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Modulation of Cortical Activity During Different Imitative Behaviors

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Koski, Lisa, Marco Iacoboni, Marie-Charlotte Dubeau, Roger P. Woods, and John C. Mazziotta. Modulation of cortical activity during different imitative behaviors. *J Neurophysiol* 89: 460–471, 2003; 10.1152/jn.00248.2002. Imitation is a basic form of motor learning during development. We have a preference to imitate the actions of others as if looking in a mirror (specular imitation: i.e., when the actor moves the left hand, the imitator moves the right hand) rather than with the anatomically congruent hand (anatomic imitation: i.e., actor and imitator both moving the right hand). We hypothesized that this preference reflects changes in activity in previously described frontoparietal cortical areas involved in directly matching observed and executed actions (mirror neuron areas). We used functional magnetic resonance imaging to study brain activity in normal volunteers imitating left and right hand movements with their right hand. Bilateral inferior frontal and right posterior parietal cortex were more active during specular imitation compared with anatomic imitation and control motor tasks. Furthermore this same pattern of activity was also observed in the rostral part of the supplementary motor area (SMA-proper) of the right hemisphere. These findings suggest that the degree of involvement of frontoparietal mirror areas in imitation depends on the nature of the imitative behavior, ruling out a linguistic mediation of these areas in imitation. Moreover, activity in the SMA appears to be tightly coupled to frontoparietal mirror areas when subjects copy the actions of others.

INTRODUCTION

The study of imitation is of importance to an increasingly wide range of neuroscientific domains, from social communication (Frith and Frith 1999; Gallese and Goldman 1998) to motor control, network modeling, and robotics (Arbib et al. 2000; Billard 2001; Schaal 1999). The neural basis of imitation, however, has been unclear until recently. The observation of rather surprising properties of neurons in the ventral premotor cortex (area F5) and posterior parietal cortex (area PF) of the macaque brain has provided insights in the neural mechanisms that may facilitate imitation. These cells, called mirror neurons, fire not only when a monkey performs a particular type of action but also when the monkey simply observes someone else performing the same action, e.g., manipulating an object (di Pellegrino et al. 1992; Fogassi et al. 1998; Gallese et al. 1996, 2001; Rizzolatti et al. 1996a). As such, the mirror system allows a direct matching of the representation of observed and executed actions, thus providing a relatively simple neural precursor mechanism for the human ability to imitate.

We recently conducted a functional magnetic resonance imaging (fMRI) study that supports the direct matching hypothesis. Regions capable of performing direct matching should be active during execution of an action regardless of how that action is elicited. Furthermore, these regions should also be active when simply observing the action. Imitation is a special case of action execution in which the action is elicited by the observation of an identical movement. Therefore activity in a direct matching region should be greater during imitation than during execution of movements elicited by other cues. This pattern of activity was found in the left frontal operculum and the right posterior parietal cortex (Iacoboni et al. 1999).

Additional evidence for the critical role of the frontal operculum and posterior parietal cortex in imitation and action observation has been provided by fMRI data (Buccino et al. 2001; Koski et al. 2002), magnetoencephalography (MEG) data (Nishitani and Hari 2000), positron emission tomography (PET) data (Decety et al. 1997, 2002; Grafton et al. 1996; Grezes et al. 1999; Krams et al. 1998; Parsons and Fox 1998; Rizzolatti et al. 1996b), and a combined cytoarchitectonic and fMRI study (Binkofski et al. 2000). Notably, these two cortical regions may be homologous to those that have been identified as containing mirror neurons in the monkey (di Pellegrino et al. 1992; Fogassi et al. 1998; Gallese et al. 1996). The ventral premotor peak reported in our previous fMRI studies (Iacoboni et al. 1999; Koski et al. 2002) was located in the frontal operculum, in putative Brodmann area 44, strengthening the hypothesis that area F5 of the macaque brain and area 44 of Brodmann in the human brain share anatomical and functional homologies (Petrides and Pandya 1994; Preuss et al. 1996; Rizzolatti and Arbib 1998; Rizzolatti et al. 1996a; von Bonin and Bailey 1947). The location of the reported activity in the posterior parietal cortex is quite variable across studies, but the peak reported in our first study (Iacoboni et al. 1999) was located at the intersection between postcentral sulcus and intraparietal sulcus; this intersection may conceivably fall within the region homologous to area PF in the monkey. Although discrepancies exist in the labeling of anatomic subdivisions within the posterior parietal cortex regions in monkey and

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human, recent functional neuroimaging studies suggest that functional subregions such as polymodal motion processing (Bremmer et al. 2001b) and attentional set shifting (Rushworth et al. 2001) are organized similarly in monkeys and in humans. Therefore measures of neural activity in the frontal operculum and the posterior parietal cortex during action observation and imitation appear to strongly support the existence of a mirror system in humans.

Different varieties of imitation may occur in the real world, even for relatively simple movements. For example, when face to face with a teacher or demonstrator, a pupil may choose to imitate actions in one of two ways. He or she may execute the movement as if looking in a mirror, so that actions performed by the teacher's left hand are imitated with the right hand. We refer to this variety of imitation as *specular imitation*. Alternatively, the pupil may imitate the movement using the same hand as the teacher so that actions performed by the teacher using the left hand are also performed by the pupil using the left hand. We refer to this variety of imitation as *anatomic imitation* because it is performed with the anatomically congruent hand.

Studies in infants indicate that children as young as 9 months old are capable of imitating novel actions (Meltzoff 1988a,b). This ability could rely on a very basic system for matching observed and executed movements, such as the mirror system described in the preceding text. The results of developmental studies indicate that specular imitation is a more natural behavior than anatomic imitation (Bekkering et al. 2000; Berges and Lezine 1963; Gleissner et al. 2000; Kephart 1971; Schofield 1976). Indeed, specular responses predominate over nonspecular responses until 10 yr of age (Wapner and Cirillo 1968). These differences in the behavioral performance of specular and anatomic imitation would predict differences in the level of activity in the brain regions underlying imitation. Thus we hypothesized that specular imitation would activate the direct observation-execution matching system more than anatomic imitation.

We tested this hypothesis by comparing patterns of cortical activity during specular imitation and anatomic imitation. Because blood oxygen level dependent fMRI profiles compatible with the mirror system have been reported in the frontal operculum and the posterior parietal cortex of the human brain, we predicted that activity in these regions would be modulated by the type of imitation performed. Specifically, we predicted that these regions would be activated more during specular imitation than during anatomic imitation.

METHODS

Subjects

Eight right-handed subjects (4 female) were recruited through newspaper advertisements. Participants gave informed consent according to the requirements of the Institutional Review Board of UCLA. The average age of the subjects was 28.6 ± 6.2 (SD) yr. The subjects were right-handed as indicated by a questionnaire adapted from the Edinburgh Handedness Inventory (Oldfield 1971). All were screened to rule out medication use, a history of neurological or psychiatric disorders, head trauma, substance abuse, or other serious medical conditions. No neurological abnormalities were identified by neurological examination performed just before the scanning session.

Image acquisition and processing

Images were acquired using a GE 3.0T MRI scanner with an upgrade for echo-planar imaging (EPI) (Advanced NMR Systems). A two-dimensional spin-echo image (TR = 4,000 ms; TE = 40 ms, 256 by 256, 4-mm-thick, 1-mm spacing) was acquired in the sagittal plane to allow prescription of the slices to be obtained in the remaining sequences and to ensure the absence of structural abnormalities in the brain. For each subject, two functional EPI scans (gradient-echo, TR = 4,000 ms, TE = 70 ms, 64 × 64, 26 slices, 4-mm-thick, 1-mm spacing) were acquired, each for a duration of 5 min and 40 s and covering the whole brain. Each scan consisted of eight task periods of 20 s alternating with nine rest periods of 20 s. A high-resolution structural T2-weighted echo-planar image (spin-echo, TR = 4,000 ms, TE 54 ms, 128 × 128, 26 slices, 4-mm-thick, 1-mm spacing) was acquired coplanar with the functional images.

The functional images were aligned with the T2-weighted structural image within each subject using a rigid-body linear registration algorithm (Woods et al. 1998a). The images were then registered to a Talairach-compatible (Talairach and Tournoux 1988) MR atlas (Woods et al. 1999) with fifth-order polynomial nonlinear warping (Woods et al. 1998b). Data were smoothed using an in-plane, Gaussian filter for a final image resolution of 8.7 × 8.7 × 8.6 mm.

