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Watching Others' Actions: Mirror Representations in the Parietal Cortex

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An observation that neurons in the motor cortex of the monkey are active both when the monkey performs a specific action and when he watches an actor executing the same action led to the mirror-system hypothesis. This hypothesis suggests that primates perceive and interpret others' actions by generating an internal motor representation (e.g., simulation). Recent evidence suggests that humans have a similar mirror system. In this review, we focus on the essential congruence between the motor and visual properties of an action. We summarize behavioral and imaging studies in humans that show that observing others' actions can interfere with our own motor execution. We discuss a framework for understanding such an internal representation and suggest that the activity in the parietal cortex during observation of others' actions is based on the sensory-to-motor remapping properties of this region, which are necessary for fine control of our own actions. NEUROSCIENTIST 13(6):667–672, 2007. DOI: 10.1177/1073858407302457

Mirror neurons are a particular class of visuomotor neurons that discharge both when the monkey performs a particular action and when it observes another monkey, or the experimenter, doing a similar action. The first mirror neurons were discovered in area F5 of the monkey's prefrontal cortex (Gallese and others 1996; Di Pellegrino and others 1992). More recently, mirror neurons were also found in the anterior part of the monkey's inferior parietal lobule (IPL; Foggasi and others 1998; Foggasi and others 2005). The functional role of mirror neurons has been hotly debated since they were first reported. Suggestions include a leading role in imitation, language development, action understanding, and social cognition. These options are discussed in detail elsewhere (Rizzolatti and others 2001; Rizzolatti and Craighero 2004) and are beyond the scope of this review. Here, we focus on the mirror-system characteristics, adopting a mechanistic approach rather than a functional one. We suggest that the mirror system may develop on the basis of the intrinsic features of the motor system (which controls our own actions) to understand and predict actions made by others.

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Visuomotor Congruence in the Mirror System

Many parietal neurons are classified as visuomotor, having specificity to both motor elements and visual aspects. For example, neurons in the lateral intraparietal (LIP) area often have a saccadic "movement field" (i.e., firing during a saccade of a specific magnitude and direction) that corresponds to their visual receptive field (Colby and others 1995). Mirror neurons are a unique class of visuomotor neurons in that they are active during a specific motor action and the visual perception of the same action made by the experimenter or by another monkey. Indeed, Gallese and others (1996) reported that 93% of the visuomotor neurons in F5 showed some congruence between their preferred observed action and the motor actions they encode. Thirty-two percent of F5 visuomotor neurons showed strict congruence (firing during both observation and execution of a specific grasping grip), whereas 61% showed broad congruence, coding only the goal of the action (such as object grasping without specificity to the way the object is grasped). The question of specificity and congruence—the degree of tight linkage between the visual and motor properties of mirror neurons—is clearly the core of the mirror-system hypothesis. In the next section, we present the evidence for this congruence in the human cortex.

Evidence for the existence of mirror neurons in humans is obviously indirect. However, behavioral studies demonstrate an interaction between an observed action and the executed one. For example, Brass and others (2000) showed that when subjects are required to move one of two fingers, observing incongruent finger movements interferes with the subjects' performance

(compared with observation of congruent finger movements), even when the observed actions are irrelevant for the task. Similarly, Kilner and others (2003) have demonstrated that the accuracy of performance of repetitive horizontal or vertical arm movements is significantly worse when subjects observe perpendicular arm movements than when they observe arm movements similar to the ones they execute.

