

Mirror neurons in humans: Consisting or confounding evidence?

Luca Turella^a, Andrea C. Pierno^a, Federico Tubaldi^a, Umberto Castiello^{a,b,*}

^a *Department of General Psychology, University of Padua, 35131 Padova, Italy*

^b *Department of Psychology, Royal Holloway, University of London, Egham, Surrey TW20 OEX, UK*

Accepted 12 November 2007

Available online 21 December 2007

Abstract

The widely known discovery of mirror neurons in macaques shows that premotor and parietal cortical areas are not only involved in executing one's own movement, but are also active when observing the action of others. The goal of this essay is to critically evaluate the substance of functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies whose aim has been to reveal the presence of a parallel system in humans. An inspection of this literature suggests that there is relatively weak evidence for the existence of a circuit with 'mirror' properties in humans, such as that described in monkeys.

© 2007 Elsevier Inc. All rights reserved.

Keywords: Mirror neurons; Imitation; Action observation; fMRI; PET; Humans; Macaque monkey; Inferior frontal cortex; Parietal cortex; Premotor cortex

1. Introduction

Mirror neurons are a class of visuomotor neurons activated by both the execution and the passive observation of object-related actions. Cells having this property were found in macaques within the convexity behind the arcuate sulcus (area F5c) within the premotor cortex (PMC; Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Fogassi, & Gallese, 1996a), and in the complex PF/PFG (PF) within the rostral part of the convexity of the inferior parietal cortex (Fogassi et al., 2005; Fogassi & Luppino, 2005; Gallese, Fogassi, Fadiga, & Rizzolatti, 2002).

Although the thorough investigation of mirror neurons has brought to the description of a number of features characterizing these cells (for review see Rizzolatti, Fogassi, & Gallese, 2001; Rizzolatti & Craighero, 2004; Rizzolatti & Luppino, 2001) the present essay focuses on their most striking property. That is, the response of these neurons to

both the execution of an action, and to the observation of either a conspecific or an experimenter carrying out that same action.

The discovery of these cells has had a revolutionary impact, turning perception-action interaction into a focus of intensive, interdisciplinary research looking for a similar 'mirror' activity in humans. However, there has been a great deal of speculation about the functions of a possible human homologue of mirror neurons. Reasonable proposals have suggested that they mediate action observation and understanding (Rizzolatti et al., 2001). Whereas, intriguing, but more speculative proposals suggest that they mediate imitation (Iacoboni, 2005a), understanding of intention (Iacoboni et al., 2005) speech processing (Rizzolatti & Craighero, 2004), music processing and misperception of emotion in music (Gridley & Hoff, 2006; Molnar-Szakacs & Overy, 2006), empathy (Leslie, Johnson-Frey, & Grafton, 2004), cigarette addiction (Pineda & Oberman, 2006), and sexual preference (Ponseti et al., 2006). However, at present, compelling experimental evidence for the possible involvement of the mirror system in any one of these functions is relatively weak. This is chiefly due to the fact that so far there is little evidence that the identified areas subserving such functions are indeed

* Corresponding author. Address: Department of General Psychology, University of Padua, 35131 Padova, Italy. Fax: +39 049 8276600.

E-mail address: umberto.castiello@unipd.it (U. Castiello).

‘mirror’. To date, the only available review aimed at evaluating activation related to movement execution and observation failed to show any reliable effect of ‘mirror’ activity in putative human homologue mirror areas (Grezes & Decety, 2001). However, since this seminal review, a number of fMRI and PET studies have been conducted to reveal a functional equivalence between observing and performing an action. Therefore such new evidence calls for a re-assessment of this literature.

Herein we pose the following question: has this body of research demonstrated without reasonable doubt that exactly the same human brain area is activated in both the execution and the observation of a similar action (as happens for the monkey mirror neurons)?

As we shall report, the majority of PET and fMRI studies on neurologically healthy subjects have not adopted an experimental design adequate enough to provide persuasive evidence for the existence of a human mirror system that has similar properties to those revealed in monkeys. The goal of the present essay is not to cast any doubt on the importance of the discovery of mirror neurons, but to critically evaluate the substance of the speculations which have been advanced in the terms of its existence in humans.

First, we will review PET and fMRI studies aimed at elucidating possible evidence in favor of brain areas showing similar activation for both the observation and the execution of action. Then, in the ensuing sections we shall critically discuss, on the basis of theoretical and empirical evidence, how reasonable it is to assume that a mirror system does exist in humans.

2. PET and fMRI studies in the human brain

Here we shall review available evidence in favour of the existence of a mirror neuron system in humans and consider whether it exhibits the same properties as those found in the ‘classic’ studies performed on non-human primates. This is a fundamental step because, before speculating about the number of functions the ‘human’ mirror neurons may subserve, it is imperative to verify that in the human’s brain areas similar to those identified in monkeys are activated for similar tasks.

We will consider only studies performed with neurologically healthy volunteers focusing on findings which have been primarily interpreted in terms of ‘mirror’ type of activity. Specifically, these findings relate to the observation and imitation of action.

Studies which have utilized Johansson (1973) type of stimuli (e.g., Bonda, Petrides, Ostry, & Evans, 1996), whole body movement (e.g., Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002) or computer graphic animated stimuli (e.g., Pelphrey, Morris, & McCarthy, 2004) will not be considered because they are not comparable with those that have been utilized to elicit mirror neurons responses in monkeys. Second, we will report on imitation

studies which, more than in other domains, have called for an involvement of ‘mirror’ type of activity.

Although the human homologues of the monkey’s mirror areas are thought to be the ventral premotor cortex, the pars opercularis of the inferior frontal gyrus (but see Petrides, 2005; Petrides, Cadoret, & Mackey, 2005), and the rostral part of the inferior parietal lobe, we will consider here any potential human homologue of the monkey mirror areas (as proposed within the literature). Therefore, in our review screening we will use liberal criteria for the inclusion of potential ‘mirror’ areas. For the frontal cortex we will consider both the ventral and the dorsal premotor cortex, the supplementary and pre-supplementary motor area and both the pars opercularis and triangularis of the inferior frontal gyrus. For the parietal cortex we will consider the inferior parietal lobule, the superior parietal lobule, and the intraparietal region.

2.1. Action observation

In this section we shall elaborate only on a number of studies which, by virtue of their experimental design and activated areas, have the potential to show ‘mirror’ activity as originally described (for a description of the criteria adopted to operate this selection please refer to the note in Table 1). These studies are marked with an asterisk in Table 1. We will not describe in detail the remaining studies because on the basis of the classic report on ‘mirror’ activity (Rizzolatti, Fadiga, Fogassi et al., 1996a, 2001) they do not meet ‘mirror’ criteria.

Inspecting Table 1, it is noticeable that only a few studies (those marked with an asterisk) meet the necessary requirements for exploring ‘mirror’ activity. That is, neuronal activity within the same area is elicited by both the execution and the observation of the same action (but also see the note in Table 1). In one of these studies, Rizzolatti, Fadiga, Matelli et al. (1996b) used PET to localize brain regions active during both the observation and the execution of grasping movements. Human subjects were tested under three conditions: in the first condition they observed grasping movements of common objects performed by the experimenter; in the second condition they reached and grasped the same objects. These two conditions were compared with a third condition consisting of object observation. This study did not reveal activation within either the frontal or parietal ‘mirror’ areas. Activation within frontal areas was found during action observation, but not during action execution. The reverse was found for parietal areas.