Behavioral conditions

Stimuli consisted of images of hands representing a simple movement, namely, lifting of the index or middle finger from a resting position on a table surface (Brass et al. 2000; Iacoboni et al. 1999). The hands were oriented with fingers toward the subject and were presented against a blue background. Eight trials (4 index finger actions, 4 middle finger actions) were presented in each task period. Each trial lasted 2,000 ms with an intertrial interval of 500 ms during which a blue screen was presented.

The full study design included two stimulus factors and one instruction factor. The first stimulus factor was stimulus type: moving versus static hand. One half of the stimuli depicted actual movement. The other half of the stimuli represented a particular movement symbolically by means of a black cross superimposed on the middle or index finger of a static hand. The black cross was present on the hand for the same duration as the action depicted in the moving condition (control condition). This variable, stimulus type, was crossed with a second variable, stimulus laterality, in which the presented hand could be a left hand or a right hand. Thus four different categories of stimuli were presented: a moving left hand, a moving right hand, a static left hand with a symbolic cue, and a static right hand with a symbolic cue. The four stimulus categories were then crossed with the instruction factor: execute versus observe. In the execution condition, subjects used their right hand to perform the movement cued by the stimulus: either the finger movement (imitation) or the black cross (control motor condition). In the observation condition, subjects simply observed the stimuli passively. Thus subjects participated in a total of eight different tasks. These tasks are illustrated in Fig. 1. Note that the execution of a movement cued by a moving left hand corresponds to what we have defined as specular imitation, whereas the execution of a movement cued by a moving right hand corresponds to what we have defined as anatomic imitation. The control motor condition for each of these tasks is represented by the execution of a movement in response to the respective static hand on which the correct movement finger was cued symbolically.

As stated in the previous section, two functional scanning runs were acquired from each subject with each run consisting of eight task periods intermixed with rest periods, so that all eight task types were presented once in each scan. The instruction factor (execute vs. observe) was blocked within a scanning run, such that subjects saw all four stimulus categories in a sequence of four alternating task and rest periods before switching tasks within the same scanning run. The

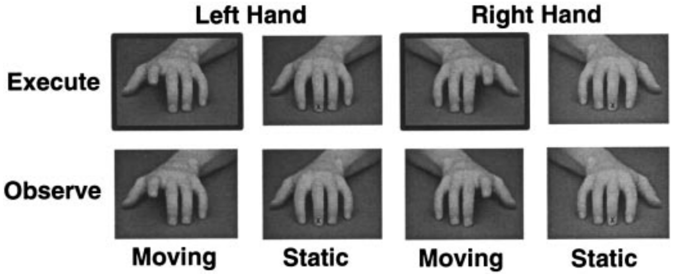

FIG. 1. Examples illustrating the endpoint of trials from the 8 conditions presented during each functional scanning run. Each block of trials corresponded to a single condition and movements of the index or middle finger were represented in a randomized trial order within each block. Subjects used their right hand to perform the action indicated by the stimulus hand during execute blocks and simply observed during observe blocks. The heavy black outline indicates those conditions that correspond to imitation.

order of the stimulus categories and the order of the instruction factor were counterbalanced across runs and across subjects.

Statistical analyses

All statistical analyses were performed after spatial normalization and smoothing, on the group data. Statistical contrasts were based on an ANOVA model (Woods et al. 1996), which factors out the run-to-run variability within subjects as well as the between-subject variability in signal intensity (Iacoboni et al. 1996–1999; Woods et al. 1996). The dependent variable was the sum of the signal intensity at each voxel throughout each task period (Iacoboni et al. 1999, 2001; Koski et al. 2002). In the following subsections, we detail the nature of each contrast tested.

Identification of motor areas

The first contrast was conducted to identify regions activated by execution of the finger movements, relative to the passive observation of hands and finger movements. A four-way ANOVA model included the following factors: subject ($n = 8$), functional scan ($n = 2$), instruction ($n = 2$: execute, observe), stimulus ($n = 4$: moving left hand, static left hand with cue, moving right hand, static right hand with cue). A simple contrast on the instruction variable was carried out: execute versus observe.

IMITATION OF A LEFT HAND. A contrast of imitation of a moving left hand minus movement in response to a symbolic cue on the static left hand was carried out to reveal any brain regions that showed activity suggestive of mirror properties during specular imitation. By the terms “mirror properties” or “mirror activity,” we refer to a pattern of activity in which there is an increase in fMRI signal during action imitation compared with performance of the control motor task. In other words, the results would reveal regions the activity of which not only increases during performance of an action but shows still further increase in signal during imitation of the same action due to the visual encoding of that action by mirror areas. This contrast is essentially a replication of that reported in one of our previous studies of imitation using fMRI (Iacoboni et al. 1999).

This contrast and all remaining contrasts were based on the data from the execution instruction tasks only. The three-way ANOVA model used for these analyses included the following factors: subject ($n = 8$), functional scan ($n = 2$), and stimulus category ($n = 4$: specular imitation, anatomic imitation, execution to cue on static left hand, execution to cue on static right hand). Note that whereas the statistical contrast compared only two of the four stimulus categories, all four stimulus categories were entered in the ANOVA model. This approach yields identical error terms for all imitation contrasts reported in this paper so that the results of the different contrasts may be compared more equitably.

IMITATION OF A RIGHT HAND. A contrast of imitation of a moving right hand minus movement in response to a symbolic cue on the static right hand was carried out to reveal any brain regions that showed activity suggestive of mirror properties during anatomic imitation, as defined in the preceding section.

MIRROR ACTIVITY SPECIFIC TO ONE IMITATION TYPE. The specular imitation hypothesis was tested using a weighted contrast of specular imitation (weight: $+3$) with anatomic imitation (weight: -1) and execution to a symbolic cue on the left hand (weight: -1) or right hand (weight: -1). This contrast was designed to reveal regions that showed a particular type of interaction, namely one in which significantly greater signal was obtained in the specular imitation condition compared with the average of the other three execution conditions. It differs from the simple subtractions performed in the preceding text in that it reveals regions that show increased activity uniquely in the specular imitation condition. The opposite contrast was used to test for regions that show increased activity uniquely in the anatomic imitation condition (anatomic imitation weight: $+3$; specular imitation weight: -1; execution to a symbolic cue on the left hand weight: -1; or right hand: weight: -1).

Statistical thresholds

The present study was intended to examine further the pattern of activity within regions of interest identified in our first study of imitation using fMRI: inferior frontal cortex, rostral posterior parietal cortex, and parietal operculum (Iacoboni et al. 1999). We allowed for bilateral regions of interest because bilateral activity could be observed in frontoparietal regions in our previous study when the statistical threshold was lowered. Our previous study (Iacoboni et al. 1999), as well as numerous other imaging studies, showed the importance of the frontal operculum and the posterior parietal cortex in the recognition and imitation of actions (Binkofski et al. 2000; Buccino et al. 2001; Decety et al. 1997, 2002; Gallese et al. 1996; Grafton et al. 1996; Grezes et al. 1999; Koski et al. 2002; Krams et al. 1998; Nishitani and Hari 2000; Rizzolatti et al. 1996b). On the basis of this strong a priori hypothesis about the brain regions involved, we adopted here a statistical cutoff criterion of $t = 3.53$ at each voxel (df $= 21$; $P = 0.001$, uncorrected for multiple spatial comparisons) for determining the statistical significance of peaks within our regions of interest. For peaks located outside these regions of interest, we used a more conservative joint intensity and spatial threshold of $P = 0.001$ and 10 voxels (Forman et al. 1995).

RESULTS

Motor areas involved in execution of finger movements: execution minus observation-only

The regions activated by execution of the finger movements are shown in Fig. 2. Strong signal increases were observed throughout the hand region of the primary sensorimotor cortex, the premotor cortex, and the motor areas of the medial wall. The activity was strongly lateralized to the left hemisphere as would be expected given that subjects performed the task with their right hand. Consistent with this pattern, strongly lateralized activity was also observed in the right cerebellum. The posterior parietal cortex also showed signal increases during execution of the finger movements, again greater in the left than in the right hemisphere.