If the mirror system is activated when seeing an action, this should be manifested in a change in the excitability of the observer's brain regions that encode the execution of the observed action (and only those). One way to assess this is by measuring the magnitude of the motor-evoked potential (MEP), recorded from the muscles, as a result of applying transcranial magnetic stimulation (TMS) to the primary motor cortex (M1) during action observation. Several TMS studies have used this approach to demonstrate that the motor system is activated during action observation (for example, Aziz-Zadeh and others 2002; Gangitano and others 2001; Theoret and others 2005). Thus, passive observation of video clips that show object grasping amplifies the amplitude of the MEP resulting from a TMS pulse applied to M1, in concordance with the kinematic profile of the observed action (Gangitano and others 2001). Aziz-Zadeh and others (2002) showed that when applying TMS to M1, MEPs are greater during observation of a contralateral hand action than during observation of an ipsilateral hand action. Furthermore, using the same technique, researchers have shown that action observation can modulate the motor cortex, even in the long run, by forming new motor memories. Classen and others (1998) demonstrated that after the repetitive execution of unidirectional, stereotyped thumb movements, the direction of thumb movements evoked by TMS over M1 was altered so that it corresponded to the direction of the movements during training. Amazingly, even mere observation of thumb movements oriented opposite to the previously determined direction of the thumb movement (for a TMS pulse) increased the probability that a TMS-evoked thumb movement will result in movement towards the observed direction (Stefan and others 2005). This result indicates that action observation not only interferes with motor execution but can also change long-lasting motor representations.

Functional-imaging studies in humans further demonstrate that some motor cortical regions are active during observation of actions made by others, following the same rules of motor representation. Buccino and others (2001) showed subjects clips of object manipulation by the hand, mouth, and foot. They found that some regions within the premotor and parietal cortex were more active during observation of these dynamic clips than during observation of static pictures of the same actions. Buccino and others also found that these regions contained a homunculus-like mapping of the seen effectors (representing the foot-, hand-, or mouth-action clips along the mediolateral axis), similar to the classic somatomotor mapping along the central sulcus. Furthermore, the activation in the parietal cortex was seen only when the subjects observed clips showing object manipulation and not while observing clips without an object.

Another guiding rule of representation in the monkey's motor cortex is the localized representation of specific actions. Thus, grasping is represented in the anterior intraparietal (AIP) area (Sakata and others 1995), reaching movements in the parietal reach region (PPR; Buneo and others 2002), and saccades in the LIP area (Colby 1998). Culham and others (2003) showed that the fMRI activation in the anterior intraparietal sulcus (aIPS) of humans is significantly greater when subjects are executing object-grasping movements than when they perform only the reaching part of the action. Based on these motor findings, we studied how grasping movements made by others are represented in the human cerebral cortex (Shmuelof and Zohary 2005, 2006). During an fMRI experiment, subjects observed video clips of a single hand reaching for and grasping various objects. We found that regions within the aIPS showed grasp-based adaptation (i.e., reduction of the fMRI signal during observation of the same grasping movement, compared to the signal elicited by viewing different grasping movements). These results suggest that there may be a correspondence between the selectivity of the anterior intraparietal cortex to visually guided self-grasping and the region's specificity for grasping actions made by others (see Fig. 1C). Furthermore, an important feature of the viewed grasping action—determining the magnitude of the fMRI response—was the identity of the observed acting hand (right or left hand). Observing grasping actions by the right hand elicited greater fMRI activation in the left aIPS, whereas observing left-hand actions resulted in greater activation in the right aIPS (Figure 1A). The fact that such a clear contralateral hand preference, a classic characteristic feature of the motor system, can be seen during viewing action (rather than self-action) lends further support to the notion that the observation of grasping movements evokes an internal simulation of the observed action, using our own motor system. Furthermore, this hand specificity is seen in parietal voxels that demonstrate congruent visual and motor properties. Thus, the same voxels show selective activation for both 1) observing object-manipulation actions and 2) manipulating objects with the contralateral hand in the absence of visual feedback (see Fig. 1B).

