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Introduction to the Mirror Neuron Forum

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"Mirror neurons will do for psychology what DNA did for biology," asserted V. S. Ramachandran in 2007. In contrast, others (e.g., Hickok & Hauser, 2010) are far less sanguine. The goal of this mirror neuron forum is to bring together experts holding a range of opinions to assess the current state of mirror neuron research and theorizing.

The forum has three sections. This first section provides a brief introduction to research on mirror neurons with a focus on work with humans. This section also includes definitions of key terms (e.g., *mirror neuron*, *mirror mechanism*) and a description of many of the techniques that have been used to investigate mirror neurons. Along with each method is a list of the criteria that are used to implicate the operation of mirror neurons.

The second section is the forum itself. The five scientists engaging in the forum (Vittorio Gallese, Morton Ann Gernsbacher, Cecilia Heyes, Gregory Hickok, and Marco Iacoboni) helped to develop the questions and structure of the interchange: Each contributor has 3,000 words to address whichever questions the contributor deems most relevant, but no single answer should exceed 750 words. Then, each contributor has another 1,800 words to comment on what others have written. Finally, the third section attempts to summarize the forum and to provide suggestions for future research.

What Are Mirror Neurons, Mirror Neuron Systems, and Mirror Mechanisms?

Mirror neurons were first discovered by Di Pellegrino, Fadiga, Fogassi, Gallese, and Rizzolatti (1992; see also Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) using single-cell recording from neurons in area F5 of the macaque monkey premotor cortex. What makes a neuron a *mirror neuron* is that it is active both when the animal engages in an activity, such as grabbing a peanut with the hand, and when the animal observes a conspecific (or the experimenter) engage in the same or closely related activity. Further research demonstrated that about one third of these mirror neurons are "strictly congruent"—that is, they require a close match in action production and action perception, whereas about two thirds are broadly congruent and respond to actions with the same goal (e.g., grabbing a peanut) but differing movement specifics (e.g., using a tool instead of the hand). Furthermore, some 17% of these mirror neurons also have auditory properties—that is, the same neuron is active during auditory perception (e.g., hearing a peanut shell being opened), visual perception (e.g., seeing a peanut being broken), and action production (e.g., breaking a peanut). Comprehensive reviews of mirror neuron research may be found in Rizzolatti and Craighero (2004) and Rizzolatti and Sinigaglia (2010).

It is, at the very least, curious that neurons in a motor area of monkey cortex respond to visual and auditory stimuli. The real excitement, however, is generated by theoretical interpretation of the function of mirror neurons. Some have proposed that mirror neurons have a causal role in the recognition of action goals and intents. That is, "resonance" in Animal A's motor system provides that animal with its own goal and intent for an observed action, and Animal A uses that goal and intent to interpret or recognize Animal B's goals and intents. In this way, mirror neurons may grease the wheels of social interaction. Further work with humans has suggested that mirror neurons play a role in empathy (Gazzola, Aziz-Zadeh, & Keysers, 2006), autistic behavior (Dapretto et al., 2006), speech perception (D'Ausilio, et al., 2009), language comprehension (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006), and imitation (Iacoboni, 2005). But in fact, the function of mirror neurons

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is hotly debated. For example, Hickok and Hauser (2010) have proposed that mirror neurons function in action selection and have little to do with recognizing goals and intent or any form of social information processing. The forum addresses the extent to which the data support contributions of mirror neurons to the functions listed above.

It is unlikely that mirror neurons in one area of cortex are doing all of the work (whatever that work may be). Instead, much like other types of neurons, they almost certainly function in conjunction with neurons in other areas of cortex. For example, Iacoboni (2005) proposed a *mirror neuron system* consisting of mirror neurons in the parietal cortex and mirror neurons in the premotor cortex working in collaboration with visual processing performed in the superior temporal sulcus. Similarly, the term *mirror mechanism* refers to a particular area of cortex (or cortical network) involved in both action production and observation.

