

Imitation, Empathy, and Mirror Neurons

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Abstract

There is a convergence between cognitive models of imitation, constructs derived from social psychology studies on mimicry and empathy, and recent empirical findings from the neurosciences. The ideomotor framework of human actions assumes a common representational format for action and perception that facilitates imitation. Furthermore, the associative sequence learning model of imitation proposes that experience-based Hebbian learning forms links between sensory processing of the actions of others and motor plans. Social psychology studies have demonstrated that imitation and mimicry are pervasive, automatic, and facilitate empathy. Neuroscience investigations have demonstrated physiological mechanisms of mirroring at single-cell and neural-system levels that support the cognitive and social psychology constructs. Why were these neural mechanisms selected, and what is their adaptive advantage? Neural mirroring solves the “problem of other minds” (how we can access and understand the minds of others) and makes intersubjectivity possible, thus facilitating social behavior.

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INTRODUCTION

Although mimicry is a pervasive phenomenon in the animal kingdom, imitation certainly achieves its highest form in humans. Past authors—for instance, de Montaigne (1575), Adam Smith (1759), Poe (1982), Nietzsche (1881), and Wittgenstein (1980)—have often associated imitation with the ability to empathize and understand other minds. The evolutionary, functional, and neural mechanisms linking imitation to empathy, however, have been unclear for many years. Recently, there has been a convergence between cognitive models of imitation, social psychology accounts of its pervasiveness and its functional links with empathy and liking, and the neuroscience discoveries of neural mechanisms of imitation and empathy. This convergence creates a solid framework in which theory and empirical data reinforce each other.

Hebbian learning: associative learning is implemented by simultaneous activation of cells that would lead to increased synaptic strength between the cells

Among cognitive models of imitation, the ideomotor model and the associative sequence learning model seem to map well onto neurophysiological mechanisms of imitation. The ideomotor model assumes a common representational format for action and perception, whereas the associative sequence learning model puts at center stage Hebbian learning as a fundamental mechanism linking sensory representations of the actions of others to motor plans. Furthermore, social psychology studies have documented the automaticity of imitation and mimicry in humans, a feature that also maps well onto some recently disclosed neurophysiological bases of imitation.

This review discusses cognitive models, social psychology constructs, and neural mechanisms of imitation under the hypothesis that these mechanisms were selected because they offer the adaptive advantage of enabling the understanding of the feelings and mental states of others, a cornerstone of social behavior.

COGNITIVE MECHANISMS OF IMITATION

The Ideomotor Framework of Imitation

Theories of action can be divided into two main frameworks. The most dominant framework may be called the sensory-motor framework of action. It assumes that actions are initiated in response to external stimuli. In this framework, perception and action have independent representational formats. Stimuli must be translated into motor responses by stimulus-response mapping mechanisms. This framework has generated a large literature and elegant experimental paradigms, as for instance the work on stimulus-response compatibility (Hommel & Prinz 1997, Proctor & Reeve 1990). Stimulus-response translational mechanisms, however, do not easily account for the similarity between the observed action and the action performed by the imitator that is required by imitation. Indeed, one of the main problems of imitation often discussed in the

literature inspired by sensory-motor models is the so-called correspondence problem (Nehaniv & Dautenhahn 2002). This problem can be summarized with the question: how is the sensory input from somebody else's action transformed into a matching motor output by the imitator?

For the ideomotor framework of action, the correspondence problem of imitation is not a problem at all. Indeed, the ideomotor framework assumes a common representational format for perception and action, an assumption that makes translational processes between stimuli and responses rather unnecessary. The roots of the ideomotor framework were established by the work of Hermann Martin Lotze (Prinz 2005) and William James (1890). The starting point of actions, for Lotze and James, is not a response to a sensory stimulation, but rather the representation of the goal that the agent intends to achieve. When an intention is unchallenged by a conflicting one, it activates the representation of the intended goal and the motor plan necessary to achieve it. The coactivation of the intended goal and the motor plan required to achieve it—according to the ideomotor framework—is the result of our experience. We have learned the effects of our own actions, and we expect certain effects when we perform certain acts. This previous learning makes it possible that just thinking about the intended goal automatically activates the representation of the action necessary to obtain it. Thus, when I think about rebooting my computer, I automatically activate the representation of the finger movement necessary to press the appropriate key.

The ideomotor framework naturally accounts for imitation. According to this framework, when I see somebody else's actions and their consequences, I activate the representations of my own actions that would produce those consequences. Here, consequences are construed in a very broad sense. For instance, a simple finger lifting has multiple perceptual consequences, among them the sight of the finger lifting. Thus, simply watching somebody else lifting a finger should activate my own mo-

tor plan to lift the same finger. Brass and colleagues tested this hypothesis in elegantly simple experiments (Brass et al. 2000, 2001). Subjects were shown two movements of the index finger from the same starting position. In half of the trials the finger would move upward, and in the other half it would move downward. Subjects were instructed to respond as fast as possible using their own index finger. Within each block of trials, subjects were instructed to use always the same motor response, either an upward or a downward movement. Thus, although perceptually subjects were seeing both upward and downward movements, motorically they were only executing one of the two movements. Given that response selection was not required, the identity of the stimulus was completely irrelevant for the initiation of the motor response. Here, the sensory-motor framework would predict similar reaction times for responses that were identical to the stimulus (e.g., upward motor response for a stimulus showing an upward finger movement) and for responses that were different from the stimulus (e.g., upward motor response for a stimulus showing a downward finger movement). In contrast, the ideomotor framework would predict faster reaction times for motor responses identical to the stimulus compared to motor responses different from the stimulus. The results demonstrated a large chronometric advantage for responses identical to the stimuli, in line with the predictions of the ideomotor framework (Brass et al. 2000, 2001).

