

# Neural Substrates for Action Understanding at Different Description Levels in the Human Brain

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## Abstract

Understanding complex movements and abstract action goals is an important skill for our social interactions. Successful social interactions entail understanding of actions at different levels of action description, ranging from detailed movement trajectories that support learning of complex motor skills through imitation to distinct features of actions that allow us to discriminate between action goals and different action styles. Previous studies have implicated premotor, parietal, and superior temporal areas in action understanding. However, the role of these different cortical areas in action understanding at different levels of action description remains largely unknown. We addressed this question using advanced animation and stimulus generation techniques in combination with sensitive functional magnetic resonance imaging adaptation or repetition suppression methods. We tested the neural sensitivity of fronto-parietal and visual areas to differences in

the kinematics and goals of actions using kinematic morphs of arm movements. Our findings provide novel evidence for differential involvement of ventral premotor, parietal, and temporal regions in action understanding. We show that the ventral premotor cortex encodes the physical similarity between movement trajectories and action goals that are important for exact copying of actions and the acquisition of complex motor skills. In contrast, parietal regions and the superior temporal sulcus process the perceptual similarity between movements and may support the perception and imitation of abstract action goals and movement styles. Thus, our findings propose that fronto-parietal and visual areas involved in action understanding mediate a cascade of visual-motor processes at different levels of action description from exact movement copies to abstract action goals achieved with different movement styles. ■

## INTRODUCTION

Our ability to interpret abstract action goals and intentions and identify action styles from their movements is critical for our social interactions in dynamic environments. Successful interactions entail a cascade of visual-motor processes that relate to different levels of action description (Byrne & Russon, 1998) from exact copies of movement trajectories to actions of different movement styles. These processes range from the observation and imitation of detailed movement trajectories that support the acquisition of complex motor skills to the generalization of such specific motor plans to actions that have the same abstract goal but may vary in their characteristics across actors or social contexts.

Understanding the neural underpinnings of this critical ability for our social interactions has recently generated large interest in cognitive neuroscience. Recent neurophysiological (Fogassi et al., 2005; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992) and imaging studies (Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006; Iacoboni et al., 2005; Buccino, Lui, et al., 2004; Buccino,

Vogt, et al., 2004; Saygin, Wilson, Hagler, Bates, & Sereno, 2004; Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003; Buccino et al., 2001; Iacoboni et al., 1999, 2001; Nishitani & Hari, 2000; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti et al., 1996; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995) have identified a mirror-neuron circuit for action understanding in frontal premotor (ventral premotor cortex [PMv]), parietal (intraparietal sulcus [IPS]), and superior temporal (superior temporal sulcus [STS]) cortical areas that respond not only to the execution but also to the observation and imitation of actions. However, the contribution of the human fronto-parietal and temporal cortical areas to action understanding remains largely unknown and rather controversial. Some studies propose that the premotor and parietal cortex are involved in the dissociable processing of abstract goals and movement kinematics, respectively (Iacoboni et al., 1999, 2001), whereas others suggest processing of action goals independent of motor trajectories in the parietal cortex (Hamilton & Grafton, 2006) and unexpected intentional actions in the STS (Pelphrey, Morris, & McCarthy, 2004; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). What is the role of the different cortical areas in the human mirror-neuron circuit in the understanding of actions at different levels of action description? Do different areas contribute to the precise observation and imitation of

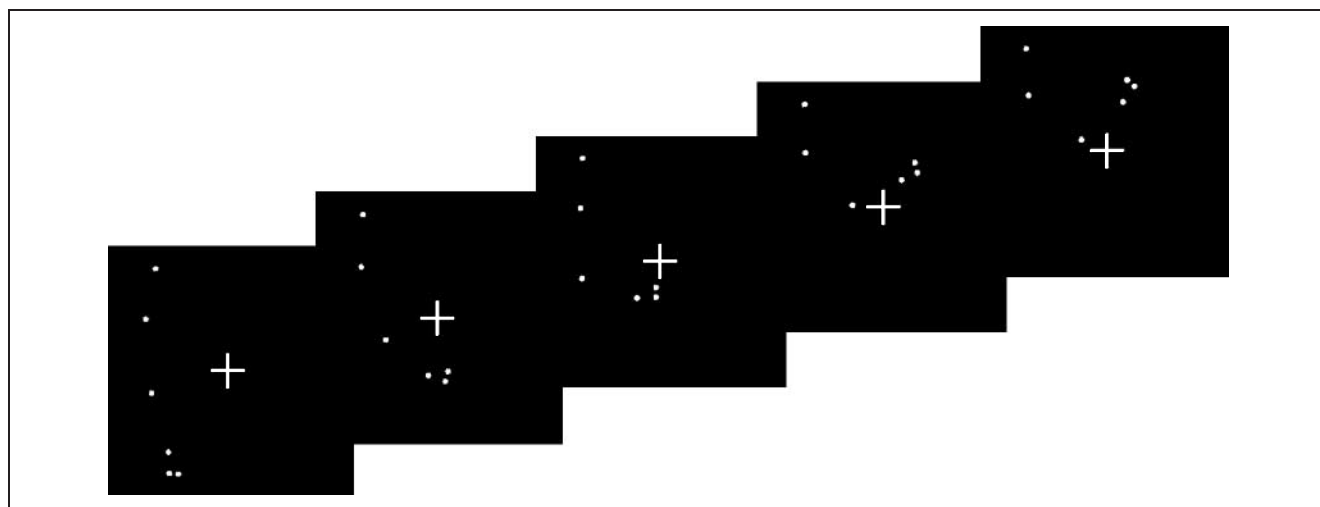
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complex movement trajectories that allow us to become experts in performing complex motor tasks and the interpretation of abstract action goals that allow us to generalize across differences in the characteristics of movements performed by different actors?

We addressed these questions by examining the sensitivity of human cortical areas involved in action understanding (PMv, SPL, IPL, STS) to changes in the abstract action goals or the kinematics (movement trajectory) that define the means by which action goals are achieved at a subordinate level of detail (Byrne & Russon, 1998; Jeannerod, 1997). To this end, we employed an event-related functional magnetic resonance imaging (fMRI) adaptation or repetition suppression paradigm (Grill-Spector, Henson, & Martin, 2006; Grill-Spector & Malach, 2001) that involves examining the fMRI response to two sequentially presented stimuli. Increased fMRI responses (i.e., rebound) for a change in a specific stimulus dimension (e.g., action goal or kinematics), compared to decreased responses for identical stimuli presented repeatedly, indicate neural populations sensitive to the modified stimulus attribute. This paradigm has been used successfully in numerous studies investigating visual processing in the occipito-temporal cortex as well as higher cognitive functions in frontal (Buckner et al., 1998) and parietal (Naccache & Dehaene, 2001) areas and the processing of action goals in the parietal cortex (Hamilton & Grafton, 2006). Further, recent electrophysiological evidence suggests that this phenomenon may reflect neural adaptation in stimulus-selective neural populations (Krekelberg, Boynton, & van Wezel, 2006; Sawamura, Orban, & Vogels, 2006; Tolia, Keliris, Smirnakis, & Logothetis, 2005).

We manipulated the differences between the action goals and kinematics of human movements in a controlled manner using the following stimulus generation methods. First, we used motion-capture recordings of four different instrumental and social (Gallagher & Frith,

2004), goal-directed human arm movements (knocking, lifting, waving and throwing) performed by different actors and rendered as point-light displays (Figure 1) that are known to be spontaneously perceived as natural biological movements (Thornton & Vuong, 2004; Pollick, Hill, Calder, & Paterson, 2003; Troje & Geyer, 2002; Shiffrar, Lichtey, & Chatterjee, 1997; Dittrich, 1993; Cutting & Kozlowski, 1977; Johansson, 1973). Second, we transformed these movements using temporal morphing (Hill & Pollick, 2000) that preserves the goal and spatial path of the movement but allows us to change the movement kinematics in a parametric manner. Third, we played sequentially presented actions forwards and backwards that preserves the average movement kinematics but may alter the goal of actions (e.g., when the movement of lifting an object is played backwards, it appears as placing the object). These stimulus manipulations allowed us to generate four types of movements: (a) movements that differed both in their goal and kinematics (different movement); (b) movements that differed only in their kinematics (different kinematics); (c) movements that shared the same average kinematics and similar goal (similar goal); and (d) movements that shared the same average kinematics but had different action goals (different goal). We evaluated the physical similarity between these movements by comparing positional and velocity differences between their trajectories (Pomplun & Matarić, 2000) and their perceptual similarity based on behavioral ratings. Unlike previous studies that focused on the role of different cortical areas in different functions for action understanding, our parametric approach revealed dissociable neural correlates of action understanding at different levels of action description. In particular, we show that the premotor cortex responds to the physical differences between actions independent of how perceptually salient these differences are. Such processing may support imitation of detailed and complex



**Figure 1.** Stimuli. Illustration of a sequence of sample frames from one of the actions (lift) used for the moving stimuli.

movements for the acquisition of fine motor skills guided by predictive comparisons between the observed and intended action. In contrast, parietal and superior temporal areas respond to perceptually salient differences between action goals or kinematics independent of the magnitude of the physical differences between movement trajectories. These action representations may allow the interpretation and possibly the imitation of abstract action goals while taking into account the style of individual actors. Thus, our findings relate to multilevel computational models that have been proposed to mediate action understanding at different levels of description based on inverse and forwards circuits (Oztop, Kawato, & Arbib, 2006; Iacoboni, 2005; Miall, 2003; Kawato, 1999).

## METHODS

### Participants

Twenty-four students from the University of Tübingen participated in two experiments (11 in Experiment 1, 13 in Experiment 2). One subject from Experiment 1 and two subjects from Experiment 2 were excluded from the analysis due to excessive head movements. All participants gave informed consent for their participation.

### Visual Stimuli

For the functional localization of the regions of interest (ROIs), we used two types of stimuli: (a) point-light displays of goal-directed arm movements (knocking, throwing, lifting, and waving), and (b) static frames from these point-light displays connected with lines that appeared as stick-figure images of arms. For the event-related designs, in Experiments 1 and 2, we presented point-light goal-directed arm movements of three types: (a) natural recordings of human movements, (b) parametric temporal morphs, or (c) movements presented with reversed frame order (played backwards). All movements were carefully matched—they were arm movements, took the same amount of time, had their temporal structure divided into three segments for the purposes of morphing, could be performed with the rest of the body roughly stationary, started and ended with the arm at the side, had similar complexity in raising up, performing the action (in some cases repetitively) and then returning the arm to the side. Further details on the stimulus generation are provided as supplementary material.

