

MIRRORS IN THE MIND

A special class of brain cells reflects the outside world, revealing a new avenue for human understanding, connecting and learning

By Giacomo Rizzolatti, Leonardo Fogassi and Vittorio Gallese

John watches Mary, who is grasping a flower. John knows what Mary is doing—she is picking up the flower—and he also knows why she is doing it. Mary is smiling at John, and he guesses that she will give him the flower as a present. The simple scene lasts just moments, and John's grasp of what is happening is nearly instantaneous. But how exactly does he understand Mary's action, as well as her intention, so effortlessly?

A decade ago most neuroscientists and psychologists would have attributed an individual's understanding of someone else's actions and, especially, intentions to a rapid reasoning process not unlike that used to solve a logical problem: some sophisticated cognitive apparatus in John's brain elaborated on the information his senses took in and compared it with similar previously stored experiences, allowing John to arrive at a conclusion about what Mary was up to and why.

Although such complex deductive operations probably do occur in some situations, particularly when someone's behavior is difficult to decipher, the ease and speed with which we typically understand simple actions suggest a much more straightforward explanation. In the early 1990s our research group at the University of Parma in Italy, which at the time included Luciano

ACTION PERFORMED by one person can activate motor pathways in another's brain responsible for performing the same action. The second understands viscerally what the first is doing because this mirror mechanism lets her experience it in own her mind.

WOLINSKY (photograph); JEN CHRISTIANSEN (photo/illustration)

Fadiga, found that answer somewhat accidentally in a surprising class of neurons in the monkey brain that fire when an individual performs simple goal-directed motor actions, such as grasping a piece of fruit. The surprising part was that these same neurons also fire when the individual sees someone else perform the same act. Because this newly discovered subset of cells seemed to directly reflect acts performed by another in the observer's brain, we named them mirror neurons.

Much as circuits of neurons are believed to store specific memories within the brain, sets of mirror neurons appear to encode templates for specific actions. This property may allow an individual not only to perform basic motor procedures without thinking about them but

Instant Recognition

OUR RESEARCH GROUP was not seeking to support or refute one philosophical position or another when we first noticed mirror neurons. We were studying the brain's motor cortex, particularly an area called F5 associated with hand and mouth movements, to learn how commands to perform certain actions are encoded by the firing patterns of neurons. For this purpose, we were recording the activity of individual neurons in the brains of macaques. Our laboratory contained a rich repertoire of stimuli for the monkeys, and as they performed various actions, such as grasping for a toy or a piece of food, we could see that distinct sets of neurons discharged during the execution of specific motor acts.

The pattern of activity was a true representation in the brain of the act itself, regardless of who was performing it.

also to comprehend those acts when they are observed, without any need for explicit reasoning about them. John grasps Mary's action because even as it is happening before his eyes, it is also happening, in effect, inside his head. It is interesting to note that philosophers in the phenomenological tradition long ago posited that one had to experience something within oneself to truly comprehend it. But for neuroscientists, this finding of a physical basis for that idea in the mirror neuron system represents a dramatic change in the way we understand the way we understand.

Then we began to notice something strange: when one of us grasped a piece of food, the monkeys' neurons would fire in the same way as when the monkeys themselves grasped the food. At first we wondered whether this phenomenon could be the result of some trivial factor, such as the monkey performing an unnoticed movement while observing our actions. Once we managed to rule out this possibility and others, including food expectation by the monkeys, we realized that the pattern of neuron activity associated with the observed action was a true representation

in the brain of the act itself, regardless of who was performing it.

Often in biological research, the most direct way to establish the function of a gene, protein or group of cells is simply to eliminate it and then look for deficits in the organism's health or behavior afterward. We could not use this technique to determine the role of mirror neurons, however, because we found them spread across important regions on both sides of the brain, including the premotor and parietal cortices. Destroying the entire mirror neuron system would have produced such broad general cognitive deficits in the monkeys that teasing out specific effects of the missing cells would have been impossible.

So we adopted a different strategy. To test whether mirror neurons play a role in understanding an action rather than just visually registering it, we assessed the neurons' responses when the monkeys could comprehend the meaning of an action without actually seeing it. If mirror neurons truly mediate understanding, we reasoned, their activity should reflect the meaning of the action rather than its visual features. We therefore carried out two series of experiments.