It is important to keep in mind that the congruent and specific fMRI response in both action observation and action execution does not necessarily imply that single neurons in the human anterior intraparietal cortex are sensitive to both the visual and motor elements of the same action. Because the spatial resolution of the fMRI signal is very coarse ($\sim$10–50 mm^3, corresponding to the average activity of $\sim$1 million to 5 million neurons), it is possible that there are various neuronal populations within a given voxel: Some are specific to the visual aspects, whereas others are specific to the motor elements. One indirect way to suggest that single neurons in the human anterior intraparietal cortex truly have a dual visuomotor-matching function is by using a visuomotor fMRI adaptation paradigm (Grill-Spector and others 1999). The fMRI signal
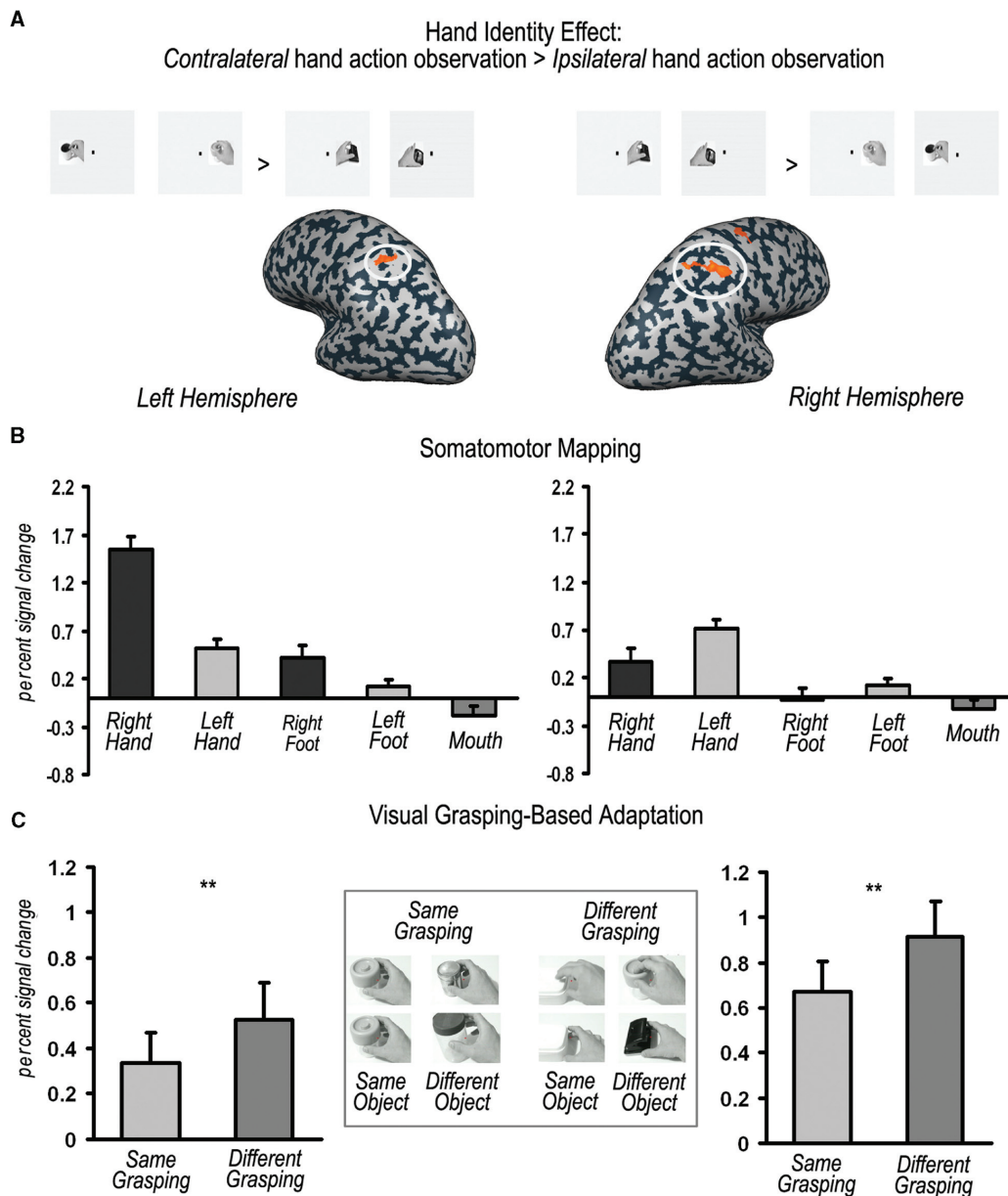
Fig. 1. Analysis of fMRI activation in the parietal areas that show selectivity to the identity of the observed hand. *A*, Hand-identity areas. This is an illustration of the cortical areas showing greater fMRI activation during observation of contralateral hand actions than during ipsilateral hand actions (irrespective of the hand position relative to the fixation point). Orange-colored regions in the right hemisphere are voxels with significantly higher activation during observation of left-hand actions than during observation of right-hand actions ($P < 0.05$, $n = 14$, cluster-size correction for multiple comparisons). In the left hemisphere, the orange areas depict voxels with the opposite selectivity (right hand > left hand). *B*, Motor properties in the hand-identity areas. This illustration shows averaged fMRI activation ($n = 9$) during a somato-motor mapping experiment in which the subjects moved their right or left hand or foot or their mouth in the dark without visual feedback. Error bars denote SEM. Significant preference can be seen for actions of the contralateral hand compared to the ipsilateral hand (paired, two-tailed t-test, $P < 0.005$) as well as compared to the other body parts. Thus, the parietal regions that are sensitive to the identity of the viewed hand show a similar contralateral specificity for one's own acting hand. *C*, Grasp-viewing–based adaptation in hand-identity areas. Repeated viewing of the same grasping behavior leads to a reduction of the fMRI signal in the same parietal areas that are sensitive to the identity of the viewed hand. Significant reduction of the fMRI signal during repeated observation of the same grasping movement (compared to the case of viewing different grasping movements) can be seen in voxels activated during both left and right parietal hand identity (paired, two-tailed t-test; $P < 0.005$). The asterisks denote significance (**$P < 0.01$). The central inset shows static samples of the video clips that were used during the same-grasping and the different-grasping conditions. In both conditions, subjects observed blocks showing a right hand reaching and grasping the same or different objects. Adapted from Shmuelof and Zohary 2006, with permission from the Society for Neuroscience.