The ideomotor framework also predicts that goals have higher priority than movements in imitation. Imitation experiments in children have confirmed this prediction. In one of these experiments (Bekkering et al. 2000), children and experimenters were sitting on the opposite sides of a desk. In half of the trials the experimenter would place her or his left hand on the left side of the desk (left ipsilateral movement) or on the right side of the desk (left contralateral movement); in the remaining half of the trials the experimenter would place her or his right hand on the right side of the desk (right ipsilateral movement) or on the left side of the desk

Associative sequence learning: imitation is based on associative, Hebbian-like learning, creating “vertical links” between sensory and motor representations

(right contralateral movement). Children were instructed to “Do what I do,” and in all cases, they imitated all these movements well. In a separate session, children and experimenters were again sitting on the opposite sides of the desk. Now, however, there were two big red dots, one on the left and one on the right side of the desk. Whenever the experimenter made a movement, either ipsilateral or contralateral with either the left or the right hand, the hand of the experimenter would end up covering the big red dot. Children were again instructed to “Do what I do.” In this situation, children imitated well the ipsilateral movements but made frequent mistakes when trying to imitate the contralateral movements. Note that these movements had been imitated well in absence of the big red dot. The presence of the big red dot had changed the goal of the action to be imitated. Whereas in the absence of the dot, the action itself was the goal to be imitated, the presence of the dot had changed the goal of the action in covering the dot. Indeed, children made mistakes when imitating contralateral movements because they used ipsilateral movements to cover the same dot that had been covered by the experimenter. In other words, children would copy the goal but used a simpler movement to achieve this goal (Bekkering et al. 2000).

One of the main assumptions of the ideomotor framework is that action and perception share a common representational format. This assumption fits well recent neuroscience discoveries, as discussed below. Another important assumption of the ideomotor framework is that our perceptual and motor experience is very important in shaping the functional aspects of imitation. This assumption is also shared by the associative sequence learning model (Heyes 2005), as described in the next section.

Associative Sequence Learning

The associative sequence learning model of imitation proposes that imitative abilities are based on associations between the sensory and motor representation of actions. These associations would be mostly shaped by experience,

although a small number of these associations may be innate. Several environmental situations may favor the establishment of these associations between sensory and motor representation of actions, for instance, visually guided actions, such as reaching and grasping, during which we can observe our own arm and hand reach and grasp for objects surrounding us. Also, mirrors and other reflecting surfaces allow the observation of one’s own facial and body movement as if they were performed by somebody else. Furthermore, early in human development, adults tend to imitate the baby (Nadel 2002), thus favoring the formation of the associations between sensory and motor representations of actions.

The basic assumption of the associative sequence learning model is that imitation is not based on dedicated functional (and neural) mechanisms. General sensory and motor systems may implement imitative abilities through mechanisms that are strongly reminiscent of Hebbian learning. One of the corollaries of this assumption is that imitation should not be confined to specific lineages. Indeed, although primates clearly show varying degrees of imitative abilities, birds (Akins et al. 2002) and dolphins (Herman 2002) also seem able to imitate. Thus, imitative behavior appears to be the product of convergent evolution. If this is true, then the hypothesis that imitation is mostly shaped by experience—as assumed by the associative sequence learning model—is obviously supported.

The role of experience and the environment in shaping imitative abilities may also account for evidence that at first sight seems at odds with the basic assumptions of the associative sequence learning model. Many animals share similar basic sensory and motor functional and neural mechanisms. In principle, this should lead to similar imitative skills in many animals. Imitation abilities, however, vary substantially between species (Boysen & Himes 1999, Hurley & Chater 2005). Is this evidence a fatal blow to the main assumption of the associative sequence learning model? Probably not. Indeed, different kinds of environments may

account for the differences in imitative abilities observed in different species. As discussed above, some elements that are quite specific to the human environment should favor the formation of the associations between sensory and motor representations posited by the associative sequence learning model. In keeping with these ideas, humans are by far the best imitators (Hurley & Chater 2005).

Empirical evidence in well-controlled laboratory experiments seems to support the role of experience in shaping imitation, as hypothesized by the associative sequence learning model. For instance, hand-opening and hand-closing gestures are typically facilitated by the observation of the same movement compared to the observation of a different movement. However, this facilitation can be abolished by a relatively short period of training during which subjects are instructed to open the hand while observing hand closing, and to close the hand while observing hand opening (Heyes et al. 2005).

In another experiment, the effect of training was measured on the speed of imitation induced by the observation of human motion versus robotic motion. A typical finding is that humans imitate more quickly the movements of another human compared to the movements of a robot. This effect, however, may be simply because humans tend to interact more with other humans than with robots. Indeed, subjects who were trained to execute hand movement in response to a robotic movement demonstrated no difference in speed of imitation while observing human and robotic movements (Press et al. 2007).

Although the associative sequence learning model and the ideomotor framework of imitation share the main idea that experience is extremely important for imitation, they also seem to differ on an important point. The associative sequence learning model assumes that separate sensory and motor representations are linked by experience. In contrast, the ideomotor framework assumes that sensory and motor functional mechanisms share a common represen-

tational format. In psychological terms, these differences are not negligible. The translation of these different concepts into neural activity, however, as discussed below, may not differ dramatically (Glimcher 2005). Indeed, the main assumptions of both the associative sequence learning model and the ideomotor framework of imitation fit well with recent neuroscience findings on imitation.

IMITATION AND EMPATHY IN SOCIAL BEHAVIOR

Pervasiveness and Automaticity of Human Imitation

Humans seem to have a strong tendency to align their behavior with their fellows during social interactions (Lieberman 2007). Some of these forms of imitation and mimicry are not only pervasive and automatic, but also operate on a quite complex level. Ap Dijksterius (2005)—following LeDoux's terminology on processing of fearful stimuli (LeDoux 1996)—suggests that there are two roads to human imitation. A low road leads to imitation in a direct fashion, such that the perceiver acts the gestures, postures, facial expressions, and speech perceived in other people. A high road leads to complex and rather subtle forms of imitation, as shown by a number of experiments with priming manipulations that lead to stereotype activation or trait activation.

