports data on the social contingencies of imitative learning in related species (Lefebvre, 2000). Even species known for mimetic abilities, such as Grey parrots, imitate only under certain conditions. Thus preexperimental generalizations about imitative abilities may be premature. Might supposedly nonimitative species imitate under appropriate conditions?

Of interesting is that the conditions under which Grey parrots acquire referential English labels (goal-directed imitation) are those that produce (1) exceptional learning—learning unlikely during normal development but possible with certain input (Pepperberg, 1985, 1988b, 1993, 1997) and (2) acquisition of language by children with specific impairments and who lack concomitant social skills (e.g., M. Rice, 1991; see Pepperberg & Sherman, 2000, 2002). Normal children, for example, but not impaired children or Grey parrots, learn from video in the absence of interactive caretakers (Pepperberg et al., 1999). Normal children, but not Grey parrots, learn labels from a single caretaker (D. Baldwin, 1991; J. de Villiers & de Villiers, 1978; Pepperberg et al., 2000). For echolalic autistic children (who are characterized by their nonreferential use of mimicked sounds; Fey, 1986), acquiring normal communication may involve exceptional learning and be responsive to M/R training (Pepperberg & Sherman, 2000, 2002).

When comparing M/R with other forms of imitative training, another issue arises. Possibly for parrots (and children with disabilities, and maybe other animals), the typical form of instruction, that is, "do as I do," might prevent the subject from separating the targeted behavior pattern or target of the command from the command and thus inhibit building a representation of the required response (Pepperberg & Sherman, 2000). Maybe such subjects must observe a model responding to the command "do as I do" (i.e., or see a response to "do *x*") to identify behavior patterns to be learned or imitated (and to correlate the action with the specific label "*x*").

10.6.1 Neurological Correlates and Levels of Imitation

My findings also suggest a search for both correlates and homologies across species for recently discovered neuroanatomical areas that are apparently involved in replicating action (mirror neurons; Iacoboni et al., 1999), and for relations between different areas and levels of imitation (Rizzolatti et al., 2001). Byrne and Russon (1998), among others, suggest that imitation encompasses a range of behavior patterns of varying complexity; they deconstruct imitation into an "action level"—specification of sequential acts—and a "program level"—description of subroutine structure and the hierarchical layout of a behavioral program. I propose three levels: simple mimicry, low-level imitation, and high-level imitation, and their connections to mirror neurons.

Simple mimicry describes replication of actions (e.g., manual or vocal) without direction—with unclear referential and functional aspects—but that involve some social interaction. Examples might be newborns' imitative acts (Meltzoff & Moore, 1977) and adults' unconscious replication of others' motions in social settings (e.g., touching their hair in specific ways; Chartrand & Bargh, 1999), also behavior like Alex's in M/R variant-1. These patterns most likely do not recruit the mirror neuron system activated when deliberate actions are viewed (what I'll call MN1), but corroborate neurobiological data on involuntary levels of imitation (Arbib et al., 2000;

what I'll call MN0)—levels that involve little or no cognitive processing, intentional reproduction, or integration of observed acts in which "an executive sector of the motor system 'resonates' during observation of an action. As a consequence the observed action is usually emitted. In this type of resonance phenomenon understanding of the meaning is neither essential nor required" (Rizzolatti & Arbib, 1999, p. 152). Thus I propose connecting the absence of reference, functionality, and intentionality, the lack of recruitment of MN1, and the lack of overt learning of a novel behavior (or, at best, replication without meaning), and the absence of "theory of mind" (TOM; see following discussion).

Low-level imitation most likely involves MN1 and some reference, functionality, and social interaction, but not improbable behavior or TOM. Examples are replication of motor acts such as movement toward objects (Rizzolatti et al., 2001) or Alex's learning the word "carrot" after trainers ate and labeled the object only a few times, because he had phonemes from "key" and "parrot" (Pepperberg, 1999). When a monkey sees a human arm move, for example, its cortical neurons homologous to those of the human become active, even if the monkey's limb remains inactive (e.g., Fogassi, 2000); the observed action, however, must be goal directed (Buccino et al., 2001; Rizzolatti et al., 2001). In humans, some activation occurs even when intransitive movements are observed (Fadiga et al., 1995). Monkey mirror neurons are not likely involved in Thorpe's improbable acts because their activation also seemingly requires experience of, or capacity for, making the observed movement (Chaminade et al., 2001b; Rizzolatti et al., 2001). How can an existing action be improbable? Of interest is that in humans some different brain areas activate during means versus goal actions (Chaminade et al., 2002), suggesting that behavior involving these neurons is not simple mimicry; instead, these neurons could be involved in the recruitment of sets of acts from one context for use in another; that is, for emulation (e.g., Tomasello, 1999), not imitation. A consistent interpretation of monkey data would be that their mirror neuron system, an MN1, recruits *innate* grasping patterns when the monkeys observe human actions, and that novel patterns—and true imitation—are not part of the system.

Higher-order imitation most likely involves considerable reference, functionality, social interaction, and creation of improbable acts. Alex's referential acquisition should qualify. Such behavior relates to, but I believe differs from, the motor actions described by Rizzolatti and co-workers—patterns requiring "refinement of the motor act or of the motor sequence" (Rizzolatti et al., 2001, p. 668), Rizzolatti et al., like Byrne (2002a), argue that new patterns arise as subjects dissect observed behavior into a string of already existing simpler sequential components (motor acts), then reconstitute them appropriately. In contrast, I argue that precisely because these are Thorpe's improbable acts, the observer is *creating* these motor patterns, a representation. The issue may be of degree, in that I am discussing creation from the most elementary motor units. In any case, these novel patterns take longer to construct than those involved in low-level imitation; they require strong levels of reference, functionality, and interaction for their inception (e.g., Pepperberg, 1985), and, I suggest, involve the construction of neural pathways that only then are recruited into a mirror system, MN2. These actions might also involve beginnings of TOM.

Might data about levels of imitation thus provide insights into TOM, assuming various TOM levels also exist? Possibly building MN2 activity allows observers to both see and somehow feel how actions look—a means of representing and categorizing actions for future replication (e.g., Hurford, 2002); the beginning of TOM. MN1 activity alone cannot be enough or monkeys would exhibit TOM. Understanding TOM requires teasing apart confounded issues. We must start by determining what neural substrates are involved in integrating information; what is needed for inferential understanding of how replicating a specific observed behavior is a specific means to obtaining a specific goal, even under delayed reward (e.g., Bandura, 1969); and what brain areas control an observer's ability to replicate behavior patterns physically, versus how much processing and what areas are involved in observers' *choosing* to replicate the behavior (e.g., so the imitative act is deliberately executed in pursuit of some goal). Of interesting is that when an observer chooses not to act, spinal (as opposed to cortical) neuronal excitation occurs in the order opposite to cortical mirror neuron excitation, possibly to prevent physical replication (Baldissera et al., 2001).

Different human mirror neurons seem to be involved with means than with goals (Chaminade et al., 2002). Are different mirror neurons involved in the awareness of achieving a different goal with a similar arm movement, or the same goal with the same arm movement, the latter being needed for intentional imitation (e.g., MN1 versus MN2)? Is awareness or recognition intentional or is learning necessary? People learning American Sign Language signs improve their acquisition and retention by delaying rather than concurrently imitating the observed motions (Weeks et al., 1996); thus functional learning most likely requires more than replication. Likewise, autistic children's echolalia but lack of controlled imitation suggests that an executive process that is missing in their mirror neuron system (see J. Williams et al., 2001) exists for true imitation. Does this relate to TOM? When is TOM required for imitation? Is TOM required for higher forms of imitation, or do creatures simply need a nonreflexive consciousness tied to some relatively low intentionality and biologically based hedonic response (Dickinson & Balleine, 2000)? A chimpanzee that attributes goals to moving blocks (Uller & Nichols, 2001) most likely attributes goals—and its mirror neurons respond—to moving human arms, and it can replicate the human action. But does the chimpanzee attribute these goals or intentions to the human connected to the arm (Povinelli & Eddy, 1996)? Data showing that particular neurons fire in monkeys only when the agent being observed attends to the object of its reaching (Jellema et al., 2000) support this inference, but monkeys rarely imitate even intentionally useful acts demonstrated by humans (Visalberghi & Fragaszy, 2002). And attributing intention to moving objects does not require fully developed TOM; children attribute intention early but fail TOM tasks until they are about 3 years of age (Baron-Cohen et al., 1985). Possibly imitation, TOM, and neural pathways involve corresponding levels of complexity.

Now, what primate mirror neuron analogues (MN0, MN1, MN2) could exist in parrots, who cannot exactly replicate human motor patterns? Do parrots have neurons that react similarly when hearing *and* speaking human labels? For oscine birds' own song, some parallels exist with primates. In songbirds, the high vocal center (HVC) sends efferents to both input and output branches of the song system; the HVC is necessary for song production and has neurons showing song-specific auditory responses (H. Williams, 1989). Furthermore, playback of the birds' own song during sleep causes neural activity comparable to actual singing (Dave & Margoliash, 2000). How these findings relate to parrot brains, which are organized differently than those of songbirds (e.g., Striedter, 1994; Jarvis & Mello, 2000), is unclear. Although studies of *ZENK* gene[2] expression show separation of budgerigar (*Melopsittacus undulatus*) response regions for hearing and vocalizing warble song (Jarvis & Mello, 2000), electrophysiological studies in the frontal neostriatum of awake budgerigars show activity during both production of and response to calls (Plumer & Striedter, 1997, 2000). Evidence also exists for additional budgerigar auditory-vocal pathways (e.g., Brauth et al., 2001). Because the *ZENK* response appears to be

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[2] Expression of the *ZENK* gene, a songbird analogue to a human transcription factor known as egr-1, is driven by actions of singing and hearing. Thus it is used to form a functional map of the avian brain for behavior related to both auditory processing and vocal production (see Jarvis & Mello, 2000).

tuned to specific song features (Ribeiro et al., 1998), the relevance of these data for mirror neurons in talking parrots is not known.

10.6.2 Connections to Communication and Possibly Language

Imitation and mirror neuron issues should, however, relate to communicative competence. Mirror neuron data suggest homologies between the monkey F5 and human Broca's area (Fogassi, 2000; Rizzolatti et al., 2001; see Grèzes & Decety, 2001) that might explain the codevelopment of gestural and verbal syntactic combinations occurring in humans and apes (i.e., simultaneous emergence of rule-governed ordering of labels and serial combination of different-sized cups; Johnson-Pynn et al., 1999). Both areas are activated by both action and observation of hand or mouth gestures, suggesting a system that not only matches observation of an action with its execution, but that could also subserve imitation and interindividual communication (Fogassi, 2000; Rizzolatti & Arbib, 1999). A similar simultaneous development of vocal and physical combinatorial actions in parrots (Pepperberg & Shive, 2001) must, however, involve nonprimate neural structures. Are these systems analogous? Or homologous (Medina & Reiner, 2000)? I have previously described parallel avian–primate developmental systems for communication (Pepperberg, 2001), but unrelated to mirror neurons or imitation. The following is a short review in the context of this discussion.

I suspect that for most creatures that learn their repertoire, early babbling mostly involves the MN0 system (e.g., Rizzolatti & Arbib, 1999), corresponding to mimicry. These utterances can be triggered by hearing, are meaningless, and involve no cognitive processing, but do involve some social interaction. They may be accompanied by simple physical actions that also "mirror" caretakers' actions, and, for both humans and parrots, may increase with adult attentiveness (Locke, 2001; Pepperberg, 1999). Data demonstrating that listening to a word produces phoneme-specific activation of speech motor centers (Craighero et al., 2002) support a mimetic interpretation. Subsequent maturation of the nervous system allows voluntary control and precise replication; possibly maturation relates to the spinal (and other) inhibitory parts of the mirror neuron system (MN1?).