in the aIPS shows clear signs of adaptation when the same grasping movement is observed repeatedly (Shmuelof and Zohary 2005). If the same aIPS neurons discharge both during observation of a specific grasping and its execution, one should see similar adaptation of the fMRI signal if one's grasping movement is preceded (or followed) by viewing the same action. On the other hand, if adjacent neural populations (in the same voxel) are separately active during grasping observation and execution, adaptation would not be expected. Such an experiment might shed more light on the neural mirror properties of the human's parietal cortex.

Another way to establish (or refute) the existence of a mirror system is to measure the correlation between the motor knowledge that is gained through repeated practice by a subject (such as a ballet dancer) and the subject's mirror (visually elicited) activity. The logic behind this approach is that if the mirror fMRI activation indeed represents the motor knowledge of the subject, there should be a clear difference between the activation elicited by viewing actions that the subject has practiced and can perform well and actions he cannot replicate. This is indeed the case: Imaging studies of professional dancers (Cross and others 2006; Calvo-Merino and others 2005; Calvo-Merino and others 2006) demonstrate greater activation in parietal and premotor areas during viewing of well-practiced dancing movements than during viewing of dancing movements that have not been practiced by the viewers.

Until this point, we have described recent evidence demonstrating a correspondence between action observation and action execution. This match can be seen in terms of 1) the cortical localization of these two functions (in parietal areas) and 2) mutual interactions between action observation and action execution: the effects of action observation on action execution (such as during motor interference) or the effects of action execution on action observation (e.g., during observation of practiced vs. novel dancing movements).