Because mirror neurons were first discovered in motor areas, much of the research has been focused on action production and recognition. Nonetheless, it now appears that mirror neurons and mirroring mechanisms are found in other areas of the brain not directly related to action. For example, Mukamel, Ekstrom, Kaplan, Iacoboni, and Fried (2010) found mirror neurons in human medial temporal cortex, a region associated with memory. Wicker et al. (2003) reported mirror mechanisms that respond to emotion production and emotion recognition. These and other discoveries suggest that what is mirrored may depend on the functional properties of different systems: Some mirror neurons may code goals, whereas others code shared emotions, learned movements, joint attention, and so on.

Techniques for Investigation and Identification of Mirror Neurons and Systems

The five methodologies described in this section provide a sense of the vibrant and quickly evolving nature of mirror neuron research. It is important to note, however, that this section also demonstrates that none of the techniques is perfect. Consequently, understanding mirror neurons and mirror mechanisms will require careful analysis.

Single-cell recording

The gold standard technique for identifying mirror neurons (although not their function) is single-cell recording. The technique requires a surgical opening of the skull and then the relatively permanent implanting of a recording electrode (or implanting a means to insert the electrode later). Because of the invasive nature of the procedure, it is used most often, but not exclusively, with animals. Mukamel et al. (2010) reported on experiments using single-cell recording in humans. The electrodes were implanted as a prelude to surgery rather than primarily for research, and thus, the location of the electrodes was not selected to test various hypotheses. Nonetheless, these data provide some of the most convincing evidence in humans for individual cells with mirror properties.

In addition to surgical skill, single-cell recording requires a type of clinical skill. Namely, the researcher must display to the animal various stimuli and coax the animal (often by presurgical training) to engage in various behaviors. Thus, although one might be recording from a mirror neuron, if the neuron is not sensitive to the stimuli being used by the experimenter, the mirroring activity might be missed.

Whereas single-cell recording provides the best evidence of mirroring at the level of the single cell, at least two important problems remain. The first is deciding on criteria that implicate mirroring. If a cell responds to visual stimulation with, say, 50% of the activity observed when the action is produced, does that count as mirroring? If the cell responds to a variety of visually presented actions but only one produced action, does that count? Or, as found by Mukamel et al. (2010), if a cell's response during presentation of visual actions is negatively correlated with the activity found during action production, does that count? This latter type of cell would seem to be particularly useful in helping an animal distinguish between self and others or suppressing overt imitative behavior upon observing another. Thus, this negative correlation could usefully be part of a mirror mechanism. Nonetheless, the criteria for these sorts of classifications are not universally accepted.

The second problem with single-cell recording is determining the cell's causal or functional role—the data are intrinsically correlational. For example, just because a cell shows mirror activity does not imply that the cell is engaged in action recognition. Alternative interpretations include action selection and correlated discharge without a particular function.

Brain imaging

Probably the most oft-used procedure for investigating mirror mechanisms in humans has been some form of brain imaging, and of those, functional magnetic resonance imaging (fMRI) is most prevalent. In this technique, the scanner detects changes in blood oxygenation, the blood oxygenated-level dependent (BOLD) signal, which tends to correlate with neural activity. The BOLD signal must be interpreted with some caution, however, because (a) the maximum change in blood flow is delayed by about 6 to 7 s, (b) the signal cannot discriminate between neural firing and suppression of firing, (c) the signal summates activity produced by hundreds of thousands or millions of neurons, (d) there are vexing statistical issues (e.g., correcting for multiple comparisons and selecting voxels to analyze; Vul, Harris, Winkielman, & Pashler, 2009), and (e) the technique is correlational—that is, observing BOLD changes in a particular area does not indicate that the area of cortex was causally efficacious in producing the observed behavior. Put differently, experimenters manipulate stimuli and cognitive tasks and then observe differences in the BOLD signal. Thus, we can safely conclude that the stimuli and tasks caused changes in brain activity. But, the interesting question is whether (and how) the brain activity affects performance of the cognitive tasks, and answering that question requires manipulating the brain and observing what behavior follows. Unfortunately, fMRI does

not lend itself to manipulating the brain (but see the following discussion of transcranial magnetic stimulation).