An example of stereotype activation on motor behavior is provided by the following experiment. Participants performed a scrambled-sentence language task. Some subjects were exposed to words such as Florida, bingo, gray; that is, words typically associated with the elderly. Some other subjects were not. After the experiment, participants left the laboratory and walked back to the elevator to leave the building. An experimenter timed this walk back to the elevator. Subjects who had been primed with the elderly stereotype were reliably slower than subjects who had not been primed (Bargh et al. 1996). The primed subjects

imitated—obviously in an unconscious way—the slowness of old people.

The high road to imitation is also at work in memory and general knowledge tasks. In one experiment, subjects sat in front of a desk full of objects. The stereotype of the elderly was primed again in some subjects by asking them questions on elderly people. Other subjects, in contrast, were asked questions about college students. Subsequently, subjects were transferred to another room and were asked to remember the objects that were on the desk in front of them. The subjects primed with the elderly stereotype remembered far fewer objects than did the other participants (Dijksterhuis et al. 2000).

In a series of experiments, participants were either asked to think about college professors (a group of people typically associated with intelligence) and to write down everything that came to mind about college professors, or they were asked to think about soccer hooligans (a group of people typically not associated with intelligence) and to write down everything that came to mind about soccer hooligans. In a later task involving general knowledge questions, a task that was ostensibly unrelated to the first one, the participants who were asked to think about college professors outperformed the participants who were asked to think about soccer hooligans. Indeed, the participants who were asked to think about college professors even outperformed participants who were not asked anything at all, and the participants who were asked to think about soccer hooligans were outperformed by participants who were not asked anything at all (Dijksterhuis & van Knippenberg 1998).

Many more studies support the concept that the high road to imitation is pervasive and automatic (Dijksterhuis 2005). The question is why pervasiveness and automaticity have been selected as distinctive properties of the high road to imitation. One possibility is that imitation facilitates social interactions, increases connectedness and liking, gets people closer to each other, and fosters mutual care. If this account

is correct, it should follow that good imitators should also be good at recognizing emotions in other people, which in turn may lead to greater empathy. Thus, this account would predict a correlation between the tendency to imitate others and the ability to empathize with them. This hypothesis was tested in a series of experiments (Chartrand & Bargh 1999). In the first experiment, subjects were asked to choose pictures in a set of photographs. The cover story was that the researchers needed some of these pictures for a psychological test and wanted to know from the subjects which pictures they considered more stimulating. While subjects were choosing the pictures, a confederate was sitting in the same room with the real subject. The confederate pretended to be another subject who was also choosing good stimulating pictures. During the experimental sessions, some confederates deliberately rubbed their nose while the others shook their foot. Subjects were videotaped and their motor behavior was measured. It was found that the real subjects unintentionally mimicked the motor behavior of the confederate with whom they were sharing the room. Subjects who shared the room with confederates who rubbed their nose, rubbed their nose more than did subjects who shared the room with confederates who shook their foot. Furthermore, subjects who shared the room with confederates who shook their foot, shook their foot more than did subjects who shared the room with confederates who rubbed their nose. These results are in line with the idea that imitation is automatic and provide the necessary prelude to the following experiments.

The second experiment tested the hypothesis that one of the functions of this automatic tendency to imitate is to increase liking between individuals. Participants were again asked to choose pictures, and confederates were again sitting with them, pretending to be participants of the study. In this second experiment, the cover task required participants and confederates to take turns in describing what they saw in various photos. At the end of the interaction

between participants and confederates, the participants were also asked to complete a questionnaire to report how much they liked the other participant (that is, the confederate) and how smoothly they thought the interaction had gone. In this second experiment, the confederates either imitated the spontaneous postures, movements, and mannerisms of the subjects or kept a neutral posture. The participants who were mimicked by confederates during the interaction liked the confederates much more than did the participants who were not imitated. Furthermore, mimicked subjects rated the smoothness of the interaction higher than did the participants who were not imitated. This experiment demonstrated that imitation and liking tend to go together. When someone is imitating us, we tend to like him or her more.

A third experiment tested the hypothesis that the more people tend to imitate others, the more they are concerned with the feelings of other people. The setting of this third experiment was identical to the first experiment. The novel aspect of this last experiment was that the participants responded to a questionnaire that measured their empathic tendencies. The experiment found a strong correlation between the tendency to empathize and the amount of imitative behavior displayed by the participants. The more a subject imitated the confederate, the more that subject was an empathic individual (Chartrand & Bargh 1999). This result suggests that through imitation and mimicry, we are able to feel what other people feel. By being able to feel what other people feel, we are also able to respond compassionately to other people's emotional states (Eisenberg 2000, Tangney et al. 2007).

Many other empirical results are consistent with these ideas (Braten 2007, Niedenthal et al. 2005). What are the neural correlates of these complex forms of human behavior? A recent discovery in the monkey premotor cortex has sparked a whole series of new studies, in monkeys and humans, that are relevant to this question.

NEURAL MECHANISMS OF IMITATION

Neural Precursors in Nonhuman Primates

The premotor cortex of the macaque brain, a cortical region important for the planning, preparation, and selection of movements and coordinated actions, is not homogeneous (Matelli et al. 1985). It is composed of several cito-architectonic fields with different physiological properties. In the lateral wall of the macaque brain, the ventral sector of the premotor cortex is composed of two main fields, area F4 and area F5 (Matelli et al. 1985). Area F5 has physiological properties relevant to the neural control of mouth and hand movements, especially grasping (Rizzolatti et al. 1988). Within area F5, there are neurons that discharge not only when the monkey performs goal-oriented actions such as grasping an object, holding it, manipulating it, and bringing it to the mouth, but also when the monkey, completely still, simply observes somebody else performing these actions. Because of these properties, which almost suggest that the monkey is observing its own actions reflected by a mirror, these cells were called mirror neurons (di Pellegrino et al. 1992, Gallese et al. 1996).

The properties of mirror neurons call to mind the concepts of the ideomotor framework of actions, according to which perception and action share common representational formats. Indeed, mirror neurons embody the overlap between perception and action predicted by the ideomotor framework by discharging both during action execution and during action observation.