Imitation of a left hand: specular imitation minus control motor task

REGIONS OF INTEREST. The areas of increased signal within our regions of interest are shown in Table 1. Significantly

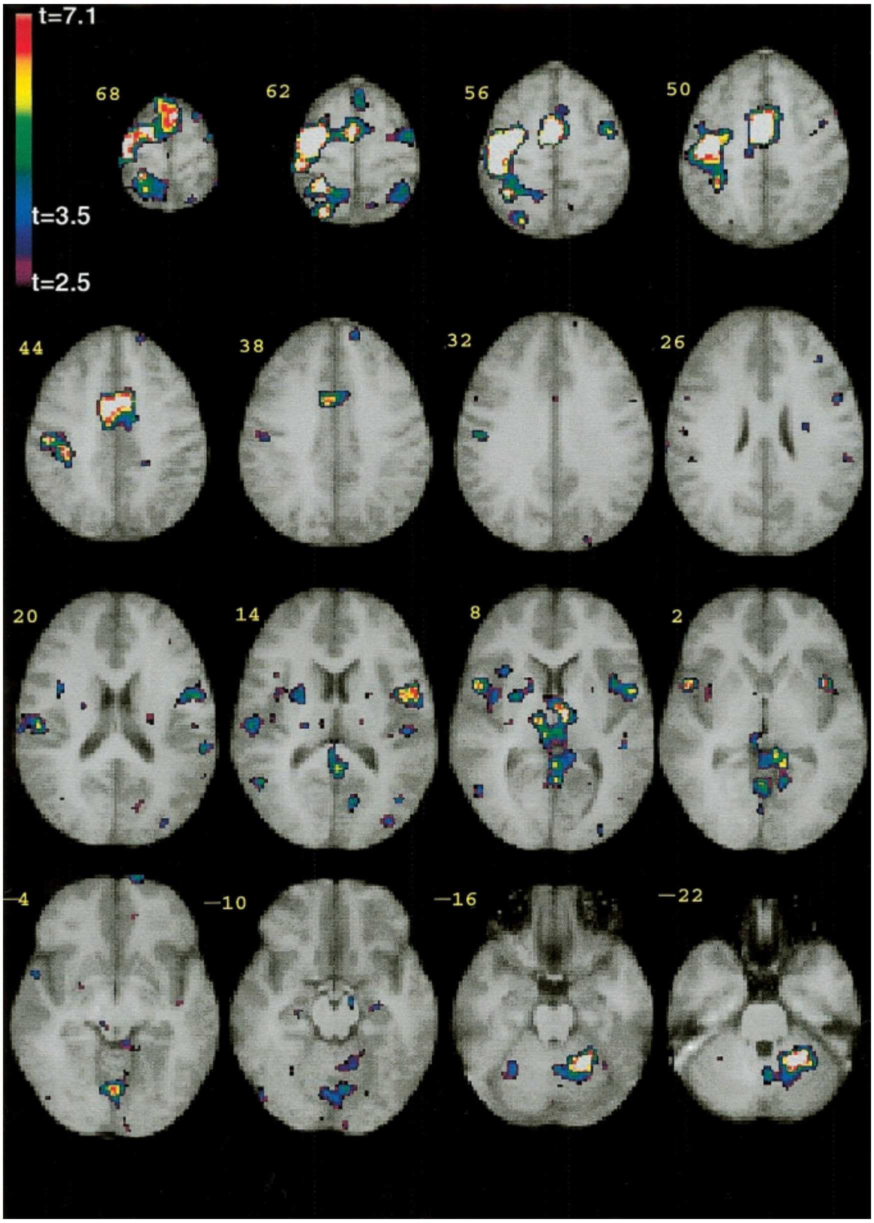

FIG. 2. Activation maps showing areas with signal intensity increases during execution tasks minus observation tasks. Slices from selected z planes within the t maps ($z = 68$ to -22) are displayed superimposed on the T1-weighted Talairach-compatible magnetic resonance (MR) atlas (Woods et al. 1999). The left and right sides of each image represent the left and right hemispheres, respectively. The color tab in the *top left corner* indicates the intensity of the signal changes, where $t = 3.5$ corresponds to a P value of 0.001 uncorrected across multiple spatial comparisons.

greater activity was observed during imitation compared with the corresponding control motor task in the intraparietal sulcus of the right posterior parietal cortex ($t = 3.65$). Significant increases in signal were also observed in the right parietal operculum.

In the frontal operculum, anterior to the precentral sulcus and ventral to the inferior frontal sulcus, we observed peaks in both the left ($t = 2.88$) and right hemisphere ($t = 3.18$). The coordinates of the peak in the left hemisphere were less than 1 cm from those identified in our previous study. The locations in

TABLE 1. *Locations within the regions of interest showing increased signal during specular imitation*

		Specular Imitation vs. Control Motor Task		Specific to Specular Imitation*	
Region	BA	*x, y, z*	*t*	*x, y, z*	*t*
L frontal operculum	44	−51, 10, 18	2.88	−50, 12, 14	3.21
R frontal operculum	44	54, 12, 20	3.18	54, 16, 20	3.13
R intraparietal sulcus	40	39, −46, 40	3.65	40, −46, 42	5.19
				34, −46, 56	4.22
R parietal operculum	40	52, −30, 28	4.40	62, −24, 30	5.00
				68, −26, 22	4.72

* Compared with anatomic imitation and motor control tasks.

TABLE 2. *Locations outside regions of interest showing increased signal during specular imitation*

		Specular Imitation vs. Control Motor Task			Specific to Specular Imitation*		
Region	BA	*x, y, z*	*t*	Voxels	*x, y, z*	*t*	Voxels
L precentral gyrus/sup. frontal sulcus	6	−30, −20, 60	4.04	17			
R precentral gyrus	4/6	34, −26, 58	4.60	27			
R supplementary motor area	6	5, −22, 64	6.56	143	2, −10, 58	6.17	325
L paracentral lobule		0, −28, 50	5.59	53			
R paracentral lobule		4, −38, 60	5.79	121	4, −38, 60	6.11	110
R posterior cingulate	31				2, −28, 48	5.58	47
R middle frontal gyrus	8	31, 26, 40	4.57	44	32, 28, 40	4.60	49
	6	38, 12, 46	4.85	82	36, 10, 48	5.08	20
	6	42, 10, 42	4.68	82	44, 8, 40	5.05	96
L sup. frontal gyrus	8	−14, 16, 52	7.06	80	−14, 16, 52	6.42	59
R sup. frontal gyrus	9				38, 32, 30	4.05	40
R sup. frontal gyrus/frontal pole	10	24, 56, 22	4.76	51	24, 56, 20	5.08	62
R ant. medial frontal gyrus		12, 44, 18	5.15	27	12, 44, 18	6.45	68
R post. middle temporal gyrus	37/39	50, −70, 18	5.98	126	50, −70, 18	6.56	147
L anterior SPL/postcentral gyrus	5	−4, −40, 64	5.70	98	−4, −40, 64	5.75	58
L medial postcentral gyrus	5	−24, −42, 64	4.29	14			
L sup. parietal lobule	7	−16, −54, 62	4.26	17			
L precuneus	7	−4, −50, 58	6.34	311	−4, −50, 60	6.03	208
R SPL/superior occ. gyrus	7/19	32, −82, 34	6.00	75	32, −80, 34	6.36	119
L cuneus	19	−20, −92, 26	5.40	34			
	19	−5, −82, 24	4.37	16			
	18	−10, −98, 20	4.87	30	−6, −100, 8	4.19	14
	18/19	−12, −92, 12	4.29	23			
R cuneus	18/19	24, −86, 26	6.00	63	24, −88, 24	4.24	22
	18/19	22, −78, 14	5.18	33			
	19	16, −96, 26	4.90	55			
L middle occ. gyrus	18	−35, −74, 16	4.01	11			
R middle occ. gyrus	18	10, −92, 14	4.32	46			
	18	40, −86, 6	4.24	24	40, −88, 10	4.93	12
L lingual gyrus		−24, −56, 2	5.01	29	−22, 56, 0	5.22	36
		−4, −78, 2	4.57	24	−4, −78, 2	4.13	
					−16, −76, −4	4.93	12

* Compared with anatomic imitation and motor control tasks. BA, Brodmann area; SPL, superior parietal lobule; occ., occipital; sup., superior; ant., anterior; post., posterior.

both hemispheres fell within the boundaries of the pars opercularis (25–50% probability) as defined by the probability map of Tomaiuolo and colleagues (1999). This *t*-value exceeds the level corresponding to a *P* value of 0.05 corrected across multiple spatial comparisons when taking the pars opercularis alone as a region of interest (average volume: 3.68 ml/hemisphere × both hemispheres; critical *t*-value = 2.57 for corresponding number of resolution elements in the present study) (Tomaiuolo et al. 1999).