The next stage, I believe, involves transition to high-, not low-level imitation. For parrots and children, first labels qualitatively differ from later labels. First labels are learned slowly, may be acoustically biased by and based on prenatal or prehatching exposure to sounds, and are predisposed, probably evolutionarily, to refer to whole objects (review in Pepperberg, 2001). First labels are often indexical (they refer to specific items, not a class), may lack communicative intent and true meaning (P. de Villiers & de Villiers, 1979), but can be goal directed. They are not based on simple associations and can be transferred across items (Pepperberg, 2001). What seems to be missing is the use of representation. Subjects might be unable to store images long enough to form representations or might not sort early labels into the categories used to form representations (i.e., form categorical images). But subjects are beginning to build such representations and the concomitant motor and vocal patterns; that is, they are beginning to construct relevant neural pathways (MN2?).

As learning of labels continues, children (Hollich et al., 2000)—and most likely parrots—begin processing information within a different context that arises through an understanding of social systems; quite likely neural development underlies such understanding and includes the functional recruitment of MN systems. Learning still appears self-directed—driven by the need to influence others and to have basic needs met—but advances because subjects now attend to others' intentions and recognize others as information sources separate from themselves. I suggest that recruitment of the MN2 system, correlated with MN1, precipitates the explosion in learning labels that occurs at about 18 months in children. MN2 provides the learning pathways and MN1 allows emulation (e.g., reorganization of sounds to create new labels) as the developing cognitive processing forms categories and representations.

Of interest is that most studies on labeling and concept formation involve older children (18–24 months, e.g., Bloom, 2000; Tomasello, 2001), ignoring transitional stages in humans and animals (cf. Hollich et al., 2000; Cheney & Seyfarth, 1990; Pepperberg, 1999). But by 18 months, a child can already take others' perspectives and see them as information sources. The child can play with one toy, notice an experimenter playing with and labeling another, and change its focus to the experimenter's toy when it hears the experimenter's label. At 12–14 months, the child is more self-centered; in the same situation, it prefers looking at its toy when it hears the experimenter's label (Hollich et al., 2000), and at about 10 months it usually associates the experimenter's label with its toy (Hirsh-Pasek et al., 2000). Thus in a brief transitional period, the child loses its self-centered bias, possibly laying the groundwork for high-level imitation. Note that autistic behavior and its communicative deficits often appear at this transition (Tager-Flusberg, 2000)—the point at which self-awareness, the need to understand the self as separate from others, and others as information sources become critical for learning. Some autistic children never move beyond the 10-month-old stage in terms of label and object associations (D.

Baldwin & Tomasello, 1998); that is, they cannot convert the actions of another into their own perspective, which is crucial for imitation and may involve MN2.

Is awareness necessary for this transition? Might its development enable the transition? Possibly, creatures learn to generalize and initially separate the self from others by categorizing and generalizing emotions first with respect to environmental events (Humphrey, 2000), then in intersubject interactions (Damasio, 1999). Damasio argues that "core" consciousness (the basic form involving awareness of the present, not the future or past) emerges when we interact with an object (including others), and is a feeling that accompanies the making of a mental image, even one retained only momentarily. His theory might explain why social interaction assists learning. The mental image allows the categorization of events with respect to their emotional content, which in intact individuals leads to categorization of involved objects and actions. A child, for example, initially does not label emotions, but talks about objects, expressing emotion by displaying positive or negative affect (Bloom, 2000). How categorizations lead to a representation of objects and actions that can be manipulated to allow advanced learning is unclear, but categorization may relate to the development of MN2 from MN1 or MN0. In this view, selfhood (not necessarily full consciousness) begins in the emotional domain, before the emergence of language, and seemingly leads to categorization, which then leads to understanding and use of representation. Our parrots' behavior—like that of children—suggests clues about the transition to advanced learning as they begin recognizing others as information sources.

Evidence for our parrots' transitions from self-centered learning comes from vocal actions like those of children, particularly sound play (described earlier), when trainers referentially map novel utterances. Apparently, Grey parrots—like children (Brown, 1973)—begin testing humans as information sources for the reference of sound patterns. They see humans in this context during training, then adapt the situation. They play with label phonetics; they also utter a label used in specific contexts, such as "wool" for a woolen pompon, while pulling at a trainer's sweater. It is rare for such action to happen by chance; by then the bird has at least three or four other labels. Our responses—of high affect, excitement, and repetition of a label, which stimulate the birds further and possibly activate mirror neurons—affirm the power of their utterances and reinforce their attempts at categorization. Even if the birds err in initial categorizations, they still receive positive reinforcement; we provide a correct, new label (e.g., state that an almond isn't a "cork," but suggest "cork nut"; Pepperberg, 1999).

Of importance is that the birds' behavior is not trial-and-error learning, but guided invention (A. Lock, 1980), from initial mapping of a label to generalization to imaginal syntax. Parrots, like children, have a repertoire of desires and purposes driving them to form and test ideas in dealing with the world; these ideas can amount to early stages of representation (categorization) in cognitive processing. And manipulation of representations is a syntax of imagery, which Damasio insists requires some self-awareness. We have creation of somewhat novel acts, maybe mirror neuron involvement.

Can training foster such emergent behavior? Preliminary data on dysfunctional children, including autistics, suggest that they respond positively to M/R input (Pepperberg & Sherman, 2000, 2002). The children in these studies have not achieved full age-appropriate behavior, but their communication abilities improve after M/R sessions. Work in progress (D. Sherman, personal communication) suggests that children with severe disabilities need to be prepared before they can accept M/R input. Data from such studies may provide additional understanding of transitional processes and their relevance to imitation.

Of course, sensitivity to input, separation of the self from others, and transition to advanced learning may not be the cause but the outcome of maturation of the brain and neural development. Many neural connections existing at birth die off early (Changeux & Danchin, 1976). Do systems used in early simple learning of labels die off, or do they get pruned and relegated for use only in mimicry? Many new connections are formed in the early years of life. Given that neural categorization occurs when a neural ensemble provides the same output from different inputs, is this connectivity—which is almost absent in year-old babies—what grows with age? Is the failure to form new connections as old ones die related to emergent autistic behavior? Possibly (see Chugani, 1999); but if behavioral shifts and the transition to different learning forms do indeed result from changes in neural connections, such reorganization is unlikely to be specific to humans because it also occurs in parrots, with their significantly different brain architecture (Medina & Reiner, 2000).

10.7 Summation

Input often affects whether imitation, like other forms of learning (e.g., Pepperberg, 1999), occurs at all, and what achievement levels exist. Careful experimentation is thus necessary to determine the extent and range of any learning ability in any species, including humans (Pepperberg & Sherman, 2000). Moreover, data on apparent true imitation in species as phylogenetically diverse as parrots and humans suggest that we must reevaluate our understanding of the phenomenon. Either such behavior arose independently multiple times, or the evolutionary precursor is further back than researchers have presumed. In any case, for parrots as well as primates, various forms and levels of imitation seemingly exist. We can label them as different phenomena, or as different aspects of one behavior, but the behavior that specifically develops is contingent upon the input received.[3]

Acknowledgment

The writing of this chapter was supported by the American Foundation.

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[3] See comments on this chapter by Byrne, vol. 1, ch. 12.3, p. 290, and by Pickering, ch. 12.4, p. 293. ED.

11 Selective Imitation in Child and Chimpanzee: A Window on the Construal of Others' Actions

Andrew Whiten, Victoria Horner, and Sarah Marshall-Pescini

11.1 Introduction

Suggesting that the behavioral repertoire of human children is shaped by the particular culture they are reared in, and that this occurs in large measure through various kinds of broadly imitative, "tradition-copying" processes, is hardly likely to provoke much debate. That the same might be true of our closest relatives, chimpanzees, has been much more controversial.

The possibility of some such fundamental similarities between chimpanzees and ourselves became a working assumption following the first substantial field studies of chimpanzees (Goodall, 1973), reinforced by impressive-looking experimental evidence for a wide-ranging imitative capacity (Hayes & Hayes, 1952). However, these conclusions were later challenged by authors who argued that the evidence was not in fact adequate to demonstrate that chimpanzees were either truly cultural, or imitative (Tomasello, 1990; Galef, 1992; Heyes, 1993), a view reinforced by new experimental studies reporting a lack of imitative copying of tool use (Tomasello et al., 1987). These and other critiques have been followed by a decade of effort in which the chimpanzee data have become more rigorously obtained and substantial. In particular, the charting of putative chimpanzee cultural variation has become more systematic (Whiten et al., 1999, 2001) and several careful experimental studies have followed the provocative findings of Tomasello et al. (1987); reviewing the field, Whiten et al. (2004) were able to cite thirty-one experimental studies completed in the intervening period. A measure of the impact of this work is that the authors of some of the sternest earlier critiques have been prepared to revise their conclusions. Thus experimentalist Tomasello joined with field ethologist Boesch to agree that "a comparison of chimpanzee and human cultures shows many deep similarities" (Boesch & Tomasello, 1998, p. 591), and

Heyes (2001a, p. 253) concluded that recent experimental studies had demonstrated chimpanzee imitation.

So it seems that "apes ape," after all, and the idea of chimpanzee cultures has become widely accepted. To a casual observer it may seem that the field has thus merely come full circle, to a picture of chimpanzee–human similarities that many long assumed existed. Indeed, broadly defined, both imitation (in Thorndike's (1898) sense of "learning to do an act from seeing it done") and "culture" (in the sense of "behavioral traditions") appear to be quite widespread among birds and mammals (Zentall, 2001; de Waal, 2001a), so that claiming the existence of both in our closest relative could be dismissed as not so very startling.

This, however, would be to neglect the fact that our current knowledge is built on much firmer scientific foundations than before, and that we have gained a significantly richer picture of the complex nature of both traditions and imitation in chimpanzees. Indeed in chimpanzees as in humans, there is more to "culture" than the mere existence of traditions (Whiten, 2000, 2001; Whiten et al., 2003). In a similar way, there can be more to imitation than implied by Thorndike's basic definition, and in this chapter we address some of these complexities in the imitation of human and nonhuman apes. Our central point is that even though a substantial cultural repertoire may be acquired by imitative copying, neither children nor chimpanzees copy all they see others around them doing. Indeed, a moment's reflection confirms they could not; if they did, they would appear to be little marionettes perpetually mimicking whoever was in view. So the question naturally arises, What determines what is copied, and what is not? This is a question little addressed by research as yet, but it is surely an important one. Thus in relation to the mechanism, or process, of imitation that is addressed by so many chapters in these two volumes, we are led to examine most fundamentally *what the imitative process selectively imitates.*[1] This in turn raises an important functional question of what purposes any such selectivity serves. Finally, this issue is important in relation to the topic of cultural transmission mentioned earlier and covered elsewhere in this volume and in volume 2, for selectivity in imitation clearly has significant potential to shape cultural stability and change.

We have been led to the question of selectivity principally because in so many of our studies, when we find evidence of imitation in apes, it is typically *partial*; some parts of what a model does are copied, others are not.

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[1] For relevant discussion, see chs. 16 by Harris and Want and 17 by Greenberg in vol. 2. ED.

This is particularly the case in chimpanzees compared with children. One interpretation of such findings, particularly likely to recommend itself to those skeptical of imitation by apes, is that this merely reflects a relatively poor imitative ability, and this is one theoretical possibility we address here. However, we also find striking biases in what children do or do not imitate and some of these, as in the chimpanzees, are suggestive of active and functional selectivity. Clearly, we need a method of distinguishing any such true and interesting selectivity from patchy copying caused merely by limited imitative competence.

Our answer has been to design experiments in which we systematically *predict* what subjects will or will not selectively copy in two contrasting conditions, *if* they are operating on adaptive or functional grounds, as opposed to being merely limited in their imitative capacity. If we can successfully predict the conditions under which particular aspects of a model's actions will be reproduced, we are getting onto firm ground in concluding that true selectivity is operating. In addition, to the extent our predictions are derived from a systematic theoretical framework, we will have made some real progress in understanding *why* the selectivity takes the form it does. We therefore explain our framework next.