Using fMRI Hamzei et al. (2003) revealed a possible overlap of activation for both observation and execution within the inferior frontal gyrus, the precentral gyrus and the parietal cortex. These authors considered the following five main conditions (but intermixed them with other conditions which were not considered within the manuscript): (i) a rest condition, in which participants fixated three stars presented on the screen; (ii) an active condition, in which

Table 1
Action observation studies in chronological order

Studies	Object related		Premotor/IFG complex					Posterior parietal complex			
	Observation	Execution	Observation	Execution	Entire body	Overlapping	Mirror	Observation	Execution	Overlapping	Mirror
Grafton et al. (1996); PET	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Rizzolatti, Fadiga, Matelli et al. (1996b)*; PET	YES	YES	YES	NO	NO	NO	NO	NO	YES	NO	NO
Decety et al. (1997); PET	NO	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Grezes et al. (1998); PET	NO	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Grezes et al. (1999); PET	NO	Not tested	NO	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Buccino et al. (2001); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Perani et al. (2001); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Grezes et al. (2003)*; fMRI	YES	YES	YES	YES	NO	NO	NO	YES	YES	NO	NO
Hamzei et al. (2003)*; fMRI	YES	YES	YES	Not tested	YES	NO	NO	YES	Not tested	NO	NO
Johnson-Frey et al. (2003); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	Not tested	Not tested	NO	NO
Manthey et al. (2003); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Gallagher and Frith (2004); fMRI	NO	Not tested	YES	Not tested	NO	NO	NO	NO	Not tested	NO	NO
Schubotz and von Cramon (2004); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Tai et al. (2004); PET	YES	Not tested	YES	Not tested	YES	NO	NO	NO	Not tested	NO	NO
Wheaton et al. (2004); fMRI	NO	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Costantini et al. (2005); fMRI	NO	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Iacoboni et al. (2005); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Sakreida et al. (2005); fMRI	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	Not tested	NO	NO
Shmuelof and Zohary (2005); fMRI	YES	Not tested	NO	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Aziz-Zadeh et al. (2006); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Cunnington et al. (2006); fMRI	NO	NO	YES	YES	NO	NO	NO	YES	YES	NO	NO
Shmuelof and Zohary (2006)*; fMRI	YES	YES	YES	YES	NO	NO	NO	YES	YES	NO	NO
Molnar-Szakacs et al. (2006); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Lotze et al. (2006); fMRI	YES	Not tested	YES	Not tested	YES	NO	NO	YES	Not tested	NO	NO
Hamilton and Grafton (2006); fMRI	YES	Not tested	NO	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Pierno, Becchio, Wall, Smith, Turella et al. (2006b); fMRI	YES	Not tested	YES	Not tested	YES	NO	NO	YES	Not tested	NO	NO
Pierno, Becchio, Wall, Smith, Castiello (2006a); fMRI	YES	Not tested	YES	Not tested	YES	NO	NO	YES	Not tested	NO	NO
Grosbras and Paus (2006); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Baumgaertner et al. (2007); fMRI	YES	Not tested	YES	Not tested	NO	NO	NO	YES	Not tested	NO	NO
Cheng et al. (2007); fMRI	YES	Not tested	YES	Not tested	YES	NO	NO	YES	Not tested	NO	NO
Dinstein et al. (2007); fMRI	NO	NO	YES	YES	NO	YES	NO	YES	YES	YES	NO
Filimon et al. (2007); fMRI	NO	NO	YES	YES	NO	YES	NO	YES	YES	YES	NO
Gazzola et al. (2007)*; fMRI	YES	YES	YES	YES	NO	YES	NO	YES	YES	YES	YES

Notes. (i) The column “Object-Related” refers to whether the observed action is object related or not. To be considered ‘mirror’, an area should be activated both when observing and when executing similar object-related actions. ‘YES’ in both the action observation and execution columns indicates that this pre-requisite has been met. (ii) The column “Premotor/IFG Complex” indicates whether activity within this potential ‘mirror’ area has been found. “Observation” indicates whether the listed study has reported (‘YES’) or has not reported (‘NO’) hand action observation type of activity. “Execution” indicates whether the listed study has reported (‘YES’) or has not reported (‘NO’) hand action execution type of activity. “Entire Body” indicates whether in the listed studies an entire person (‘YES’) or a hand detached from the body (‘NO’) was presented as a model (remember that in monkey studies F5 mirror neurons were only activated by an action demonstrated by an entire human model). “Overlapping” indicates whether overlapping activations for both observation and execution (‘YES’) were found or not (‘NO’) within the same area, as a result of conjunction analysis. The column termed “Mirror” allows for the definition of a brain area as mirror. In order for these criteria to be met, ‘YES’ should be reported within the “Object related”, “Entire body”, and “Overlapping” columns. (iii) The main column “Parietal Complex” indicates whether in the listed studies activity within this potential ‘mirror’ area has been found. This column is subdivided into four of the five categories reported above: observation, execution, overlapping, and mirror.

participants observed the picture of people grasping a cup; (iii) a passive condition, in which participants observed a person sitting on a chair; (iv) a verb condition, in which participants were requested to generate silently verbs which were related to visually presented nouns; and (v) a move condition, in which participants grasped a cup. Although both execution and observation conditions were included, this fMRI study does not allow us to draw any firm conclusion about ‘mirror’ type of activity, mainly because of methodological problems. First, the analyses were performed by merging data from two different experiments (one considering only execution and one considering both action observation and execution) with a small population sample ($N = 6$). Second, data were analyzed with a fixed effect analysis. Fixed effect analysis only allows a sample-based inference and does not allow for a generalization to the population. When the same data are processed in a more stringent fashion, using a random effect analysis, the authors did not explicitly test the overlap of activations for both observation and execution. Specifically, significant activation within the inferior frontal gyrus, the precentral gyrus and the inferior parietal cortex were only evident for action observation. Therefore, a close inspection of the results presented in this study does not seem to support ‘mirror’ properties within the human brain.