The point-light displays of goal-directed arm movements were natural human movement recordings of knocking, throwing, lifting, and waving movements presented as quick-time movies. These displays were rendered with small white dots on a black background, subtending a  $300 \times 300$  pixel squares in the middle of the computer screen. The maximum movement extent

was  $9^\circ$  of visual angle (Figure 1). Four action types were used for this purpose: knocking, lifting, waving, and throwing movements. All movements were presented from the right sagittal view, apart from the waving movements that were presented from the frontal plane, as pilot experiments showed that the waving movements were confused with the knocking movements when presented from the right or left sagittal view. The static arm displays were  $300 \times 300$  pixel single frames taken from knocking, throwing, waving, and lifting movements. The stick-like figures were created by joining the point-light markers of the natural movement recordings with straight lines. A fixation cross was drawn in the center of all visual displays.

### Procedure and Design

Each experiment consisted of eight scans: three localizer scans and five event-related adaptation scans. The order of the scans was counterbalanced across subjects. Before each scanning session begun, the participants were familiarized with the stimuli during a short practice session.

The localizer scans (block design) were used to functionally localize the cortical areas implicated in action understanding. As in previous fMRI studies in humans (Grossman & Blake, 2001, 2002; Grossman et al., 2000) and monkeys (Nelissen, Vanduffel, & Orban, 2006), to localize areas involved in the processing of movements, we presented observers with arm movements and static arm displays. Previous studies have shown that the same fronto-parietal areas are engaged in the planning, mental simulation (motor imagery), imitation, and observation of actions (Molnar-Szakacs, Kaplan, Greenfield, & Iacoboni, 2006; Blakemore & Frith, 2005; Clark, Tremblay, & Ste-Marie, 2004; Johnson-Frey et al., 2003; Manthey, Schubotz, & von Cramon, 2003; Grezes & Decety, 2001; Binkofski et al., 2000), with stronger activations for mental simulation than observation, and imitation than simulation or observation. In accordance with these studies, to localize areas involved in action understanding, we instructed observers (written instruction on the screen for 2 sec before each block) to perform two tasks: either observe (observation task) or imagine to imitate (mental simulation task) these visual displays. As execution of the presented arm movements during imitation in the scanner would result in motion artifacts in the fMRI images, we instructed the observers to mentally simulate (imagine themselves to imitate) the presented arm movements and static postures, in accordance with previous studies. Each scan consisted of sixteen 16-sec stimulus blocks and five fixation periods (16 sec each) interleaved. That is, each of the four conditions (observe movements, observe static displays, imagine to imitate movements, imagine to imitate static displays) was repeated four times in each scan. Ten different images of static arm

displays or four movies were presented in each block. Each static arm display was presented for 500 msec with a blank interval of 1100 msec between stimuli. Each movement-type stimulus was presented for 3 sec with a blank interval of 1 sec between stimuli. All of the stimulus types were presented in all blocks within each scan, in a design that balanced for the order of the conditions. Each subject was run on three localizer scans, each of which lasted 6 min and 32 sec.

Experiments 1 and 2 used an event-related fMRI adaptation paradigm in which two movements were presented sequentially in a trial. Each event-related scan lasted 7 min and 44 sec and consisted of one 7-min and 12-sec epoch of experimental trials and two 16-sec fixation epochs, one at the beginning and one at the end of the scan. Each scan consisted of 16 experimental trials in each of three conditions and 16 interleaved fixation trials. As in previous studies, the order of the trials was counterbalanced so that trials from each condition, including the fixation condition, were preceded (two trials back matched history) equally often by trials from each of the other conditions. A new trial began every 8 sec: the first movement (3 sec) was followed by an interstimulus interval (100 msec), a second movement (3 sec), and a blank interval for 1900 msec. Subjects were instructed to imagine to imitate (mental simulation task) the movements while fixating, and at the end of each trial, to perform a movement matching task (identical vs. different) that ensured the participants' attention across all stimulus conditions.

In Experiment 1, we tested the following conditions: (a) identical movement, where the same type of movement (identical in both the kinematics and the action goal) was presented twice; (b) different kinematics, where two different kinematic morphs with the same goal were presented in a trial; and (c) different movement, where the two stimuli in a trial differed both in the goal of the movement and the kinematics. In Experiment 2, we tested the following conditions: (a) identical movement, where the same movement was presented twice in a trial; (b) similar goal, where the two movements in a trial had the same kinematics but when one of the two was played in the reverse sequence the goal of the movements remained perceptually similar (knocks and waves); and (c) different goal, where the two movements in a trial had the same kinematics but the goal of the movements appeared different when one of the two was played in the reverse sequence (throws and lifts).

### Magnetic Resonance Imaging Acquisition

For all experiments, scanning was performed at the 3-T Trio Siemens scanner at the University Clinic, Tübingen, Germany. A gradient-echo pulse sequence (TR = 2 sec, TE = 90 msec) was used for both the localizer and the

event-related scans. Twenty-four (3 mm thick by 3 mm × 5 mm in-plane resolution) axial slices covering the whole-brain volume were collected with a head coil.

### Data Analysis

fMRI data were processed using the Brain Voyager 2000 software package. Preprocessing of all the functional data included head movement correction and linear trends. The functional images were aligned to the 3-D anatomical data and the complete dataset was transformed to Talairach coordinates.

For each individual subject, we localized ROIs by correlating the signal time course with a box-car reference function, based on the hemodynamic response properties. Table 1 shows the Talairach coordinates for each ROI. For each event-related scan, we extracted the fMRI responses by averaging the data from all the voxels within the independently defined ROIs, as described previously (Kourtzi & Kanwisher, 2001). The average signal time course across trials in each condition was converted to percent signal change relative to the fixation trials. We then averaged the time courses for each condition across scans for each subject and then across subjects. Because of the hemodynamic lag in fMRI response, the peak in overall response and, therefore, the differences across conditions are expected to occur at a lag of several seconds after stimulus onset. To find the peak latencies of the fMRI time courses for each condition and ROI, we fit the data using two (one for

**Table 1.** Talairach Coordinates across ROIs: Average Talairach Coordinates [Mean (SD)] across Subjects for the Left and Right Hemispheres of the PMv, SPL, IPL, STS, and hMT+/V5 Defined by the Localizer Scans in Each Subject

ROIs	Average Talairach Coordinates		
	<i>x</i>	<i>y</i>	<i>z</i>
<i>Left Hemisphere</i>			
PMv	-49 (4)	8 (4)	12 (5)
SPL	-21 (7)	-61 (9)	50 (7)
IPL	-42 (8)	-43 (6)	38 (9)
STS	-50 (5)	-44 (6)	11 (5)
hMT+/V5	-43 (3)	-66 (6)	0 (5)
<i>Right Hemisphere</i>			
PMv	50 (5)	6 (6)	14 (5)
SPL	21 (9)	-63 (9)	48 (6)
IPL	41 (11)	-43 (7)	36 (7)
STS	51 (5)	-41 (5)	10 (6)
hMT+/V5	44 (3)	-64 (4)	-2 (3)

the initial response and one for the undershoot) Gamma functions (Boynton, Engel, Glover, & Heeger, 1996). This analysis showed image peak points for the fMRI time courses between 8 and 12 sec after trial onset; that is, 2–6 sec after the end of the presentation of the two stimuli (3 sec per stimulus) per trial. Therefore, the average response at these peak points was taken as the measure of response magnitude for each condition and ROI in subsequent analyses. For statistical analysis of differences between conditions in the average fMRI response at these time points, we used repeated measures analyses of variance (ANOVAs) and contrast analyses (Greenhouse–Geisser). We further tested whether other cortical areas beyond the functionally mapped ROIs were engaged in the analysis of arm movements during mental simulation. We performed a whole-brain analysis using a GLM across subjects in each experiment (random effects analysis at the group level) consistent with previous studies (Thoenissen, Zilles, & Toni, 2002; Toni et al., 2002). For each experiment, we identified clusters that showed significantly stronger activation for different than for identical movements ( $p < .01$  uncorrected) and characterized the responses across conditions within each cluster based on beta weights.

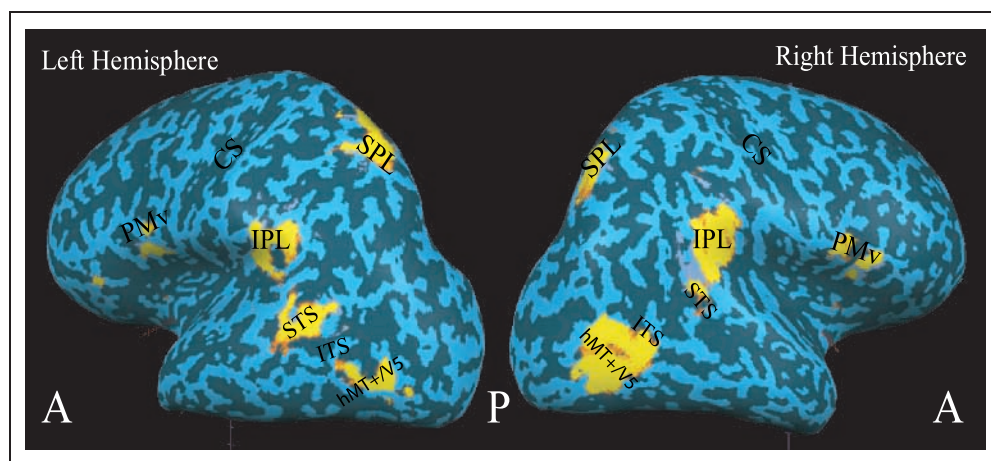
## RESULTS

### Localization of Regions of Interest

For each observer, we localized independently the cortical circuit previously implicated in the observation and imitation of actions; that is, the PMv, the inferior (inferior parietal lobule [IPL]) and superior (superior parietal lobule [SPL]) parietal cortex (Figure 2). As in previous studies (Grezes & Decety, 2001; Binkofski et al., 2000), these regions were identified as the sets of contiguous voxels that showed significantly ( $p < .001$ , corrected) stronger fMRI responses when the observers

imagined to imitate (mental simulation task) than observed moving, goal-directed arm movements (knocks, lifts, waves, throws). Similarly, stronger activations were observed in these regions when the observers imagined to imitate than observed the posture of static arm displays (frames from the same actions). As similar patterns of activation were observed for moving and static displays, we combined data across these conditions in order to maximize detection power when functionally localizing the cortical areas activated more strongly in the mental simulation than the observation task. We further localized visual motion areas hMT+/V5, and STS. hMT+/V5 is known to be involved in motion analysis (Orban et al., 2003; Tootell et al., 1995; Zeki et al., 1991). The STS has been implicated in the processing of biological motion (Saygin et al., 2004; Jellema & Perrett, 2003; Pelphrey et al., 2003; Puce & Perrett, 2003; Grossman & Blake, 2002; Grezes et al., 2001; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001; Allison, Puce, & McCarthy, 2000; Grossman et al., 2000; Decety & Grezes, 1999; Bonda, Petrides, Ostry, & Evans, 1996; Oram & Perrett, 1994; Perrett et al., 1989) and is thought to be part of the cortical circuit for action understanding (Iacoboni et al., 2005; Koski et al., 2003; Iacoboni et al., 1999). hMT+/V5 and the STS were defined as the set of contiguous voxels that showed significantly ( $p < .001$ , corrected) stronger fMRI responses for moving than static arm displays independent of whether the observers were instructed to imagine imitating or observe the displays. As similar patterns of activation were observed for the mental simulation and observation tasks (i.e., stronger activations for moving than static displays), we combined data from both tasks in order to maximize detection power when functionally localizing the cortical areas activated more strongly for moving than static displays. Finally, we investigated the processing of actions in the primary visual cortex (V1) that is the first stage of analysis of visual input. We defined V1

**Figure 2.** Localization of ROIs. Functional activation maps for one subject showing the ventral premotor (PMv), superior (SPL) and inferior parietal lobule (IPL), superior temporal sulcus (STS), and hMT+/V5 regions. The functional activations are superimposed on the inflated cortical surfaces of the right and left hemispheres of one subject. The sulci are coded in darker blue than the gyri and the anterior–posterior orientation is noted by A and P. Major sulci are labeled: STS = superior temporal sulcus; ITS = inferior temporal sulcus; CS = central sulcus.



as the set of contiguous voxels around the calcarine sulcus that were activated by both static and moving displays.