11.1.1 A Framework for Analyzing Selective Imitation

Our framework for these studies draws on theoretical discussions in the literature of the past 15 years or so (Whiten et al., 2004) and is illustrated in figure 11.1. As indicated, we envisage the processes involved in copying from another's actions as constituting a continuum ranging between imitation and emulation. The core idea we wish to capture is that at the emulation pole of the continuum, the observer may be actively ignoring—"selecting out"—various aspects of the actions of the model, which at the imitative pole would instead be "selected in." We can envisage various contexts in which such a flexible, selective strategy could be adaptive, as indicated in figure 11.1. For example, some actions may be seen as accidental rather than intended, or as not causally linked to an outcome of interest, and thus not copied. Or it might be that even though certain acts *are* perceived as intended and/or causally necessary, the observer has at his or her disposal alternative behavioral techniques for gaining the results of interest, which are preferred over those performed by the model (and of course even if components are selected out because they are seen as *not* intended or *not* causal, emulation requires that the observer be able to come up with actions that can be substituted for those used by the model).

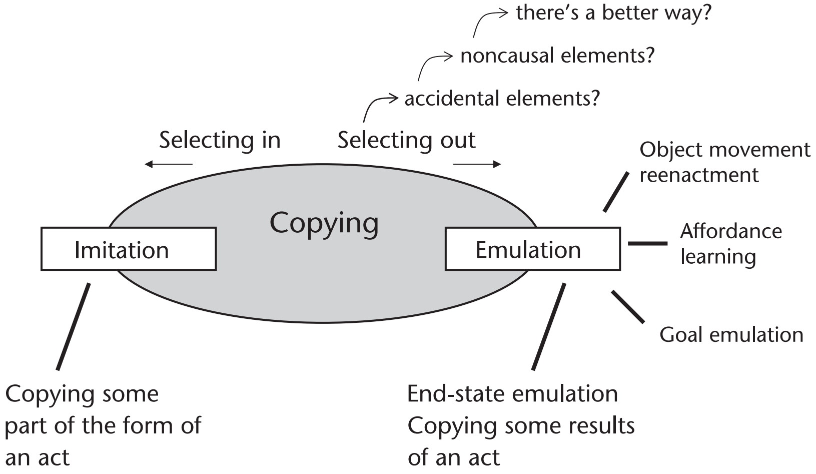


Figure 11.1
Framework for analyzing selective imitation. Copying is conceptualized as a continuum. At one pole, emulation may involve copying only the results the model achieved, or their goal, or the way objects are moved; at the other pole, imitation involves a more complete copy of the form of the actions of the model. Thus in emulation there is a relative selecting out of certain parts of the model that at the imitative pole are selected in. Three possible bases for selecting out elements of the model are suggested: they are perceived as accidental rather than intended; they are perceived as noncausal rather than causing a desirable outcome; or the observer simply knows a better way to achieve such an outcome (see the text and Whiten et al., 2004, for further discussion and references).

The hypothesis we wish to explore goes beyond a common preoccupation in the recent literature about whether any particular species is an imitator or an emulator, to propose that instead there may be adaptive flexibility, so that a learner might switch between the imitation and emulation poles of the copying continuum according to context. In this chapter we focus on the opportunities to select in or select out information on the causal relevance of actions the model performs. Our previous research suggests that imitative copying is favored in tasks where such causal connections are relatively opaque to the learner; under these constraints, it may be adaptive to imitate rather comprehensively all the actions taken by the model. By contrast, where causal connections are more transparent to the observer, emulation becomes more feasible. Emulation may be preferred for reasons such as those suggested earlier, and may be more efficient than what can be achieved through the higher-fidelity copying that distinguishes the imitation end of the continuum.

We have turned these ideas into experiments that we describe in more detail in the following sections. The basic strategy is to create two different forms of the same task, one of which we predict will generate relatively full imitation, and the other a more restricted copy limited to end results of the sequence of actions. Such an approach not only probes the mechanisms of observational learning, but can also give us, as we indicate in our subtitle, a window on the construal of others' actions. Thus in the present case, they may tell us something of the extent to which chimpanzees' and children's perceptions of others actively assess the causal significance of the actions performed and use this assessment to shape the kind of social learning process activated. This issue is given added topicality because of a suite of experimental studies by Povinelli (2000) that led him to conclude that chimpanzees actually understand rather little about causality.

11.2 Imitation in Chimpanzees: Ill Formed or Selective?

Before describing the experiments designed explicitly to test the hypothesis outlined earlier, repeated findings in earlier work need to be reviewed briefly. The basic finding of interest in our earlier studies on evidence of imitation, whether in chimpanzees or children, is that the copying tends to be partial. Overall, especially in chimpanzees, we have tended to find patchy fidelity to the actions of the model. As noted earlier, it is often inherently difficult to discern whether this reflects an imperfect imitative ability or is instead demonstrating the kind of adaptive selectivity described in the foregoing section. This is why we have performed the prospective experiments described here, which were specifically designed to differentiate these possibilities. Nevertheless, it is important to review certain earlier findings precisely because they do form the background and platform for the new experiments; moreover, they repeatedly present puzzles of interpretation that may be solved at least in part by the theory and experimental approaches described in this chapter.

11.2.1 Copying Some Components of a Task, but Not Others

In three studies of the observational learning of chimpanzees we have used an "artificial fruit" (figure 11.2), designed as an experimental analogue of foraging problems encountered in the wild (Whiten, 1998, 2002a; Whiten et al., 1996). As with certain real fruits, the animal is faced with a task

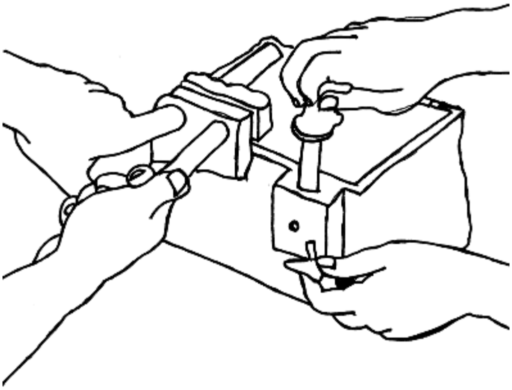


Figure 11.2
"Pin-apple" artificial fruit for experimental investigation of imitation. The actions illustrated are poking through the outer bolt, pulling and twisting out the inner bolt, removing the pin, and pulling up the handle. Once all defenses are removed in these ways or others, the lid can be opened to gain access to an edible core.

that involves removal of the food's defenses (e.g., shelling, breaking off) to allow access to an edible core. In addition, the fruit was designed to implement a two-action approach (B. Dawson & Foss, 1965) to assessing imitation. Each defense can be removed in one of two ways, only one of which is seen by each subject before they are given the chance to try to open the fruit themselves. The extent to which the two groups of subjects subsequently perform differently, and in particular the extent to which their actions match those of the model variant they watched earlier, gives us a robust measure of imitative learning. Differences cannot be due to stimulus enhancement, since both of the two variant techniques are applied to the same part of the fruit.

We have consistently found that chimpanzees performed imitative copying of certain parts of this task and not others (Whiten, 1998, 2002a; Whiten et al., 1996). The two alternatives of *poking* the "bolts" out of the way, versus *pulling and twisting* them out (see figure 11.2), elicited matching behaviors in chimpanzees. These behaviors could be identified by videotape coders blind to which variant the subjects had actually seen. Such results were similar to those for preschool children tested in similar ways (in these experiments, adult human models who were familiar to the subjects were used in all cases). By contrast, chimpanzees that had witnessed a model either pulling out the "handle" (as in figure 11.2) or twisting it out of the way, did not show significantly different approaches when they had their turn at the task; their tendency was efficiently to pull out the bolt, whichever method they had seen modeled. From the perspective of figure 11.1, the chimpanzees' actions were relatively *imitative* with respect to the bolts, but relatively *emulative* with respect to the handle; for the latter they appeared to have learned something about a useful end result (disabling the handle defense), but applied their own technique to achieving this. However, children continued to imitate this part of the task, as they had with the bolts.

The basic contrast between these two sets of subjects is thus that the children exhibited imitation of a quite high fidelity throughout, whereas the chimpanzees imitated only partially—on the bolts but not the handle. One interpretation of these results is that chimpanzees are simply less proficient imitators. However, we found that the chimpanzees were in fact faster at opening the fruit, apparently because they did not copy all they had seen in the relatively painstaking way characteristic of the children. Instead, by applying their own preferred method of disabling the handle defense, they turned in a more efficient performance than the children. This argues for seeing the chimpanzees' approach as not necessarily expressing an inability, but instead a possible case of adaptive, selective imitation.

This appears to leave us with the question of why the children were not acting in such an adaptive way, a puzzle we postpone for discussion after some other relevant results have been outlined. For the chimpanzees, the question is why they copied one component and not the other. Our guess is that from the chimpanzees' perspective, the two components differed in transparency. As chimpanzees acted on the handle, even if they were turning it, they would tend to discover it could be pulled out, and they preferred to do so subsequently (unlike the more faithfully copying children). By contrast, if the chimpanzees started to poke out the bolts when they had seen the model do this, it appeared to be not so transparent to them that the bolts could in fact be pulled out instead.

This interpretation of the chimpanzees' approach as adaptive, selective imitation of some components but not others is, of course, post hoc. It can be tested only by further experiments of the kind we report further here, but experiments informed by the kinds of results we have just described.

11.2.2 Differential Copying of the Sequential Structure of a Technique versus Its Components

Extending the concept of the two-action methodology (Whiten, 2002a), the artificial fruit described earlier was designed so the steps to opening it could be performed in different sequential orders (figure 11.2). In an earlier study, two chimpanzees saw each of the two bolts removed first; then the pin was taken out, the handle was disabled, and the lid opened to reveal the edible part inside. Another pair of subjects saw the alternative sequence of pin-handle-outer bolt-inner bolt. Within each pair, one subject saw one technique for each component (e.g., poke the bolts) and the other subject saw the alternative (e.g., pull and twist the bolts) (Whiten, 1998).

By the third and final trial, there was a statistically significant match to the particular sequential structure each subject had witnessed. In three cases the match was perfect and in the fourth the only difference was the relatively trivial one that the bolts were taken out in a different order. By contrast, these subjects varied in the extent to which they matched details of the ways in which the component acts had been performed. Two showed quite extensive matching of techniques applied to the bolts; one replicated the spinning action it had seen on the pin and one subject did neither of these. Thus, in these results we may be seeing selective imitation (to varying extents in different individuals) of the overall sequential structure, at the expense of details of the technique for each component. This might constitute adaptive selectivity to the extent that in many complex natural tasks it may be more critical to learn the overall structure than the individual actions (R. Byrne & Russon, 1998), at least when the animal is competent enough to generate its own local solutions to the latter.

However, if we take a less static view and consider the development, or learning, of a skill, the selectivity may be more complex than this. As noted earlier, the subjects came to match the sequential structure only after several trials (whether this reflects repeated opportunities to observe the model, or repeated opportunities to perform the task, or an interaction between these, we do not yet know). By contrast, there was evidence of copying component techniques (twisting bolts and spinning the pin, neither of which are in fact physically necessary) from the outset. This raises the possibility that there is differential selectivity during the social learning of a complex sequence of actions, with selectivity initially focusing on the shape of the component acts, then later shifting to higher-level sequential patterning (Whiten et al., 2004). This might vary among species. Testing gorillas, we found no evidence of sequence learning in equivalent tests, yet there was evidence that they copied aspects of the components, such as spinning the pin versus pulling it straight out, the two variants demonstrated by models (Stoinksi et al., 2001).

As in the previous study, however, we must be cautious about these interpretations. It remains possible that the apparent "selectivity" observed in this study in fact reflects merely individual differences in imitative competence, rather than active selectivity. We have here important background findings that require the new experiments we report in the following discussion, and are no substitute for them.

11.2.3 Differential Copying of Hierarchical versus Sequential Structure

Imitation might occur at the level of the hierarchical structure that characterizes skills such as foraging techniques among apes (R. Byrne, 1994 and vol. 1, ch. 9). Although the copying of sequential structure described earlier may be an instance of this, it is possible, at least in principle, that it reflects only the copying of a linear, sequential chain of actions, A-B-C, etc. To actually test for the copying of hierarchical structure, we need materials specifically designed for this purpose (Whiten, 2002a,b).