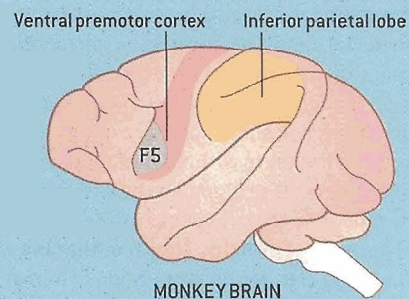
First we tested whether the F5 mirror neurons could "recognize" actions merely from their sounds. We recorded the mirror neurons while a monkey was observing a hand motor act, such as ripping a sheet of paper or breaking a peanut shell, that is accompanied by a distinctive sound. Then we presented the monkey with the sound alone. We found that many F5 mirror neurons that had responded to the visual observation of acts accompanied by sounds also responded to the sounds alone, and we dubbed these cell subsets audiovisual mirror neurons.

Next we theorized that if mirror neurons are truly involved in understanding an action, they should also discharge when the monkey does not actually see the action but has sufficient clues to create a mental representation of it. Thus, we first showed a monkey an experimenter reaching for and grasping a piece of food. Next, a screen was positioned in front of the monkey so that it could not

Overview/Meeting of Minds

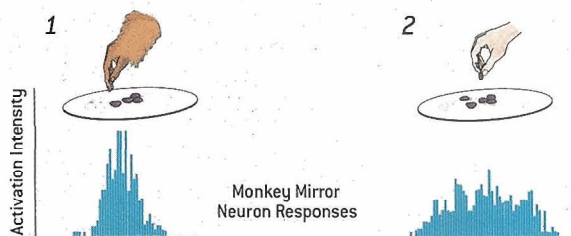
- Subsets of neurons in human and monkey brains respond when an individual performs certain actions and also when the subject observes others performing the same movements. These "mirror neurons" provide a direct internal experience, and therefore understanding, of another person's act, intention or emotion.
- Mirror neurons may also underlie the ability to imitate another's action, and thereby learn, making the mirror mechanism a bridge between individual brains for communication and connection on multiple levels.

In experiments with monkeys, the authors discovered subsets of neurons in brain-motor areas (right) whose activation appeared to represent actions themselves. Firing by these "mirror neurons" could therefore produce in one individual an internal recognition of another's act. Because the neurons' response also reflected comprehension of the movement's goal, the authors concluded that action understanding is a primary purpose of the mirror mechanism. Involvement of the mirror neurons in comprehending the actor's final intention was also seen in their responses, which distinguished between identical grasping actions performed with different intentions.



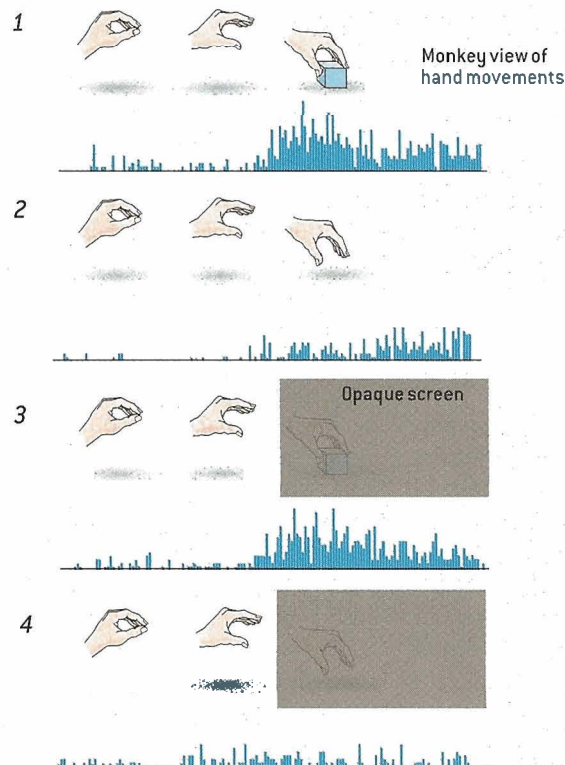
UNDERSTANDING ACTION

In early tests, a neuron in the premotor area F5, associated with hand and mouth acts, became highly active when the monkey grasped a raisin on a plate (1). The same neuron also responded intensely when an experimenter grasped the raisin as the monkey watched (2).