### Experiment 1: Processing of Action Goals and Kinematics

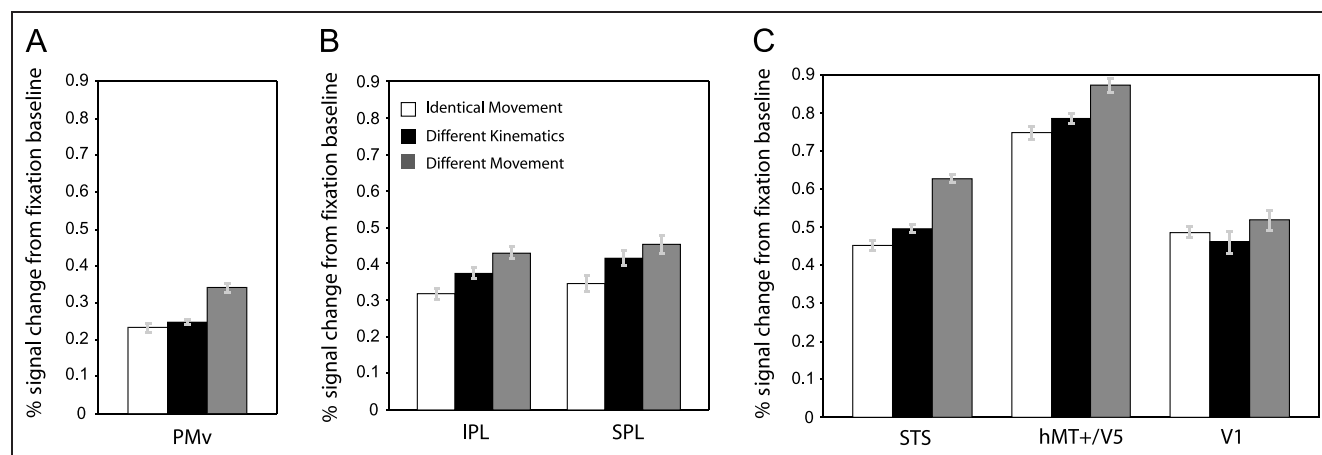
We examined whether ventral premotor, parietal, and visual areas, localized as ROIs in each individual observer, differently process the kinematics and goals of actions. Specifically, we tested for fMRI rebound effects (i.e., increased responses from adaptation) for changes in (a) the kinematics of the actions when there was no change in the goal of the movement (different kinematics), and (b) the goal and the kinematics of the actions (different movement). As shown in Figure 3, we observed increased responses for different (different movement) than identical movements across all areas providing evidence for the basic adaptation or repetition suppression effect in these areas. Interestingly, significant fMRI rebound effects for movements that differed in the kinematics but not the goal of actions were observed in parietal regions (IPL, SPL) and the STS but not in the PMv, hMT+/V5, or V1. These findings suggest that parietal regions and the STS encode information about movement kinematics and may mediate the interpretation and imitation of actions that share the same goal but differ in their kinematics when performed by different actors.

In particular, a repeated measures ANOVA on the average peak responses for condition (identical, different kinematics, different movement) and ROI (PMv, IPL, SPL, STS, hMT+/V5, V1) showed significant main effects of condition [ $F(2, 18) = 17.68, p < .001$ ] and ROI [ $F(5, 45) = 15.77, p < .001$ ], and a significant interaction between condition and ROI [ $F(10, 90) = 2.242, p < .05$ ].

A significant effect of condition was observed in the PMv [ $F(2, 18) = 19.020, p < .001$ ], IPL [ $F(2, 18) = 9.078, p < .001$ ], SPL [ $F(2, 18) = 4.331, p < .05$ ], STS [ $F(2, 18) = 41.992, p < .001$ ], and hMT+/V5 [ $F(2, 18) = 9.629, p < .001$ ], but not in V1 [ $F(2, 18) < 1, p = .3946$ ]. Further analysis (contrast analysis) of the fMRI responses in each ROI revealed the following findings.

First, the PMv showed sensitivity for movements that differed both in their goal and kinematics rather than for movements that differed only in their kinematics (Figure 3A). That is, contrast analysis showed significantly stronger fMRI responses for the different movement condition than for the identical condition [ $F(1, 18) = 23.71, p < .001$ ]. In contrast, no significant differences were observed between the different kinematics and the identical conditions [ $F(1, 18) = 0.71, p = .41$ ]. This rebound effect in the PMv for changes in the goal of the movement is consistent with previous imaging and physiological studies, suggesting that the PMv is involved in the processing of higher-order features of the action, such as action goals. Interestingly, a similar pattern of results was observed in hMT+/V5 (Figure 3C); that is, we observed significantly stronger responses for the different movement than the identical condition [ $F(1, 18) = 18.29, p < .001$ ] but no differences between the different kinematics and the identical condition [ $F(1, 18) = 1.66, p = .21$ ]. These adaptation effects suggest that hMT+/V5 may also be involved in the processing of action goals. However, it is possible that these results in the PMv and hMT+/V5 were due to the larger physical differences in the motion trajectories between the two actions presented in a trial in the different movement than the different kinematics condition. We test this possibility further in Experiment 2.

Second, in contrast to the effects observed in the premotor cortex, we observed rebound effects in the



**Figure 3.** fMRI responses for Experiment 1. Average peak fMRI responses (percent signal changes from the fixation baseline trials). Responses are plotted for the identical movement condition (white bars), the different kinematics condition (black bars), and the different movement condition (gray bars). The fMRI responses are shown averaged across hemispheres for (A) the ventral premotor cortex (PMv), (B) the inferior and superior parietal lobules (IPL, SPL), and (C) the superior temporal sulcus (STS), area hMT+/V5, and the primary visual cortex (V1). Error bars indicate standard error of the mean across subjects.

parietal cortex for movements that differed in their goal and kinematics and movements that had the same action goal but differed in their kinematics (Figure 3B). In particular, contrast analysis showed that fMRI responses in the IPL for the different kinematics [ $F(1, 18) = 18.15, p < .001$ ] and the different movement [ $F(1, 18) = 4.75, p < .05$ ] conditions were significantly stronger than the identical condition. Similar analysis of the fMRI responses in the SPL showed that fMRI responses for the different kinematics [ $F(1, 18) = 3.53, p < .05$ ] and the different movement [ $F(1, 18) = 8.42, p < .01$ ] conditions were significantly stronger than the identical condition. These findings suggest that regions in the parietal cortex are involved in the processing of the kinematics of actions. Interestingly, adaptation effects in the STS (Figure 3C) were similar to those observed in the parietal cortex. In particular, we observed significantly stronger responses for the different movement [ $F(1, 18) = 77.72, p < .001$ ] and the different kinematics [ $F(1, 18) = 5.02, p < .05$ ] than the identical condition. These results suggest that the STS is involved in the processing of the goal and the kinematics of movements. Finally, no significant differences were observed across conditions in V1 [ $F(2, 18) < 1, p = .394$ ], suggesting that the fMRI adaptation effects observed in other ROIs could not be due to low-level differences across conditions.

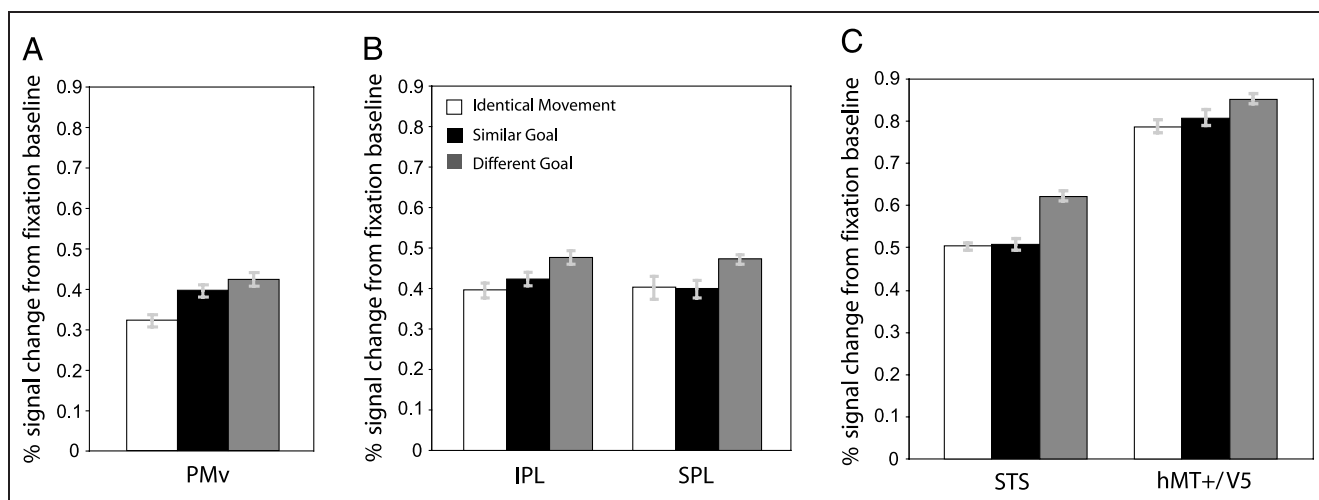
### Experiment 2: Processing of Movements with Different versus Similar Goals