Working with preschool children, we have used a "key-way" "fruit" that requires sixteen component actions to allow a lid to be finally removed to obtain a reward (Whiten, 2002a,b; see also figure 11.3). The sixteen actions can be performed by models in one of two different, hierarchically organized ways. Imagining the sixteen actions as a 4 × 4 array, one can characterize the two different approaches as either "column-wise" or "row-wise." In the column-wise approach, a handle is selected and stabbed into a shaped tablet to make a "key"; this is then inserted into an appropriate lock (figure 11.3), pushing a restraining rod out of the way, which is in turn removed. This process is repeated a further three times with new handles and tablets, until all the restraining rods are removed and the lid can be lifted off. In the alternative row-wise approach, all the handles are picked up and stabbed into the tablets in turn; all the keys are then inserted, and finally all the rods are removed and the lid lifted off. It was found that preschool children were really quite faithful in copying whichever of the two overall approaches they had seen, which provides the first direct evidence of the imitation of hierarchical structure in any species.

However, each of the two sets of subjects had been further subdivided. Half of each group saw the components of the task performed left-to-right and half saw them done right-to-left. Thus, in addition to testing for imitation of overall hierarchical structure, we could examine whether the particular, chainlike sequence of components modeled was copied. We found that in these young children it was not. There was a stark contrast between copying of the hierarchical structure itself and ignoring of the particular sequential chain of component actions witnessed.

Presenting this task to chimpanzees is problematic because its small parts are so easily stolen and chewed! One of us (SM-P) therefore designed

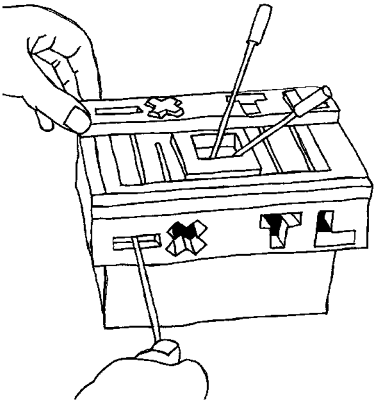


Figure 11.3

"Key-way" fruit for identifying imitation of hierarchical structure. A lid is held on an underlying box by four horizontal rods that can be seen through the transparent lid. One way in which a model opens the fruit is by taking one of the handles from the central cup, stabbing it into a tablet held in a recess at the back of the lid and thus making a key, pushing this key into a correspondingly shaped slot at the front (illustrated here) to eject one of the rods, pulling out the rod thus protruding from the back of the box, and finally removing the key. A similar "column" of actions is performed for each of the shapes indicated (– X T L). In the alternative "row" method, all the handles are first stabbed into all the tablets; then all the keys are placed in the appropriate locks, all the rods are pushed through and taken out, and finally all the keys are removed. The two approaches thus include the same set of sixteen actions, organized into two alternative hierarchical structures ("columns" versus "rows").

another task to test for copying hierarchical structure, built on the same principles as the key-way, but somewhat simpler in that it incorporated only a 3 × 4 array of component actions (figure 11.4). The column-wise approach to this task involves removing a bolt of the kind used in the pin-apple described earlier, folding back the hinged door that had been held shut by the bolt, flicking aside a sliding door, and turning a knurled knob underneath it several times. Once all three columns are completed, a drawer opens, offering a reward. The row-wise approach, of course, involves performing all bolt removals, then all door folds, and so on to overall completion.

Juvenile chimpanzees have shown a significant tendency to follow whichever of the two approaches they have seen (Marshall-Pescini & Whiten, unpublished), which to our knowledge is the first quantitative

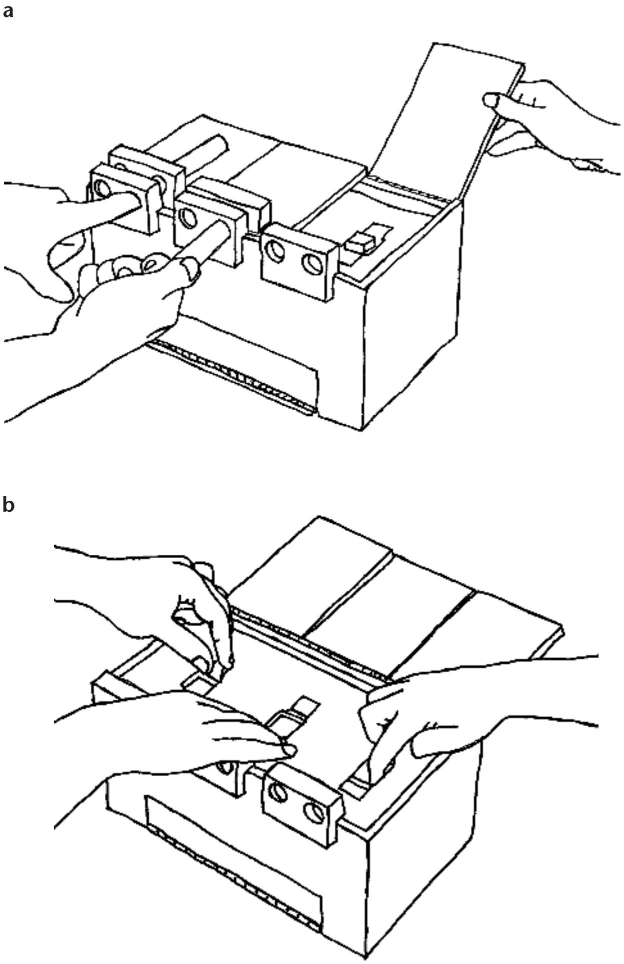


Figure 11.4
Task used for identifying imitation of hierarchical structure in chimpanzees. (*a*) The actions illustrated are poking a bolt through (left), pulling and twisting it out (center), and opening the lid once the bolt is removed (right). (*b*) Additional actions illustrated are flicking the sliding door away (left), flicking it in the opposite direction (middle), and inserting a finger to turn the knurled knob underneath (right). Once all twelve operations are completed, the door at the base drops open to reveal food. See the text for a further explanation of alternative hierarchical approaches to the task.

evidence for copying of hierarchical structure in a nonhuman primate. It thus complements the similar finding for children on the key-way fruit described earlier. There is also a similarity with the earlier study of sequential imitation (Whiten, 1998) in that a significant match emerged only after several trials. However, as in the key-way study, the chimpanzees were exposed to different chains of actions (working left-to-right versus right-to-left) within each of the hierarchical approaches. And like the children, the chimpanzees did *not* copy this specific chain of actions, even though they picked up the higher-level hierarchical structure they saw modeled.

The results of the child and chimpanzee versions of this task thus show a remarkable convergence. In both cases we appear to have selective imitation of hierarchical structure, ignoring sequential chaining of component actions. As before, we must of course consider the possibility that this might be explicable as poor, rather than selective, imitation. However in this case, such an explanation seems most unlikely. We know through experiments with the pin-apple of the kind described earlier that in certain contexts both children and chimpanzees can and do imitate the particular sequential order in which they see a series of actions performed. Accordingly, we seem to have true selective imitation in these studies, with both chimpanzees and children.

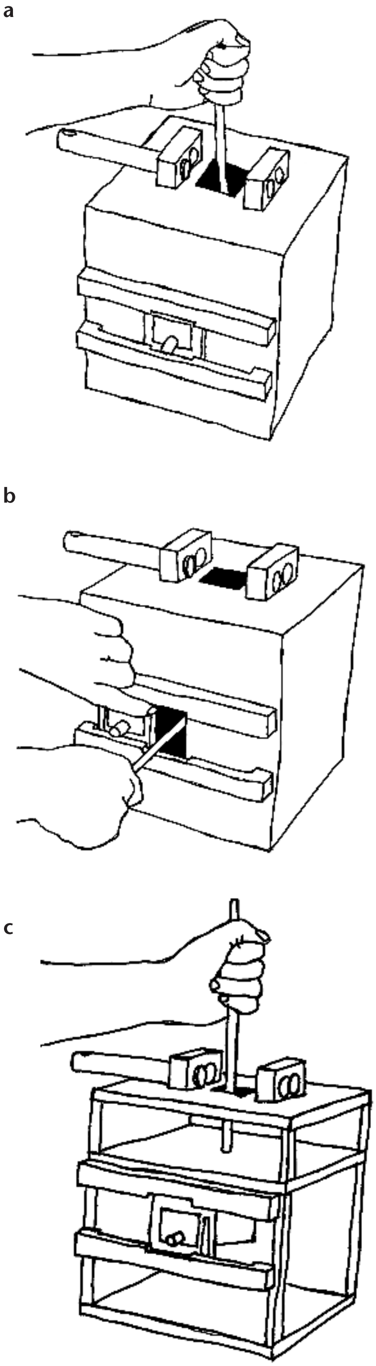
Why might this be? We suspect, in part by intuition in observing the modeled actions ourselves, that the subjects may find it relatively transparent that the left-right order of operation is not critical; one can ''just see'' that it's not going to matter whether one starts on the left or right. By contrast, it may be a more sophisticated operation to recognize that there is an alternative solution to the particular, efficient-looking hierarchical alternative each subject sees. However, this is speculation; and we must remember that in actuality, both the sequential and hierarchical alternatives are arbitrary, so that in purely logical terms there is no reason to copy one and not the other. The device *might* have been built so that its internal structure meant that the particular chain of actions shown *was* the only one that would work. Hence these experiments, in concert with those described previously, leads us directly to a study specifically designed to test whether our speculative interpretations of selectivity are on the right track.

11.3 Selectivity of Imitation Contingent on Recognizing Causal Structure

The interpretations of earlier findings reviewed earlier are not the only foundations for the experiment outlined here. Another important one is a study by Want and Harris (2001 and vol. 2, ch. 8 by Harris and Want). Want and Harris presented preschool children with a horizontal tube containing a reward that could be pushed out using a stick. However, if the reward were pushed in one direction, it fell into a trap; only pushing from the alternative end constituted a correct solution for this task. In one condition of the study, the children were presented with a demonstration of the correct approach; in another, they were first shown an incorrect approach (pushing the reward to the edge of the trap, accompanied with the exclamation ''Whoops''), followed by a correct one. Want and Harris found that 3-year-old children were subsequently more proficient at the task themselves if they had seen the incorrect-then-correct model, than the more straightforwardly correct one. Moreover, these children did not copy the incorrect part of the demonstration they had seen. Accordingly, we have here an apparent case of selective imitation. In the terms of our figure 11.1, the children selected out the causally irrelevant part of the incorrect-then-correct demonstration, presumably because their understanding of causality was sufficient to allow them to recognize it as such.

One of us (VH) conducted a study using 3-year-old children and young chimpanzees that incorporated some principles similar to those of Want and Harris, but had some extra twists. In this experiment, the subjects watched a model ''stab-fishing'' in one of two identically structured boxes. One of these boxes was opaque. The subjects watched as a model took a stick tool, used it to remove a bolt covering a hole in the top of this box, then stabbed the stick down through the hole three times (figure 11.5a). The stick was then removed; a small door on one side of the box was opened; and the stick was finally poked along the tunnel so revealed to fish out a small item of food (figure 11.5b).

The reader might like to imagine how he or she would perform the task given the opportunity. Our prediction is that the approach would be different than that elicited by observing the other version of the task, in which the box is transparent, except for the tunnel concealing the food reward. In this condition, an observer can see that when the stick is stabbed down through the top hole, it merely strikes a false ceiling and does no useful work in relation to the tunnel containing the food (figure 11.5c). We reasoned that after having seen this transparent version of the task, a chimpanzee or child might be more likely to omit the stabbing action in the top hole, assuming they could recognize it as causally irrelevant. In other words, they would veer to the emulation pole of copying shown in figure 11.1. By contrast, in the opaque condition there is less basis for recognizing the stabbing action as irrelevant, and we predicted that here a


a
b
c

more fully imitative copy would be adaptive, and more likely to be performed by both child and chimpanzee.