The initial hypothesis about the functional role of mirror neurons focused on action recognition. By firing during actions of the self and of other individuals, mirror neurons may provide a remarkably simple neural mechanism for recognizing the actions of others. Early observations on firing-rate changes in mirror neurons demonstrated that these cells do not fire at the sight of a pantomime (Rizzolatti et al. 1996,

Premotor cortex: anterior sector of the agranular frontal cortex containing neurons that are relevant to the planning, preparation, and selection of actions

Mirror neurons: neurons with motor properties in premotor and posterior parietal cortex that fire not only during action execution, but also while observing somebody else performing the same or a similar action

Strictly congruent mirror neurons:

mirror neurons that fire during the observation of exactly the same action they code motorically

Broadly congruent mirror neurons:

mirror neurons that fire during the observation of an action achieving the same goal or logically related to the action they code motorically

Rizzolatti & Arbib 1998). For instance, the pantomime of whole-hand grasp (when the whole hand is used to grasp a relatively large object, as an orange) does not trigger the discharge of a mirror neuron that fires during execution and observation of whole-hand grasps. This makes sense because monkeys typically do not pantomime. These early findings suggested that the properties of this neural system were remarkable but relatively simple, some sort of “monkey see, monkey do” neural mechanisms. However, many other findings contradict this view and rather suggest that mirror neurons form a sophisticated, nuanced system for shared coding of motor and perceptual aspects of actions of self and others (Rizzolatti & Craighero 2004).

For instance, although the term “mirror” implies a strong similarity between the executed and the observed actions, only one third of mirror neurons—the so-called strictly congruent mirror neurons—fire for the same executed and observed action. The remaining two-thirds of mirror neurons—the so-called broadly congruent mirror neurons—fire for executed and observed actions that are not the same but either achieve the same goal or are logically related (di Pellegrino et al. 1992, Gallese et al. 1996, Rizzolatti & Craighero 2004), thus forming some sort of sequence of acts, as for instance observed placing food on the table and executed grasping food and bringing it to the mouth.

The properties of broadly congruent mirror neurons suggest that these cells provide a flexible coding of actions of self and others. This flexibility is an important property for successful social interactions because even though imitation is a pervasive phenomenon in humans, people do not imitate each other all the time but rather often perform coordinated, cooperative, complementary actions. Broadly congruent mirror neurons seem ideal cells to support cooperative behavior among people (Newman-Norlund et al. 2007).

Following the initial observations (di Pellegrino et al. 1992, Gallese et al. 1996), a series of more recent experiments have demonstrated other complex properties of mirror neurons. For instance, we often easily recognize actions

that are partially occluded. The role of mirror neurons in the recognition of hidden actions was tested by using a screen that occluded the completion of the grasping action (Umiltà et al. 2001). In two baseline conditions, the firing of the cells was measured for observation of grasping and of grasp pantomime. As expected, mirror neurons fired for grasping observation but not for observation of the pantomime. In a new experimental condition, the subject watched a graspable object placed on a desk in front of the monkey. Subsequently, a screen occluded the sight of the graspable object and a human experimenter reached with her or his hand behind the screen. The monkey was able to see the experimenter’s hand moving toward the object but was not able to see the actual grasping action, which was occluded by the screen. Approximately half of the mirror neurons tested in this experiment discharged even though the grasping action was occluded. The firing rate changes of these neurons were tested also in an additional control condition. Here, at the beginning of the trial, the monkey saw that there was no graspable object on the table. As in the previous experimental conditions, a screen subsequently occluded the sight of the table and a human experimenter reached with her or his hand behind the screen. Consider that at this point, this additional control condition is visually identical to the previous experimental conditions involving the screen occluding the sight of the grasping action. The only difference here is the prior knowledge of the absence of a graspable object behind the screen. Mirror neurons tested under this experimental condition did not change their firing rate, suggesting that the unseen action behind the screen was indeed coded as a pantomime (or, better, as a nongrasping action) (Umiltà et al. 2001).

The experiment on hidden actions demonstrates another aspect of the properties of mirror neurons that suggests that these cells code actions in a fairly sophisticated way. The same visual information is coded differently, on the basis of prior knowledge about the presence or absence of a graspable object behind the screen. A subsequent experiment

demonstrated that mirror neurons also code in absence of any visual input (Kohler et al. 2002). In this study, after the necessary baseline conditions were performed and mirror neurons were identified, the experimenters measured the firing-rate changes of mirror neurons to the sound of actions. The sound stimuli used in this study were associated with common actions such as tearing a piece of paper, breaking peanuts, and so on. Control sounds not associated with actions, for instance white noise, were also used (Keysers et al. 2003, Kohler et al. 2002). The single-cell recordings demonstrated that mirror neurons can also discharge to the sound of an action, even in absence of the visual input related to the action. These auditory properties of mirror neurons have two important theoretical implications. One implication is relevant to the evolution of language. Area F5 of the macaque brain (where mirror neurons were originally discovered) is the anatomical homologue of Brodmann area 44 of the human brain (Rizzolatti & Arbib 1998), a brain area with important language properties. This anatomical correspondence, together with other considerations, led to the hypothesis that mirror neurons may have facilitated the emergence of language in the human brain (Rizzolatti & Arbib 1998). However, language is not only written and read but also (and mostly) spoken and heard. Mirror neuron responses to auditory stimuli are essential evidence for the hypothesis that mirror neurons are important neural elements in language evolution. The other implication of the auditory properties of mirror neurons is that they show that mirror neurons are multimodal cells. This functional property is theoretically important because it is compatible with associative models of how mirror neurons may be formed, which is discussed in more detail below. When we break a peanut, the visual input of our fingers breaking the peanut and the auditory input of the sound of breaking the peanut almost always co-occur, especially when we are initially learning to perform the action. Associative models can easily account for multimodal responses that are produced by the

co-occurrence of sensory stimuli from multiple modalities (Fanselow & Poulos 2005, Keysers & Perrett 2004, Wasserman & Miller 1997).