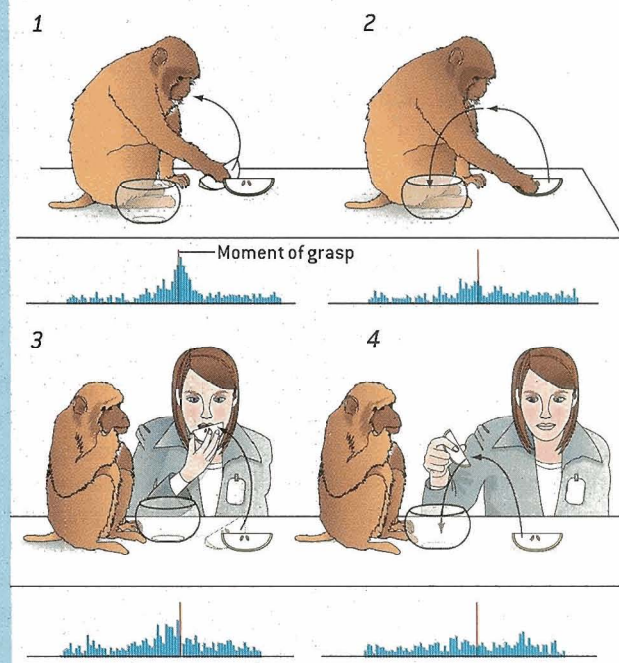
DISCRIMINATING GOAL

An F5 mirror neuron fired intensely when the monkey observed an experimenter's hand moving to grasp an object (1) but not when the hand motioned with no object as its goal (2). The same neuron did respond to goal-directed action when the monkey knew an object was behind an opaque screen, although the animal could not see the act's completion (3). The neuron responded weakly when the monkey knew no object was behind the screen (4).



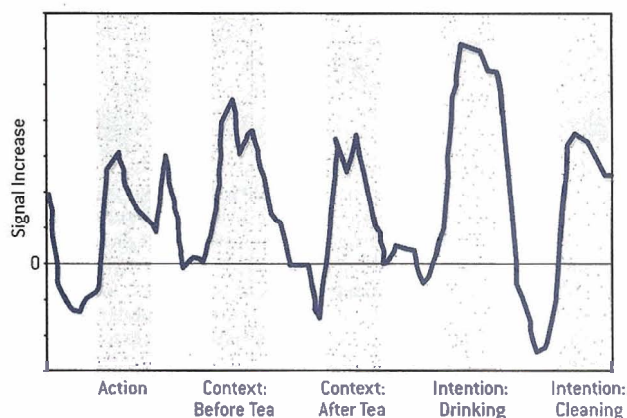
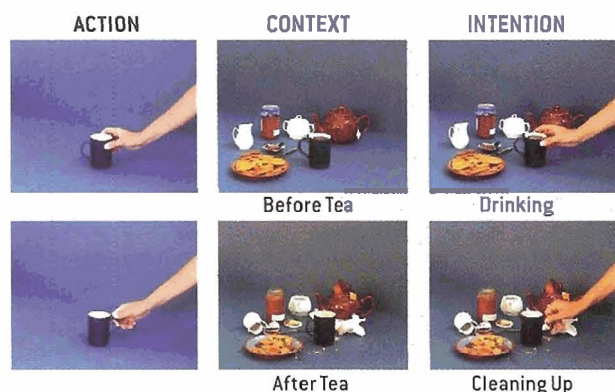
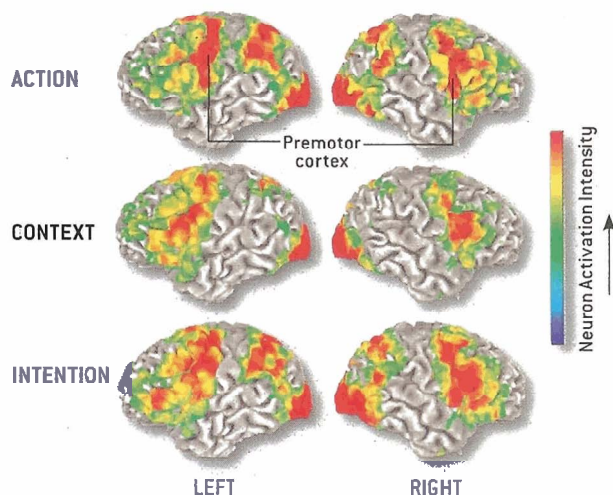
DISCERNING INTENTION