PEAKS OUTSIDE THE REGIONS OF INTEREST. Areas of increased activity outside our regions of interest are shown in Table 2. We observed peaks within the posterior portion of the right superior parietal lobule, close to the superior occipital gyrus. Increased activity was also seen in the left parietal cortex in the medial wall of the postcentral gyrus (Brodmann area 5), in the superior parietal lobule (Brodmann area 7), and the precuneus. In medial frontal regions, the paracentral lobule was activated bilaterally as was the caudal part of the supplementary motor area (SMA) and an anterior region of the medial frontal gyrus near the pole in the right hemisphere. Within the dorsal premotor cortex, peaks were observed in the precentral gyrus bilaterally and in the posterior part of the middle frontal gyrus in the right hemisphere. More anteriorly, peaks were observed in the dorsal prefrontal cortex bilaterally as well as in the frontal pole of the right hemisphere. Finally, increased signal was also observed in the dorsal end of the ascending limb of the right inferior temporal sulcus [Brodmann area (BA) 39], in the left lingual gyrus, and in bilateral cuneus and middle occipital gyrus.

Imitation of a right hand: anatomic imitation—control motor task

The results of this contrast are presented in Table 3. One peak was observed in the posterior region of the right parietal operculum. Increased signal was also found in the paracentral lobule of the left parietal cortex and in the ventral bank of the right superior temporal sulcus.

TABLE 3. *Regions showing increased signal during anatomic imitation versus control motor task*

Regions of Interest	Brodmann Area	*x, y, z*	*t*	Voxels
R parietal operculum	40	64, −38, 32	6.98	
Outside regions of interest				
L paracentral lobule		−2, −38, 66	4.80	15
R posterior middle temporal gyrus	21	54, −26, −10	7.06	26

Mirror activity specific to specular imitation: interaction contrast

Figure 3 illustrates the brain regions showing increased activity in this contrast.

REGIONS OF INTEREST. Greater activity during imitation than during the control motor task was observed in a pattern that was unique to specular imitation in the right intraparietal sulcus, right parietal operculum, and left frontal operculum (Table 1). For the right intraparietal sulcus, two locations showed increased signal, one located more anteroventrally, and one more dorsally, within the dorsomedial bank of the intraparietal sulcus. Significant increases in signal were also observed in the right parietal operculum.

Bilateral increases in activity were seen in the frontal operculum in the left ($t = 3.21$) and right ($t = 3.13$) pars opercularis. The coordinates of both peaks fall within the boundaries of the pars opercularis (left: 50–75% probability; right: 25–50% probability) (Tomaiuolo et al. 1999). As shown in Fig. 4, the location of the increased activity observed in the left pars opercularis overlaps with that observed in our previous study of imitation (Iacoboni et al. 1999)

PEAKS OUTSIDE THE REGIONS OF INTEREST. The results of this contrast were largely consistent with those obtained in the simple comparison of specular imitation minus the control motor task (Table 2). Significantly greater activity during specular imitation relative to the other execution conditions was observed in the right superior parietal lobule close to the superior occipital gyrus and in the posterior cingulate region (Brodmann area 31). In the left parietal cortex, the medial wall of the postcentral gyrus and the precuneus both showed increased signal. In the right medial frontal regions, increased activity was seen in the paracentral lobule, the rostral part of the supplementary motor area, and anteriorly near the frontal pole. The coordinates of the peak of activity in the SMA were located in the rostral part of the SMA proper (Fig. 5), just anterior to the border between the rostral and caudal SMA (Rizzolatti et al. 1996c; Vorobiev et al. 1998). The anterior part of the dorsal premotor cortex was activated in the right hemisphere. Peaks were also observed in the dorsal prefrontal cortex bilaterally and in the frontal pole of the right hemisphere. Outside the frontal and parietal cortex we observed increased activity in the right hemisphere in the middle temporal gyrus (BA 39) and middle occipital gyrus of the right

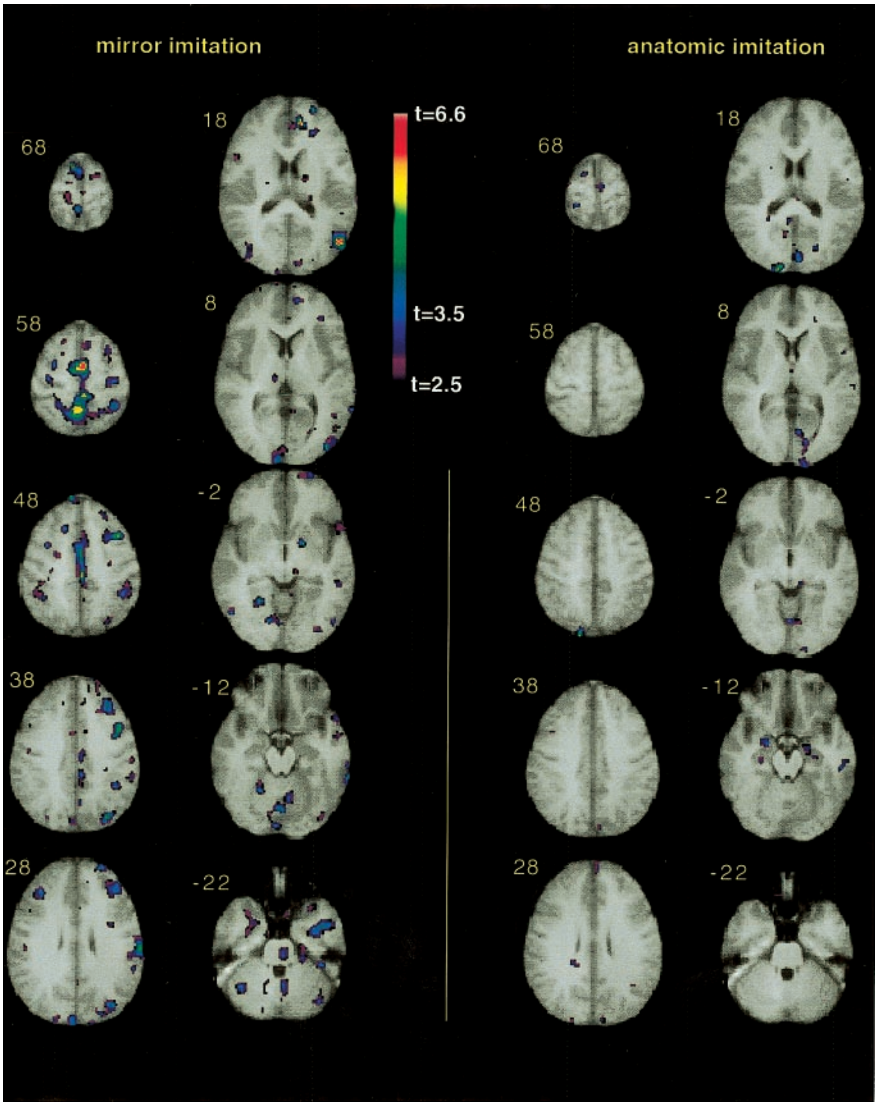

FIG. 3. Activation maps showing areas with increased signal intensity specific to the specular imitation condition when contrasted with the other three execution instruction tasks (*left*) and specific to the anatomic imitation condition when contrasted with the other 3 execution instruction tasks (*right*). Slices from selected z planes ($z = 68$ to -22) are displayed superimposed on the T1-weighted Talairach-compatible MR atlas (Woods et al. 1999). The left and right sides of each image represent the left and right hemispheres, respectively. The color tab in the top middle of the figure indicates the intensity of the signal changes, where $t = 3.5$ corresponds to a P value of 0.001 uncorrected.