The key results are summarized in figure 11.6 (Horner & Whiten, 2004). Three-year-old children clearly did not conform to our prediction. Instead, they largely imitated the whole routine they had witnessed, including stabbing in the top hole first, even when they had seen the transparent version of the model. This was true whether they saw the opaque version first or the transparent one first. It even occurred when the children were left alone to attempt the task. The children were not encouraged to imitate in any way, but merely invited to attempt to reach the reward themselves.

By contrast, the chimpanzees did conform to our prediction. Although with the opaque version of the task they did not copy as faithfully as the children did, they clearly implemented a different, more emulative strategy after observing the transparent version of the task modeled. Whether they saw this first or after a series of trials with the opaque version, they were significantly more likely to leave out the irrelevant action in the transparent condition than in the opaque one. We believe this is the first empirical demonstration of such an effect in nonhuman primates and now discuss its implications.

11.4 General Discussion

11.4.1 Adaptive Use of Imitation versus Emulation by Chimpanzees

Most discussion of the evidence for emulation and imitation has focused on whether a particular study of a particular species shows it to be emulating *or* imitating. Implicit in many such analyses is that that species might be characterized as showing one of these, but not the other. For example, Byrne and Tomasello (1995) argued that the claim by Heyes et al. (1992) to have shown imitation in rats might instead result from the rats being emulators. Likewise, Tomasello (1996), reviewing several experimental studies with apes undertaken up to that date, concluded that apes that had

◄ **Figure 11.5**

Task for studing selective imitation. (*a*) Once the top bolt is moved out of the way, the stick is stabbed repeatedly into the top hole of the opaque box. (*b*) The bottom door is then opened (here by sliding to the left) and the stick is used to fish out a reward from a tunnel. (*c*) When the transparent box is used, an observer can see that the stabbing action in the top hole is ineffective, for it terminates on a transparent false ceiling above the reward location.

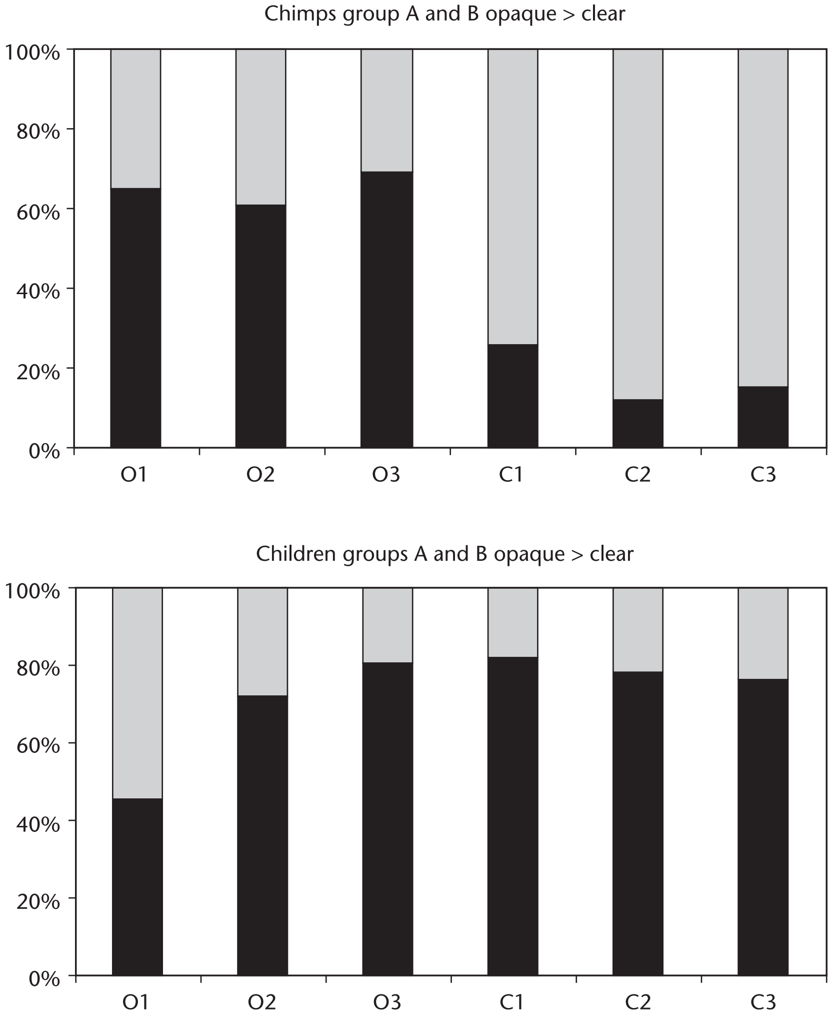


Figure 11.6

Results of the tests for selective imitation, showing percentage of actions first directed to the irrelevant top hole (dark portion of bar) versus causally relevant bottom hole (light portion). (*Above*) Chimpanzees showed a preference for starting with the irrelevant action on the top hole (dark portion of bar) in three trials of the opaque condition (O), shifting, as predicted, to focus more on the final, causally relevant action on the bottom hole once they were switched to the clear (C) condition (other subjects who started with the transparent box showed similar behavior). (*Below*) Young children did not show the shift in selective imitation seen in the chimpanzee subjects; in all conditions, they tended to copy both causally relevant *and* irrelevant components of the task.

not been exposed to human enculturation could be best characterized as emulators and not imitators. Our stab-fishing experiment suggests instead that for chimpanzees at least, aspects of the information available in the model may be selected in (a more fully imitative response) or selected out (a more emulative response) according to the subject's appraisal of the significance of this information. In our experiment, ''significance'' concerned the perceivable, noncausal role of the stabbing action in the top of the transparent box. Further studies will be needed to discover if similar flexibility in social learning applies to other information that might be used to guide the selectivity of copying, such as whether certain components are accidental or intended, an issue already addressed in the case of children (Meltzoff, 1995; Carpenter et al., 1998a; 2003) and beginning to be addressed in primate studies (Myowa-Yamakoshi & Matsuzawa, 2000).

It will be evident that these results lead us to believe the answer to the question, Do apes ape? (Tomasello, 1996) is ''yes,'' but only insofar as this will depend on context. ''Aping'' seems traditionally to carry a connotation of relatively unintelligent mimicking, with little understanding of the meaning of the act copied. Our data suggest that instead, apes may copy intelligently; they will appraise the ''meaning'' of components of an act they see associated with desirable outcomes, such as those perceived as causally connected with such outcomes.

We do not wish to overinterpret what the chimpanzees are doing in making the discrimination about ''causality'' that our results confirm. Povinelli (2000) has reported extensive suites of experiments designed to find out just how much chimpanzees understand about causality. From these he concluded that chimpanzees take into account causality that can be directly perceived, but they do not appreciate underlying physical principles that are unobservable, such as force, which we humans do. Our results are not inconsistent with such conclusions, for the sense of causality that swung the imitation-emulation pendulum for our subjects hinged only on recognizing that (1) the transparent false ceiling blocked effective connection with the food location and/or (2) the stick had to make contact with the food location to have an effective role, two factors we have checked in separate experiments.

In this connection, it is worth putting our results in context by referring to some important bird studies, where we find some of the few other experiments to have examined selectivity in social learning. Palameta and Lefebvre (1985) showed that pigeons would learn by observation to peck through paper covers over food dishes, but they would do this only if the models they witnessed had obtained food in this way, in contrast to models that were observed pecking but gaining no food. Akins and Zentall (1998) have shown a similar effect in Japanese quail. There is a parallel with our own study in that these birds are showing adaptive selectivity, that picks out others' actions that are effective in gaining a desirable outcome. However, although the birds also detect causally relevant actions in this way, they may be doing so only at an associative level (''perform acts seen in others that are associated with feeding''). Our own results cannot be interpreted in this way. Actions on both opaque and transparent boxes were correlated with food reward, as was the stabbing action in both cases. The discrimination made by the chimpanzees must have relied on the cognitive appraisal of causality, at least in terms of the relevant connectivity of tool and food location.

11.4.2 ''Blanket'' Copying by Children

In our stab-fishing experiment, the children differed from the chimpanzees in copying in much more ''blanket fashion,'' persisting in copying the irrelevant actions even with the transparent box, and even when the model left the room to remove social pressure for conformity.[2]

Two kinds of interpretation of such results can be entertained. The first acknowledges that this is not a freak result, but in fact mirrors many others provided by our own and others' research. For example with the pinapple task, as noted earlier, the children tended to copy much more of the task than the chimpanzees, even though they might, as a result, have taken longer to complete the whole task. We are thus led to recognize a real tendency of children, at least in contrast to nonhuman primates, to ''overcopy.'' A plausible explanation for this is simply that we are such a thorough-going cultural species that it pays children, as a kind of default strategy, to copy willy-nilly much of the behavioral repertoire they see enacted before them. Children have the longest childhoods of any primate, much of which is spent in play, practice, and exploration, so there is plenty of opportunity to weed out wrongly assimilated aspects of the actions observed. Overcopying coupled with play might even provide a measure of serendipitous innovation in the culture at large.

A second interpretation acknowledges that there are other findings in the literature that do show selectivity; for example, those of Want and Harris (2001) and Carpenter et al. (1998a) have already been alluded to. So of

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[2] We invite the reader to imagine what kind of interpretations would have been offered by themselves and various theorists in the social learning community if the child and chimpanzee results had come out the other way round!

course we would not wish to claim that our result show that children never exhibit selectivity. Even with our specific task, it becomes an important question as to whether older children—or perhaps even younger ones—will see the social world differently and copy in a less blanket fashion. One factor that may well explain why Want and Harris and Carpenter et al. obtained different results is that the models in their studies marked the irrelevant actions with a vocalization, like "Whoops." Another factor might be that we repeated the demonstrations several times, even before a child made its first attempt. This may have been construed by the child as indicating that the stabbing action was indeed important, perhaps because it appeared necessary rather than inconsequential, or because it was intended rather than accidental. This line of thinking leads to the intriguing possibility that the children copied all they saw done on the transparent box, not because they were less inclined to be selective than were the chimpanzees, but because they were also actively assessing the meaning of what they saw, yet unlike the chimpanzees saw stabbing as a repeated, therefore intended, and therefore likely important component of the task. Further experimental manipulations would be required to examine such possibilities.

11.4.3 Imitation of Sequential and Hierarchical Structure

In discussing our experiments designed specifically to assess the imitation of these aspects of the structure of actions, we noted selective assimilation of hierarchical structure while aspects of sequencing were ignored by both children and chimpanzees. However, the stab-fishing task also casts light on this issue and in fact shows the opposite effect: copying of both hierarchy *and* sequence. Our reasoning about this rests on the conjunction of two of the findings: (1) that in one condition the subjects performed the whole task, but in the other only the second part of it; and (2) that in the full performance they carried out the sequence of actions they had witnessed (i.e., stab in the top hole, then fish in the side hole). Finding (1) shows that the chimpanzees could decompose the task (parse it, in Byrne's, 1999, linguistic analogy; see also vol. 1, ch. 9) and thus perceived its hierarchical structure, and finding (2) shows that they recognized and copied the correct sequential structure when they performed the whole task. One of us has argued elsewhere (Whiten, 2002a) that one reason the concept of program-level imitation (Byrne, 1994) may be misleading is that it conflates what are in principle (and, it seems, in practice) the two separable issues of imitating sequential versus hierarchical structure. However, to the extent that the definition of program-level imitation includes copying both sequence and subroutine structure (R. Byrne & Russon, 1998, p. 677), we believe the stab-fishing results provide the first quantitative evidence for this particular conjunction in a nonhuman species.