A recent study on mirror neuron responses to the sight of actions involving the use of tools is also consistent with the hypothesis that the properties of mirror neurons are shaped by experience. Early observations on mirror neuron responses to observed actions suggested that these cells do not fire at the sight of an action involving the use of a tool. For instance, a mirror neuron discharging during the execution and observation of precision grips (when grasping small objects with two fingers) would not fire at the sight of the experimenter using a hand tool such as a pliers to grasp the same small object (Rizzolatti & Arbib 1998). However, a recent study recording in the inferolateral aspect of area F5 has reported robust discharges in approximately 20% of recorded mirror neurons when the monkey observed the experimenters using tools (Ferrari et al. 2005). Indeed, these discharges were even more robust than the discharges of the same cells during the observation of a grasping action without the tool (Ferrari et al. 2005). Although it is not possible to demonstrate unequivocally that the mirror neuron responses to tool use actions were acquired through the daily experience of observing human experimenters using tools in the lab, this seems a likely explanation. It is unlikely that tool-use mirror neurons were already present in area F5 of the macaque brain but never recorded for more than ten years. This recently discovered functional property of mirror neurons and its likely underlying forming mechanisms is also obviously relevant to the psychological theories discussed above.

Furthermore, described above, the ideomotor framework of action puts intentions front and center. Is it possible that the discharge of mirror neurons may represent the coding of the intention associated with the performed and observed action rather than the action itself? A recent single-cell recording study has addressed this question (Fogassi et al. 2005). The depth electrode recordings first demonstrated that neurons in area PF/PFG—a cortical

area located in the anterior part of the inferior parietal lobule that is anatomically connected with area F5 in the ventral premotor cortex (see **Figure 1**) and that also contains mirror neurons—had differential discharges for the same grasping action that led to, say, eating food rather than placing the food in a container (note that the monkeys were rewarded after placing the food in the container; thus, the amount of reward was identical for both actions). Not surprisingly, grasping for eating was preferred by the majority of grasping cells in this parietal area, although approximately 25% of neurons coding differently the same grasping action on the basis of its intention preferred grasping for placing over grasping for eating (Fogassi et al. 2005).

This pattern of firing-rate changes demonstrates that these cells code the same executed grasping action rather differently, according to the intention (or the goal) associated with the grasping action. The same pattern of firing-rate changes was also observed during action observation. Here, the monkey was simply observing the human experimenter performing grasping actions. The intention of the experimenter was cued by the presence of a container. When the container was present, the experimenter grasped the food and placed it in the container. When the container was absent, the experimenter grasped the food and ate it. At the time of grasping, the cells that discharged more robustly for grasping to eat when the monkey performed the actions also discharged more robustly when the monkey simply observed the human experimenter grasping the food in order to eat it. Likewise, the cells that discharged more robustly for grasping to place when the monkey performed the actions also discharged more robustly when the monkey simply observed the human experimenter grasping the food in order to place it in the container (Fogassi et al. 2005). Thus, rather than coding the observed grasping action, these neurons seem to be coding the goal associated with the action, the intention to eat or to place.

The most dramatic demonstration of the role of goal coding in these cells has been pro-

vided by a very recent study (Umiltà et al. 2008). Here, single-cell recordings in area F5 were performed after monkeys were trained to use pliers to grasp objects. Ventral premotor neurons active during grasping actions were also active when the monkey used pliers to grasp objects. Monkeys were trained to use reverse pliers that required hand opening rather than hand closing (as in natural grasps). Remarkably, neurons that fired during hand closing in natural grasps and during use of normal pliers did fire during hand opening when the monkeys used the reverse pliers. The activity of these motor neurons is evidently centered on coding the goal of the action rather than the motor detail of hand closing or opening. Among these motor neurons, the cells with mirroring properties also demonstrated a pattern of firing-rate changes centered on goal coding, discharging when the tips of the pliers were closing on the objects to be grasped during observation of action with both normal and reverse pliers (Umiltà et al. 2008).

Mirror neurons do not mirror only grasping actions performed with the hand or with tools controlled by the hand. There is evidence of mirror neurons coding facial actions, in particular with the mouth. Both ingestive (such as biting and sucking) and communicative actions are coded by mirror neurons (Ferrari et al. 2003). This is especially important for the hypothesis that mirror neurons may facilitate our understanding of the emotions of other people, because the face is the body part that we use most often to express our own emotions.

Macaque Mirror Neurons and Imitation in Monkeys

Do monkeys imitate? This is a contentious issue, and the answer to this question is heavily dependent on the definition of imitation. Among scholars, it was widely held at the end of the nineteenth century that monkeys not only are able to imitate, but they actually do it "...at ludicrous length." (Romanes 1883). In those times, imitation was not typically associated with high forms of intelligence. This

view of imitation has changed considerably in the past 30 years (Hurley & Chater 2005), calling also for a revision of previously held ideas on monkeys' ability to imitate. Indeed, such revision had at some point taken the form of a true backlash, with many scholars denying that monkeys had any imitative ability. This position raised the issue of what is the adaptive advantage of mirror neurons for monkeys and inspired new and better-controlled studies. There is now well-controlled evidence that monkeys are indeed able to imitate (Ferrari et al. 2006; Subiaul et al. 2004; Voelkl & Huber 2000, 2007), and it is likely—although there is no direct evidence yet—that this ability is supported by mirror neurons. For instance, marmosets observed a demonstrator removing the lids from a series of plastic canisters to obtain a mealworm. Subsequently, marmosets that observed a demonstrator using its hands to remove the lids used only their hands, whereas marmosets that observed a demonstrator using its mouth used their mouth to remove the lids (Voelkl & Huber 2000). In another study, marmosets observed another marmoset (the model) that was previously trained to open a box in a peculiar way. Detailed motion analyses demonstrated that the highly unusual movement pattern of the model was faithfully replicated by the observers (Voelkl & Huber 2007). A recent study has also shown that rhesus macaques display neonatal imitation abilities that are similar to the abilities displayed by human neonates (Ferrari et al. 2006).