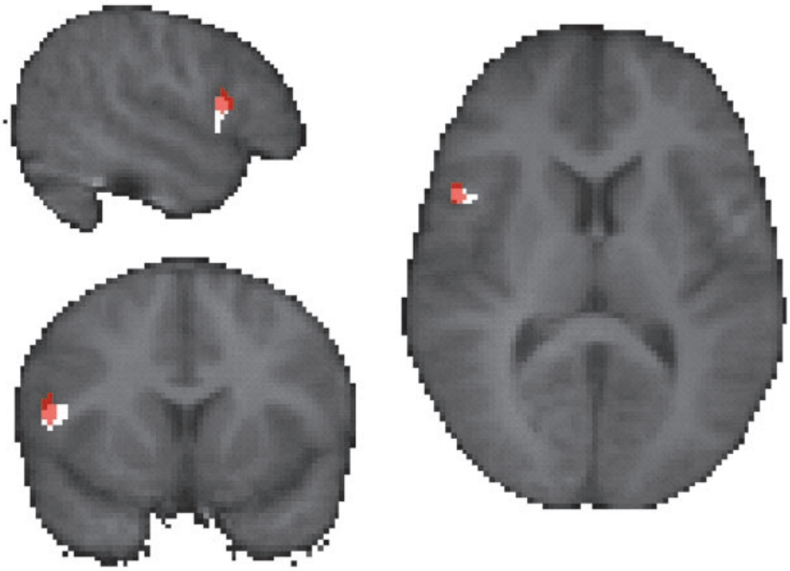

FIG. 4. Slices in the sagittal ($x = -50$), coronal ($y = 10$), and transverse ($z = 12$) planes illustrating the overlap (pink) in the pars opercularis of the left hemisphere between the region activated in our earlier study of imitation (Iacoboni et al. 1999) and in the present study. The region identified in the present study was created by labeling voxels in the left pars opercularis region that had a value of $t = 2.5$ or greater in the contrast map of specular imitation vs. the other three execution conditions (red). These labeled voxels are shown superimposed on the pars opercularis region activated in the earlier study (white), which is itself overlaid on the T1-weighted brain atlas for anatomic localization.

hemisphere, in the lingual gyrus of the left hemisphere and in the cuneus bilaterally.

Mirror activity specific to anatomic imitation: interaction contrast

We also analyzed the data to determine whether there were brain regions that showed a pattern of activity opposite to the hypothesized pattern, i.e., greater activity for anatomic imitation than specular imitation and the two control motor tasks. This pattern was not found within our regions of interest even when lowering the threshold for statistical significance further to $P = 0.01$ ($t = 2.5$). The results of the contrast are illustrated in Fig. 3 (*right*). One significant peak was observed in the middle occipital gyrus (BA 18) of the left hemisphere ($x = -16$, $y = -98$, $z = 16$; $t = 5.27$; number voxels above threshold = 49).

DISCUSSION

We report here the results of a follow-up study of the neural substrates of imitation. In a previous study, we demonstrated that the frontal opercular and posterior parietal regions in the human brain showed patterns of activity compatible with the

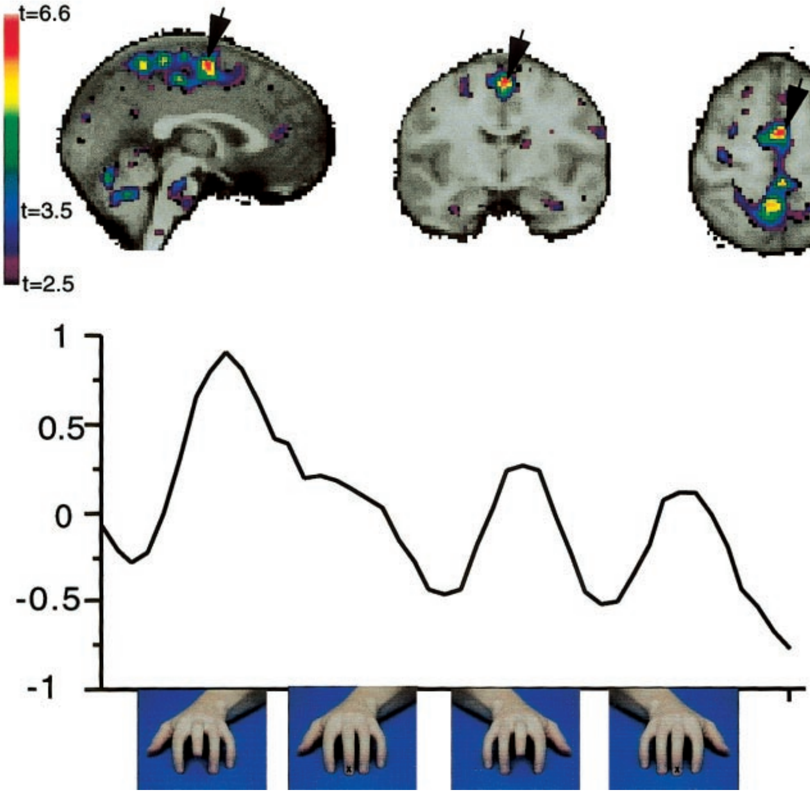

FIG. 5. *Top*: areas of increased signal intensity in the supplementary motor area (see black arrows) from the weighted contrast of specular imitation vs. the other 3 execution instruction conditions. The location of these regions is presented in transverse, sagittal, and coronal views selected to display the voxel of highest signal intensity and superimposed on a T1-weighted Talairach-compatible MR atlas (Woods et al. 1999). The color tab on the *top left* of the figure indicates the intensity of the signal changes, where $t = 3.5$ corresponds to a P value of 0.001 uncorrected. It is clear that although the peak of greatest significance was located in the right hemisphere, the activity is actually bilateral and extends well into the left hemisphere as well. *Bottom*: graph illustrates the time series of activity across the task and rest blocks for the execution instruction conditions. The time series was constructed by first creating a region of interest for the peak that included all contiguous voxels activated at or above $t = 3.53$ and then calculating the average signal within this region. Activity is expressed as the percent change in MR signal relative to the average resting baseline signal calculated for each subject (y axis). The time series line is calculated from the average signal at each point in time, across 4 task periods and 5 rest periods, averaged across the 2 functional scans and across all subjects. The gray textured boxes represent the task periods. The order of conditions as presented in the figure is represented in the small photographs below the x axis: specular imitation, left control motor task, anatomic imitation, and right control motor task. These conditions were presented in counterbalanced order across functional scans and subjects in the experiment but are shown here in a fixed order for display purposes only.

existence of a mirror system capable of representing or matching both observed and executed actions. This mechanism may underlie the development of the human ability to imitate. In the present study, we show that activity in the frontal opercular and posterior parietal regions varies as a function of the type of imitation being performed. Differences in the behavioral characteristics of specular and anatomic imitation appear to be associated with differences in the patterns of activity within underlying neural systems. The results support our hypothesis that the mirror system is engaged to a greater degree when imitating the actions of others in the specular configuration, rather than in an anatomic configuration. This suggests that the relative facility with which humans imitate in the specular configuration may be a function of greater dependence on a simple mechanism for matching observed and executed actions.

It is important to consider whether the results obtained here could be explained on the basis of stimulus-response compatibility rather than imitation because the anatomic imitation condition requires subjects to perform an action in a spatial location that is not congruent with that of the observed action. This argument maybe rejected for two reasons. First, the behavioral literature on visually cued actions performed by adult subjects indicates that reaction times for imitating a finger movement are almost 100 ms faster than reaction times for performing the same movement in response to a symbolic cue regardless of the spatial stimulus-response relation (Brass et al. 2000, 2001). This suggests a privileged mechanism for imitation over a more laborious spatial stimulus-response mapping strategy. Moreover, imitation and spatial stimulus-response compatibility show dissociable effects on reaction times (Brass 2001, experiment 3). Second, if the differences in activity observed across imitation types in the present study were attributable to differences in spatial compatibility, we would expect anatomic imitation to be associated with greater activity than specular imitation in regions known to be activated during incompatible stimulus-response conditions, such as the dorsal premotor and posterior parietal cortex (Iacoboni et al. 1996–1998). A simple contrast of anatomic minus specular imitation did not yield such a pattern of activity.