Grezes, Armony, Rowe, and Passingham (2003) conducted an fMRI study specifically designed to test ‘mirror’ activity within the human brain. For the ‘observation’ conditions subjects viewed an object, observed a grasp, or observed an object being grasped. The ‘observation’ baseline condition consisted of viewing a stationary background. For the ‘execution’ conditions, the subjects executed the grasp appropriate for the object that they viewed, imitated the pantomime they viewed, or imitated the hand grasping an object. In the ‘execution’ baseline condition subjects performed the same grasp (power grip) on all trials while viewing a stationary background. As for the previous studies, the analyses did not reveal any activity within ‘mirror’ brain areas for the conditions which in principle were particularly suited to elicit such activity (i.e., observation of objects being grasped, and grasping execution). For instance, the inferior frontal gyrus (the proposed homologue of premotor area F5) showed the least activation in response to the observation of object-related grasping, whereas it showed a greater response for the observation of the object presented alone or for the observation of grasping pantomimes. We suspect that the lack of clear results implicating ‘mirror’ activity might be due to several confounding factors. First, the activations reported for the ‘execution’ conditions actually refer to activations obtained from both execution and observation conditions. Second, the baseline conditions might not be ideal: for the ‘observation’ baseline condition the subjects viewed a stationary background, whereas for the ‘execution’ baseline condition subjects performed only power grip tasks (note that in the execution conditions both power and precision grips were tested). A final concern is that only the hand

of the acting model was presented. In both single-cell recordings and fMRI studies in monkeys, ‘mirror’ activity within this area is only evident when the experimenter was entirely visible. With respect to this latter issue Nelissen, Luppino, Vanduffel, Rizzolatti, and Orban (2005) used fMRI in monkeys to map the activation of the anterior part of the frontal lobe during action observation. Specifically, the targeted brain area was the region near the arcuate sulcus. Interestingly area F5c, in which mirror neurons are usually found, responded only when the individual grasping the object was in full view. Merely seeing a hand (detached from a body) grasping an object did not elicit a response. This observation supports single-cell findings in which monkeys always saw the entire experimenter, and not a hand acting alone (Gallese et al., 1996; Rizzolatti, Fadiga, Fogassi et al., 1996a). Crucially it also means that the view of the entire agent performing the action is a prerequisite to activating this area.

Another study conducted by Shmuelof and Zohary (2006) claims the existence of mirror representations of other people’s actions within the anterior sector of the intraparietal sulcus. The authors presented participants with the following stimuli: clips of (i) objects grasped by the right hand, shown in the left peripheral visual field; (ii) objects grasped by the right hand, shown in the right peripheral visual field; (iii) objects grasped by the left hand, shown in the left peripheral visual field; (iv) objects grasped by the left hand, shown in the right peripheral visual field; (v) spatially scrambled version of the object-grasping clips, shown in the left and (vi) the right peripheral visual fields. In addition, a separate somatomotor localizer experiment was conducted in which participants (only 9 out of the 14 who took part in the previous experiment) were requested to move specific body parts such as the right hand, the left hand, the right foot, the left foot, and the mouth. First the authors conducted a group factorial analysis on the observation conditions (i.e., i–iv) which indicated that, whereas activation in the occipital and posterior parietal cortices was specific to the visual-field location of the clips, activation in an area located between the superior bank of the anterior intraparietal sulcus and the postcentral sulcus was specific to the identity of the observed hand. Then, to establish whether activity in the latter areas was indeed the product of an internal motor representation of someone else’s action (in other words part of a mirror system) the authors tested whether the same areas were selectively active during execution of motor acts performed with the same body part. To this end, they mixed results from the two experiments by identifying common voxels that responded to hand action observations (all observation conditions > scrambled conditions) and to hand action executions. It is worth noting that the action execution voxels were quite unusually defined by contrasting hand object-related actions with foot non object-related movements. Second, the identified common voxels were utilized to define separate regions of interest (ROI) for each participant. Third, within these ROI subsequent analyses con-

firming the hand-identity effects found in the factorial group analysis were conducted. On the basis of these findings the authors argued that the activity found within the superior bank of the anterior intraparietal sulcus, both during action observation and during action execution, provides support for the human mirror system hypothesis. However, a close inspection of methodological and anatomical aspects of the study casts doubt on the strength of this claim: (i) the locus of activation was not within the rostral part of the inferior parietal lobule, but between the superior bank of the anterior intraparietal sulcus and the postcentral gyrus; (ii) the experimenters mixed results from two different experiments testing 14 participants for the action observation conditions and only 9 out of these 14 for the action execution conditions—more importantly, there was no exact match between the hand actions tested in the action execution experiment with those tested in the action observation experiment; (iii) even considering these data as evidence for the existence of a human mirror system, it should be noted that the supposed mirror areas identified in this study were only confined to parietal regions and did not extend to the ventral premotor cortex.

A recent paper aimed at unraveling the visual requirements of the mirror-neuron system has partially addressed some of the above issues (Gazzola, Rizzolatti, Wicker, & Keysers, 2007; see also Gazzola, Aziz-Zadeh, & Keysers, 2006). Although this study was chiefly designed to investigate whether mirror neurons respond to robotic actions, it contains some aspects which are of relevance for the present review. This study, for the first time, tested both action execution and observation using the same participants (though in separate sessions administered with a fixed order in different days). In the observation conditions subjects were requested to passively watch a human hand (not an entire agent) (i) performing simple actions, (ii) performing complex actions, (iii) resting still on a surface behind the objects used in complex actions and lastly, (iv) entering the scene without objects. In the execution conditions participants were requested to perform, without being able to see either their hands or the objects, some of the complex actions watched during the observation session. Actions were executed with the right as well as with the left hand. First, the authors identified brain areas involved in both left- and right-hand action execution. This map was subsequently utilized to inclusively mask the observation conditions (conditions i–iv); in addition the authors excluded voxels that generally responded to meaningless visual patterns. By using this strategy the authors were able to identify brain areas which were activated both during action execution and observation. Motor-masked results from two key contrasts comparing the observation of the two goal-directed conditions (conditions i and ii) with the observation of the static control (iii) revealed activation within a symmetric network involving temporal, parietal, and frontal areas. The temporal activation was located in the posterior mid-temporal gyrus. The parietal activation was very extensive, including both superior and inferior

parietal lobes, the parietal operculum, and the primary somatosensory cortex. The frontal activation comprised a dorsal node including the precentral gyrus and a ventral node located in the pars opercularis of the inferior frontal gyrus as well as cytoarchitectonically unassigned regions of the inferior frontal gyrus and of the precentral gyrus. Additional activations surviving masking were found bilaterally in the mid-cingulate cortex and in the cerebellum.

Although this study provides some evidence of mirror activity in humans by demonstrating that a number of areas are activated during both the execution and the observation of hand actions, a number of issues should be considered. First, the analysis performed revealed that a striking number of areas (not previously considered as mirror), were activated during execution as well as observation of hand actions (i.e., the posterior mid-temporal gyrus, the superior parietal cortex, the dorsal premotor cortex, the cerebellum, the putamen, the insula, and the mid-cingulate cortex). This result may have been, at least in part, determined by the rather liberal threshold ($p < .001$; uncorrected) adopted to inclusively mask all the action-observation results with the motor-execution results (note that for the action observation results a similar threshold was applied). Using this strategy may have maximized the probability of finding a large number of commonly activated voxels for both observation and execution (as indeed the authors reported). Adopting a more conservative threshold would have probably allowed for a more precise anatomical definition of the core mirror system which, on the basis of the neurophysiological literature, is unlikely to be as broad as that identified by the authors. In this respect, it would be difficult to interpret in terms of classic ‘action understanding’ mirror mechanisms all the reported areas showing overlapping activation for action execution and action observation.