Why do we find copying of both sequential and hierarchical structure in stab-fishing, but not in the other tasks we used to investigate this issue? We suggest that the most likely interpretation hinges on the arbitrariness built into the two-action experimental design. In the case of the key-way fruit, for example, it does not matter whether the task is started on the left or the right, and both children and chimpanzees appeared to recognize this. In the stab-fishing task, however, if one recognizes the stabbing as an element to be copied, it can only be done sensibly before the fishing element or it is redundant. Of course, the nature of the experimental design means that in reality, whether the stabbing or the fishing is done first *is* arbitrary to the extent that a subject may perform these in either order, i.e., stab then fish, or fish then stab (and note that likewise, in the key-way task, in reality there are numerous ways to complete the task, yet the subjects tended to use the one demonstrated). Thus the word "sensibly" is important in the earlier sentence; we are not appealing here to arbitrariness in the reality of the task as set by the experimenter, but rather we are making a suggestion about how the subjects are construing the task, and more particularly, why they might rationally apply different rules of selective imitation in each.

11.4.4 Extending the Two-Action Methodology

We end with a methodological point, which given continuing controversies in this field (Caldwell & Whiten, 2002), seems worth emphasizing. The principle of the two-action task has been advocated by many in the field of social learning to be an important tool in discriminating forms of social learning, imitation in particular (e.g., Galef et al., 1986; Heyes, 1996; Zentall, 2001). By contrast, Byrne (2002a) has argued that the approach fails to identify imitation because the tasks are insufficiently novel to do so. It is true that the two-action method has mainly been celebrated by those working on birds and nonprimate mammals and using relatively simple action alternatives, such as pushing a bar to the left or the right, or pecking versus stepping on a treadle. However, this is not an intrinsic limitation in the concept of the two-action method. If novelty is the problem, then it just requires that the two alternative actions modeled (or minimally, perhaps at least one of them) be shown to be "novel" according to some agreed-upon operational criterion, such as that provided by a baseline, no-model condition. More important, the two-action approach need not be limited to a too-myopic definition of action, which limits the alternatives to relatively small differences in the type of bodily actions (e.g., push left versus push right), as Byrne appears to assume.

To the contrary, we hope we have shown that the fundamental approach can be applied with rigor and with interesting results in relation to higher levels of complexity, such as those of sequential and hierarchical structures, and the availability of causal information. In principle, the approach appears to be a powerful way to investigate selective imitation in relation to just about any contrasting aspects of actions, however complex, that can be copied and that we psychologists can imagine.[3]

Acknowledgments

We thank the Biotechnology and Biological Sciences Research Council for funding the recent research by SM-P and VH described here. We are grateful for the exceptional support of Debby Cox, Cherie Montgomery, and the trustees and staff of Ngamba Island Chimpanzee Sanctuary and Wildlife Conservation Trust, where these studies were conducted.

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[3] See comments on this chapter by Galef vol. 1, ch. 12.5, p. 295, and by Jones ch. 12.6, p. 297. For relevant discussion see chs. 6, 16, 17, and 18 in vol. 2, by Harris and Want, Gil-White, Greenberg, and Chater, respectively.

12 Commentary and Discussion on Imitation in Animals

12.1 Imitation in Animals: Function versus Mechanism and the Issue of Novelty

Thomas Zentall on Byrne

Much of the disagreement over what constitutes imitation comes from different origins of the question, Can animals imitate? More specifically, developmental and comparative psychologists typically ask, Can animals imitate as children do, and if they can, by what mechanism do they do it? whereas those who study animal behavior and behavioral ecologists (biologists) more typically ask, Can animals imitate and if they do, of what use is it to them?

In an attempt to integrate these two perspectives, Byrne ventures courageously beyond the narrow confines of the imitation of simple motor behavior typically studied by psychologists, into the complex actions involved in naturally occurring problems that animals encounter. However, he does so without adequately dealing with two important theoretical issues that have dominated the field of animal imitation.

First, Byrne admits that his behavioral parsing model does not speak to the issue of how an observer is able to translate the observed response of another into its own felt, but not seen, behavior (the opaque correspondence problem). At a functional level, it does not matter how an animal that is in the presence of other responding animals comes to respond in a similar way. Thus, for the behavioral parsing model, it does not matter if the mere presence of others increases the likelihood of the target response (social facilitation), or if the response of others draws attention to the objects involved in making the target response (stimulus enhancement), or even if manipulation of the object (e.g., breaking open nuts) shows the observer that nuts can be opened (affordance learning). It only matters that the response has adaptive value. However, to psychologists interested in how animals are able to imitate, these are important alternative mechanisms that should be distinguished from imitation.

Second, Byrne distinguishes between *contextual learning,* in which behaviors already in the animal's repertoire are produced in novel contexts, and *production learning,* in which the behavior or behavioral sequence is not already in the animal's repertoire. The distinction between imitation of familiar and novel responses can be traced to Thorpe (1963). It may not be a useful distinction, however, because in a sense all behavior is an extension of, or generalization from, behavior already in the animal's repertoire. Byrne does not disagree, but he argues that in the case of more complex *sequences* of responses, it can be assumed that the particular sequence has probably never been performed. This assumption is questionable for two reasons. First, one must allow for the fact that the start and end points of the sequence (and perhaps even points in between) are likely to be determined by the nature of the task. More specifically, in the case of Byrne's example, processing of nettle leaves by mountain gorillas, the task must start with picking the leaves and end with placing the leaves in the mouth and chewing them. Furthermore, although the sequence of the remaining responses appears to be arbitrary (e.g., twisting off the stems that have nettles and folding the leaves so that the nettles are not on the outside), some responses may be more easily made before others and thus the order of those responses would also be influenced by trial-and-error learning, rather than imitation. If the probability of the target sequence of responses in the absence of observation of the sequence of responses made by others is not zero, then the distinction between novel and improbable is no longer useful because what Byrne calls contextual imitation could account for these results.

A more useful distinction in defining imitation involves the probability of the occurrence of the demonstrated behavior relative to that of an appropriate control condition. Although some have argued for the use of a predemonstration baseline control (see Anisfeld, vol. 2, ch. 4), typically such a control neglects many of the nonimitative factors mentioned earlier. Instead, a more appropriate control condition is one in which the effects of the response on the environment are the same and only the topography of the response is different (e.g., depressing a lever with a different part of the body). Ideally, the two responses would be selected so that observation of either would greatly increase the probability that the observer would then make a similar response. For example, Akins and Zentall (1996) found that Japanese quail that observed a demonstrator stepping on a treadle to obtain food learned to obtain food themselves by stepping on the treadle, whereas those that observed a demonstrator pecking at a treadle to obtain food learned to obtain food themselves by pecking. Byrne (and others) would argue that both stepping (walking) and pecking were in the observers' repertoire prior to observation, but it is also unlikely that any of the birds had ever stepped on or pecked at anything like the treadle (a small, flat, elevated, platformlike device) used in this experiment. Furthermore, given the anatomy of the birds (they could not see their foot while stepping or their beak while pecking), it can be argued that both responses were perceptually opaque (Heyes & Ray, 2000).

Byrne proposes that this form of imitation should be treated as *response facilitation*. The presumption is that because both behaviors are familiar, observation results in the priming of the brain records of those motor behaviors. Evidence for the existence of mirror neurons that respond similarly to behavior performed and behavior observed supports the possibility of such priming (see Rizzolatti, vol. 1, ch. 1 and Gallese, vol. 1, ch. 3). However, in the case of mirror neurons, the perceptual features of the behavior observed and the behavior performed are generally quite similar (e.g., a grasping response with the hand). Therefore the problem of correspondence is greatly reduced. Furthermore, Byrne suggests that priming as a source of contextual imitation would be unlikely if testing were delayed, and as he notes, we have reported such deferred imitation in Japanese quail when observation and performance are separated by as much as 30 minutes (Dorrance & Zentall, 2001; see also Heyes, vol. 1, ch. 6). Thus we propose that experiments that have used the two-action method provide the best means that we currently have for studying imitation in animals. Finally, if, as Byrne proposes, it is the imitation of a sequence of actions that bestows a special cognitive status on an organism, we have recently found that pigeons show some ability to copy a two-response sequence (stepping on or pecking at a treadle, followed by pushing a screen, either to the right or to the left, that is blocking access to food; Nguyen, Klein, & Zentall, in press).

12.2 Novelty and Complexity: Two Problems in Animal (and Human) Imitation

Birgit Elsner on Byrne

Byrne highlights some aspects of imitation that have been neglected by researchers thus far: the observational learning of novel, complex, action sequences. These behaviors are especially relevant in animals, but also in everyday actions by humans. If individuals were able to acquire complex skills by observation, they could learn from merely watching others' behaviors without needing explicit modeling. In the experimental investigation of imitation, novelty and complexity are difficult to define and to control, and this is probably the reason why evidence for production learning is weak at present. However, I doubt that Byrne's proposal to turn to observational data would overcome the problems of novelty and complexity. Moreover, although Byrne's examples of plant feeding techniques show that great apes perform standardized, remarkably complex actions, it remains unclear whether these behaviors actually represent observational learning of novel skills, and whether the acquisition of complex behaviors is actually driven by different processes than the acquisition of simple actions.

12.2.1 The Problem of Novelty

To Byrne, novelty will prove to be a cardinal requirement of imitation. However, the range of behaviors he accepts as being "novel" seems to be quite narrow. For example, he claims that nothing new is being learned in two-action experiments because the copied movements are in the individual's repertoire and are just applied to new situations. The question is, however, how individuals could imitate behaviors that are not in their repertoire. This becomes especially obvious in imitation by infants. A 9-month-old who has difficulty in releasing a small object from her hand will not imitate putting a ball in a cup (Elsner & Aschersleben, 2003). Nevertheless, deferred imitation of novel behaviors is a milestone in cognitive development (Piaget, 1951/1962). So the problem is how to define "novelty."

According to Meltzoff (1988a), an act can be novel in six senses: (1) It has never been seen, (2) performed, or (3) imitated by the infant before. (4) It is not a well-practiced game. (5) It has not been performed with a particular object before. (6) It occurs with near-zero probability in spontaneous play. The experimental evidence for "true imitation" fulfills at least criterion (6). Nevertheless, Byrne proposes to turn to observational data for evidence of imitation of novel, complex actions. But what is "novel" in the plant feeding techniques? Because the components of the action should be highly familiar to apes (e.g., stripping, folding), the novel part is the *organization* of the components, and this adds a seventh sense to Meltzoff's definition.

Byrne's second concern about the two-action method is that "true imitation" involves only contextual learning, whereas plant feeding requires the acquisition of a new behavioral complex, and thus production learning. Yet, according to Janik and Slater (2000), rearranging familiar, pre-existing signals into new combinations is *contextual* learning: "Production learning refers to instances where the signals themselves are modified in form as a result of experience with those of other individuals" (2000, p. 2). If Byrne wants to transfer these definitions to plant feeding, it should not only include rearranging existing actions into novel sequences but also the addition of structurally different elements. However, the problem with the observational data thus far is that we know only the outcome of the learning process. If Byrne could present observations of juvenile gorillas who watched skilled models and added acts to their plant processing that they had never done before, this would be stronger evidence for production learning. But as long as we do not know how the action sequences are acquired, it is hard to accept the observational data as evidence for production imitation of novel behaviors.

12.2.2 The Problem of Complexity

Byrne's model provides an important theoretical contribution on how apes and humans could segment the fluid streams of movements they are confronted with while observing other agents. Although I highly value the model, I am skeptical about the idea that mirror neurons are the neuronal basis of behavior parsing (BP). Mirror neurons become active when a monkey observes a given action and when it performs that action (Gallese et al., 1996). Thus, all that mirror neurons can do is match an observed action to an action that is in the individual's repertoire. This is problematic in two senses. First, how could an individual parse an action that is *not* in its repertoire? To understand an action, an individual needs additional neurons that can process novel actions at least perceptually. Second, mirror neurons allow only action-level imitation; the observer performs the action he has seen. However, gorillas imitate behavioral organization on a program level, and this cannot rely on kinesthetic-visual matching, but has to take into account other aspects of the action sequence.

Byrne proposes that a string comparison enables the ape to detect the underlying structure of the observed behavior. However, a string comparison requires high cognitive capacity. The ape has to store the parsed sequences, decide which sequences lead to the same end, and then has to compute the statistical regularities within and between the components of these sequences. The question is whether and how great apes can actually do all that. An alternative idea would be that individuals parse behaviors, not in terms of movements, but in terms of subgoals.