It is evident, however, that imitative learning is not developed in monkeys as it is in humans (Hurley & Chater 2005). What then would be the main function of mirror neurons in the monkey brain? One possibility might be that mirror neurons facilitate the ability to recognize the actions of others. A recent behavioral study, however, has also revealed that monkeys are able to recognize when they are being imitated (Paukner et al. 2005). In this study, monkeys observed two experimenters, each manipulating a wooden cube with a hole in each side. Initially, the monkeys did not show any preferential looking between the two experimenters.

Subsequently, a cube was given to the monkey. When the monkey started manipulating the cube, one of the two experimenters imitated accurately the monkey's actions directed at the cube. The second experimenter, in contrast, performed different actions. At this point, the monkey preferentially looked at the experimenter imitating her own actions. This capacity, which is likely supported by mirror neurons, may have an important social function and may be one of the early functional precursors of the highly developed imitative behavior of humans.

Human Brain Mechanisms of Mirroring

The exquisite spatial and temporal resolution afforded by depth electrode recordings of single-cell activity can be obtained only with techniques of brain investigation that are quite invasive. These techniques cannot typically be used in humans. The neural properties revealed by single-unit recordings in monkeys are usually investigated in humans at the system level, with lesion studies (behavioral observations on neurological patients), brain imaging, and recently transcranial magnetic stimulation (TMS). Although the relationships between all these markers of brain activity are far from being fully defined, there is evidence that they tend to correlate relatively well. Spiking neuronal activity recorded with in-depth electrodes correlates well with the blood-oxygenation-level dependent (BOLD) signal measured by functional magnetic resonance imaging (fMRI) (Logothetis et al. 2001). In some cases, however, spiking activity and BOLD seem to dissociate (Logothetis & Wandell 2004), for instance when spiking responses show adaptation (that is, a reduced response to repeated stimuli) while BOLD does not (Goense & Logothetis 2008). Nevertheless, a recent TMS study has shown similar stimulation effects on both neural and hemodynamic signals (Allen et al. 2007), supporting the practice of inferring neural activity from signals based on hemodynamic changes, such as BOLD fMRI.

TMS: transcranial magnetic stimulation

BOLD: blood-oxygenation-level dependent

fMRI: functional magnetic resonance imaging

Pars opercularis:

posterior sector of the inferior frontal gyrus delimited superiorly by the inferior frontal sulcus, inferiorly by the Sylvian fissure, posteriorly by the ventral sector of the precentral gyrus, and anteriorly by the ascending branch of the Sylvian fissure. Pars opercularis in the left hemisphere is classically considered the posterior part of Broca's area, a major language area of the human brain

Indeed, this practice is widely used in systems neuroscience. For instance, single-cell recordings with depth electrodes have revealed in the dorsal premotor cortex of macaques cellular mechanisms of conditional motor learning, the fundamental ability that allows the association of motor responses to arbitrary sensory stimuli, as when we brake at a red traffic light. In humans, the dorsal premotor cortex has also been associated with conditional motor learning by brain imaging and lesion studies (Passingham 1993). Even though single-cell recordings of human dorsal premotor neurons have not been performed, the obvious assumption is that the human brain must have dorsal premotor cellular mechanisms that enable conditional motor learning and that are likely similar to—albeit probably more sophisticated than—the ones recorded in monkeys.

This very same logic applies to the investigation of mirror neurons in the human brain. Given that the information typically obtained in human studies is at system level, the term “mirror neuron system” is often used in these studies. Two positron emission tomography studies (Grafton et al. 1996, Rizzolatti et al. 1996) and a TMS study (Fadiga et al. 1995) provided early evidence compatible with the idea that the human ventral premotor and inferior frontal cortex had mirroring properties. However, these studies did not investigate the role of these human brain areas in imitation. In a later fMRI study (Iacoboni et al. 1999), subjects were required to imitate simple finger movements and to perform motor and visual control tasks. The logic of the study was as follows: The neuronal discharge measured by depth electrode recordings in macaques during action observation is approximately 50% of the discharge measured during action execution (Gallese et al. 1996). Thus, human brain areas with mirror neurons should also have an increased BOLD signal (which roughly correlates with brain activity in fMRI) during action observation that is approximately 50% of the BOLD increase measured during action execution. Furthermore, during imitation, subjects were simultaneously watch-

ing the finger movement and copying it. Thus, mirror neuron areas may have a BOLD signal increase during imitation that is approximately the sum of the BOLD signal increases observed during action observation and during action execution. The fMRI study found that two cortical areas had this predicted pattern of activity: They were located in the posterior part of the inferior frontal gyrus and in the rostral part of the posterior parietal cortex (Iacoboni et al. 1999), in anatomical locations (**Figure 2**) that were homologous to the anatomical locations of the macaque brain areas with mirror neurons, that is, area F5 in the ventral premotor cortex and area PF/PFG in the rostral sector of the inferior parietal lobule.

The inferior frontal area with mirroring properties overlapped with the posterior part of Broca's area, a major language area. On one hand, these findings supported the evolutionary hypothesis about the role of mirror neurons in language (Rizzolatti & Arbib 1998). On the other hand, an activation in a language area during a nonlanguage task may be induced by covert verbalization occurring during the activation tasks. It is unclear why imitation should induce more covert verbalization than motor execution, which in turn should induce more covert verbalization than action observation (the pattern predicted for a mirror neuron area and observed in the posterior part of the inferior frontal gyrus and in the rostral part of the posterior parietal cortex), and this issue cannot be conclusively resolved by fMRI, which is a technique that provides only correlational data between brain areas and human behavior. TMS, on the other hand, provides information on the causal role of the activity in a brain area and human behavior. A high-frequency repetitive TMS study indeed demonstrated later that activity in the pars opercularis, the posterior part of the inferior frontal gyrus, is essential to imitation (Heiser et al. 2003).

A series of brain-imaging studies has suggested a core cortical circuitry for imitation composed of the posterior part of the superior

temporal sulcus, a higher-order visual area that responds to watching biological motion and intentional actions (Allison et al. 2000, Jellema et al. 2000, Perrett et al. 1989, Puce & Perrett 2003, Puce et al. 1998), and by the parietal and frontal mirror neuron areas. Within this cortical circuitry, the superior temporal cortex would provide a higher-order visual description of the actions of other people and would feed this information to the fronto-parietal mirror neuron areas (Iacoboni et al. 2001). The parietal mirror neuron area would code the motor aspect of the action (Iacoboni et al. 1999), whereas the frontal mirror neuron area would be more concerned with the goal of the action (Iacoboni 2005, Iacoboni et al. 2005, Iacoboni & Dapretto 2006, Koski et al. 2002).