In the inferior parietal lobe, readings from one neuron show intense firing when the monkey grasped a fruit to bring it to its mouth (1). The neuron's response was weaker when the monkey grasped the food to place it in a container (2). The same mirror neuron also responded intensely when the monkey watched an experimenter perform the grasp-to-eat gesture (3) and weakly to the grasp-to-place action (4). In all cases, the responses were associated with the grasping act, indicating that the neuron's initial activation encoded an understanding of final intention.



GRASPING INTENTION

Understanding the intentions of others is fundamental to human social behavior, and human mirror neurons appeared to confer that ability in an experiment designed to test their intention recognition. Volunteers were shown film clips (*below left*) depicting two similar cup-grasping actions without context, two contexts without action, and combinations of acts and context that signaled the action's intention: settings for afternoon tea that suggested the cup was being grasped for the purpose of drinking from it or that tea was over and the cup was being cleaned up. Activation of mirror neuron populations in premotor cortex areas in both hemispheres of subjects' brains (*right*) increased most strongly in response to scenes of action with a clear intention. Mirror neurons also distinguished between possible intentions, responding more intensely to the basic biological function of drinking than to the culturally acquired act of cleaning (*below right*).



see the experimenter's hand grasping the food but could only guess the action's conclusion. Nevertheless, more than half the F5 mirror neurons also discharged when the monkey could just imagine what was happening behind the screen.

These experiments confirmed, therefore, that the activity of mirror neurons underpins understanding of motor acts: when comprehension of an action is possible on a nonvisual basis, such as sound or mental representation, mirror neurons do still discharge to signal the act's meaning.

Following these discoveries in the monkey brain, we naturally wondered whether a mirror neuron system also exists in humans. We first obtained strong evidence that it does through a series of experiments that employed various techniques for detecting changes in motor cortex activity. As volunteers ob-

served an experimenter grasping objects or performing meaningless arm gestures, for example, increased neural activation in their hand and arm muscles that would be involved in the same movements suggested a mirror neuron response in the motor areas of their brains. Further investigations using different external measures of cortical activity, such as electroencephalography, also supported the existence of a mirror neuron system in humans. But none of the technologies we had used up to this point allowed us to identify the exact brain areas activated when the volunteers observed motor acts, so we set out to explore this question with direct brain-imaging techniques.

In those experiments, carried out at San Raffaele Hospital in Milan, we used positron-emission tomography (PET) to observe neuronal activity in the brains of

human volunteers as they watched grasping actions performed with different hand grips and then, as a control, looked at stationary objects. In these situations, seeing actions performed by others activated three main areas of the brain's cortex. One of these, the superior temporal sulcus (STS), is known to contain neurons that respond to observations of moving body parts. The other two—the inferior parietal lobule (IPL) and the inferior frontal gyrus (IFG)—correspond, respectively, to the monkey IPL and the monkey ventral premotor cortex, including F5, the areas where we had previously recorded mirror neurons.

These encouraging results suggested a mirror mechanism at work in the human brain as well but still did not fully reveal its scope. If mirror neurons permit an observed act to be directly understood by experiencing it, for example,

SOURCE: "GRASPING THE INTENTIONS OF OTHERS WITH ONE'S OWN MIRROR NEURON SYSTEM," BY M. IACOBONI ET AL., IN *PLOS BIOLOGY*, VOL. 3, NO. 3, 2005; LUCY READING-IRKANDA (graph illustration)

we wondered to what extent the ultimate goal of the action is also a component of that “understanding.”