By speculating that apes should be sensitive to the distribution of pauses in execution, Byrne highlights the role of functional modules within the sequence. D. Baldwin and Baird (2001) have shown that 10- to 11-month-old human infants parse continuous everyday actions along "intention boundaries." They are surprised if an action is interrupted before the subgoal has been achieved. Similarly, Bauer and Mandler (1989) found that 19- to 31-month-old infants process the causal structure of action sequences. Thus, human infants process observed sequences of actions in terms of steps that lead to a final goal.

Concentration on subgoals reduces the complexity of behavior and would explain both the consistent ordering of the plant feeding sequences (which is guided by the succession of subgoals) and the idiosyncratic variation at lower hierarchical levels. Each animal may perform the parsed action in a slightly different fashion, but all animals obtain the same subgoal. However, this does not imply that apes have to understand the causality of the actions. They only have to memorize that action *x* leads to environmental state *y*, no matter why. Parsing behaviors along their subgoal structure would help the ape to determine whether its own action will lead to the observed consequence.

Taken together, the acquisition of complex behaviors by observational learning is an important issue in imitation research. The question is, however, whether we should assume separate processes for the acquisition of simple and complex behaviors. It is hard to imagine that an ape copies an observed novel sequence as a whole after extensive behavior parsing and string comparison. It seems more likely that the individual would begin with copying subgoals of the sequence by performing single actions, and finally arrive at performing the whole sequence by combining observational and trial-and-error learning. Taken this way, learning a complex skill may not be that different from the imitation of single actions investigated with the two-action method. The same processes of subgoal-oriented observational learning may help the individual to either achieve one goal by applying a single action from its repertoire in novel circumstances, or to achieve a hierarchical goal structure by rearranging multiple actions.

12.3 Do Parrots (and Children) Emulate Speech Sounds?

Richard W. Byrne on Pepperberg

Almost single-handedly, Irene Pepperberg has changed our view of vocal copying by parrots from a relatively trivial curiosity to an important window into the cognition of another species and a valuable foil for interpreting quasi-linguistic data from nonhuman apes. Whereas the average pet parrot blindly copies speech sounds, Alex and the other African Grey parrots exposed to the model/rival method use English words to answer questions and to make requests and comments. It seems that several aspects of the model/rival technique are important, including speaker-hearer role reversal, corrective feedback and demonstration, and constant social interaction; when *any* of these aspects are altered, the parrots fail to learn instrumental, referential use of human speech. This should serve as a reminder of how likely it is that our methods of examining animal cognitive abilities are not yet optimal, and that we are probably underestimating their abilities. In her chapter, Pepperberg has for the first time evaluated these data for what they tell us specifically about imitation.

She makes a telling comparison with learning birdsong, which is often regarded as the canonical form of vocal imitation. Pepperberg notes that the biological constraints that guide song learning, the limitations on what can be learned, and the fact that what is acquired is seldom quite the same as the model, make it difficult to claim most song learning as imitation at all. In contrast, when the vocalizations of *another* species are learned, evolved predispositions do not muddy the water, and we can safely attribute any close resemblance of the vocalization to imitative copying. The same has been found in motor learning. While we may strongly suspect that wild great apes learn many of their everyday skills by imitation, when those skills are natural ones for the species, it is very hard to be sure. In contrast, when captive great apes copy human actions, we can be sure that the actions were not somehow latent parts of the animal's natural repertoire, nor was their acquisition guided by evolved constraints (e.g., Russon & Galdikas, 1993, 1995).

Pepperberg makes a sharp distinction between Alex's imitation, which is referential and purposeful, and the ''mere mimicry'' of the pet parrot—following Tomasello in this dismissal (e.g., see Tomasello et al., 1993a). How such a classification would apply to birdsong is unclear, since song is clearly functional in many ways yet is not referential in its detailed content, and it is sometimes acquired by mimicry of more-or-less random environmental sounds, including ringing telephones, chainsaws, and car alarms. Pepperberg and Tomasello agree in treating mimicry as less cognitively demanding than imitation, but this seems to confuse the copying process (which is surely no less difficult in mimicry, or indeed different from it) with any subsequent use of the signal in cognitively sophisticated communication.

Pepperberg summarizes detailed acoustic analyses, which convincingly show that Alex and his kind produce human speech much the same way as we do: filtering (by cavity resonance) source vibrations (of the syrinx, in his case). This lays to rest the more exotic idea, previously current, that independent sounds from the two sides of the syrinx interfere to produce a composite that resembles human speech. It also brings to the fore the central question: Are these parrots *imitating* speech, or copying it in some other way? Tomasello and his colleagues, following D. Wood (1989), have introduced a distinction between imitation *sensu stricto*, in which movement patterns are copied by observation, and emulation, in which what is copied are the results of actions, not the way in which they are produced (Tomasello, 1990; Tomasello et al., 1993a). Since the means of production are limited in any given species, when a result is attained by emulation, the method chosen will very often coincidentally be the same as that used by the model, and human observers may mistake the process for one of imitation. Alex, of course, cannot observe the movements of the human vocal chords in the supralaryngeal tract, and what he is copying with such fidelity is the result of those movements. By Tomasello's definition, his copying therefore reflects emulation, not imitation. (Note that Pepperberg uses the term "emulation" for "reorganization of sounds to create new labels," which would seem rather different.)

But surely, children can no more see the movements of adults' vocal tracts than can parrots. Should what they do also be described as emulation? In the sense of imitation beloved of comparative psychologists (e.g., Heyes, 1993) and sometimes called true imitation—characterized by rather detailed, element-by-element matching between model and mimic—the answer is probably "yes." However, there is more to it than that.

A child's copy of an adult's word is by no means an exact match; it differs in a distinctive way. All vowels are shifted upward because children have smaller vocal tracts. Hearing a child speak, adults automatically correct for this shift, in effect modeling the child's supralaryngeal tract, and correctly hear the vowel phonemes intended. Moreover, if the "real" adult vowel sounds were artificially inserted into the child's speech, we would hear them as different vowels or even just noises. This shows that when a child copies an adult's word, the process is not a simple, echoic one; the spoken word is analyzed or parsed into components, and the child then generates its own, synthetic version. Children's phonemes are produced the same way as those of adults, but they do not sound the same because of the difference in vocal tract size. Thus, when children copy adult words, the process is clearly not emulation, in the sense of copying a result, but is better described as a sort of imitation. Specifically, it is *program-level imitation* (R. Byrne, 1994, 1998b; R. Byrne & Russon, 1998), a synthetic process in which a novel organizational structure of behavior is learned by perceiving the organization within another individual's behavior, and then copying the relevant section—building the same structure out of component elements that are already within the repertoire.

Evidently Alex can parse human speech at the words-within-sentences level, since he answers questions in ways that show he understands them. (Probably, then, he could imitate the sentences by resynthesizing the structure he perceives, out of words.) But I am not sure whether Alex's copying of human speech shows any evidence that the words themselves have been acquired by program-level imitation, as in the case of a young child. Careful examination of the details of his vocalizations for any comparable evidence of program-level imitation will be needed, and the result will throw new light on how Alex perceives the words he uses.

12.4 Some Reflections on Imitation in Human Language

Martin J. Pickering on Pepperberg

Human language makes use of a great deal of largely automatic imitation and is an ideal example of an application of current theories of imitation. I start by reviewing imitation-related work in human dialogue, and then relate this to Pepperberg's fascinating chapter. Given the current realization of the central importance of imitation to theories of mind and behavior, it is striking how little crosstalk there has been between theories of imitation on the one hand and cognitive psychology and psycholinguistics on the other. By drawing on some issues raised by Pepperberg, I hope to show how this connection can be made.

Most psycholinguistics has concentrated on isolated acts of production or comprehension, where there is little room for imitation. However, the most natural and basic form of language is dialogue, and it is quite clear that it involves a great deal of imitation. Studies using corpora show that it is highly repetitive in many ways (e.g., Tannen, 1989). In controlled experiments, interlocutors tend to "entrain" on referring expressions, so that if one refers to an object as a "sofa" or a "couch," the other will normally use the same expression (Brennan & Clark, 1996). They also entrain on particular "situation models," so that if one interlocutor refers to her position in a maze as "I'm in E4," the other will tend to say "I'm at A5," and will count in the same way (e.g., letters = columns, starting from the left); but if the first speaker says "I'm at the T-shape," the other might say "I'm at the L on its side" (Garrod & Anderson, 1987). Explicit negotiation is extremely rare, instead, interlocutors tend to imitate each other directly.

There are also strong tendencies to imitate grammatical form. Branigan et al. (2000) had interlocutors take turns describing pictures to each other (and in finding the appropriate picture in an array). One speaker was actually a confederate of the experimenter and produced scripted responses, such as "the cowboy offering the banana to the robber" or "the cowboy offering the robber the banana." The syntactic structure of the confederate's description strongly influenced the syntactic structure of the experimental subject's description, even when lexical items were not repeated. Interlocutors are of course unaware that they are imitating each other's grammar.

All this provides clear evidence that an automatic process of imitation occurs, and that it takes place at a range of different linguistic levels. This is particularly useful for theories of imitation because psycholinguistics draws upon very precisely defined levels of representation (e.g., syntax, semantics, the lexicon), so that we can say exactly what is being imitated. It also shows how important imitation is to real interactive language, simply because the effects are so strong (e.g., people find it quite hard not to refer to objects in the way that their interlocutor has just done). Pickering and Garrod (in press) argue that dialogue "succeeds" if interlocutors converge on the same understanding of a situation, and that imitation (which they call alignment) is the fundamental mechanism leading to such success. Dialogue therefore seems to involve a "perception-behavior expressway" at a range of linguistic levels (Dijksterhuis & Bargh, 2001).

Participants in a dialogue differ in their "status," so that a speaker seems to share a closer relationship with his or her addressee than with someone who is not currently being addressed, and indeed addressees seem to imitate speakers more than other people do. But it is interesting that experimental participants imitate speakers even when the speakers have not addressed them (Branigan et al., unpublished). Such a situation appears to occur in Pepperberg's model/rival training where the parrot watches an interaction between people. It is interesting that imitation appears to require that the trainers exchange roles, because this is clearly in keeping with forms of natural dialogue where a nonaddressee is "listening in" on a conversation or where two interlocutors are speaking to each other, but for the benefit of an audience (as in television interviews). We do not know precisely how forms of multiparty interaction differentially affect linguistic imitation; Pepperberg's studies may provide some insights into such effects.

It may also be of interest that intrinsic reinforcers are so necessary for learning. It is reasonable to argue that the reward that occurs during most dialogue involves successful understanding (either personal understanding or realization that one's interlocutor has understood one). If so, understanding can perhaps be regarded as an intrinsic reinforcer, for the obvious reason that what is understood is the content of the dialogue. If an interlocutor received a reward for successfully participating in a dialogue, but successfully communicating a message was not really the interlocutor's goal (e.g., in an oral examination of linguistic competence), then imitation might be less likely.

Pepperberg's classification of levels of imitation is particularly interesting because, as she says, language involves considerable reference, functionality, and social interaction, and must involve higher-order imitation. She therefore suggests that it must be very different from the unconscious replication of others' motions in social settings (Chartrand & Bargh, 1999). It is not, however, exactly clear whether imitation needs to be improbable. I think that this depends on precisely what is being imitated and what is regarded as improbable. As I have said, interlocutors tend to refer to objects in the same way. If it is 60% likely that I will refer to an object as a "sofa" on first mention, but 90% likely after my interlocutor has called it a sofa, then this is surely imitation, even though it is not improbable. In contrast, it is of course extremely unlikely that I will utter "sofa" at a particular point, or that I will utter "sofa" with a particular set of acoustic characteristics. That said, the suggestion that most forms of linguistic imitation are higher order is almost certainly correct.