Another thorny problem for fMRI research is that interpretation often depends on the logic of the subtraction method. Because all areas of the brain show some activity in every task, experimenters need to determine that an area is particularly active for the task of interest. One way to make this determination is to use a control task that differs from the critical task in just one way—the way that is critical to the proposed function under study. For example, in Rueschemeyer, Glenberg, Kaschak, Mueller, and Friederici (2010), the critical task was understanding sentences describing visual motion (e.g., "The car approaches you") and the control task was understanding sentences describing a visual scene but with no motion (e.g., "The car is large"). Then, one subtracts activity measured during the control task from activity measured during the critical task to determine those areas of the brain differentially active during the critical task.

There are at least two problems, however, with the subtractive methodology. The first is that there is generally no way to determine that the two tasks differ in one and only one way. Note that the two sentences above differ in several ways (e.g., number of letters, number of syllables, description of the size of the car) in addition to whether they describe motion or not. Second, the two tasks may differ in subtle ways that complicate interpretation. For example, one control task may be more variable than another control task. Then, whether or not there is a significant difference between the control task and the critical task might reflect variability rather than differences between means.

Given the difficulty in interpreting the BOLD signal, how does one characterize activity as being produced by mirror neurons or a mirror mechanism? In general, the criteria have been (a) particularly strong activity observed in an area of cortex during action production, (b) similarly strong activity observed in the same area during action recognition, and (c) the area has been associated with mirror neurons using single-cell recording. (Keep in mind, however, that usually the single-cell recording is of the monkey cortex whereas the fMRI is of the human cortex. It is a good bet, although not guaranteed, that the areas are homologous given the conservative nature of evolution and given that homologies in brain structure are the norm in closely related species.) An additional criterion used in some studies is to demonstrate somatotopy. For example, Aziz-Zadeh et al. (2006) studied the fMRI signal in human premotor cortex and observed (a) BOLD activity during observation of actions involving the hand that matched BOLD activity during reading about hand actions, (b) BOLD activity during observation of actions involving the foot that matched BOLD activity during reading about foot action, and (c) that those two sets of matches occurred in spatially different areas of the cortex.

A recent innovation in the use of fMRI to study mirror mechanisms has been the development of the cross-modal repetition suppression paradigm. Researchers have often found that the BOLD response is reduced upon repetition of a stimulus. Mirror neurons are supposedly active both upon action production and action recognition. Consequently, if imaging a mirror mechanism, one should expect a decreased BOLD signal not only when the same action is produced repeatedly, but also when that action production is followed by the observation of the same action. In addition, there should be repetition suppression of the BOLD signal when observation of an action is followed by production of that action. These predictions have been confirmed by Kilner, Neal, Weiskopf, and Frith (2009), although Lingnau, Gesierich, and Caramazza (2009) only found repetition suppression when action observation was followed by action production and not when production was followed by observation. However, there are potential problems with fMRI repetition suppression paradigms (Bartels, Logothetis, & Moutoussis, 2008) and with the logic of cross-modal adaptation (Sawamura, Orban, & Vogels, 2006). For example, repetition may affect the input synapse and not the firing of the neuron itself. In this case, input using different synapses (e.g., cross-modal input) may show no effect of the repetition.

Mu rhythm suppression

Neural activity is often coordinated so that rhythmic electrical signals are generated, and this rhythmical activity can be detected by both magnetoencephalography (MEG) and electroencephalography (EEG). At rest, motor areas generate activity with a frequency around 10 Hz, called *mu rhythm*, and mu rhythm is suppressed during motor execution. It is interesting to note that mu rhythm is also suppressed during action observation (e.g., Cheng et al., 2008), and this has been taken as evidence for mirroring. Although the technique has many of the interpretive problems of fMRI, it is particularly useful for studying putative mirror activity in infants.

Transcranial magnetic stimulation (TMS)

When using TMS, an electromagnetic coil, often figure-eight shaped, is held near the head. When the coil is pulsed, a magnetic field is generated, and the field penetrates the skin, skull, and outer layers of cortex. Neurons that are perpendicular to the magnetic field act like conductors, and an electric pulse is induced in those neurons. In this way, the TMS pulse literally affects brain activity.