Another relevant issue concerns with the differences between the classic mirror conditions and those utilized in the above experiment. Specifically, during the observation trials subjects watched only a hand, rather than the entire body, moving (see Nelissen et al., 2005). In addition, although the study was conducted on the same pool of subjects, action observation and action execution were never intermixed within the same experiment, but rather tested in separate daily sessions with action execution always following action observation. This lack of randomization could have led to systematic bias in the data.

A number of confounds can also be identified in the way action execution was tested. First, the stimuli presentation that the authors opted for was an event-related design, whereas for the action observation experiment a block design was adopted. Second, the executed actions did not fully match those utilized for action observation. During execution, participants were only requested to perform one out of three possible complex actions. By contrast, during action observation, participants observed a set of six, and not three, possible complex actions. Third, during action execution the participants could not see the to-be-

grasped objects in the scanner. Even though to demonstrate the motor properties of mirror neurons the self-executed action must not be seen (e.g., Gallese et al., 1996; Keysers & Perrett, 2004), the strategy adopted by Gazzola and co-workers to have participants not only unable to see their own action, but also unable to see the objects appears to be rather unnatural. This entails spatial search and memory components that visually guided grasping does not require, and would result in a very different hand kinematic profile for the two grasping situations (i.e., blind and visible). Following this line of reasoning, it could be advanced that the more complex situation involved in the blind-grasp condition may have triggered different activation patterns from those usually evoked by reach-to-grasp actions towards visually available objects. The way motor events were modeled in the execution experiment suggests, indeed, that components such as blind-searching for the object and recalling from memory the spatial location of the object contributed to determine the action execution activations. These components were certainly not involved in the observation phase of the study in which the objects were fully available to the observers.

Put together, the above studies do not provide consistent evidence in favor of ‘mirror’ type of activity within the frontal and the parietal complex as found in monkeys. This does not mean that mirror neurons do not exist in humans, but it highlights that what has been so far demonstrated is the existence of brain areas which respond to action observation, but not necessarily to both observation and execution and, even when they do, the loci and pattern of activation appears to be more extended than the classic ‘mirror’ system entails.

2.2. Imitation

The discovery of mirror neurons has stimulated considerable interest in the field of action imitation and many neuroimaging studies have now investigated the brain regions involved in imitation (for review see Heyes, 2001; Iacoboni, 2005a; see also Table 2). These studies have identified a limited number of areas involved in imitative processes, including the inferior frontal gyrus, the dorsal and the ventral premotor cortex, the inferior parietal cortex, the superior parietal lobule and the posterior superior temporal sulcus (Brass & Heyes, 2005).

Specifically, particular emphasis has been given to the posterior section of the inferior frontal gyrus activation (the proposed human homologue of premotor area F5 in monkey) even though the role played by this area and more generally by mirror neurons in imitative behavior is still controversial (Brass & Heyes, 2005).

Here we put forward the same argument made for the ‘action observation’ studies: before assigning a specific function, i.e., imitation, to mirror neurons it is necessary to demonstrate that the areas activated for such functions do have ‘mirror’ properties. The failure to reveal specific brain loci that are active during imitation, passive observa-

Table 2
Imitation studies in chronological order

Studies	Object related		Premotor/IFG complex			Posterior parietal complex				
	Observation	Execution	Observation	Execution	Entire body	Overlapping	Mirror	Execution	Overlapping	Mirror
Krams et al. (1998); PET	Not tested	NO	Not tested	YES	NO	NO	NO	Not tested	NO	NO
Iacoboni et al. (1999)*; fMRI	NO	Not tested	YES	Not tested	NO	NO	NO	Not tested	NO	NO
Iacoboni et al. (2000); fMRI	NO	Not tested	NO	Not tested	NO	NO	NO	NO	NO	NO
Iacoboni et al. (2001); fMRI	NO	Not tested	NO	Not tested	NO	NO	NO	NO	NO	NO
Tanaka et al. (2001); fMRI	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	NO	NO
Tanaka and Inui (2002); fMRI	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	NO	NO
Decety et al. (2002); PET	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	NO	NO
Koski et al. (2002); fMRI	NO	Not tested	NO	Not tested	NO	NO	NO	Not tested	NO	NO
Koski et al. (2003); fMRI	Not tested	YES	Not tested	YES	NO	NO	NO	Not tested	NO	NO
Buccino et al. (2004)*; fMRI	YES	YES	YES	YES	NO	NO	NO	YES	NO	NO
Leslie et al. (2004); fMRI	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	NO	NO
Chaminade et al. (2005); fMRI	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO
Makuchi (2005); fMRI	Not tested	NO	Not tested	YES	NO	NO	NO	Not tested	NO	NO
Molnar-Szakacs et al. (2005); fMRI	NO	Not tested	YES	Not tested	NO	NO	NO	Not tested	NO	NO
Muhlau et al. (2005); fMRI	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	NO	NO
Rumiati et al. (2005); PET	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	NO	NO
Aziz-Zadeh et al. (2006) fMRI	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	NO	NO
Jackson et al. (2006); fMRI	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	NO	NO
Williams et al. (2006); fMRI	Not tested	Not tested	Not tested	Not tested	NO	NO	NO	Not tested	NO	NO
Jonas et al. (2007); fMRI	NO	NO	YES	YES	NO	NO	NO	YES	NO	NO

Notes: Conventions are as for Table 1. Although imitation entails execution of an observed action, please note that here ‘Execution’, as in Table 1, exclusively indicates whether the listed study has tested pure action execution conditions and not imitation.

tion, and execution of an action, would signify that no inference regarding mirror type of activity can be drawn. We use an approach similar to that adopted for the ‘action observation’ section to classify the imitation neuroimaging studies on the basis of the reported possible ‘mirror’ activations within the frontal and the parietal complex (see Table 2). Within the main text we shall elaborate only on those studies which, with regard to experimental design and activated areas, may have the potential to show that areas involved in action imitation also show ‘mirror’ activity as originally described. These studies are marked with an asterisk in Table 2. We will not describe in detail the remaining studies because, on the basis of the classic report on ‘mirror’ activity (Rizzolatti, Fadiga, Fogassi et al., 1996a, 2001), they don’t meet ‘mirror’ criteria.

A great deal of insight regarding the possible role played by mirror neurons in imitation comes from a study conducted by Iacoboni et al. (1999). In this study participants were asked to observe and to immediately imitate finger movements (imitation condition), as well as to perform the same movements after the delivery of either spatial or symbolic cues prompting participants on which finger to move (execution condition). Pure action observation conditions (observation condition), in which participants were simply requested to watch an animated hand whose index or middle finger moved at random, were also included. Although in this study activity within the posterior section of the inferior frontal gyrus was revealed, it has been suggested that this activation was due to experimental confounds (Jonas et al., 2007). First, the performed action was not object related. Therefore these studies lack an important pre-requisite necessary to consider the obtained activations ‘mirror’. In this vein, a recent execution study demonstrated differential activations for object related actions versus gestures (Kroliczac, Cavina-Pratesi, Goodman, & Culham, 2007). Second, the fact that only a hand acting is presented, and not an entire person, may create a possible confound when interpreting the inferior frontal gyrus activation (Nelissen et al., 2005). Third, another issue concerned with the Iacoboni et al. (1999) work refers to the basic logic underlying this study. They suggest that during imitation there is both observation and execution of an action. Thus, activity during imitation should roughly correspond to the sum of the activity measured during action observation and action execution (Iacoboni, 2005b). To us such interpretation is rather simplistic and does not catch the complexity underlying the imitation process (e.g., Tessari & Ruminati, 2004). Final and most important, this study does not distinguish between activity time-locked to observation, execution, and imitation. This is partly due to the fact that in the imitation condition participants were requested to observe and imitate finger movements. Thus it might well be that in the imitation condition, both imitation and action observation were intermixed.