Overall, the connection between vocal imitation in Grey parrots and imitation in human dialogue may seem a distant one, but I suspect that some common principles relating to levels of imitation, type of social interaction, and perhaps nature of reinforcement can be found. I also hope to have demonstrated that studies of imitation, whether in humans or nonhumans, need to address the question of exactly what is being imitated. In this respect, linguistic imitation is particularly helpful because the levels of representation involved are (fairly) well defined.

12.5 Breathing New Life into the Study of Imitation by Animals: What and When Do Chimpanzees Imitate?

Bennett Galef on Whiten, Horner, and Marshall-Pescini

It took a hundred years, more or less, for behavioral scientists to come even close to a generally accepted demonstration of learning by imitation in any nonhuman animal (Galef, 1998). Whiten et al. now take it for granted that he, and others, have provided compelling examples of imitation in chimpanzees. Consequently, Whiten has moved on to a new stage in the study of imitation. He asks, not whether chimpanzees can imitate, but what chimpanzees do imitate (acts, portions of acts, sequential structures of acts, hierarchical structures of complex sequences of acts), under what conditions chimpanzees imitate, and in what ways, if any, imitation differs in chimps and children.

Well, have they done it? Have Whiten et al. demonstrated imitation in chimpanzees? Personally, I am convinced that if the present evidence of imitation by chimpanzees in two-action procedures is replicated in other laboratories (and there is every reason to believe that it will be), the answer is "yes." Imitation in our great ape cousins will have been demonstrated.

We skeptics have thrown challenge after challenge to those claiming to demonstrate learning by imitation in animals. Happily, one after another those challenges have been overcome. It would be churlish to continue to demur, without solid grounds for demurral. The view that evidence of imitation is unacceptable unless an "imitated" act is novel (see Pepperberg, vol. 1, ch. 10) seems to me to foreclose the possibility of demonstrating imitation in species other than those that, like African Grey parrots, can produce an effectively infinite number of distinct outputs. We have no way of knowing whether an act "imitated" by an animal with a restricted behavioral repertoire is truly novel or a modification of a familiar act.

Why were we skeptics so hard to convince? It is not, as some have implied, that those who refused to accept early evidence of imitation in apes had a philosophical commitment to an unbridgeable gap in intellect between humans and apes. Nor are we unreconstructed radical behaviorists, unable to accept evidence of cognition in animals. Rather, until recently, the evidence for imitation in apes was not compelling (Galef, 1988), and if the scientific community were to accept weak evidence of imitation in animals, there would be no motivation to seek stronger evidence. In my view, if the field of social learning is to continue to move forward, as it has so remarkably for the past 30 years (Galef, 1998), it will do so only by parsimonious interpretation of strong evidence.

Whiten et al.'s chapter makes a convincing and substantial contribution to that forward momentum. It celebrates the opening of a new era in studies of imitation, the importance of which can best be understood in historical context.

Nineteenth-century naturalists considered imitation to be characteristic of women, children, savages, the mentally impaired, and animals, all believed to have little ability to reason for themselves (Darwin, 1871; Romanes, 1884; C. Morgan, 1896). Creative problem solving, what we today call individual learning, was considered the hallmark of rational minds and was believed to be more or less restricted to mature European males who, because they could reason, only infrequently needed to imitate.

In the late 1890s, Edward Thorndike (1898), among others, started to see things the other way round. Thorndike felt, as most do today, that imitation required cognitive abilities beyond those needed to learn for oneself about environmental contingencies.

As is well known, Thorndike (1898) was unable to find evidence of imitation in the chickens, cats, dogs, and monkeys that he brought into his laboratory, though all learned by trial and error. He interpreted this failure of animals to imitate and their ability to learn by trial and error as revealing animals' inability to manipulate representations to solve problems. His views formed the basis of the behaviorist revolution.

The continued search for evidence of imitation in animals for the first 70 years of the twentieth century reflected an implicit questioning of the behaviorist *Zeitgeist*. For, in the Thorndikian view, if animals could imitate, then they must be able to manipulate representations.

The antibehaviorist revolution (Baars, 1986) of the past 30 years led to broad acceptance of the view that the behavior of animals as lowly as pigeons and rats is supported by cognitive activity. Consequently, the quest for evidence of imitation in animals lost its theoretical rationale in the search for evidence of animal cognition. The quest became a somewhat intellectually hollow, self-perpetuating enterprise.

That is why it is particularly important that Whiten and his colleagues have taken the next step. They have moved study of imitation in animals beyond an atheoretical, autonomously motivated search for evidence of a phenomenon to ask what is imitated, who imitates, and under what conditions is imitation most likely to occur. Such investigations have already breathed new life into a classic problem area in animal psychology that had been stagnant for decades.

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12.6 Why Don't Apes Ape More?

Susan Jones on Whiten, Horner, and Marshall-Pescini

The larger context of the research by Whiten, Horner, and Marshall-Pescini is the question of the phylogenetic origins of imitation. A cross-species comparative approach to this question can't help but be interesting to developmentalists like myself. I want therefore to comment on this broader aspect of the work instead of on the specific issue of whether chimpanzees are selective in their imitating. This is a bit hard on the authors, since the way they address the latter question is also interesting and perhaps more successful. However, it is what chimpanzee imitation can tell us about the origins of our own imitative behavior that I think may be of primary concern to many readers.

Actually, I do not think that much can be learned about the similarities and differences between the mechanisms underlying chimpanzee and human imitation in the kinds of studies reported here. Although in all of their comparative work the researchers model the same behaviors for the two species and then measure the same imitative responses, the chimpanzees and children are never really facing the same tasks. The two species come into the experiments with very different histories (including, for example, different amounts of experience with Plexiglas food boxes with complex fasteners) and ways of construing events in those histories that are likely to differ in unspecified but significant ways. The chimpanzees and children are on different cognitive developmental trajectories, have been on them for different lengths of time, and are moving along them at different rates. For at least these reasons, the tasks cannot be comparable for the two species, and thus it is not clear how similarities and differences in their rates and types of behavioral copying are to be interpreted.

What is clear and very interesting in this work is the revelation that imitation plays such different roles in chimpanzee and human lives. I am not referring here to the (unexplained) rigidity of the human children's copying versus the less faithful but perhaps more efficiently functional copying of the chimpanzees. Instead, I refer to differences in how common and how important imitation seems to be in the everyday behavior of each species.

I was surprised to learn how difficult it has been to demonstrate that chimpanzees do in fact imitate at all. And although that point seems to be settled, it is still striking that the copying that chimpanzees do do (at least in captivity) seems so unnatural to and effortful for the animals. Spontaneous imitation is apparently not observed among captive chimpanzees. And the copying elicited in experiments always seems to be extrinsically motivated, for example, by the prospect of special food rewards. Even then, the imitation that results is typically partial, which might be because it is selective, as the authors argue. However, it may also be because chimpanzees are not only not inclined to imitate, but are also just not very good at it.

In contrast, spontaneous imitation is easy to find in human behavior. It's everywhere, across ages and across cultures. And it does not seem to be tied at all (or at least not at all tightly) to any particular biological functions. Humans from an early age may learn clearly functional things through imitation: how to cross a busy street, pronounce a word, use a spear-thrower, or grind corn. But imitation can also occur in the service of just about any of the motivations that humans experience. It often looks intrinsically rewarding; toddlers touch their foreheads to a table just because it's their turn to do so. It can be done for a wide range of social purposes; think of how you learned to dance or to extend or accept an invitation to dance. Human imitation is often playful. And any parent with more than one child knows that imitation can be used as a method of torture. So, imitation is a very flexible and effortless multipurpose kind of behavior in humans.

The big comparative questions, then, would seem to be, first, how to account for the qualitative differences in the nature of chimpanzee and human imitation, and second, what that account might tell us about the nature of imitation as observed in each species. There are, of course, a variety of approaches to these questions. Until recently, one entirely respectable approach would have been to look for commonalities and differences in imitation by chimpanzees and humans. The commonalities might be attributed to a common hominoid ancestor, or perhaps to parallel evolution of similar mechanisms for dealing with similar environmental challenges. The differences might be attributed to selective pressures encountered since the two species diverged. The expectation would be that imitation in the nonhumans would be more limited, fragile, and harder to find than in humans (as it doubtless is) because the human imitative capacity, like so many other human capacities, is more highly evolved.

The trouble with this kind of approach is that it is associated with a highly questionable sort of folk psychology that posits the existence of modular cognitive and behavioral capacities that can be inherited as units. Historically, attributing behavior to innate modules has been a convenient way for psychologists to beg the explanatory questions. Now, however, neuroscientists have developed the tools to begin looking for these modules in human brains and they are not finding them. And while the evidence for innate behaviors remains poor, evidence for alternative ways of explaining our observations (for example, from connectionist models) becomes more and more compelling (e.g., Elman et al., 1999).

I would therefore like to argue for a different question and a different approach to cross-species comparisons of imitative behavior. The question is, What common processes are at work in different instances of imitation? The approach is developmental. Unfortunately, I cannot point to a model in human developmental psychology. We who study humans have a very long way to go to account for the instances of imitation we see in human children. Contrary to widespread belief, however, I would argue that no inborn imitative capacity has been shown or will be shown to exist in humans (Jones, 1996, 2001). Therefore, I think there is a developmental story to tell.

Imitation seems just as unlikely as any other complex, flexible behavior to turn out to be a unitary or modular capacity. That means that imitation is unlikely to be something that is inherited. It seems much more likely that specific instances of imitation are produced by, or "emergent from," some combination of subunits of different skills and different kinds of knowledge, each with its own developmental history. A number of those components may well be learned in the typical human caregiver–infant relationship. And one product of some subset of those acquired components may be a general-purpose ability to copy the behavior of others.

Two apparently unrelated bits of knowledge seem relevant here. First is the fact that mothers across different cultures imitate their babies and in particular that they imitate the babies' vocalizations (e.g., Parton, 1976; Papousek & Papousek, 1989; Kokkinaki & Kugiumutzakis, 2000). So babies have months of experience of face-to-face interaction in which imitation is demonstrated to them in a turn-taking situation. And during those months, they begin to imitate the sounds their caregivers make. But the caregiver's imitation comes first.

Second is a bit of information about those uncommon humans who do not follow the normative developmental course (whatever that is) to free and flexible imitative abilities. I refer to the subset of autistic children who do not imitate. The failure to imitate, along with other cognitive deficits in autism, is often studied as one among many symptoms of the lack of a "theory of mind" and this lack is often made to sound like the result of a missing module.

However, many years ago Ovar Lovaas at the University of California at Los Angeles worked out a way to teach autistic children a wealth of different things using discrete trial training (e.g., Lovaas, 1987; Lovaas & Buch, 1997). And his very effective intervention starts with teaching the autistic child to imitate. Through Lovaas-inspired discrete trial training, many, many autistic children have learned to imitate first one specific behavior and then another. After learning to imitate some number of individual behaviors, many autistic children have shown a more general copying capacity. Some of these children have then gone on to master language, false-belief tests, and all kinds of other things.

The relevant point for the present discussion is that imitation can be learned. This suggests that imitation may in fact usually be learned, in the usual course of development. Or put another way, some combination of behavioral experiences, expectations, awareness, and knowledge of self–other physical and cognitive and motivational similarities, as well as other kinds of knowledge may occur or emerge in development, and may combine to enable and motivate behavioral copying. So now, what if human children actually do begin to learn to imitate in the context of thousands of social exchanges with their caregivers? Well then, the poor chimpanzee is at a distinct disadvantage unless someone imitates thousands of his actions from an early age. In short, I wonder if what the chimpanzee needs to develop a much stronger and more obvious imitative ability is not several million more years of evolution, but instead a large dose, administered early, of appropriate (though not typical for the species) experience.

Perhaps then, someone ought to use discrete trial training to teach young chimpanzees to imitate first one behavior and then another and another. Whoever does it should teach imitation for its own sake rather than as a means to another experimental end. Then they should go on to test for generalization of the learned imitation, and they should look for the emergence of an imitative motive in instances of spontaneous imitation. I think the results of this kind of enterprise are potentially fascinating, and the contemplation of such an enterprise is potentially important to anyone interested in how behavior works in any species.

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