Both the left and right frontal opercular peaks reported here are consistent with those described in a recent study of action observation (Buccino et al. 2001). The area of greatest increase in the left frontal operculum overlapped spatially (Fig. 4) with the area reported in our earlier study of imitation (Iacoboni et al. 1999). Finally, the location of the peaks is the same (within the spatial resolution of our scanning methods) as that reported in a recent study in which we demonstrated the importance of the frontal operculum for representing the goal of an action (Koski et al. 2002). These peaks are located anterior to the precentral sulcus and therefore can be said to fall within the boundaries of Brodmann area 44.

The interpretation of the activity seen in the frontal operculum during tasks such as action observation, imagery, execution, and imitation is currently a topic of much debate. Considerable evidence supports the view that Brodmann area 44 constitutes the human homologue of area F5 in the monkey (Petrides and Pandya 1994; Preuss et al. 1996; Rizzolatti et al. 1996b, 1998; von Bonin and Bailey 1947). What explanation can account for a relationship between a mirror system and an area of the brain typically known for its role in linguistic processing? According to the *evolutionary precursor* view, the human capacity for language evolved from the existence of a mirror system in nonhuman primates. This mirror system provided the capacity to recognize actions, which led to a capacity to imitate actions, which in turn developed into a capacity for manual-based communication, and, finally, speech (Arbib 2002; Rizzolatti and Arbib 1998). In contrast, the *silent speech* view hypothesizes that the observation of meaningful actions and the performance of motor imagery tasks automatically engage subvocal speech processing of the stimuli (Grezes et al. 1998). Grezes and Decety (2001) recently reviewed the neuroimaging studies of action observation, motor imagery, and action execution as well as action naming. In support of the silent speech hypothesis, they concluded that of these four task types only action naming consistently activated Broca's area (Brodmann area 44/45), whereas the remainder tended to involve more posterior portions of the inferior frontal cortex located on the precentral gyrus corresponding to Brodmann area 6.

The data presented here, however, are not consistent with the silent speech hypothesis. In our study, imitation of left hand actions yields greater activation in pars opercularis than imitation of right hand actions. We do not see any cause to suggest that left hand actions would invoke silent speech more than right hand actions. Thus the results of the present study are difficult to reconcile with the view that activation in Broca's area during imitation is due to silent speech.

Both types of imitation were associated with activity in the parietal operculum when compared with their control motor tasks. This was also described in our previous report of fMRI activity during imitation in which it was suggested (Iacoboni et al. 1999) that the activity in the parietal operculum might reflect input from reafferent signals associated with action performance. Such input could underlie the preservation of a sense of self or body identity during action imitation (Georgieff and Jeannerod 1998). Because action observation increases activity in motor related areas, the brain must have some way of representing the ownership of actions during imitation to discriminate between merely observing an action and performing it oneself.

Sirigu and colleagues (1999) made a similar suggestion in their report on apraxic patients with parietal lesions. The patients performed hand movements while receiving visual feedback by video and were unable to judge whether the movement shown on the video was from their own hand or that of the examiner. Their impairment suggested an inability to incorporate internal feedback about movement into a model of the ongoing action. The patients studied had lesions of vascular origin that likely included the opercular region of the parietal lobe. Thus the converging evidence from these two very different research methods appear to strongly support the importance of the parietal operculum in integrating feedback from motor and kinesthetic regions to form a continuously evolving representation of movement. This representation may function not only to indicate ownership of an observed action but may have a more general role in motor imagery and planning as suggested by the impairments in motor imagery tasks seen in after parietal lesions (Sirigu et al. 1996) or in disengaging motor attention during disruption of the supramarginal gyrus by transcranial magnetic stimulation (Rushworth et al. 2001a).

Moderating this interpretation, however, we note some differences between our fMRI results and the other studies cited here. First, the other studies have tended to implicate the left hemisphere (Rushworth et al. 2001a; Sirigu et al. 1999), whereas the activity we observed in the parietal operculum was lateralized to the right hemisphere despite the use of the ipsilateral hand to respond. The lateralized pattern we observed could not be related to simple sensorimotor aspects of the movement, which are typically contralateral to the motor effector, but it does fit with the observation that body schema disorders occur primarily after lesions to the parietal cortex of the right, rather than left, hemisphere (Berlucchi and Aglioti 1997). Second, the other studies cited here do not point specifically to the opercular region of the parietal cortex, but involve the supramarginal gyrus or more widespread lesions involving the temporoparietal region. Clearly, understanding the specificity and lateralization of function within the parietal operculum will require more direct investigation.

A number of areas outside the regions of interest also showed greater signal for specular imitation (see RESULTS and Tables 2 and 3). These regions encompass visual, motor, and integrative areas, suggesting that during specular imitation, the greater activity in mirror areas spreads upstream and downstream in the cortical network activated by imitative behavior. Among these regions, we want to emphasize the role of the SMA, an area known to play an important role in action representation.

The motor regions of the medial wall may be subdivided into the SMA (or SMA-proper) and the pre-SMA on the basis of their cytoarchitecture, their pattern of cortical and subcortical connectivity, and their functional properties observed in neuroimaging studies (see Grezes and Decety 2001; Picard and Strick 1996, 2001 for reviews). The SMA can be subdivided still further into rostral and caudal regions based on anatomic (Rizzolatti et al. 1996c; Vorobiev et al. 1998) and functional (Grafton et al. 1996; Stephan et al. 1995) considerations. The boundary between the caudal and rostral subdivisions of the SMA may be considered to fall at the midpoint of a line drawn between the anterior and posterior commissures (Vorobiev et al. 1998). This midpoint corresponds to $y = -12$ in the coordinate system of Talairach and Tournoux (1988). The peak of greatest signal increase in the current study was located at $y = -10$ in Talairach coordinates, very close to the boundary between the rostral and caudal SMA. The activity extended slightly asymmetrically in a rostral and ventral direction from this peak, suggesting that it falls within the rostral SMA.

The right SMA was more active during specular imitation than during anatomic imitation and the two control motor conditions despite identical motor output requirements. This location was also activated at a subthreshold level when comparing imitation with control motor tasks in our previous study of imitation but was not reported because it did not reach the rather conservative threshold chosen for that very first study on imitation (Iacoboni et al. 1999). Another interesting feature is the presence of task-related activity during the observation-only conditions (see Fig. 6). This finding is consistent with the results of neuroimaging studies that demonstrated an association between activity in SMA and action execution, motor imagery, and observation of actions (see Grezes and Decety 2001, for a review). Previous studies suggest that the rostral SMA in particular may be active when a mental representation of a movement is engaged, in the absence of actual movement execution (Grafton et al. 1996; Stephan et al. 1995).

The present results showed similar imitation-related modulation of activity in the SMA and in other regions important for action representation. As illustrated in Fig. 6, we observed a complex dissociation between the pattern of activity obtained during imitation and that obtained during observation of hands and hand actions in the SMA, ipsilateral posterior parietal, and superior temporal sulcus (STS) regions. Imitation of a left hand (specular imitation) was associated with the greatest signal increase during the execution tasks. During observation-only, however, activity increased to a comparable degree for both moving and static right hands and to a *lesser* extent for moving and static left hands. Thus the processes involved in imitation appear to modify the pattern of activity in brain regions important for representing action.