Internal Simulation and Action Control

What underlying mechanisms may explain this congruence? It has been argued that the internal simulation of observed actions is based on the same mechanisms of forward modeling that naturally take place during action execution (Oztop and others 2005; Blakemore and Decety 2001). Thus, internal simulation that allows the observer to predict the kinematics and outcome of his or her own observed action may also be used for predicting others' actions.

Forward Modeling during Action Execution

Based on computational and psychophysical results from motor-control experiments, Wolpert and Miall (1996) have suggested that the central nervous system can learn to estimate the sensory outcome of one's own specific commands to the motor system (such as the trajectory of the hand) using an internal simulation, a forward model. This assessm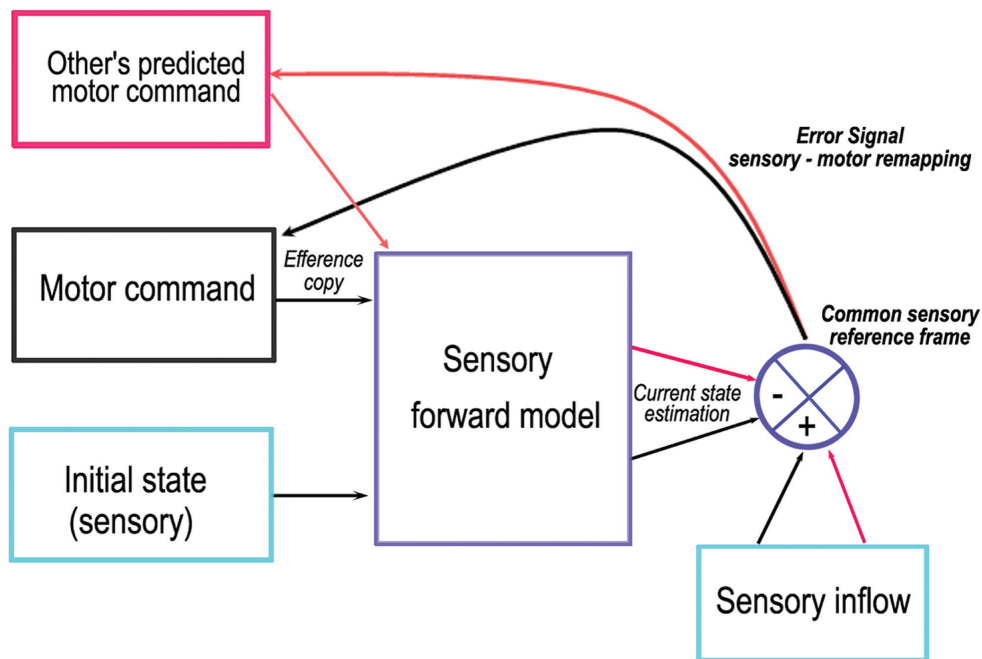ent is based on an efference copy of the motor command and sensory inflow about the current state of the acting effector. Based on these two inputs, the forward model predicts the sensory outcome of the motor command at any given time and compares it to the (delayed) sensory feedback from the environment. In the case of incongruence between these two signals, an error signal emerges, leading to correction of the action during its unfolding (see Fig. 2). Thus, to detect and correct errors in the trajectory of the hand in its reach, a comparison between the predicted location of the hand (the sensory-forward model) and the online, sensory-based location of the hand has to be made on a common sensory frame of reference (presumably eye centered; see Batista and others 1999). The results of this comparison (i.e., the error signal) is subsequently remapped to the relevant motor reference frame, according to the acting effector (right hand, left hand, etc.), the executed action (grasping, reaching, etc.), and the location of the object relative to the hand (Colby 1998; Buneo and others 2002).