A possible limitation of Experiment 1 is that movements with different goals have larger differences in their kinematics than movements with the same goal but different kinematics. As a result, it is possible that the stronger rebound effects observed for the different movement than for the different kinematics condition (Figure 3) indicate sensitivity to large changes in the kinematics rather than the goal of actions. We tested this possibility in Experiment 2 by comparing fMRI responses for movements that shared the same average kinematics but had similar or different action goals. To this end, we manipulated the order in which the frames of the movement sequences were presented. That is, the two movements presented sequentially in a trial were played forwards versus backwards (in reverse frame order). Playing a movement backwards preserves the same average kinematics as when playing the same movement forwards. However, this manipulation can result in movements that have either a similar goal (i.e., wave, knock) or a different goal (i.e., lift, throw) when played in forwards versus reverse order (see supplementary material). For example, playing backwards a waving or knocking movement displays the same goal as when the movement is played forwards. In contrast, when the movement of lifting an object is played backwards, the action goal changes from lifting to placing. Similarly,

playing backwards throwing movements changes the perceived action goal from throwing to catching or pulling an object toward oneself. It is possible that these perceived differences in action goals due to physical changes in motion direction are mediated by processing of movements in various body-centered coordinate systems (Buneo & Andersen, 2006; Graziano, Cooke, & Taylor, 2000; Colby & Goldberg, 1999). We verified these interpretations of actions goals when the movements were played forwards versus backwards by asking participants to describe the actions presented in these displays. All participants perceived movements played forwards or backwards as natural and gave interpretations consistent with lifting versus placing and throwing versus catching or pulling. Furthermore, perceptual similarity ratings (supplementary material) showed that actions that differed in their goals when played forwards versus backwards (i.e., lift, throw) were perceived as different (Figure 5B) compared to actions that had similar goals when played forwards versus backwards (i.e., wave, knock).

Using these stimuli, we tested fMRI responses for three conditions in which the trials consisted of (a) the same movement played either forwards or backwards twice (identical), (b) the same movement played once forwards and once backwards with perceptually similar goal (similar goal: wave, knock movements), and (c) the same movement played once forwards and once backwards with perceptually dissimilar goal (different goal: lift, throw movements). As shown in Figure 4, we observed that parietal areas and the STS encode differences between movements with dissimilar action goals even when the kinematics remain in average the same between these movements. Interestingly, the premotor cortex appears to encode differences between movements even when they have a similar goal, whereas fMRI responses in hMT+/V5 reflect the differences in the physical motion across action sequences. In particular, a repeated measures ANOVA on the average peak responses for condition (identical, similar goal, different Goal) and ROI (PMv, IPL, SPL, STS, hMT+/V5) showed a significant main effect of condition [ $F(2, 20) = 8.58, p < .01$ ], ROI [ $F(4, 40) = 27.52, p < .001$ ], and a significant interaction between condition and ROI [ $F(8, 80) = 2.31, p < .05$ ]. A significant effect of condition was observed in the PMv [ $F(2, 20) = 7.38, p < .01$ ], IPL [ $F(2, 20) = 3.84, p < .05$ ], STS [ $F(2, 20) = 20.9, p < .001$ ], and SPL [ $F(2, 20) = 3.51, p < .05$ ], but not in hMT+/V5 [ $F(2, 20) = 2.66, p = .095$ ].

Further analysis of the fMRI responses in the PMv showed rebound effects for movements with different or similar action goals. That is, the fMRI responses for the similar goal [ $F(1, 20) = 7.4, p < .05$ ] and different goal [ $F(1, 20) = 13.76, p < .01$ ] conditions were significantly stronger than the identical condition. These rebound effects were not significantly different for the similar and different goal conditions [ $F(1, 20) = 0.98,$



**Figure 4.** fMRI responses for Experiment 2. Average peak fMRI responses (percent signal changes from the fixation baseline trials). Responses are plotted for the identical movement condition (white bars), the similar goal condition (black bars), and the different goal condition (gray bars). The fMRI responses are shown averaged across hemispheres for (A) the ventral premotor cortex (BA 44 on the left and the right pars opercularis, respectively), (B) the inferior and superior parietal lobules, and (C) the superior temporal sulcus (STS), and area hMT+/V5. Error bars indicate standard error of the mean across subjects.

$p = .33$ ]. Similar analysis in the parietal areas showed fMRI rebound effects for the action goal only when the movements had different goals. In the IPL, fMRI responses were significantly stronger for the different goal than the identical condition [ $F(1, 20) = 7.46, p < .05$ ]. However, no significant differences were observed between the similar goal and identical condition [ $F(1, 20) = 0.93, p = .35$ ]. Similarly in the SPL, fMRI responses were significantly stronger for the different goal than for the identical condition [ $F(1, 20) = 4.99, p < .05$ ]. However, no significant differences were observed between the similar goal and identical condition [ $F(1, 20) = 0.013, p = .91$ ].

Finally, analysis of the fMRI responses in the STS showed a similar pattern of results as in the parietal areas. That is, we observed significantly stronger fMRI responses for the different goal than the identical condition [ $F(1, 20) = 32.42, p < .001$ ]. However, no significant differences were observed between the similar goal and identical condition [ $F(1, 20) = 0.038, p = .85$ ]. These results suggest that the STS is engaged in the processing of the action goals even when the average kinematics remain the same. Finally, no significant differences were observed across conditions [ $F(2, 20) = 2.66, p = .1$ ] in hMT+/V5, suggesting that the fMRI activations in Experiment 1 reflect the dissimilarities in the physical motion trajectories between actions with different goals and kinematics.

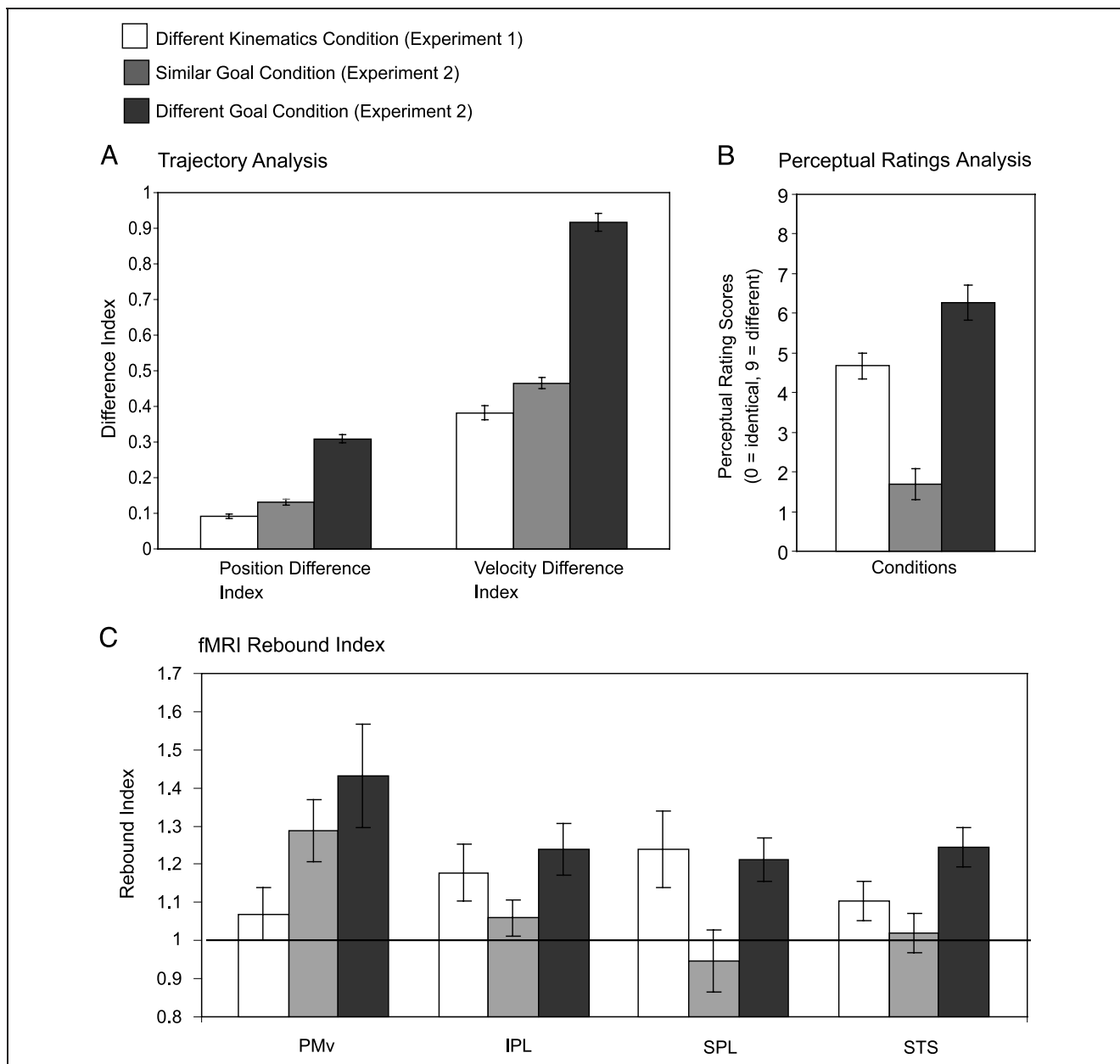
Taken together, these results suggest that areas in the premotor cortex, parietal cortex, and STS encode differences in action goals even when the average movement kinematics remain the same. Thus, the effects observed in Experiment 1 were not simply due to larger differences in the kinematics between movements with different than the same goal but also due to changes in the

goal of the movements. Interestingly, parietal areas and the STS were shown to represent differences between movements with different goals, whereas premotor areas were shown to encode differences between movements even when they shared similar action goals.