We have recently proposed a model in which different kinds of action description are represented in the STS region and the mirror system (Iacoboni et al. 2001) for the purpose of monitoring performance during imitation. The STS, known to be

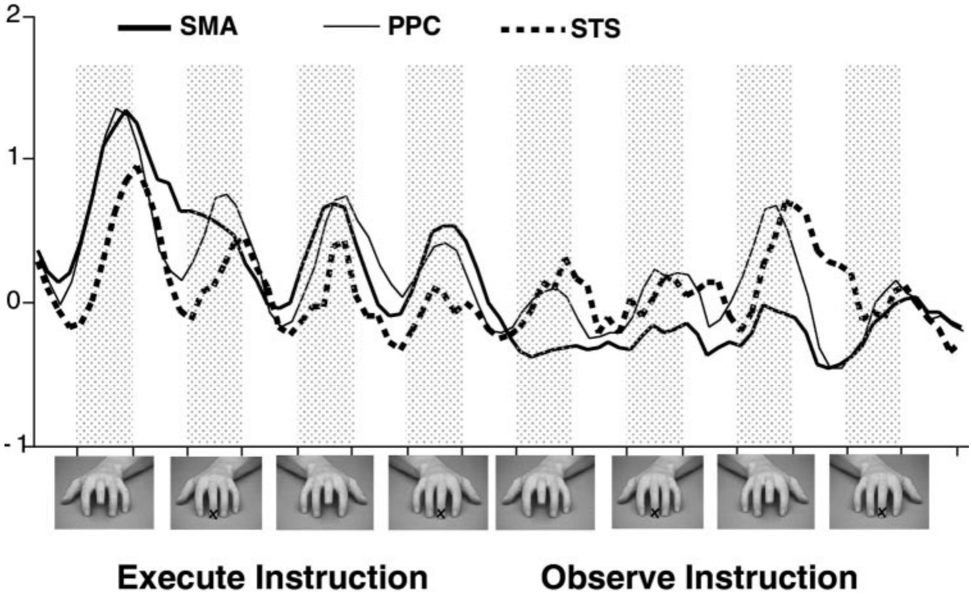

FIG. 6. Graph illustrates the time series of activity in the posterior parietal cortex (thin line), supplementary motor area (thick line) and superior temporal sulcus regions (dotted line) across the task and rest blocks for all conditions. The time series for each of the 3 regions was constructed as in Fig. 5. Activity is expressed as the percent change in MR signal relative to the average resting baseline signal calculated for each subject (*y* axis). The time series line is calculated from the average signal at each point in time, across 8 task periods and 9 rest periods, averaged across the 2 functional scans and across all subjects. Other display details are as in Fig. 5.

important for the perception of biological motion (Allison et al. 2000; Frith and Frith 1999; Grafton et al. 1996; Puce et al. 1998), provides a high-order visual description of an observed action and matches this description with the predicted sensory consequences of imitating that same action. These consequences are represented in the form of efferent copies of motor plans and are provided by motor-related mirror regions in the posterior parietal and/or frontal opercular regions. We hypothesize that SMA function may be included in this model, influencing and being influenced by the processing of these other regions within the network for representing actions. Consistent with this proposal are the well-documented anatomic connections between the posterior parietal cortex (areas PC, PE, and PEA) in the monkey brain and the SMA (area F3: Luppino et al. 1993) and STS regions (Seltzer and Pandya 1994).

Outlining the interaction of these regions within the context of the present data is a complex task. We can begin by hypothesizing that in addition to the tendency to imitate in the specular configuration, there may also be an opposing tendency to map observed actions onto a dominant, i.e., right, hand. Thus we speculate that the observation of right hands was associated with greater activity in STS that was carried forward to posterior parietal cortex, then to inferior frontal cortex, and finally to SMA. From the differences in the degree of task-related activity during observation, it appears that the SMA is less responsive than the posterior parietal cortex and the STS to the visual properties of the stimuli when no response is required. This would be consistent with its predominant role in motor control, although clearly this control is influenced by visual input. When an observed action has to be copied, however, subjects would tend to map the observed left hand onto their own right hand due to their preference for specular imitation. In this case, greater activity for left hand actions would originate in the frontal operculum and the posterior parietal cortex and spread downstream to SMA and upstream to the STS. This description of how actions might be represented within a model that includes the SMA, STS and mirror areas constitutes a set of testable hypotheses that may drive future work in imitation.

Could the increased activity during specular imitation observed in this study reflect the operation of an attentional mechanism? This possibility is suggested by the presence of increased signal in early visual processing regions such as the extrastriate, occipitotemporal and occipitoparietal cortex. The results are not consistent, however, with the effects that would be predicted from a general attentional mechanism. Because anatomic imitation is the less natural task if one considers the developmental literature (Bekkering et al. 2000; Gleissner et al. 2000; Kephart 1971; Schofield 1976), it should require greater attentional resources, yet the opposite pattern was obtained.

The observed pattern of activity could, however, be predicted by a version of the premotor theory of attention, in which processing of visual stimuli may be facilitated by feedback from the activation of motor programs for carrying out an action (Craighero et al. 1999). The concept of motor to sensory modulation of activity was first elaborated in the notion that when a command is made to move the eyes, a corollary signal is sent back to visual areas in preparation for the anticipated change of visual scene (Sperry 1950). The results of recent neuroimaging studies are consistent with this principle, demonstrating modulation of early visual and auditory processing areas as a function of the frequency of saccadic eye movements and spoken syllables, respectively (Paus et al. 1995, 1996a,b). Interpreted in the context of the present study, posterior parietal regions could contribute to the preparation of the motor program during specular imitation, subsequently feeding back to enhance (rather than decrease as in primary sensory regions) activity in higher order visual processing areas. Both the network model described above for action imitation and the type of attentional enhancement mechanism proposed here are consistent with the overall principle of an ongoing pattern of forward and inverse signals between neural networks during performance of an action.

To conclude, the results of this study demonstrate differential activity in frontoparietal regions during different forms of imitative behavior. In particular, they suggest the importance of the mirror system for imitating in the specular configuration. Taken in the context of developmental studies of imitation, the results may be interpreted as evidence that the mirror system provides a basic mechanism that allows for some types of simple imitation. The development of more complex imitative skills may emerge as a function of the maturation of other systems important for visuospatial transformation. A recent review of imitation studies suggested a need for further research directed at determining what cognitive and neural capacities may work in conjunction with the mirror system to support imitation (Williams et al. 2001). The present study begins to answer this question, suggesting how frontoparietal mirror areas may operate within larger neural networks during particular types of imitation.

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REFERENCES

Allison T, Puce A, and McCarthy G. Social perception from visual cues: role of the STS region. *Trends Cogn Sci* 4: 267–278, 2000.

Arbib MA. The mirror system, imitation, and the evolution of language. In: *Imitation in Animals and Artifacts*, edited by C. Nehaniv and K. Dautenhahn: The MIT Press, 2002, p. 229–280.

Arbib MA, Billard A, Iacoboni M, and Oztop E. Synthetic brain imaging: grasping, mirror neurons and imitation. *Neural Networks* 13: 975–997, 2000.

Bekkering H, Wohlschlager A, and Gattis M. Imitation of gestures in children is goal-directed. *Q J Exp Psychol A* 53: 153–164, 2000.

Berges J and Lezine I. *Test d'Imitation de Gestes: Techniques d'Exploration du Schema Corporel et des Praxies Chez l'Enfant de 3 A 6 Ans.* Paris, France: Masson and Cie, 1963.

Berlucchi G and Aglioti S. The body in the brain: neural bases of corporeal awareness. *Trends Neurosci* 20: 560–564, 1997.

Billard A. Learning motor skills by imitation: a biologically inspired robotic model. *Cybern Syst* 32: 155–193, 2001.

Binkofski F, Amunts K, Stephan KM, Posse S, Schormann T, Freund H-J, Zilles K, and Seitz RJ. Broca's region subserves imagery of motion: a combined cytoarchitectonic and fMRI study. *Hum Brain Map* 11: 273–285, 2000.

Brass M, Bekkering H, and Prinz W. Movement observation affects movement execution in a simple response task. *Acta Psychol* 106: 3–22, 2001.

Brass M, Bekkering H, Wohlschlaeger A, and Prinz W. Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. *Brain Cogn* 44: 124–143, 2000.

Bremmer F, Schlack A, Shah NJ, Zafiris O, Kubischik M, Hoffmann K-P, Zilles K, and Fink GR. Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* 25: 287–296, 2001.

Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, and Freund HJ. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci* 13: 400–404, 2001.

Colby CL, Gattass R, Olson CR, and Gross CG. Topographical organization of cortical afferents to extrastriate visual area PO in the macaque: a dual tracer study. *J Comp Neurol* 269: 392–413, 1988.

Craighero L, Fadiga L, Rizzolatti G, and Umilta C. Action for perception: a motor-visual attentional effect. *J Exp Psychol Hum Percept Perform* 25: 1673–1692, 1999.

Decety J, Chaminade T, Grezes J, and Meltzoff AN. A PET exploration of the neural mechanisms involved in reciprocal imitation. *Neuroimage* 15: 265–272, 2002.