To establish the involvement of the anterior parietal cortex in error-signal processing, Tunik and others (2005) have shown (using TMS) that virtual lesions to the human anterior parietal cortex (contralateral to the acting hand) caused errors in reach-to-grasp kinematics towards a rotating target only immediately after (65 ms) target rotation. Interestingly, if the rotation of the target was such that it did not require a change in the grasping posture (because of target symmetry), the TMS pulse to the aIPS did not cause significant errors in the kinematics of the grasp movements. This result suggests that this area might be engaged in the correction of the hand kinematics in the early stages of its unfolding (based on a calculated error signal). An elegant way to identify brain areas that are associated with error-signal processing is by following the time course of classical visuomotor-association learning tasks. Imaging studies have found a positive correlation between the behavioral end-point error and the fMRI activation magnitude in the intraparietal sulcus, contralateral to the acting hand (during a force-field, center-out task; Tunik and others 2007), and in the posterior parietal cortex (during visuomotor rotation; Graydon and others 2005). The correlation between the fMRI signal and the behavioral error supports the claim that the anterior parietal cortex is engaged in building or monitoring associations between motor commands and sensory inputs. Furthermore, the fact that the effects were mainly found in the intraparietal sulcus contralateral to the acting hand suggests that the error signal in this region already has been remapped to motor coordinates.

Forward Modeling during Action Observation

The remapping properties of the parietal cortex may be used not only for monitoring one's own course of action but also for predicting the outcome of others' actions (Oztop and others 2005). Thus, based on the early stages of an observed action, the observer builds an internal simulation of the action's course and final outcome. This outcome is constantly compared to the (visual) sensory inflow regarding the actor's actions. If there is congruence between the predicted outcome of the inferred

Fig. 2. Simplified illustration of the internal forward model during action execution (black arrows) and action observation (red arrows). During action execution, the forward model receives a copy of the motor command (efference copy) and sensory information regarding the state of the effector. Based on these two inputs, the sensory-forward model generates a prediction of the (sensory) expected outcome of the motor command in each moment. This estimation is subsequently compared to the sensory inflow from the environment in a common sensory reference frame. In case of a discrepancy between the two signals, an error signal emerges. Sensory-to-motor remapping of the error signal leads to correction of the motor command. During action observation (red arrows), the observer builds a prediction about the intended motor action of the actor, based on visual information. The predicted command is fed into the forward model, resulting in an estimation of the sensory outcome of the actor's action. This estimation is compared with the visual inflow, and in case of a marked difference between the predicted state (the predicted location of the hand) and the current state (the real location of the hand), the remapped error signal leads to correction of the observer's prediction regarding the actor's action.

action and the sensory inflow, the prediction of the observer is probably correct; if not, the emerging error signal (in motor reference frame) leads to an update of the observer's prediction about the actor's action (see Fig. 2). This model is supported by our recent findings in the human parietal cortex. The selectivity of voxels in the anterior parietal cortex to the identity of the acting hand, both when performing grasping actions and when viewing similar actions made by others, may be explained as the sensory-to-motor remapping of the error signal to the relevant motor coordinates. Interestingly, this parietal activation is prominent during tasks, such as imitation and mental rotation of hand posture, that facilitate the remapping of external actions to our own motor system (Iacoboni and others 1999; de Lange and others 2005). For example, the fMRI activation in the intraparietal sulcus was correlated with the degree of mental rotation necessary to determine the identity (left or right) of pictures of hands but not when similar mental rotation was applied to letters. Recently, a modulation of the activation in the intraparietal sulcus during this task was demonstrated as a function of the subject's hand postures in the scanner, as well (de Lange and others 2006).

Conclusion

In this review, we describe recent functional-imaging, behavioral, and TMS studies that suggest that self-evoked and observed actions may share similar cortical (motor) representations and that these can interfere with each other. We speculate here that this common representation (of our own and others' action) is a result of the comparison between the internal forward modeling and the incoming sensory inflow that leads to generation of error signals. This (motor-registered) error signal allows fine control over our own actions. We suggest that the same system can be used to predict and react to actions made by others.

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