This latter issue has been better tackled by Buccino et al. (2004). In their study they used a guitar-chords imitation task. The subjects in the scanner were requested to imitate

on a guitar the finger configurations made by a guitar player (model). Importantly, this study was appropriately designed to separately sample brain activity time-locked to action execution, observation, imitation, and planning. The results indicated ventral premotor cortex activation for action execution and observation which, in principle, could account for a ‘mirror’ type activity. However, the very fact that the same area also responds for the object presented alone and during action planning does not allow for firm conclusions. Similarly, activation within the inferior frontal gyrus was found during either action planning, action execution, or action observation. Therefore, the role of the pars opercularis of the inferior frontal gyrus cannot be fully discriminated. Within the inferior parietal lobule a similar pattern of activation was found. Furthermore, the authors did not perform any type of analysis (such as conjunction analysis) allowing for the precise definition of any ‘mirror’ regions. The ‘mirror’ explanation has also to be mitigated by the fact that only the model’s hand was presented. Finally, the subjects were naïve to guitar playing, which is very good for testing imitation of novel actions, but not for testing classical mirror properties, especially if subjects were required to perform slightly different actions during different conditions which were mainly related to playing guitar chords. The activity of mirror neurons is chiefly elicited by the observation of actions which belong to the motor repertoire of the subject (Rizzolatti, Fadiga, Fogassi et al., 1996a), and in particular to object-related grasping actions.

Altogether, none of the above imitation experiments has clearly demonstrated activation specifically related to mirror areas. This is especially so if we consider the classic mirror neurons properties investigated in monkeys. For example, whereas in monkeys F5 mirror neurons are particularly active for hand movements, in humans the proposed homologue (the posterior section of the inferior frontal gyrus, area 44) is activated when contrasting finger-immediate imitation with static-hand observation, but not when performing the contrast hand-movement-immediate imitation against finger-immediate imitation (Tanaka & Inui, 2002). Even compared with a control static condition, the activation for the imitation of intransitive hand movement did not elicit BA 44 activity, but immediate imitation of fingers’ movement did. Support for the role of BA 44 in finger, rather than hand, movements imitation comes from a study in apraxic patients (Goldenberg & Karnath, 2006). The authors show that finger imitation impairment is related to an inferior frontal gyrus lesion, whereas hand imitation deficit is related to a lesion of the inferior parietal lobule and the temporo-parietal-occipital junction.

Continuing this analysis, Molnar-Szakacs, Iacoboni, Koski, and Mazziotta (2005) found that both the ventral and the dorsal sectors of area 44 mainly responded to immediate imitation of finger movements. The ventral sector responded to imitation of finger movements, but not to observation and execution of finger movements, or to static visual control. For the dorsal sector only data concerned

with immediate imitation and observation are presented, therefore no conclusions in terms of mirror activity for this area can be drawn.

Finally, these considerations are strengthened by an elegant study conducted by Makuuchi (2005; see also Jonas et al., 2007 and Williams et al., 2006) that aimed to assess the involvement of area 44 in imitative behavior. Results from this study not only indicated that area 44 is not a crucial neural component for imitation, but they also attributed to this area a role in delayed action execution (see also Toni, Schluter, Josephs, Friston, & Passingham, 1999).

As suggested by the above author (Makuuchi, 2005), in the majority of previous studies aimed at ascribing to mirror neurons a role in imitation, participants were continuously requested to observe and then perform the same observed movement (e.g., finger movements; Iacoboni et al., 1999). This implies that visuo-motor transformations are not necessary for subjects to imitate continuously, since they could simply perform the movements using the same motor program. In such a situation, the visually presented movements may serve as cues as to when to perform the requested movements rather than a specification of what is required to be performed. As activation in the left area 44 has also been observed in delayed motor execution tasks (Toni et al., 1999) it may well be that the inferior frontal gyrus activation reported in previous studies should be ascribed to delayed action execution, and not to imitation *per se*.

Altogether evidence from these studies (Jonas et al., 2007; Makuuchi, 2005; Williams et al., 2006) indicates a lack of a signature of mirror neuron activity in the inferior fronto-parietal cortex for imitation processes. Rather, they suggest that responsiveness of this fronto-parietal system during imitation of intransitive movements critically depends on the experimental context.

3. Theoretical considerations

From a theoretical perspective, at least for the two interconnected processes considered here (i.e., action observation and imitation), the idea of a mirror system in humans appears premature. Particularly so considering that ‘mirror’ areas, such as the inferior frontal gyrus, have also been proposed as relevant loci for a number of processes such as ‘prediction’ and ‘selection’ even in non-semantic tasks (e.g., Schubotz, 2007; Zhang, Feng, Fox, Gao, & Hai Tan, 2004).

Certainly the step towards the reproduction of an observed action is not as small as it may appear. The question is whether the reproduction of a seen action requires a full activation of the motor representations that are primed during action observation. In the majority of the relevant action observation fMRI and PET studies participants are not required to perform any action at all. Therefore, these studies provide evidence that the passive observation of actions is sufficient to generate premotor activations. Assigning to these areas the ‘mirror’ label is based on the

inference that in some circumstances the observation of actions leads to activation of a set of brain regions known to be involved also in movement execution. However, as we have highlighted, very often the areas involved in observation and execution do not match, or areas that are active for action observation are not active for action execution and so on. We suggest that results from action observation studies, thus far, are not suited to properly demonstrate mirror activity in humans.

Studies which required overt imitation have not demonstrated that the activated areas are indeed ‘mirror’. Therefore, these studies do not substantiate a role of ‘mirror’ areas in imitation that goes beyond pure action observation. Does this mean that mirror neurons cannot do imitation? Or are they capable of imitation without having imitation as their function? In this respect, ‘Generalist’ theories of imitation imply the possibility that areas involved in action observation, including mirror neurons, *can do* imitation but are not *for* imitation (Greenwald, 1970; Heyes, 2001; Heyes & Ray, 2004; Prinz, 2002). In other words mirror neurons could be involved in generating imitative behavior without imitation being the function that favored their evolution. Mirror neurons may thus acquire their properties in the course of ontogeny as a side-effect of the operation of general associative learning, and motor control mechanisms, that led to their formation evolved in response to much more general adaptive problems. It might be that the environment in which humans develop yields mirror neurons with imitative specificity. Furthermore there is an issue which needs some clarification before any firm conclusion can be drawn regarding the link between mirror neurons and imitation. This concerns the claim that monkeys have mirror neurons but, according to some authors, they do not imitate (Lyons, Santos, & Keil, 2006; Roth & Dicke, 2005). If proved, this evidence would go against the hypothesis that mirror neurons are for imitation.