### Comparison across Experiments

To summarize and compare the results across experiments (Figure 5), we calculated three indices: (a) physical movement similarity index, (b) perceptual similarity index, and (c) fMRI activation rebound index. We computed the physical similarity between movements by comparing positional and velocity differences between their trajectories (Pomplun & Matarić, 2000) and their perceptual similarity based on behavioral ratings (supplementary material). As shown in Figure 5A, analysis of the movement trajectories showed significant differences in position [ $F(2, 261) = 353.12, p < .001$ ] and velocity [ $F(2, 261) = 173.69, p < .001$ ] between movements presented across the different conditions with the smallest positional and velocity differences for movements with different kinematics (different kinematics condition, Experiment 1) and increasingly larger differences for movements with similar [ $t_{(\text{scheffe})}, p < .05$ ] (similar goal condition, Experiment 2) or different goals [ $t_{(\text{scheffe})}, p < .001$ ] (different goal condition, Experiment 2). Behavioral measures (ratings from 0 = identical to 9 = different) of the perceptual similarity between the sequentially presented movements (Figure 5B) showed that actions that differed in their goals (different goal condition, Experiment 2) were perceived as different compared to actions with similar goals (similar goal condition, Experiment 2) that were perceived as more similar to each other [ $t(9) =$





**Figure 5.** Comparison of trajectories, perceptual ratings, and fMRI rebound effects. (A) Trajectory analysis: index of position and velocity differences between movement pairs presented in the different kinematics (Experiment 1), similar goal (Experiment 2), and different goal (Experiment 2) conditions. Average indices across four different markers (elbow, wrist, first metacarpal, fourth metacarpal) with error bars showing the standard error of the mean (*SEM*) across the different marker locations. This analysis showed a difference between similar (knocks and waves) and different (throws and lifts) goal conditions. This difference appears to arise from the inherent symmetry of the movements themselves. Both knocks and waves had, on average, symmetric patterns of movement directed around the front midpoint of the body, and thus, when reversed, had similar kinematics both forwards and backwards. Lifts and throws, on the other hand, had less symmetric patterns of movement, and thus, the difference index across forwards and backwards patterns of movement were greater. This is particularly evident for the lifting movement that involves motion near the body at the beginning and away from the body at the end. For throwing, this difference in symmetry appears more subtle and seems to involve the three components of the movement (windup, throw, return) being distributed so that the windup and throw were completed in the first 60% of the movement time and the return, by itself, taking 40% of the movement time. (B) Perceptual ratings analysis: scores of perceptual similarity (0 = identical, 9 = different) for movements presented sequentially in a trial for the different kinematics, similar goal, and the different goal conditions. Error bars indicate standard error of the mean rating across subjects ( $n = 10$ ). (C) fMRI rebound index: An fMRI rebound index (percent signal change in each condition divided by percent signal change in the identical movement condition) is plotted for the different kinematics, similar goal, and the different goal conditions for each ROI. A ratio of 1 (horizontal dashed line) indicates adaptation. Error bars indicate standard error of the mean across subjects and are large as they are computed based on individual subjects' mean ratios.

13.981,  $p < .001$ ]. Interestingly, movements that shared the same goal but differed in their kinematics (different kinematics condition, Experiment 1) were rated as more dissimilar [ $t(9) = 9.089$ ,  $p < .001$ ] than movements with similar action goals (similar goal condition, Experiment 2). These behavioral measurements suggest that small differences in the movement trajectories of actions that share the same goal but differ in their kinematics are more salient perceptually than larger physical differences between actions that have similar action goals, consistent with previous studies (Troje, Westhoff, & Lavrov, 2005; Pollick, Fidopiastis, & Braden, 2001; Hill & Pollick, 2000), showing that observers discriminate between different actors performing the same movement, and generalize between actions with similar goals.

Comparison of the movement trajectory measurements and the perceptual similarity ratings predicts two different patterns of cortical activations. Higher sensitivity for the larger trajectory differences between movements with similar goals than movements with different kinematics would indicate cortical areas that process the physical (e.g., position, velocity) differences between movement trajectories. In contrast, higher sensitivity for differences between movements that differ in their kinematics than movements that have similar action goal would indicate areas that respond in accordance with the perceptual salience of the differences between movements (i.e., the ability of the observers to discriminate between movements).

As shown in Figure 5C, fMRI responses in the premotor cortex were consistent with processing of physical differences between movement trajectories and their actions (Figure 5A: trajectory analysis), whereas fMRI responses in the parietal cortex (IPL, SPL) and the STS were in accordance with the perceptual salience of the differences between movements (Figure 5B: perceptual ratings). To compare the fMRI responses for different cortical areas across conditions in the two experiments, we calculated a rebound index by dividing the percent signal change for each condition by the percent signal change for the identical movement condition in each experiment for each ROI separately. A ratio of 1 indicates adaptation, whereas a significantly stronger response than 1 indicates release from adaptation (rebound effect). In the premotor cortex, significant rebound effects were observed for increasingly larger physical differences between movement trajectories independent of whether these changes were of low [Similar goal:  $t(10) = 2.36$ ,  $p < .05$ ] or high [Different goal:  $t(10) = 2.33$ ,  $p < .05$ ] perceptual salience. However, no significant rebound effects were observed for movements with the smallest physical trajectory differences [Different kinematics:  $t(9) = 0.99$ ,  $p = .35$ ], although these movements were perceived as different by the observers. In contrast, in the parietal cortex and the STS, significant rebound effects were observed for per-

ceptually salient differences between movements with small [Different kinematics: SPL,  $t(9) = 2.26$ ,  $p < .05$ ; IPL,  $t(9) = 2.1$ ,  $p < .05$ ; STS,  $t(9) = 1.64$ ,  $p < .13$ ] or large [Different goal: SPL,  $t(10) = 3.01$ ,  $p < .01$ ; IPL,  $t(10) = 3.3$ ,  $p < .01$ ; STS,  $t(10) = 8.45$ ,  $p < .001$ ] physical trajectory differences. However, no significant rebound effects were observed for movements that were rated by the observers as similar despite differences in their physical trajectories [Similar goal: IPL,  $t(10) = 0.64$ ,  $p = .54$ ; SPL,  $t(10) = -0.48$ ,  $p = .64$ ; STS,  $t(10) = 0.39$ ,  $p = .7$ ].

### Whole-brain Analysis

We further investigated the processing of action goals and kinematics in areas engaged in the processing of arm movements during mental simulation beyond the functionally mapped ROIs known to be involved in action understanding. We compared activations for different and identical movements based on a whole-brain analysis across subjects. This analysis revealed activations in left frontal areas (premotor dorsal [PMd]; dorsolateral prefrontal [DLPFC]; cingulate), medial parietal regions (parietal occipital junction [POJ]; left precuneus), and temporal cortex (bilateral STS; right hMT+/V5; right fusiform face area [FFA], right posterior fusiform gyrus [PFs]). However, the whole-brain analysis did not reveal significant activations in areas PMv, IPL, or SPL, whereas these areas showed significantly higher activation during mental simulation than observation of movements. Although potential differences in statistical power and signal-to-noise across analyses (whole brain, ROI analysis) limit the interpretation of null effects in fMRI signals (i.e., nonsignificant activations), activations revealed by the whole-brain analyses, in addition to those shown by the localization of ROIs, relate to differences in the comparisons conducted in these analyses. That is, comparison across tasks (mental simulation vs. observation) reveals areas involved in action understanding, whereas comparison of different and identical movements reveals areas that differ in the processing of action goals and kinematics during mental simulation of movements as well as higher cognitive processes (e.g., discrimination of novel vs. familiar stimuli) known to engage fronto-parietal cortical circuits (Culham & Kanwisher, 2001; Duncan & Owen, 2000).

In particular, in Experiment 1, we observed significantly higher activations (random effects uncorrected:  $p < .01$ ; small volume correction, Bonferroni corrected:  $p < .05$ ; fixed effects, Bonferroni corrected:  $p < .01$ ) for different than identical movements in left frontal (PMd, DLPFC), medial parietal (bilateral POJ and left precuneus), and right temporal (FFA, PFs) areas, in addition to activations in the bilateral STS and right hMT+/V5 that were previously defined based on the ROI analysis (Figure S3). Analysis based on the beta weights across conditions in these areas showed significant differences

between the different movement and identical movement conditions ( $p < .001$ ) and between the different movement and different kinematics conditions ( $p < .01$ ), but no significant difference between the different kinematics and identical movement conditions ( $p > .5$ ). These results suggest that the left dorsal premotor and left DLPFC represent differences between movement trajectories similarly to ventral premotor areas, as shown by the ROI analysis. In contrast to the effects observed in the IPL and SPL based on the ROI analysis, activations in medial parietal regions (POJ, precuneus) did not show significant differences for movements that differed only in their kinematics. This result suggests a special role for areas IPL and SPL in representing the perceptually salient differences between movements compared to other parietal areas engaged in the mental simulation of arm movements. Interestingly, activations in the temporal cortex (right FFA, right PFs) are consistent with the involvement of these areas in processing complex movements (Beauchamp, Lee, Haxby, & Martin, 2003; Grossman & Blake, 2002). Similar analysis in Experiment 2 showed significantly higher activations (random effects uncorrected:  $p < .01$ ; small volume correction, Bonferroni corrected:  $p < .05$ ; fixed effects, Bonferroni corrected:  $p < .05$ ) for movements of different goal than identical movements in the left PMd and left cingulate cortex, in addition to activations in the right STS that was previously defined based on the ROI analysis (Figure S4). Further, in contrast to the activation patterns in PMv based on the ROI analysis, activations in the PMd were not significantly ( $p = .318$ ) different for movements of similar goal than identical movements. This result suggests that the premotor cortex may support representations of actions at different description levels: The dorsal region may represent the perceptually salient differences between action goals similar to the IPL and SPL, whereas the ventral region appears to represent a detailed copy of movement trajectories. Finally, the lateralization effects observed in frontal areas (left PMd, left DLPFC, left cingulate) are consistent with previous studies (Aziz-Zadeh et al., 2006) showing that laterality in the stimulus affector (e.g., right hand actions for the stimuli used in our study) results in contralateral activations in frontal areas (e.g., left hemispheric dominance in our studies). Further, previous studies have shown right hemispheric dominance in the temporal cortex (right STS, right FFA) for biological movements (Grossman, Blake, & Kim, 2004; Pelphrey et al., 2003; Grossman et al., 2000).

## DISCUSSION

The goal of our study was to investigate the role of different cortical areas implicated in the human mirror-neuron circuit in the understanding of actions at different levels of action description from the precise reproduc-

tion of detailed movements to the interpretation of abstract actions. By using kinematic morphs of different types of arm movements, by matching movements for goals or average kinematics, and by employing sensitive fMRI adaptation/repetition suppression methods, we provide novel evidence for differential involvement of premotor areas and parietal and temporal regions in action understanding. In particular, our results show that the PMv encodes the physical similarity between movement trajectories and their goals, whereas parietal regions and the STS process the perceptual similarity between movements that differ either in their action goal or the kinematic profiles of different actors. These findings suggest that processing in the PMv may mediate the exact copying of complex movements, whereas processing in parietal and superior temporal areas may support the interpretation of abstract action goals and movement styles. These differences in the functions of frontal, parietal, and temporal areas engaged in action understanding are supported by recent evidence for a double dissociation between the imitation of finger configurations and the imitation of hand postures in patients with apraxia (Goldenberg & Karnath, 2006). In particular, lesions in the middle temporal gyrus, middle occipital gyrus, and the IPL were associated with deficits in imitating hand postures, whereas lesions in the inferior frontal gyrus, insula, and subcortical areas were associated with deficits at imitating finger configurations. These findings suggest that parietal areas process the goal of actions as expressed by hand movements, whereas premotor areas represent the detailed description of finger movements that is critical for copying complex actions.