TMS can be used in at least three ways. First, a single pulse directed at motor areas of the brain can generate activity in targeted muscles. This activity is called a motor evoked potential (MEP). Once there is measurable activity in the muscle, one can study modulating effects of cognitive tasks. Any such modulation indicates that the cognitive activity and motor activity share some portion of the cortico-spinal pathway. As one example, Fadiga, Craighero, Buccino, and Rizzolatti (2002) directed TMS pulses at areas of motor cortex that control the tongue to elicit MEPs at the tongue. These MEPs were then modulated by listening to speech with an Italian trilled "r" (produced by the tongue), but not with an Italian double "f" (produced by the lips). They concluded that the pathways

involved in listening to speech are shared with motor activity involved in speech production.

Two TMS pulses delivered in quick succession can sometimes facilitate performance. D'Ausilio et al. (2009) directed a double TMS pulse at motor areas used in controlling the tongue or the lips while the participant tried to discriminate between tongue-produced phonemes and lip-produced phonemes. The tongue-directed double pulses facilitated processing of tongue-produced phonemes more than lip-produced phonemes, and the opposite effect was found for lip-directed double TMS pulses.

The third use of TMS is called repetitive TMS (rTMS). In this procedure a series of pulses, often several a second, is directed at a particular area of cortex for seconds or minutes. Subsequent to rTMS, processing in the stimulated area is disrupted, often for several minutes.

TMS procedures are able to deal with some, but not all, of the problems associated with fMRI. Most important, TMS (particularly double-pulse TMS and rTMS) can be used to demonstrate a causal relation because manipulating the brain can be shown to affect behavior. However, as noted before, proper interpretation of TMS admits the possibility that effects of the pulse are produced anywhere along the cortico-spinal pathway. Also, the TMS pulse has a spatial distribution of about 0.5 to 1 cm, and thus, millions of neurons are affected by the pulse. In this case, one could argue that the pulse affects separate systems: one used in action production and one used in action recognition.

With TMS, the criteria used to identify a mirror mechanism are relatively simple. Namely, if the TMS pulse is directed at a motor area (and produces measurable motor activity) and the same pulse affects action recognition (e.g., speech perception), that is *prima facie* evidence for a mirror mechanism. Adding a demonstration of somatotopic organization is generally accepted as increasing the probability of having tapped a mirror mechanism. Nonetheless, as noted above, the possibility exists that the TMS pulse has multiple effects such as affecting a motor system and a separate recognition system that happen to be located in the same cortical area.

Behavioral methods

A variety of behavioral methods have been proposed for investigating putative mirror mechanisms. Here, the focus is on three methods that have been useful in demonstrating causal relations. All three methods involve some form of learning.

The first method for demonstrating a causal relation, teaching a new action, was used by Casile and Giese (2006). They trained participants to produce a novel, upper body motion. During training, participants were blindfolded to minimize visual experience. Next, the participants classified pairs of point-light walkers as using the same gait or different gaits. Remarkably, discrimination (i.e., action recognition) improved for the gait using the trained upper body motion, and discrimination performance was correlated with the success that participants had in learning the novel upper body motion. How do

these findings implicate a mirror mechanism? If we agree that the blindfold eliminated visual experience, then the results demonstrate a causal effect of motor training on action recognition, which is one of the signature claims of a mirror mechanism. Note, however, that it is difficult to map these data to the underlying neurophysiology: Did the training affect the same sort of mirror mechanism as identified by single-cell recording? It is impossible to say.