Imitative behavior can take many forms (Hurley & Chater 2005). The core circuitry for imitation, composed of superior temporal cortex, inferior parietal lobule, and inferior frontal cortex, interacts with other neural systems to support different forms of imitative behavior. For instance, the interactions between the core circuitry for imitation and the dorsolateral prefrontal cortex seem critical during imitative learning (Buccino et al. 2004). In contrast, social mirroring and the ability to empathize with others may be supported by the interactions between the core circuitry for imitation and the limbic system (Iacoboni 2005). An fMRI study of imitation and observation of facial emotional expressions (Carr et al. 2003) tested the hypothesis that empathy is enabled by a large-scale neural network composed of the mirror neuron system, the limbic system, and the insula connecting these two neural systems. Within this network, mirror neurons would support the simulation of the facial expressions observed in other people, which in turn would trigger activity in limbic areas, thus producing in the observer the emotion that other people are feeling. This model predicts activation of mirror neuron areas, insula, and limbic areas during both observation and imitation of facial emotional expressions. Furthermore, the model predicts that the increased activity in mirror neuron ar-

reas during imitation should also spread to insula and limbic areas, if these brain centers are indeed functionally connected with mirror neuron areas. Both predictions were supported by the empirical findings (Carr et al. 2003).

In functional terms, the large-scale network composed of mirror neuron areas, insula, and the limbic system likely provides a simulation-based form of empathy (Goldman 2006, Goldman & Sripada 2005). Recent data also suggest that the activity in this network provides a biomarker of sociality and empathy. Indeed, an fMRI study of imitation and observation of facial expressions in children with autism and in typically developing children demonstrated not only a deficit in mirror neuron areas in the children with autism, but also a correlation between the severity of the disease and activity in these areas: The lower the activity in mirror neuron areas, the more severe the autism (Dapretto et al. 2006). Furthermore, a separate fMRI study on typically developing preadolescents—in which the activation task was again the observation and imitation of facial emotional expressions—has recently demonstrated that activity in mirror neuron areas was positively correlated with interpersonal competence and empathic concern (Pfeifer et al. 2008). Two additional fMRI studies on adults also support the findings obtained in children. In one study, subjects observed simple grasping actions (Kaplan & Iacoboni 2006). In the other study, subjects listened to action sounds (Gazzola et al. 2006). Both studies found a positive correlation between empathy scores and activity in premotor areas activated during action observation and while listening to action sounds, thus likely containing mirror neurons.

Neural Mirroring and Psychological Theories of Imitation

The ideomotor model of imitation and the associative sequence learning model share many concepts but diverge on a fundamental one: The former assumes overlap between

perceptual and motor representations, whereas the latter assumes that sensory and motor representations are separated but functionally connected through vertical links formed by associative learning. Both models also map well onto the functional properties of mirror neurons and neural systems for mirroring. Do the neuroscience findings on mirror neurons better support the assumptions of the ideomotor model on perceptual and motor representations or those of the associative sequence learning model? It is difficult to answer this question because the levels of description of psychological theories and those of neuroscience empirical work are radically different.

The discharge of mirror neurons during action execution and action observation seems to fulfill the main assumption of the ideomotor model, a common representational format for perception and action. Preliminary results on individual neuronal activity obtained with depth electrode recordings in humans (R. Mukamel, A. Ekstrom, J. Kaplan, M. Iacoboni and I. Fried, unpublished observations) seem also to support the ideomotor model. Using a rare clinical opportunity, we recently recorded single-cell activity in epileptic patients implanted for surgical evaluation. We found human neurons with mirror properties in the frontal lobe as well as in the medial temporal cortex. Although the discharge of these cells during action execution and action observation seems to imply a common representational format for perception and action implemented at single cell level, it is also true that lesions in the frontal lobe are more often associated with motor deficits, and lesions in the medial temporal lobe are more often associated with perceptual deficits. Perception and action, which are united at the level of single cells, seem to be more easily separated at the system level. In principle, the discharge during action execution and during action observation of frontal and medial temporal neurons may represent in neural terms the “vertical links” posited by the associative sequence learning model between a sensory unit (the medial temporal neuron) and

a motor unit (the frontal neuron) that fire together as a result of associative learning.

WHY NEURAL MIRRORING AND IMITATION?

The fundamental Darwinian question is why mirror neurons were selected by evolution. What is the adaptive advantage of having these neurons? The properties of these cells seem to solve—or better, dis-solve—what is called the “problem of other minds”: if one has access only to one’s own mind, how can one possibly understand the minds of other people? How can one possibly share one’s own mental states with others, making intersubjectivity possible?

A classical solution to the problem of other minds is the so-called argument from analogy. The argument from analogy posits that we first observe certain relations between our mental states and our bodily states and then find an analogy between our body and the body of other people. If there is an analogy between our body and the body of others, there may be also an analogy between our mental states/bodily states relations and those of other people. This way of reasoning about the mental states of other people seems too complex for something we seem to accomplish so naturally, effortlessly, and quickly. Mirror neurons, in contrast, provide a prereflective, automatic mechanism of mirroring what is going on in the brain of other people that seems more compatible with our ability to understand others effortlessly and with our tendency to imitate others automatically, as we have discussed in this review.

A further implication of the recent work on the relationships between mirror neurons, imitation, and empathy is the consideration that the evolutionary process made us wired for empathy. This is a major revision of widely held beliefs. Traditionally, our biology is considered the basis of self-serving individualism, whereas our ideas and our social codes enable us to rise above our neurobiological makeup. The research on mirror neurons, imitation, and empathy, in contrast, tells us that our

ability to empathize, a building block of our sociality (Adolphs 2009) and morality (de Waal 2008, Tangney et al. 2007), has been built “bot-

tom up” from relatively simple mechanisms of action production and perception (Iacoboni 2008).