Interestingly, our findings relate to multilevel computational models that propose inverse and forwards circuits for action understanding at these different levels of description (Oztop et al., 2006; Iacoboni, 2005; Miall, 2003; Wolpert, Doya, & Kawato, 2003; Kawato, 1999; Wolpert & Kawato, 1998). In particular, it has been suggested that the visual representation of an observed action is translated into a motor plan based on inverse models that map the relationship between the action goal that the observer intends to imitate and the motor commands that will allow the observer to achieve this goal. This motor plan is then converted into a predicted visual representation of the intended action based on a forwards model that compares the internal motor plan to the outcome of the intended action and allows the observer to evaluate whether the intended action approximates that of the observed model. Possible links between these models and the mirror-neuron circuit suggest that action understanding may recruit inverse models that support the translation of the visual representations of observed actions in the STS to motor plans in parietal and premotor areas, and forwards models that mediate the translation of motor plans to predicted actions from the PMv to the STS via the

parietal cortex. Recent neuroimaging studies provide evidence for the role of the parietal cortex in integrating information from motor and visual areas for guiding actions (Shmuelof & Zohary, 2006; Tunik, Frey, & Grafton, 2005). We suggest that the PMv may support action understanding and the imitation of motor acts by representing the physical trajectory differences between the intended and observed action. In contrast, comparison of observed to intended action based on perceptual similarity in the parietal cortex and the STS may support the interpretation and imitation of abstract goals and their translation to motor plans that reflect idiosyncrasies in movements of different styles.

### fMRI Adaptation: Interpretation and Controls

To study the sensitivity of neural populations to differences between movements in their goals or kinematics at a resolution beyond that of the typical human fMRI voxel, we used an fMRI selective adaptation paradigm (Grill-Spector & Malach, 2001; Kourtzi & Kanwisher, 2000). This paradigm allows us to study neural sensitivity to feature differences that mediate discrimination between stimuli, as neurons responding to these features are intermingled within each voxel, and thus, could not be measured at the standard fMRI resolution. Recent electrophysiological studies provide evidence that fMRI adaptation effects are related to neural adaptation at the level of single neurons (Krekelberg et al., 2006; Sawamura et al., 2006; Tolias et al., 2005). fMRI selective adaptation has been used extensively for studying the processing of motion patterns (Huettel, Obembe, Song, & Woldorff, 2004; Huk, Dougherty, & Heeger, 2002; Tolias, Smirnakis, Augath, Trinath, & Logothetis, 2001). Given the complexity of the blood oxygenation level-dependent signal, fMRI selective adaptation studies cannot discern whether the neural sensitivity observed at the scale of large neural populations reflects selectivity as measured by the spike output of individual neurons or adapted input from other neural populations within or across cortical areas (Sawamura et al., 2006; Tolias et al., 2005). These limitations notwithstanding, fMRI selective adaptation for motion has been verified in several single-cell recording studies in area MT (Petersen, Baker, & Allman, 1985). In our study, the lack of fMRI selective adaptation (rebound effect) in V1 suggests that sensitivity in other cortical areas (premotor, parietal cortex, STS) could not be simply attributed to adaptation of input responses to low-level stimulus features from the primary visual cortex.

Might our findings be due to differences in the attentional demands of the matching task across conditions? Analysis of the behavioral accuracy and reaction time data showed that our findings could not be simply due to differences in the difficulty or the duration of

stimulus processing across conditions. In particular, lower fMRI responses were observed when the task was more difficult [ $F(9, 18) = 81.32, p < .001$ ]; that is, fMRI responses were lower for the different kinematics compared to the different goal condition. Consistently, although reaction times were slower [ $F(9, 18) = 3.88, p < .05$ ] for the different kinematics than different goal changes, fMRI responses were lower in the first than in the later condition. Could the stronger rebound effects observed for changes in the goal than the kinematics be attributed to increased attention of the subjects to the most salient changes (i.e., goal than kinematics changes, different than similar goal changes)? Previous neuroimaging studies have implicated parietal areas in guiding visual attention (Culham & Kanwisher, 2001) and proposed a higher-level saliency based motion system in the IPL (Claeys, Lindsey, De Schutter, & Orban, 2003). However, if our results were due to these general arousal/interest confounds, a similar pattern of results would be also expected in visual areas, where responses are known to be modulated by attention (Kastner & Ungerleider, 2000; Ress, Backus, & Heeger, 2000). Moreover, it is highly unlikely that the observers selectively chose to attend to a particular condition as all trials were presented rapidly and were randomly interleaved. Thus, it is unlikely that our results could be significantly confounded by these general attentional confounds.

Could the stronger rebound effects observed for changes in the goal than the kinematics be attributed to subjects silently verbally reciting the goal of the movement? Although we cannot rule out this argument completely, the rebound effect for the similar goal condition contradicts this hypothesis. That is, if verbalization/silent speech shaped the responses in the PMv, then no rebound effects should have been observed for actions that have similar goals (i.e., wave, knock) and cannot be distinguished based on verbal labels. In contrast to this hypothesis, our results are consistent and extend previous neurophysiological studies, suggesting that the premotor cortex processes motor engrams rather than movement kinematics.

An alternative interpretation of our findings would suggest that responses in the PMv reflect categorization of movements at the basic level, whereas responses in the parieto-temporal regions are in accordance with categorization at the subordinate level of discriminating between actions performed by different actors. Previous studies have implicated areas in the frontal and parietal cortex in the categorization of static patterns (Vogels, Sary, Dupont, & Orban, 2002), but their role in the categorization of actions remains unknown. However, the rebound effects observed in the PMv for movements with similar goals that reflect a subordinate-level discrimination are consistent with the role of the premotor cortex in the fine analysis of action goals rather than basic-level categorization. Future studies on the role of

these areas in action categorization would be of further interest.

Finally, it is not likely that our results could be significantly confounded by eye movements. We recorded subjects' eye movements for both experiments using a video-based Eye-Link system (SR Research, Mississauga, Ontario, Canada; 250 Hz sample rate). No significant differences were observed across conditions in the average eye position [Experiment 1:  $F(3, 9) < 1$ ,  $p = .45$ ; Experiment 2:  $F(2, 6) < 1$ ,  $p = .82$ ], suggesting that subjects could fixate for prolonged periods. The average saccade number [Experiment 1:  $F(3, 9) = 1.39$ ,  $p = .31$ ; Experiment 2:  $F(2, 6) = 1.11$ ,  $p = .41$ ] and amplitude [Experiment 1:  $F(3, 9) < 1$ ,  $p = .79$ ; Experiment 2:  $F(2, 6) = 1.00$ ,  $p = .49$ ] did not differ significantly across conditions. Although eye movements could only be collected outside the scanner (due to technical limitations), the lack of any significant differences in the above measurements showed that observers could maintain stable fixation while performing the same tasks as in the scanner.

### Action Processing from Visual Motion Areas to the Premotor Cortex

Our findings relate to the visuomotor representation of actions, as the observers in these experiments were asked to imagine themselves imitating the presented movements. As in previous studies (Grezes & Decety, 2001; Binkofski et al., 2000), this mental simulation task was employed to avoid distortions on the fMRI images that could occur due to body movement if the observers were instructed to execute the presented actions. The validity of this task for studying action understanding was supported by several studies showing that (a) observation, mental simulation (i.e., imagery) and execution of action share common representations (Prinz, 2002; Vogt, 1996; Jeannerod & Decety, 1995), and (b) imagery activates body parts in a somatotopic manner similar to that of voluntary movements (Ehrsson, Geyer, & Naito, 2003). Although we did not control whether the participants performed the mental simulation task, when debriefed after scanning, all observers reported an impulse to move while watching the actions presented during scanning. Thus, our findings in the ventral premotor, parietal, and temporal cortex could be extended to understand the mechanisms that mediate pure visual or motor representations of actions.

This visual-motor link for action understanding was supported by several neurophysiological and imaging studies that suggest that processing of movements may implicate areas not only in the motor cortex but also in the visual cortex. In particular, in the monkey brain, two possible streams involved in action processing have been identified: one from area PO (primarily area V6), sending its output to two relay stations in the SPL, areas

V6a and MIP; the other from MT/V5, projecting to MST, PF/PG (the human homologue of IPL), and areas F4 and F5 (Rizzolatti & Matelli, 2003). Previous human neuroimaging studies have reported activation for motor execution, imitation, and observation in parietal areas: the inferior parietal lobule, the superior part of the parietal lobule at the postcentral sulcus (Buccino, Vogt, et al., 2004; Koski et al., 2003; Iacoboni et al., 1999). Numerous imaging studies on biological movement processing (Pelphrey et al., 2004; Puce & Perrett, 2003; Grossman & Blake, 2002; Grezes & Decety, 2001; Grezes et al., 2001; Vaina et al., 2001; Allison et al., 2000; Grossman et al., 2000; Decety & Grezes, 1999; Bonda et al., 1996) have shown activations in the visual cortex; that is, in the STS and the fusiform gyrus. Additionally, two recent neuroimaging studies report activations for biological movements presented as point-light displays beyond the STS in the parietal and the premotor cortex (Saygin et al., 2004; Pelphrey et al., 2003).

Our study advances our understanding of this visual-motor link by investigating processing of human actions in both visual and parieto-frontal areas. In particular, our findings in the visual cortex suggest that action processing in hMT+/V5 focuses on the analysis of the physical motion in action sequences rather than processing of their goals or kinematics. Processing of action goals and kinematics is evident in the STS that is known to be engaged in the visual perception of biological movements in the human (Pelphrey et al., 2003, 2004; Saygin et al., 2004; Puce & Perrett, 2003; Grossman & Blake, 2002; Grezes et al., 2001; Vaina et al., 2001; Allison et al., 2000; Grossman et al., 2000; Grezes & Costes, 1998; Bonda et al., 1996) and monkey brain (Jellema & Perrett, 2003; Puce & Perrett, 2003; Oram & Perrett, 1994; Perrett et al., 1989) as well as in animacy perception (Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005; Castelli, Happe, Frith, & Frith, 2000). Moreover, recent studies have shown activation in the superior temporal cortex during observation or imitation of hand actions even in the absence of direct vision of the imitator's hand, suggesting that the STS is involved in the cortical circuit for action understanding. It is also possible that the processing of actions in the STS is modulated by feedback projections from the IPL, as in the monkey, where area PF that is thought to be the homologue of human IPL is connected with the rostral part of the STS (Rizzolatti & Matelli, 2003; Rizzolatti & Luppino, 2001).