Although this view might be consistent with the above mentioned generalist approach, a firm demonstration of the existence of the interplay between mirror neurons and more complex cognitive abilities is needed. Imitation is not a unitary component and might not be dependent upon a unitary ‘mirror’ system in the human brain. Thus, a much more detailed scheme should be considered (Tessari & Ruminati, 2004). Even when low-level visual and motor parameters are equated, different brain activations have been found for meaningful, as compared to meaningless, gestures (Rumiati et al., 2005). These data indicate that imitation behavior cannot be localized to a single brain system, but rather different types of imitation involve different cognitive and neural systems.

4. Methodological considerations

Data from single-cell recordings and imaging techniques are difficult to reconcile. The obvious reason is that they register different signals with different sensitivities (Orban,

Van Essen, & Vanduffel, 2004). In one case the signal is related to the activity of a single neuron. In the other case the signal is concerned with a population of neurons. The BOLD signal reflects modification in cerebral blood volume, cerebral blood flow, and oxygen consumption, and therefore it is difficult to compare with neuronal activity (Logothetis & Wandell, 2004). This aspect is particularly relevant for ‘mirror’ studies. In analogy with electrophysiological recordings in monkeys, to demonstrate that the same region is activated during both execution and observation may not suffice. A more appropriate parallelism should consider similar activity within the same voxel (with the same stereotaxic coordinates) for both execution and observation.

Although this may prove to be a difficult task, this problem might be partially solved since fMRI studies have also been conducted in monkeys. The study by Nelissen et al. (2005) provides a compelling example within the mirror neurons literature. Noticeably, this study not only has confirmed neurophysiological evidence, but has revealed a new important aspect of the F5 mirror neurons. F5 mirror neurons respond only when the model performing the action is visible in her entirety. This observation supports the single-cell findings in which monkeys always saw the entire experimenter, and not the hand acting alone (Gallese et al., 1996; Rizzolatti, Fadiga, Fogassi et al., 1996a). It also means that the view of the agent performing the action is a prerequisite to trigger a response in this area (which is a factor rarely considered in human neuroimaging studies).

Although using fMRI techniques may allow for a more direct comparison between monkeys and humans, it does not solve another critical issue; i.e., the possibility of establishing homologies between brain regions within different species. Homologies between species can only be inferred with some considerable degree of caution. Even for areas in which a high degree of homology would be expected (e.g., visual areas) agreement in terms of homologies has been reached only for a few areas (e.g., V1, V2, MT/V5; Orban et al., 2004; Sereno & Tootell, 2005). Thus when advancing homologies for other brain regions, in which a lesser degree of similarity would be expected (e.g., prefrontal and parietal cortices), a great deal of caution should be taken. The most recent proposal is that the main areas that may comprise the human mirror system are the ventral premotor cortex and the pars opercularis of the inferior frontal gyrus, together with the rostral part of the inferior parietal lobule (Rizzolatti & Craighero, 2004). Although some authors agree that monkey area F5 is the homologue of human area 44, the pars opercularis of the inferior frontal gyrus (Geyer, Matelli, Luppino, & Zilles, 2000; but see also Petrides, 2005; Petrides et al., 2005), it is worth noting that this area in humans has rarely been found active for both action observation and execution. Furthermore, with imitation it appears to be activated only for fingers but not for hand movements (as it is in monkeys’ studies). For the human homologue of the monkey PF (the other area containing mirror cells), there is no clear consensus. A likely

candidate seems to be the rostral posterior parietal cortex, but the evidence is far from definitive.

A final methodological issue is concerned with the interpretation of fMRI results revealing overlapping activations from independent contrasts. When a cluster is commonly activated by two (or more) contrasts between experimental conditions, two interpretations are possible. According to a common-coding interpretation, the activated cluster is thought to contain neurons that are engaged in a common computational process. This interpretation has been the favored account for the overlapping activations elicited by both observed and performed actions. In other words, it has often been taken as evidence for the existence of a mirror neuron system in the human brain. In contrast, according to a functional-independence interpretation, the activated cluster may contain functionally independent neural populations. For instance, using a multivariate approach such as the multi-voxel pattern analysis (for review see Norman, Polyn, Detre, & Haxby, 2006) Peelen, Wiggett, and Downing (2006) have recently demonstrated functional independence in overlapping extrastriate cortical regions. Therefore, even when activation maps from independent contrasts overlap (i.e., one for action observation and the other for action execution) an interpretation in terms of common neural mechanisms, should be taken with caution, especially when only univariate analysis are performed.

5. Conclusions

More than a decade of research on mirror neurons has left us with a crucial problem: is there a mirror neuron system in humans? In the present work we have considered whether recent fMRI and PET evidence has helped us to resolve this problem. From the reported research it seems that only a handful of studies have been designed to address the problem directly, and even these studies have not provided compelling evidence for a special purpose mechanism that can match the mirror neurons system as originally described in monkey. There may be a number of reasons for this lack of evidence. The simple reason is that for humans an experiment reflecting the exact conditions designed for the relevant monkey studies has not yet been performed (but see Gazzola et al., 2007). It might be reasonable to assume that action observation, imitation, and execution, share a common network of overlapping areas, but simply drawing such conclusions by comparing results from different experiments does not support the claim that some areas, for example area 44 (or part of it) are ‘mirror’.

In conclusion, within the field of research on mirror neurons a priority for future fMRI and PET research is to make a step back and to provide clear evidence for the existence of a mirror system in humans which closely resembles that found in monkeys in terms of brain areas and functions. We suggest that only after such a process is completed will it be possible to assign mirror neurons those

functions which, on the basis of current experimentation, can only be speculatively inferred.

Acknowledgments

This work was supported by a grant from the Italian Ministry of Research (MUR) to U.C. The authors thank Anthony Hayes and Roger Wales for their extremely constructive comments on earlier drafts of this manuscript.