SUMMARY POINTS

1. Imitation is pervasive and automatic in humans.
2. Psychological models of imitation that assume an overlap or strong associative links between perception and action are supported by neural mirroring.
3. The core neural circuitry of imitation is composed of a higher-order visual area (the posterior part of the superior temporal sulcus) and by the fronto-parietal mirror neuron system.
4. Empathy is implemented by a simulation of the mental states of other people.
5. A large-scale network for empathy is composed of the mirror neuron system, the insula, and the limbic system.
6. Mirror neurons were selected because they provide the adaptive advantage of intersubjectivity.

FUTURE ISSUES

1. What are the anatomical locations and physiological properties of mirror neurons in humans? Depth electrode recordings in neurological patients may be able to investigate this issue.
2. How can we more precisely map the predictions of psychological models onto empirical findings from the neurosciences?
3. What are the developmental mechanisms that shape the mirror neuron system?
4. What are the factors that influence the ability to empathize with other people?

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The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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fMRI study that demonstrated that the reduced activity in putative mirror neuron areas in patients with autism correlates with the severity of the disease.

First article to describe mirror neurons. Although the term "mirror neuron" had not been coined yet, the cells described in this article are mirror neurons.

Describes single-cell recordings in macaques demonstrating that the majority of mirror neurons code the intention associated with an observed action, rather than the action itself.

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Reviews not only the evidence on mirror neurons in macaques and humans, but also the evidence suggesting a mirror neuron deficit in autism.

This brain imaging study shows that human mirror neuron areas code differently the same action associated with different intentions.

Describes auditory responses in mirror neurons, demonstrating that mirror neurons also fire to the sound of action, even when the action is not seen.

Comprehensively reviews physiological properties and anatomical location of mirror neurons in macaques and putative mirror neuron areas in humans.

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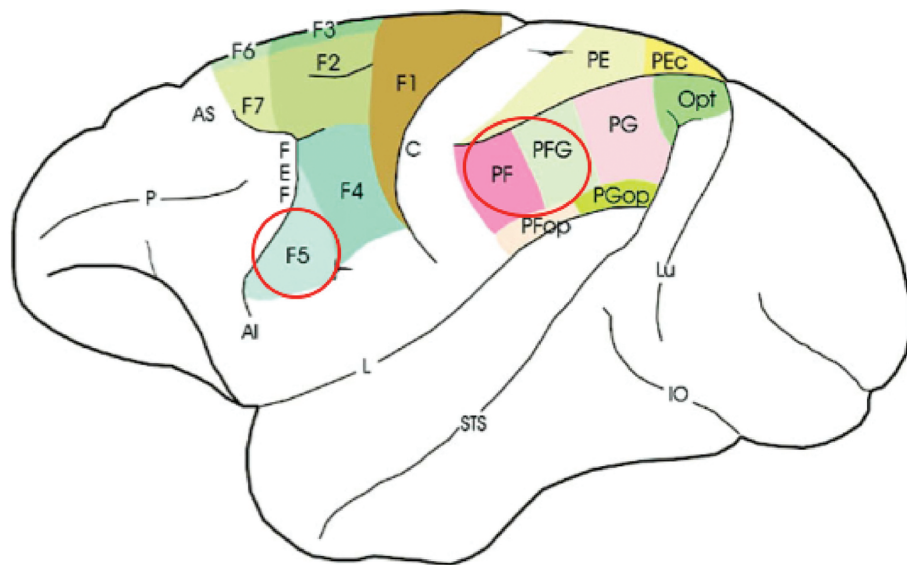


Figure 1

Schematic drawing of the lateral wall of the macaque brain. The inferior frontal (ventral premotor area F5) and inferior parietal (PF and PFG) areas circled in red contain mirror neurons. (Modified from figure 1 of Rizzolatti & Craighero 2004.)

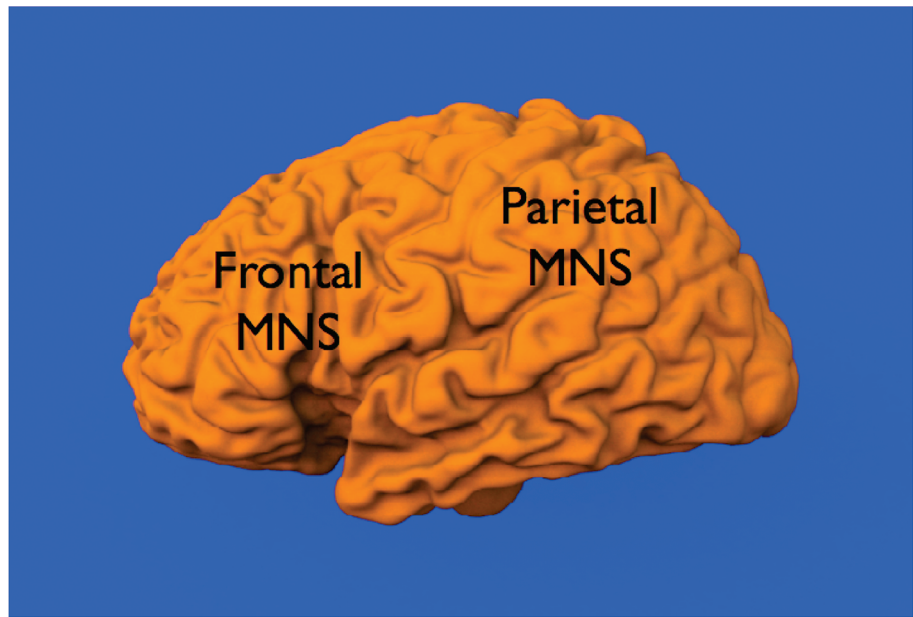


Figure 2

Lateral wall of the human brain. Human areas presumed to contain mirror neurons are in the posterior part of the inferior frontal gyrus and in the anterior part of the inferior parietal lobule.



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Errata

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