Further, our findings in the parietal cortex (IPL, SPL) are consistent with previous neuroimaging studies suggesting that the parietal cortex is involved in action processing (Jackson, Meltzoff, & Decety, 2006; Fogassi et al., 2005; Iacoboni et al., 2005; Buccino, Vogt, et al., 2004; Rizzolatti & Craighero, 2004; Tanaka & Inui, 2002; Tanaka, Inui, Iwaki, Konishi, & Nakai, 2001). In particular, activation in the IPL has been reported for changes in the movement goal (Hamilton & Grafton, 2006), perspective taking in imitation tasks (Chaminade &

Decety, 2002), and the imitation of novel action sequences (Buccino, Vogt, et al., 2004). The SPL activation observed in our studies for internally simulated actions are consistent with previous imaging studies that have reported SPL activation for imitation of hand, arm, and foot movements (Jackson et al., 2006; Buccino, Vogt, et al., 2004; Tanaka & Inui, 2002; Grezes & Costes, 1998), suggesting that SPL activations are related to proprioceptive coding of the imitated or executed action (Buccino, Vogt, et al., 2004; Rizzolatti & Craighero, 2004). Further evidence for the role of the parietal cortex in action processing comes from studies on patients with optic ataxia that have impaired control of visually guided actions or action organization due to lesions in the SPL/IPS junction (Glover, 2003, 2004; Rizzolatti & Matelli, 2003; Rossetti, Pisella, & Vighetto, 2003; Pisella et al., 2000). In addition, transient lesions over the posterior parietal cortex with transcranial magnetic stimulation were shown to disrupt the adjustments of movement trajectories (Della-Maggiore, Malfait, Ostry, & Paus, 2004). Interestingly, previous studies have implicated the IPL and the SPL in different processes (i.e., planning and ongoing control of actions, respectively) (Glover, 2004) and have suggested differences in the connectivity of these area with ventral and dorsal premotor areas (Rushworth, Behrens, & Johansen-Berg, 2006). However, our results showed similar activation patterns in the IPL and SPL. This result could be due to the design used in our experiments that does not allow us to discern between planning and ongoing control processes. Further, the lack of significant activations in areas along the IPS (e.g., AIP, VIP, LIP, MIP) known to be involved in the presentation of arm movements (Kroliczak, Cavina-Pratesi, Goodman, & Culham, 2007; Culham & Valyear, 2006; Frey, Vinton, Norlund, & Grafton, 2005; Astafiev et al., 2003; Culham et al., 2003; Grefkes, Weiss, Zilles, & Fink, 2002; Bremmer et al., 2001) could be the result of activation comparisons between conditions that involved the presentation of the same arm movements.

Finally, our findings in the premotor cortex are consistent with reports of mirror neurons in the monkey premotor cortex that are selective for the observation and imitation of actions that differ in their goals (Hamilton & Grafton, 2006; Buccino, Lui, et al., 2004; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004; Johnson-Frey et al., 2003; Umiltà et al., 2001; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti et al., 1996). Interestingly, recent studies have reported a subset of neurons in the macaque, referred to as “strictly congruent,” with mirroring properties for observed and executed actions that corresponded not only in their general goal but also in their precise description (Rizzolatti, Fadiga, Fogassi, & Gallese, 1999). The sensitivity to differences in the movement trajectories observed in our data for the premotor cortex, even when these differences are of low perceptual salience, is

consistent with this finding and suggests a possibly similar mechanism in humans.

### Theories of Imitation

Different models of imitation have been summarized by Rumiati and Bekkering (2003) to lay along a continuum with the direct matching approach at one end (Gray, Neisser, Shapiro, & Kouns, 1991; Butterworth, 1990), the active intermodal matching approach (Meltzoff & Moore, 1997) in the middle, and the goal-directed theory (Bekkering, Wohlschlaeger, & Gattis, 2000) and the dual-route theory (Rumiati & Tessari, 2002) at the opposite end. In contrast, Brass and Heyes (2005) have discussed the dichotomy between generalist theories that assume imitation is mediated by general learning and motor control mechanisms versus specialist theories (e.g., active intermodal matching), which hold that imitation depends upon special purpose mechanisms and supramodal representations. Rizzolatti, Fogassi, and Gallese (2001) draw a distinction between imitative mechanisms of direct matching that can map visual input directly onto motor structures such as mirror neurons and visual matching mechanisms that utilize ever more complex visual representations. Finally, Byrne and Russon (1998) discuss the distinction between action-level imitation that matches the surface form of a movement and program-level imitation that matches the hierarchical organization of a complex action. Addressing the complexity of these various theories and their interrelations is a challenging task.

The current findings, consistent with recent findings from neuroscience, hold that a distributed network of brain areas supports the imitation process. The complexity of this network precludes a simple conclusion to be reached between specialist and generalist theories from our study alone. However, Brass and Heyes (2005) argue that the overall body of evidence points toward generalist theories. Regardless of whether the cortical network of areas involved in action understanding subserves a specialist or generalist function, it is instructive to see how action properties are represented in the network. Our experiments address this question through a novel approach for manipulating movement goals and kinematics.

### Conclusions

In sum, our findings advance our understanding of the functional involvement of both parieto-frontal and visual areas in a neural circuit that processes the physical motion in visual action displays, the movement kinematics, and the abstract goals of actions. Unlike previous studies that have focused on the role of these areas in different aspects of action understanding (e.g., processing of action goals vs. kinematics), our study

provides novel evidence for the neural basis of a cascade of processes that mediate action understanding at different levels of action description. That is, the PMv may support the interpretation of actions and the acquisition of fine motor skills by encoding the physical differences between movement trajectories and their goals, whereas parietal and temporal areas encode the perceptually distinct features that allow us to discriminate between movements with different action goals and actors performing the same action with different styles.

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## REFERENCES

- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, *4*, 267–278.
- Astafiev, S. V., Shulman, G. L., Stanley, C. M., Snyder, A. Z., Van Essen, D. C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *Journal of Neuroscience*, *23*, 4689–4699.
- Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., & Iacoboni, M. (2006). Lateralization of the human mirror neuron system. *Journal of Neuroscience*, *26*, 2964–2970.
- Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2003). fMRI responses to video and point-light displays of moving humans and manipulable objects. *Journal of Cognitive Neuroscience*, *15*, 991–1001.
- Bekkering, H., Wohlschlagel, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Quarterly Journal of Experimental Psychology, Series A*, *53*, 153–164.
- Binkofski, F., Amunts, K., Stephan, K. M., Posse, S., Schormann, T., Freund, H. J., et al. (2000). Broca's region subserves imagery of motion: A combined cytoarchitectonic and fMRI study. *Human Brain Mapping*, *11*, 273–285.
- Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, *43*, 260–267.
- 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.
- Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience*, *16*, 4207–4221.
- Brass, M., & Heyes, C. (2005). Imitation: Is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, *9*, 489–495.
- Bremner, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K., et al. (2001). Polymodal motion processing in posterior parietal and premotor cortex: A human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, *29*, 287–296.
- 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., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *Journal of Cognitive Neuroscience*, *16*, 114–126.
- 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.
- Buckner, R. L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., et al. (1998). Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron*, *20*, 285–296.
- Buneo, C. A., & Andersen, R. A. (2006). The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia*, *44*, 2594–2606.
- Butterworth, G. (Ed.). (1990). *On reconceptualizing sensori-motor coordination in dynamic system terms*. The Netherlands: Kluwer Academic Publishing.
- Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences*, *21*, 667–684; discussion 684–721.
- Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage*, *12*, 314–325.
- Chaminade, T., & Decety, J. (2002). Leader or follower? Involvement of the inferior parietal lobule in agency. *NeuroReport*, *13*, 1975–1978.
- Claeys, K. G., Lindsey, D. T., De Schutter, E., & Orban, G. A. (2003). A higher order motion region in human inferior parietal lobule: Evidence from fMRI. *Neuron*, *40*, 631–642.
- Clark, S., Tremblay, F., & Ste-Marie, D. (2004). Differential modulation of corticospinal excitability during observation, mental imagery and imitation of hand actions. *Neuropsychologia*, *42*, 105–112.
- Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Neuroscience*, *22*, 319–349.
- Culham, J. C., Danckert, S. L., DeSouza, J. F., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research*, *153*, 180–189.
- Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Current Opinion in Neurobiology*, *11*, 157–163.
- Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Current Opinion in Neurobiology*, *16*, 205–212.
- Cutting, J. E., & Kozlowski, L. T. (1977). Recognizing friends by their walk—Gait perception without familiarity cues. *Bulletin of the Psychonomic Society*, *9*, 353–356.
- Decety, J., & Grezes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends in Cognitive Sciences*, *3*, 172–178.
- Della-Maggiore, V., Malfait, N., Ostry, D. J., & Paus, T. (2004). Stimulation of the posterior parietal cortex interferes with arm trajectory adjustments during the learning of new dynamics. *Journal of Neuroscience*, *24*, 9971–9976.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180.