On Purpose

RETURNING TO our example of John and Mary, we said John knows both that Mary is picking up the flower and that she plans to hand it to him. Her smile gave him a contextual clue to her intention, and in this situation, John’s knowledge of Mary’s goal is fundamental to his understanding of her action, because giving him the flower is the completion of the movements that make up her act.

When we perform such a gesture ourselves, in reality we are performing a series of linked motor acts whose sequence is determined by our intent: one series of movements picks the flower and brings it to one’s own nose to smell, but a partly different set of movements grasps the flower and hands it to someone else. Therefore, our research group set out to explore whether mirror neurons provide an understanding of intention by distinguishing between similar actions with different goals.

For this purpose, we returned to our monkeys to record their parietal neurons under varying conditions. In one set of experiments, a monkey’s task was to grasp a piece of food and bring it to its mouth. Next we had the monkey grasp the same item and place it into a container. Interestingly, we found that most of the neurons we recorded discharged differently during the grasping part of the monkey’s action, depending on its final goal. This evidence illustrated that the motor system is organized in neuronal chains, each of which encodes the specific intention of the act. We then asked whether this mechanism explains how we understand the intentions of others.

We tested the same grasping neurons for their mirror properties by having a monkey observe an experimenter performing the tasks the monkey itself had done earlier [see box on page 57]. In each instance, most of the mirror neurons were activated differently, depending on whether the experimenter brought the food to his mouth or put it

in the container. The patterns of firing in the monkey’s brain exactly matched those we observed when the monkey itself performed the acts—mirror neurons that discharged most strongly during grasping-to-eat rather than grasping-to-place did the same when the monkey watched the experimenter perform the corresponding action.

A strict link thus appears to exist between the motor organization of intentional actions and the capacity to understand the intentions of others. When the monkeys observed an action in a particular context, seeing just the first

ing objects such as plates and cutlery, arranged in one instance as though they were ready for someone to have afternoon tea and in the other as though they were left over from a previously eaten snack and were ready to be cleaned up. The third stimulus set showed a hand grasping a cup in either of those two contexts.

We wanted to establish whether human mirror neurons would distinguish between grasping a cup to drink, as suggested by the ready-for-tea context, and grabbing the cup to take it away, as suggested by the cleanup setting. Our re-

When people use the expression “I feel your pain,” they may not realize how literally it could be true.

grasping component of the complete movement activated mirror neurons forming a motor chain that also encoded a specific intention. Which chain was activated during their observation of the beginning of an action depended on a variety of factors, such as the nature of the object acted on, the context and the memory of what the observed agent did before.

To see whether a similar mechanism for reading intentions exists in humans, we teamed with Marco Iacoboni and his colleagues at the University of California, Los Angeles, for a functional magnetic resonance imaging (fMRI) experiment on volunteers. Participants in these tests were presented with three kinds of stimuli, all contained within video clips. The first set of images showed a hand grasping a cup against an empty background using two different grips. The second consisted of two scenes contain-

sults demonstrated not only that they do but also that the mirror neuron system responded strongly to the intention component of an act. Test subjects observing the hand motor acts in the “drinking” or “cleaning” contexts showed differing activation of their mirror neuron systems, and mirror neuron activity was stronger in both those situations than when subjects observed the hand grasping a cup without any context or when looking only at the place settings [see box on opposite page].

Given that humans and monkeys are social species, it is not difficult to see the potential survival advantage of a mechanism, based on mirror neurons, that locks basic motor acts onto a larger motor semantic network, permitting the direct and immediate comprehension of others’ behavior without complex cognitive machinery. In social life, however, understanding others’ emotions is equal-

THE AUTHORS

GIACOMO RIZZOLATTI, LEONARDO FOGASSI and VITTORIO GALLESE work together at the University of Parma in Italy, where Rizzolatti is director of the neurosciences department and Fogassi and Gallese are associate professors. In the early 1990s their studies of motor systems in the brains of monkeys and humans first revealed the existence of neurons with mirror properties. They have since continued to investigate those mirror neurons in both species as well as the role of the motor system in general cognition. They frequently collaborate with the many other research groups in Europe and the U.S. now also studying the breadth and functions of the mirror neuron system in humans and animals.

ly important. Indeed, emotion is often a key contextual element that signals the intent of an action. That is why we and other research groups have also been exploring whether the mirror system allows us to understand what others feel in addition to what they do.