Rather than modifying a mirror mechanism by training a novel task, the second method involves retraining a familiar task. Catmur, Walsh, and Heyes (2007) used single-pulse TMS to measure muscle activity in the fingers while participants watched a display of a hand moving the index finger or the little finger. Sensibly enough, MEPs in the index finger were enhanced by watching a display of index finger movement, and MEPs in the little finger were enhanced by watching a display of little finger movement. This finding suggests a mirror mechanism in that action observation modulates motor activity. Next, participants learned to produce an action upon seeing the moving hand displays. Participants in the control condition produced imitative actions (e.g., moved the index finger when the display was of a moving index finger), and participants in the incompatible condition learned to produce "countermirror" actions (e.g., moved the index finger when the display was of a moving little finger). One day later, TMS was again used to measure muscle activity in response to the visual displays. For the control condition, MEPs were similar to those used in pre-training, but for the incompatible condition, the MEP effects were reversed: There was greater activity in the muscles controlling the finger opposite to that in the display. These data clearly indicate malleability of a mirrorlike mechanism. Nonetheless, as with Casile and Giese, it is not clear how to map these results onto the underlying neurophysiology (see Catmur, Mars, Rushworth & Heyes, in press, for work addressing this question). Also, whereas it is clear from Catmur et al. (2007) that visual action observation affects muscle activity, it is not clear that the muscle activity (or the neural systems underlying that activity) contribute to visual action recognition (e.g., classification of the action as a particular kind or identification of the goal or intent of the action). It is this latter claim that is central to the interpretation of mirror mechanism function.

The third method relies on the multimodality of mirror neurons (and by extension, mirror mechanisms). Therefore, much as with cross-modal repetition suppression in fMRI research, if a mirror mechanism plays a causal role, then modifying the mechanism through one modality should affect performance in the other modality. This reasoning was used by Glenberg et al. (2010), who developed a behavioral paradigm for investigating mirror mechanisms. In their experiment, blindfolded participants transferred 15, 45, 135, or 405 beans from a source container to a target container. The containers were arranged so that the action was either toward the participant or away from the participant. Following these movements, the participant engaged in a psychophysical task that measured the threshold for classifying ambiguous movement in depth as toward or away. The stimuli that moved in depth in the psychophysical

task were pictures of (a) a hand holding a small object using a precision grip (as used in holding a bean), (b) the palm side of a hand with fingers outstretched, and (c) a geometrical diamond shape. The results satisfied four criteria consistent with a mirror mechanism. First, there was cross-modal adaptation; that is, moving beans while blindfolded systematically changed the threshold for seeing movement in depth. Second, the adaptation was specific to movement direction; that is, moving the beans toward the participant made it more difficult to see movement toward, and moving beans away from the participant made it more difficult to see movement away. Third, consistent with an interpretation of neural adaptation, the size of the shift in threshold was linearly related to the number of beans moved. Fourth, changes in threshold were found for the stimuli with biological verisimilitude (the two- hand stimuli), but not for the nonbiological stimulus (the diamond). This finding corresponds to work with macaque monkeys showing that mirror neurons have a preference for biological movement.

These data provide strong evidence for a causal connection between the motor system and visual action recognition (adapting the motor system affects action recognition), and that is certainly consistent with the predictions of a mirror mechanism used in action recognition. The data do not provide a strong connection to underlying neurophysiology, however. To provide some evidence regarding that link, Cattaneo et al. (in press) combined a variant of the motor adaptation paradigm with TMS. The critical finding was that after repeated motor actions, TMS directed at the premotor cortex (where mirror neurons are prevalent, at least in macaques) eliminated the adaptation of action recognition, whereas TMS directed at the motor cortex (where mirror neurons are less prevalent) left the adaptation of action recognition unchanged.

Conclusion

The discussion of methodologies leads to two conclusion. First, no method is perfect. Single-cell recording provides the most reliable method for identifying individual mirror neurons, but not neural systems, and the method does not easily yield causal conclusions. In humans, brain imaging allows for some localization of activity, but fMRI brings along with it many interpretive problems, the most important being the difficulty of making causal claims. TMS can be used to make causal claims, but localization is not precise and hence it is difficult to conclude that the TMS pulse is affecting one functional system or multiple systems. Behavioral methods are also useful for making causal claims, but then it is difficult to relate those claims to the neurophysiology that most clearly identifies mirror neurons.

The second conclusion is that progress will most likely be made by employing multiple methods, perhaps in conjunction with one another (e.g., the joint use of behavioral methods and TMS as illustrated by Catmur et al., 2007, and Cattaneo et al., in press). Nonetheless, even the results from multiple methods will require careful interpretation. Hence, the need for a forum such as the one in this issue of *Perspectives on Psychological Science*.

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