References

- Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing Actions. *Current Biology*, *16*, 1818–1823.
- Baumgaertner, A., Buccino, G., Lange, R., Mcnamara, A., & Binkofski, F. (2007). Polymodal conceptual processing of human biological actions in left inferior frontal lobe. *European Journal of Neuroscience*, *25*, 881–889.
- Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience*, *16*, 3737–3744.
- Brass, M., & Heyes, C. M. (2005). Imitation: Is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, *9*, 489–495.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., et al. (2004). Neural circuits underlying imitation learning of hand actions: An event related fMRI study. *Neuron*, *42*, 323–334.
- Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An FMRI study with expert dancers. *Cerebral Cortex*, *15*, 1243–1249.
- Chaminade, T., Meltzoff, A. N., & Decety, J. (2005). An fMRI study of imitation: Action representation and body schema. *Neuropsychologia*, *43*, 115–127.
- Cheng, Y., Meltzoff, A. N., & Decety, J. (2007). Motivation modulates the activity of the human mirror-neuron system. *Cerebral Cortex*, *17*, 1979–1986.
- Costantini, M., Galati, G., Ferretti, A., Caulo, M., Tartaro, A., Romani, G. L., et al. (2005). Neural systems underlying observation of humanly impossible movements: An fMRI study. *Cerebral Cortex*, *15*, 1761–1767.
- Cunnington, R., Windischberger, C., Robinson, S., & Moser, E. (2006). The selection of intended actions and the observation of others' actions: A time-resolved fMRI study. *Neuroimage*, *29*, 1294–1302.
- Decety, J., Chaminade, T., Grezes, J., & Meltzoff, A. N. (2002). A PET exploration of the neural mechanisms involved in reciprocal imitation. *Neuroimage*, *15*, 265–272.
- Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., et al. (1997). Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain*, *120*, 1763–1777.
- Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180.
- Dinstein, I., Hasson, U., Rubin, N., & Heeger, D. (2007). Brain areas selective for both observed and executed movements. *Journal of Neurophysiology*, *98*, 1415–1427.
- Filimon, F., Nelson, J. N., Hagler, D. J., & Sereno, M. I. (2007). Human cortical representations for reaching: Mirror neurons for execution, observation, and imagery. *Neuroimage*, *37*, 1315–1328.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*, 662–667.
- Fogassi, L., & Luppino, G. (2005). Motor functions of the parietal lobe. *Current Opinion in Neurobiology*, *15*, 626–631.
- Gallagher, H. L., & Frith, C. D. (2004). Dissociable neural pathways for the perception and recognition of expressive and instrumental gestures. *Neuropsychologia*, *42*, 1725–1736.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.
- Gallese, V., Fogassi, L., Fadiga, L., & Rizzolatti, G. (2002). Action representation and the inferior parietal lobule. In W. Prinz & B. Hommel (Eds.), *Common mechanisms in perception and action: Attention and performance* (Vol. XIX, pp. 247–266). New York: Oxford University Press.
- Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in humans. *Current Biology*, *16*, 1824–1829.
- Gazzola, V., Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *Neuroimage*, *35*, 1674–1684.
- Geyer, S., Matelli, M., Luppino, G., & Zilles, K. (2000). Functional neuroanatomy of the primate cortical motor system. *Anatomy and Embryology*, *202*, 443–474.
- Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography: 2. Observation compared with imagination. *Experimental Brain Research*, *112*, 103–111.
- Greenwald, A. G. (1970). Sensory feedback mechanisms in performance control: With special reference to the ideomotor mechanisms. *Psychological Review*, *77*, 73–99.
- Grezes, J., Costes, N., & Decety, J. (1998). Top-down effect of strategy on the perception of human biological motion: A PET investigation. *Cognitive Neuropsychology*, *15*, 553–582.
- Grezes, J., Costes, N., & Decety, J. (1999). The effects of learning and intention on the neural network involved in the perception of meaningless actions. *Brain*, *122*, 1875–1887.
- Grezes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*, 1–19.
- Grezes, J., Armony, J. L., Rowe, J., & Passingham, R. M. (2003). Activations related to “mirror” and “canonical” neurons in the human brain: An fMRI study. *Neuroimage*, *18*, 928–937.
- Gridley, M. C., & Hoff, R. (2006). Do mirror neurons explain misattribution of emotions in music? *Perceptual and Motor Skills*, *102*, 600–602.
- Goldenberg, G., & Karnath, H. O. (2006). The neural basis of imitation is body part specific. *Journal of Neuroscience*, *26*, 6282–6287.
- Grosbras, M. H., & Paus, T. (2006). Brain networks involved in viewing angry hands and faces. *Cerebral Cortex*, *16*, 1087–1096.
- Hamilton, A. C., & Grafton, S. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience*, *26*, 1133–1137.
- Hamzei, F., Rijntjes, M., Dettmers, C., Glauche, V., Weiller, C., & Buchel, C. (2003). The human action recognition system and its relationship to Broca's area: An fMRI study. *Neuroimage*, *19*, 637–644.
- Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences*, *5*, 253–261.
- Heyes, C., & Ray, E. (2004). Spatial S–R compatibility effects in an intentional imitation task. *Psychonomic Bulletin and Review*, *11*, 703–708.
- Iacoboni, M. (2005a). Neural mechanisms of imitation. *Current Opinion in Neurobiology*, *15*, 632–637.
- Iacoboni, M. (2005b). Understanding others: Imitation, language, empathy. In S. Hurlley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science* (Vol. 1, pp. 77–100). Cambridge, MA: MIT Press.
- Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M. C., et al. (2001). Reafferent copies of imitated actions in