Connect and Learn

AS WITH ACTIONS, humans undoubtedly understand emotions in more than one way. Observing another person experiencing emotion can trigger a cognitive elaboration of that sensory information, which ultimately results in a logical conclusion about what the other is feeling. It may also, however, result in direct mapping of that sensory information onto the motor structures that would produce the experience of that emotion in the observer. These two means of recognizing emotions are profoundly different: with the first, the observer deduces the emotion but does not feel it; via the second, recognition is firsthand because the mirror mechanism elicits the same emotional state in

the observer. Thus, when people use the expression "I feel your pain" to indicate both comprehension and empathy, they may not realize just how literally true their statement could be.

A paradigmatic example is the emotion of disgust, a basic reaction whose expression has important survival value for fellow members of a species. In its most primitive form, disgust indicates that something the individual tastes or smells is bad and, most likely, dangerous. Once again using fMRI studies, we collaborated with French neuroscientists to show that experiencing disgust as a result of inhaling foul odorants and witnessing disgust on the face of someone else activate the same neural structure—the anterior insula—at some of the very same locations within that structure [see box below]. These results indicate that populations of mirror neurons in the insula become active both when the test participants experience the emotion and when they see it expressed by others. In other words, the observer and the observed share a neural mechanism

that enables a form of direct experiential understanding.

Tania Singer and her colleagues at University College London found similar matches between experienced and observed emotions in the context of pain. In that experiment, the participants felt pain produced by electrodes placed on their hands and then watched electrodes placed on a test partner's hand followed by a cue for painful stimulation. Both situations activated the same regions of the anterior insula and the anterior cingulate cortex in the subjects.

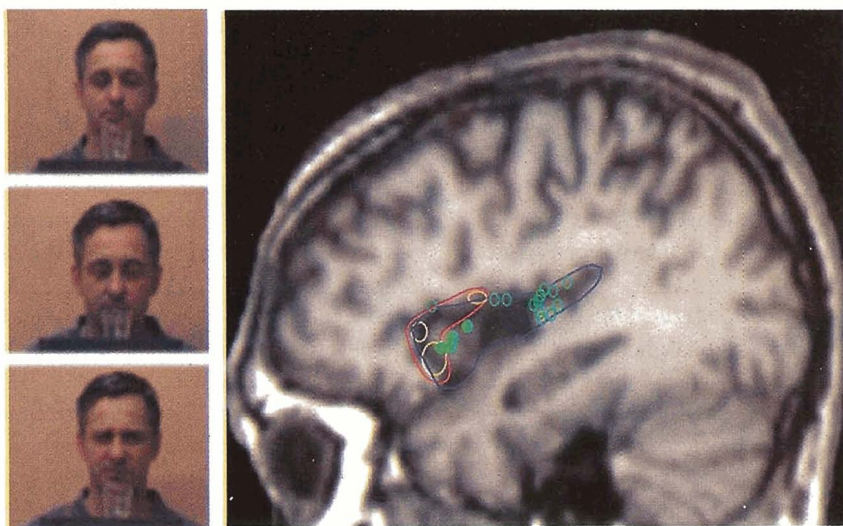
Taken together, such data strongly suggest that humans may comprehend emotions, or at least powerful negative emotions, through a direct mapping mechanism involving parts of the brain that generate visceral motor responses. Such a mirror mechanism for understanding emotions cannot, of course, fully explain all social cognition, but it does provide for the first time a functional neural basis for some of the interpersonal relations on which more complex social behaviors are built. It may be a substrate that allows us to empathize with others, for example. Dysfunction in this mirroring system may also be implicated in empathy deficits, such as those seen in children with autism [see "Broken Mirrors: A Theory of Autism," by Vilayanur S. Ramachandran and Lindsay M. Oberman, on page 62].