- Dittrich, W. H. (1993). Action categories and the perception of biological motion. *Perception*, *22*, 15–22.
- Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences*, *23*, 475–483.
- Ehrsson, H. H., Geyer, S., & Naito, E. (2003). Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of Neurophysiology*, *90*, 3304–3316.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.
- 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.
- Frey, S. H., Vinton, D., Norlund, R., & Grafton, S. T. (2005). Cortical topography of human anterior intraparietal cortex active during visually guided grasping. *Brain Research, Cognitive Brain Research*, *23*, 397–405.
- 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.
- Glover, S. (2003). Optic ataxia as a deficit specific to the on-line control of actions. *Neuroscience and Biobehavioral Reviews*, *27*, 447–456.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, *27*, 3–24; discussion 24–78.
- Goldenberg, G., & Karnath, H. O. (2006). The neural basis of imitation is body part specific. *Journal of Neuroscience*, *26*, 6282–6287.
- 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.
- Gray, J. T., Neisser, U., Shapiro, B. A., & Kouss, S. (1991). Observational learning of ballet sequences: The role of kinematic information. *Ecological Psychology*, *3*, 121–134.
- Graziano, M. S., Cooke, D. F., & Taylor, C. S. (2000). Coding the location of the arm by sight. *Science*, *290*, 1782–1786.
- Grefkes, C., Weiss, P. H., Zilles, K., & Fink, G. R. (2002). Crossmodal processing of object features in human anterior intraparietal cortex: An fMRI study implies equivalencies between humans and monkeys. *Neuron*, *35*, 173–184.
- Grezes, J., & Costes, N. (1998). Top-down effect of strategy on the perception of human biological motion: A PET investigation. *Cognitive Neuropsychology*, *15*, 553–582.
- 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., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., & Decety, J. (2001). Does perception of biological motion rely on specific brain regions? *Neuroimage*, *13*, 775–785.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*, 14–23.
- Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica (Amsterdam)*, *107*, 293–321.
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience*, *12*, 711–720.
- Grossman, E. D., & Blake, R. (2001). Brain activity evoked by inverted and imagined biological motion. *Vision Research*, *41*, 1475–1482.
- Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, *35*, 1167–1175.
- Grossman, E. D., Blake, R., & Kim, C. Y. (2004). Learning to see biological motion: Brain activity parallels behavior. *Journal of Cognitive Neuroscience*, *16*, 1669–1679.
- Hamilton, A. F., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience*, *26*, 1133–1137.
- Hill, H., & Pollick, F. E. (2000). Exaggerating temporal differences enhances recognition of individuals from point light displays. *Psychological Science*, *11*, 223–228.
- Huettel, S. A., Obembe, O. O., Song, A. W., & Woldorff, M. G. (2004). The BOLD fMRI refractory effect is specific to stimulus attributes: Evidence from a visual motion paradigm. *Neuroimage*, *23*, 402–408.
- Huk, A. C., Dougherty, R. F., & Heeger, D. J. (2002). Retinotopy and functional subdivision of human areas MT and MST. *Journal of Neuroscience*, *22*, 7195–7205.
- Iacoboni, M. (2003). Understanding others: Imitation, language, empathy. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science* (Vol. 1). MIT Press.
- Iacoboni, M. (2005). Understanding others: Imitation, language, empathy. In S. H. Chater (Ed.), *Perspectives on Imitation. From Cognitive Neuroscience to Soci Mechanisms of Imitation and Imitation in Animals* (Vol. 1, pp. 77–100). Cambridge 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, U.S.A.*, *98*, 13995–13999.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, *3*, e79.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*, 2526–2528.
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *Neuroimage*, *31*, 429–439.
- Jeannerod, M. (1997). *The cognitive neuroscience of action*. Oxford: Blackwell Publishers.
- Jeannerod, M., & Decety, J. (1995). Mental motor imagery: A window into the representational stages of action. *Current Opinion in Neurobiology*, *5*, 727–732.
- Jellema, T., & Perrett, D. I. (2003). Cells in monkey STS responsive to articulated body motions and consequent static posture: A case of implied motion? *Neuropsychologia*, *41*, 1728–1737.
- 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-Norlund, 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.



- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, 23, 315–341.
- Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, 9, 718–727.
- 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.
- Kourtzi, Z., & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *Journal of Neuroscience*, 20, 3310–3318.
- Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science*, 293, 1506–1509.
- Krekelberg, B., Boynton, G. M., & van Wezel, R. J. (2006). Adaptation: From single cells to BOLD signals. *Trends in Neurosciences*, 29, 250–256.
- Kroliczak, 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.
- 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.
- Meltzoff, A. N., & Moore, M. K. (1997). Explaining facial imitation: A theoretical model. *Early Development & Parenting*, 6, 179–192.
- Miall, R. C. (2003). Connecting mirror neurons and forward models. *NeuroReport*, 14, 2135–2137.
- 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.
- Naccache, L., & Dehaene, S. (2001). The priming method: Imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cerebral Cortex*, 11, 966–974.
- Nelissen, K., Vanduffel, W., & Orban, G. A. (2006). Charting the lower superior temporal region, a new motion-sensitive region in monkey superior temporal sulcus. *Journal of Neuroscience*, 26, 5929–5947.
- Nishitani, N., & Hari, R. (2000). Temporal dynamics of cortical representation for action. *Proceedings of the National Academy of Sciences, U.S.A.*, 97, 913–918.
- Oram, M. W., & Perrett, D. I. (1994). Responses of anterior superior temporal polysensory (Stpa) neurons to biological motion stimuli. *Journal of Cognitive Neuroscience*, 6, 99–116.
- Orban, G. A., Fize, D., Peuskens, H., Denys, K., Nelissen, K., Sunaert, S., et al. (2003). Similarities and differences in motion processing between the human and macaque brain: Evidence from fMRI. *Neuropsychologia*, 41, 1757–1768.
- Oztop, E., Kawato, M., & Arbib, M. (2006). Mirror neurons and imitation: A computationally guided review. *Neural Networks*, 19, 254–271.
- Pelphrey, K. A., Mitchell, T. V., McKeown, M. J., Goldstein, J., Allison, T., & McCarthy, G. (2003). Brain activity evoked by the perception of human walking: Controlling for meaningful coherent motion. *Journal of Neuroscience*, 23, 6819–6825.
- Pelphrey, K. A., 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*, 16, 1706–1716.
- Perrett, D. I., Harries, M. H., Bevan, R., Thomas, S., Benson, P. J., Mistlin, A. J., et al. (1989). Frameworks of analysis for the neural representation of animate objects and actions. *Journal of Experimental Biology*, 146, 87–113.
- Petersen, S. E., Baker, J. F., & Allman, J. M. (1985). Direction-specific adaptation in area MT of the owl monkey. *Brain Research*, 346, 146–150.
- Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., et al. (2000). An “automatic pilot” for the hand in human posterior parietal cortex: Toward reinterpreting optic ataxia. *Nature Neuroscience*, 3, 729–736.
- Pollick, F. E., Fidopiastis, C., & Braden, V. (2001). Recognising the style of spatially exaggerated tennis serves. *Perception*, 30, 323–338.
- Pollick, F. E., Hill, H., Calder, A., & Paterson, H. (2003). Recognizing facial expression from spatially and temporally modified movements. *Perception*, 32, 813–826.
- Pomplun, M., & Matarić, M. J. (2000, September 7–8). *Evaluation metrics and results of human arm movement imitation*. Paper presented at the First IEEE–RAS International Conference on Humanoid Robotics (Humanoids-2000), MIT, Cambridge, MA.
- Prinz, W. (2002). *Experimental approaches to imitation*. Cambridge: Cambridge University Press.
- Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 358, 435–445.
- Ress, D., Backus, B. T., & Heeger, D. J. (2000). Activity in primary visual cortex predicts performance in a visual detection task. *Nature Neuroscience*, 3, 940–945.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1999). Resonance behaviors and mirror neurons. *Archives Italiennes de Biologie*, 137, 85–100.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research, Cognitive Brain Research*, 3, 131–141.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, 2, 661–670.
- Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, 31, 889–901.
- Rizzolatti, G., & Matelli, M. (2003). Two different streams form the dorsal visual system: Anatomy and functions. *Experimental Brain Research*, 153, 146–157.
- Rossetti, Y., Pisella, L., & Vighetto, A. (2003). Optic ataxia revisited: Visually guided action versus immediate visuomotor control. *Experimental Brain Research*, 153, 171–179.
- Rumiati, R. I., & Bekkering, H. (2003). To imitate or not to imitate? How the brain can do it, that is the question! *Brain and Cognition*, 53, 479–482.
- Rumiati, R. I., & Tessari, A. (2002). Imitation of novel and well-known actions: The role of short-term memory. *Experimental Brain Research*, 142, 425–433.
- Rushworth, M. F., Behrens, T. E., & Johansen-Berg, H. (2006). Connection patterns distinguish 3 regions of human parietal cortex. *Cerebral Cortex*, 16, 1418–1430.
- Sawamura, H., Orban, G. A., & Vogels, R. (2006). Selectivity of neuronal adaptation does not match response selectivity: A single-cell study of the fMRI adaptation paradigm. *Neuron*, 49, 307–318.
- Saxe, R., Xiao, D. K., Kovacs, G., Perrett, D. I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus

- responds to observed intentional actions. *Neuropsychologia*, *42*, 1435–1446.
- Saygin, A. P., Wilson, S. M., Hagler, D. J., Jr., Bates, E., & Sereno, M. I. (2004). Point-light biological motion perception activates human premotor cortex. *Journal of Neuroscience*, *24*, 6181–6188.
- Schultz, J., Friston, K. J., O’Doherty, J., Wolpert, D. M., & Frith, C. D. (2005). Activation in posterior superior temporal sulcus parallels parameter inducing the percept of animacy. *Neuron*, *45*, 625–635.
- Shiffrar, M., Lichtey, L., & Chatterjee, S. H. (1997). The perception of biological motion across apertures. *Perception & Psychophysics*, *59*, 51–59.
- Shmuelof, L., & Zohary, E. (2006). A mirror representation of others’ actions in the human anterior parietal cortex. *Journal of Neuroscience*, *26*, 9736–9742.
- Tai, Y. F., Scherfner, 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. (2002). Cortical involvement for action imitation of hand/arm postures versus finger configurations: An fMRI study. *NeuroReport*, *13*, 1599–1602.
- 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.
- Thoenissen, D., Zilles, K., & Toni, I. (2002). Differential involvement of parietal and precentral regions in movement preparation and motor intention. *Journal of Neuroscience*, *22*, 9024–9034.
- Thornton, I. M., & Vuong, Q. C. (2004). Incidental processing of biological motion. *Current Biology*, *14*, 1084–1089.
- Tolias, A. S., Keliris, G. A., Smirnakis, S. M., & Logothetis, N. K. (2005). Neurons in macaque area V4 acquire directional tuning after adaptation to motion stimuli. *Nature Neuroscience*, *8*, 591–593.
- Tolias, A. S., Smirnakis, S. M., Augath, M. A., Trinath, T., & Logothetis, N. K. (2001). Motion processing in the macaque: Revisited with functional magnetic resonance imaging. *Journal of Neuroscience*, *21*, 8594–8601.
- Toni, I., Shah, N. J., Fink, G. R., Thoenissen, D., Passingham, R. E., & Zilles, K. (2002). Multiple movement representations in the human brain: An event-related fMRI study. *Journal of Cognitive Neuroscience*, *14*, 769–784.
- Tootell, R. B. H., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., et al. (1995). Functional-analysis of human Mt and related visual cortical areas using magnetic-resonance-imaging. *Journal of Neuroscience*, *15*, 3215–3230.
- Troje, N. F., & Geyer, H. (2002). Aftereffects in biological motion perception. *Perception*, *31*, 152.
- Troje, N. F., Westhoff, C., & Lavrov, M. (2005). Person identification from biological motion: Effects of structural and kinematic cues. *Perception & Psychophysics*, *67*, 667–675.
- Tunik, E., Frey, S. H., & Grafton, S. T. (2005). Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. *Nature Neuroscience*, *8*, 505–511.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I know what you are doing. A neurophysiological study. *Neuron*, *31*, 155–165.
- Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proceedings of the National Academy of Sciences, U.S.A.*, *98*, 11656–11661.
- Vogels, R., Sary, G., Dupont, P., & Orban, G. A. (2002). Human brain regions involved in visual categorization. *NeuroImage*, *16*, 401–414.
- Vogt, S. (1996). Imagery and perception–action mediation in imitative actions. *Brain Research, Cognitive Brain Research*, *3*, 79–86.
- Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *358*, 593–602.
- Wolpert, D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural Networks*, *11*, 1317–1329.
- Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. J. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience*, *11*, 641–649.