- the right superior temporal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 13995–13999.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, M., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *Public Library of Science, Biology*, 79, 529–535.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526–2528.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (2000). Mirror properties in a sulcus angularis area. *Neuroimage*, 5, S821.
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *Neuroimage*, 31, 429–439.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, 14, 201–211.
- Johnson-Frey, S. H., Maloof, F. R., Newman-orlund, R., Farrer, C., Inati, S., & Grafton, S. T. (2003). Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron*, 39, 1053–1058.
- Jonas, M., Siebner, H. R., Biermann-Ruben, K., Kessler, K., Bäumer, T., Büchel, C., et al. (2007). Do simple intransitive finger movements consistently activate frontoparietal mirror neuron areas in humans? *Neuroimage*, 36, T44–T53.
- Keysers, C., & Perrett, D. I. (2004). Demystifying social cognition: A Hebbian perspective. *Trends in Cognitive Sciences*, 8, 501–507.
- Krams, M., Rushworth, M. F., Deiber, M. P., Frackowiak, R. S., & Passingham, R. E. (1998). The preparation, execution and suppression of copied movements in the human brain. *Experimental Brain Research*, 120, 386–398.
- Koski, L., Wohlschlagel, A., Bekkering, H., Woods, R. P., & Dubeau, M. C. (2002). Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebral Cortex*, 12, 847–855.
- Koski, L., Iacoboni, M., Dubeau, M. C., Woods, R. P., & Mazziotta, J. C. (2003). Modulation of cortical activity during different imitative behaviors. *Journal of Neurophysiology*, 89, 460–471.
- Krolicz, G., Cavina-Pratesi, C., Goodman, D. A., & Culham, J. C. (2007). What does the brain do when you fake it? An fMRI study of pantomimed and real grasping. *Journal of Neurophysiology*, 97, 2410–2422.
- Leslie, K. R., Johnson-Frey, S. H., & Grafton, S. T. (2004). Functional imaging of face and hand imitation: Towards a motor theory of empathy. *Neuroimage*, 21, 601–607.
- Logothetis, N. K., & Wandell, B. A. (2004). Interpreting the BOLD signal. *Annual Review of Physiology*, 66, 735–769.
- Lotze, M., Heymansa, U., Birbaumer, N., Veita, R., Erbc, M., Flor, H., et al. (2006). Differential cerebral activation during observation of expressive gestures and motor acts. *Neuropsychologia*, 44, 1787–1795.
- Lyons, D. E., Santos, L. R., & Keil, C. K. (2006). Reflections of other minds: How primate social cognition can inform the function of mirror neurons. *Current Opinion in Neurobiology*, 16, 230–234.
- Makuuchi, M. (2005). Is Broca's area crucial for imitation? *Cerebral Cortex*, 15, 563–570.
- Manthey, S., Schubotz, R. I., & von Cramon, D. Y. (2003). Premotor cortex in observing erroneous action: An fMRI study. *Brain Research: Cognitive Brain Research*, 15, 296–307.
- Molnar-Szakacs, I., Iacoboni, M., Koski, L., & Mazziotta, J. C. (2005). Functional segregation within pars opercularis of the inferior frontal gyrus: Evidence from fMRI studies of imitation and action observation. *Cerebral Cortex*, 15, 986–994.
- Molnar-Szakacs, I., & Overy, K. (2006). Music and mirror neurons: From motion to 'e'emotion. *Social Cognitive and Affective Neuroscience*, 1, 235–241.
- Molnar-Szakacs, I., Kaplan, J., Greenfield, P. M., & Iacoboni, M. (2006). Observing complex action sequences: The role of the fronto-parietal mirror neuron system. *Neuroimage*, 33, 923–935.
- Muhlau, M., Hermsdorfer, J., Goldenberg, G., Wohlschlagel, A. M., Castrop, F., Stahl, et al. (2005). Left inferior parietal dominance in gesture imitation: An fMRI study. *Neuropsychologia*, 43, 1086–1098.
- Nelissen, K., Luppino, G., Vanduffel, W., Rizzolatti, G., & Orban, G. A. (2005). Observing others: Multiple action representation in the frontal lobe. *Science*, 310, 332–336.
- Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, 10, 424–430.
- Orban, G. A., Van Essen, D., & Vanduffel, W. (2004). Comparative mapping of higher visual areas in monkeys and humans. *Trends in Cognitive Sciences*, 8, 315–324.
- Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*, 49, 815–822.
- Pelphrey, A. K., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of Cognitive Neuroscience*, 10, 1706–1716.
- Perani, D., Fazio, F., Borghese, N. A., Tettamanti, M., Ferrari, S., Decety, J., et al. (2001). Different brain correlates for watching real and virtual hand actions. *Neuroimage*, 14, 749–758.
- Petrides, M. (2005). Lateral prefrontal cortex: Architectonic and functional organization. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*, 360, 781–795.
- Petrides, M., Cadoret, G., & Mackey, S. (2005). Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature*, 435, 1235–1238.
- Pierno, A. C., Becchio, C., Wall, M. B., Smith, A. T., & Castiello, U. (2006a). Transfer of interfered motor patterns to self from others. *European Journal of Neuroscience*, 23, 1949–1955.
- Pierno, A. C., Becchio, C., Wall, M. B., Smith, A. T., Turella, L., & Castiello, U. (2006b). When gaze turns into grasp. *Journal of Cognitive Neuroscience*, 18, 2130–2137.
- Pineda, J. O. A., & Oberman, L. M. (2006). What goads cigarette smokers to smoke? Neural adaptation and the mirror neuron system. *Brain Research*, 1121, 128–135.
- Ponseti, J., Bosinski, H. A., Wolff, S., Peller, M., Jansen, O., Mehdorn, H. M., et al. (2006). A functional endophenotype for sexual orientation in humans. *Neuroimage*, 33, 825–833.
- Prinz, W. (2002). Experimental approaches to imitation. In A. N. Meltzoff & W. Prinz (Eds.), *The imitative mind: Development, evolution and brain bases*. Cambridge, MA: Cambridge University Press.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1996a). Premotor cortex and the recognition of motor actions. *Brain Research: Cognitive Brain Research*, 3, 131–141.
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., et al. (1996b). Localization of grasp representation in humans by PET: 1. Observation versus execution. *Experimental Brain Research*, 111, 246–252.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, 2, 661–670.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, 31, 889–901.
- Roth, G., & Dicke, U. (2005). Evolution of the brain and intelligence. *Trends in Cognitive Sciences*, 9, 250–257.
- Rumiati, R. I., Weiss, P. H., Tessari, A., Assmus, A., Zilles, K., Herzog, H., et al. (2005). Common and differential neural mechanisms supporting imitation of meaningful and meaningless actions. *Journal of Cognitive Neuroscience*, 17, 1420–1431.
- Sakreida, K., Schubotz, R. I., Wolfensteller, U., & Cramon, D. Y. (2005). Motion class dependency in observer' motor areas revealed by functional magnetic resonance imaging. *Journal of Neuroscience*, 25, 1335–1342.
- Schubotz, R. I. (2007). Prediction of external events with our motor system: Towards a new framework. *Trends in Cognitive Sciences*, 11, 211–218.

- Schubotz, R. I., & von Cramon, D. Y. (2004). Sequences of abstract non-biological stimuli share ventral premotor cortex with action observation and imagery. *Journal of Neuroscience*, *24*, 5467–5474.
- Sereno, M. I., & Tootell, R. B. (2005). From monkeys to humans: What do we now know about brain homologies? *Current Opinion in Neurobiology*, *15*, 135–144.
- Shmuelof, L., & Zohary, E. (2005). Dissociation between ventral and dorsal fMRI activation during object and action recognition. *Neuron*, *47*, 457–470.
- Shmuelof, L., & Zohary, E. (2006). A mirror representation of others' actions in the human anterior parietal cortex. *Journal of Neuroscience*, *26*, 9736–9742.
- Simon, O. J., Mangin, L., Cohen, D., Le Bihan, S., & Dehaene, S. (2002). Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron*, *33*, 475–487.
- Tai, Y. F., Scherfler, C., Brooks, D. J., Sawamoto, N., & Castiello, U. (2004). The human premotor cortex is mirror only for biological actions. *Current Biology*, *14*, 117–120.
- Tanaka, S., Inui, T., Iwaki, S., Konishi, J., & Nakai, T. (2001). Neural substrates involved in imitating finger configurations: An fMRI study. *Neuroreport*, *12*, 1171–1174.
- Tanaka, S., & Inui, T. (2002). Cortical involvement for action imitation of hand/arm postures versus finger configurations: An fMRI study. *Neuroreport*, *13*, 1599–1602.
- Tessari, A., & Ruminati, R. I. (2004). The strategic control of multiple routes in imitation of actions. *Journal of Experimental Psychology: Human Perception and Performance*, *30*, 1107–1116.
- Toni, I., Schluter, N. D., Josephs, O., Friston, K., & Passingham, R. E. (1999). Signal-, set-, and movement-related activity in the human brain: An event-related fMRI study. *Cerebral Cortex*, *9*, 35–49.
- Wheaton, K. J., Thompson, J. C., Syngieniotis, A., Abbott, D. F., & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *Neuroimage*, *22*, 277–288.
- Williams, J. H. G., Waiter, G. D., Gilchrist, A., Perrett, D. I., Murray, A. D., & Whiten, A. (2006). Neural mechanisms of imitation and mirror neuron functioning in autistic spectrum disorder. *Neuropsychologia*, *44*, 610–621.
- Zhang, J. X., Feng, C.-M., Fox, P. T., Gao, J.-H., & Hai Tan, L. (2004). Is left inferior frontal gyrus a general mechanism for selection? *Neuroimage*, *23*, 596–603.