Many laboratories, including our own, are continuing to explore these questions, both for their inherent interest and their potential therapeutic applications. If the mirror neuron template of a motor action is partly inscribed in the brain by experience, for instance, then it should theoretically be possible to alleviate motor impairments, such as those suffered following a stroke, by potentiating undamaged action templates. Recent evidence indicates, in fact, that the mirror mechanism also plays a role in the way we initially learn new skills.

Although the word "ape" is often used to denote mimicry, imitation is not an especially well developed ability among nonhuman primates. It is rare in monkeys and limited in the great apes, including chimpanzees and gorillas. For

EMOTIONAL MIRRORS

Feeling disgust activated similar parts of the brain when human volunteers experienced the emotion while smelling a disgusting odor or when the same subjects watched a film clip (left) of someone else disgusted. In this brain cross section, neuron populations activated by the experience of disgust are outlined in red, and those activated by seeing disgust are circled in yellow. (Blue outlines the region of investigation, and green indicates areas examined in a previous study.) These overlapping neuron groups may represent a physical neural mechanism for human empathy that permits understanding the emotions of others.





IMITATION requires reproduction of actions performed by another person. If mirror neurons underlie the uniquely human facility for imitation, the mirror system may serve as a bridge that allows us to teach and learn new skills.

humans, in contrast, imitation is a very important means by which we learn and transmit skills, language and culture. Did this advance over our primate relatives evolve on the neural substrate of the mirror neuron system? Iacoboni and his group provided the first evidence that this might be the case when they used fMRI to observe human subjects who were watching and imitating finger movements. Both activities triggered the IFG, part of the mirror neuron system, in particular when the movement had a specific goal.

In all these experiments, however, the movements to be imitated were simple and highly practiced. What role might mirror neurons play when we have to learn completely new and complex motor acts by imitation? To answer this question, Giovanni Buccino at our university and collaborators in Germany recently used fMRI to study participants imitating guitar chords after seeing them played by an expert guitarist. While test subjects observed the expert, their parietofrontal mirror neuron systems became active. And the same area was even more strongly activated during the subjects' imitation of the chord movements. Interestingly, in the interval following observation, while the participants were programming their own imitation of the guitar chords, an additional brain region became active.

Known as prefrontal area 46, this part of the brain is traditionally associated with motor planning and working memory and may therefore play a central role in properly assembling the elementary motor acts that constitute the action the subject is about to imitate.

Many aspects of imitation have long perplexed neuroscientists, including the basic question of how an individual's brain takes in visual information and translates it to be reproduced in motor terms. If the mirror neuron system serves as a bridge in this process, then in addition to providing an understanding of other people's actions, intentions and emotions, it may have evolved to become an important component in the human capacity for observation-based learning of sophisticated cognitive skills.

Scientists do not yet know if the mirror neuron system is unique to primates or if other animals possess it as well. Our own research group is currently testing rats to see if that species also

demonstrates mirror neuron responses. Such internal mirroring may be an ability that developed late in evolution, which would explain why it is more extensive in humans than in monkeys. Because even newborn human and monkey babies can imitate simple gestures such as sticking out the tongue, however, the ability to create mirror templates for observed actions could be innate. And because lack of emotional mirroring ability appears to be a hallmark of autism, we are also working with young autistic children to learn whether they have detectable motor deficits that could signal a general dysfunction of the mirror neuron system.

Only a decade has passed since we published our first discoveries about mirror neurons, and many questions remain to be answered, including the mirror system's possible role in language—one of humanity's most sophisticated cognitive skills. The human mirror neuron system does include Broca's area, a fundamental language-related cortical center. And if, as some linguists believe, human communication first began with facial and hand gestures, then mirror neurons would have played an important role in language evolution. In fact, the mirror mechanism solves two fundamental communication problems: parity and direct comprehension. Parity requires that meaning within the message is the same for the sender as for the recipient. Direct comprehension means that no previous agreement between individuals—on arbitrary symbols, for instance—is needed for them to understand each other. The accord is inherent in the neural organization of both people. Internal mirrors may thus be what allow John and Mary to connect wordlessly and permit human beings in general to communicate on multiple levels. ■

MORE TO EXPLORE

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