Decety J, Grezes J, Costes N, Perani D, JEannerod M, Procyk E, Grassi F, and Fazio F. Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* 120: 1763–1777, 1997.

di Pellegrino G, Fadiga L, Fogassi L, Gallese V, and Rizzolatti G. Understanding motor events: a neurophysiological study. *Exp Brain Res* 91: 176–180, 1992.

Duvernoy H. *The Human Brain. Surface, Three-Dimensional Sectional Anatomy and MRI.* New York: Springer-Verlag, 1991.

Fogassi L, Gallese V, Fadiga L, and Rizzolatti G. Neurons responding to the sight of goal-directed hand/arm actions in the parietal area PF (7b) of the macaque monkey. *Soc Neurosci Abstr* 24: 654, 1998.

Forman SD, Cohen JD, Fitzgerald M, Eddy WF, Mintun MA, and Noll DC. Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magn Reson Med* 33: 636–847, 1995.

Frith CD and Frith U. Interacting minds—a biological basis. *Science* 286: 1692–1695, 1999.

Gallese V, Fadiga L, Fogassi L, and Rizzolatti G. Action recognition in the premotor cortex. *Brain* 119: 593–609, 1996.

Gallese V, Fogassi L, Fadiga L, and Rizzolatti G. Action representation and the inferior parietal lobule. In: *Attention and Performance. XIX. Common Mechanisms in Perception and Action*, edited by Prinz W and Hommel B. Oxford, UK: Oxford Univ. Press, 2001, p. 334–355.

Gallese V and Goldman A. Mirror neurons and the simulation theory of mind-reading. *Trends Cogn Sci* 2: 493–501, 1998.

Galletti C, Fattori P, Kutz DF, and Battaglini PP. Arm movement-related neurons in the visual area V6A of the macaque superior parietal lobule. *Eur J Neurosci* 9: 410–413, 1997.

Georgieff N and Jeannerod M. Beyond consciousness of external reality: a "who" system for consciousness of action and self-consciousness. *Conscious Cogn* 7: 465–477, 1998.

Gleissner B, Meltzoff AN, and Bekkering H. Children's coding of human action: cognitive factors influencing imitation in 3-year-olds. *Dev Sci* 3: 405–414, 2000.

Grafton ST, Arbib MA, Fadiga L, and Rizzolatti G. Localization of grasp representations in humans by positron emission tomography. II. Observation compared with imagination. *Exp Brain Res* 112: 103–111, 1996.

Grezes J, Costes N, and Decety J. The effects of learning and intention on the neural network involved in the perception of meaningless actions. *Brain* 122: 1875–1887, 1999.

Grezes J, Costes N, and Decety J. Top-down effect of strategy on the perception of human biological motion: a PET investigation. *Cogn Neuropsychol* 15: 553–582, 1998.

Grezes J and Decety J. Functional anatomic of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Hum Brain Map* 12: 1–19, 2001.

Iacoboni M, Koski L, Brass M, Bekkering H, Woods RP, Dubeau M-C, Mazziotta JC, and Rizzolatti G. Reafferent copies of imitated actions in the right superior temporal cortex. *Proc Natl Acad Sci USA* 98: 13995–13999, 2001.

Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, and Rizzolatti G. Cortical mechanisms of human imitation. *Science* 286: 2526–2528, 1999.

Iacoboni M, Woods RP, Lenzi GL, and Mazziotta JC. Merging of oculomotor and somatomotor space coding in the human right precentral gyrus. *Brain* 120: 1635–1645, 1997.

Iacoboni M, Woods RP, and Mazziotta JC. Brain-behavior relationships: evidence from practice effects in spatial stimulus-response compatibility. *J Neurophysiol* 76: 321–331, 1996.

Iacoboni M, Woods RP, and Mazziotta JC. Bimodal (auditory and visual) left frontoparietal circuitry for sensorimotor integration and sensorimotor learning. *Brain* 121: 2135–43, 1998.

Kephart NC. *The Slow Learner in the Classroom.* Columbus, OH: Charles Merill, 1971.

Koski L, Wohlschläger A, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, and Iacoboni M. Modulation of motor and premotor activity during imitation of target-directed actions. *Cereb Cortex* 12: 847–855, 2002.

Krams M, Rushworth MFS, Deiber M-P, Frackowiak RSJ, and Passingham RE. The preparation, execution and suppression of copied movements in the human brain. *Exp Brain Res* 120: 386–398, 1998.

Luppino G, Matelli M, Camarda R, and Rizzolatti G. Corticocortical connections of area F3 (SMA-proper) and area F6 (pre- SMA) in the macaque monkey. *J Comp Neurol* 338: 114–140, 1993.

Meltzoff AN. Infant imitation after a 1-week delay: long-term memory for novel acts and multiple stimuli. *Dev Psychol* 24: 470–476, 1988a.

Meltzoff AN. Infant imitation and memory: nine-month-olds in immediate and deferred tests. *Child Dev* 59: 217–225, 1988b.

Nishitani N and Hari R. Temporal dynamics of cortical representation for action. *Proc Natl Acad Sci USA* 97: 913–8, 2000.

Oldfield RC. The Assessment and Analysis of Handedness: the Edinburgh Inventory. *Neuropsychologia* 9: 97–113, 1971.

Parsons LM and Fox PT. The neural basis of implicit movements used in recognising hand shape. *Cogn Neuropsychol* 15: 583–615, 1998.

Paus T, Jech R, Thompson CJ, Comeau R, Peters T, and Evans AC. Transcranial magnetic stimulation during positron emission tomography: a new method for studying connectivity of the human cerebral cortex. *J Neurosci* 17: 3178–3184, 1997.

Paus T, Marrett S, Worsley KJ, and Evans AC. Extraretinal modulation of cerebral blood flow in the human visual cortex: implications for saccadic suppression. *J Neurophysiol* 74: 2179–2183, 1995.

Paus T, Marrett S, Worsley K, and Evans A. Imaging motor-to-sensory discharges in the human brain: an experimental tool for the assessment of functional connectivity. *Neuroimage* 4: 78–86, 1996a.

Paus T, Perry DW, Zatorre RJ, Worsley KJ, and Evans AC. Modulation of cerebral blood flow in the human auditory cortex during speech: role of motor-to-sensory discharges. *Eur J Neurosci* 8: 2236–2246, 1996b.

Petrides M and Pandya DN. Comparative architectonic analysis of the human and the macaque frontal cortex. In: *Handbook of Neuropsychology,* edited by Boller F and Grafman J. Amsterdam: Elsevier, 1994, p. 17–58.

Picard N and Strick PL. Motor areas of the medial wall: a review of their location and functional activation. *Cereb Cortex* 6: 342–53, 1996.

Picard N and Strick PL. Imaging the premotor areas. *Curr Opin Neurobiol* 11: 663–72, 2001.

Preuss TM, Stepniewska I, and Kaas JH. Movement representation in the dorsal and ventral premotor areas of owl monkeys: a microstimulation study. *J Comp Neurol* 371: 649–676, 1996.

Puce A, Allison T, Bentin S, Gore JC, and McCarthy G. Temporal cortex activation in humans viewing eye and mouth movements. *J Neurosci* 18: 2188–2199, 1998.

Rizzolatti G and Arbib MA. Language within our grasp. *Trends Neurosci* 21: 188–194, 1998.

Rizzolatti G, Fadiga L, Gallese V, and Fogassi L. Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Res* 3: 131–141, 1996a.

Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, Perani D, and Fazio F. Localization of grasp representations in humans by PET. I. Observation versus execution. *Exp Brain Res* 111: 246–252, 1996b.

Rizzolatti G, Luppino G, and Matelli M. The classic supplementary motor area is formed by two independent areas. *Adv Neurol* 70: 45–56, 1996c.

Rushworth M, Ellison A, and Walsh V. Complementary localization and lateralization of orienting and motor attention. *Nat Neurosci* 4: 656–661, 2001a.

Rushworth M, Paus T, and Sipila PK. Attention systems and the organization of the human parietal cortex. *J Neurosci* 21: 5262–5271, 2001b.

Schaal S. Is imitation learning the route to humanoid robots? *Trends Cogn Sci* 3: 233–242, 1999.

Schofield WN. Do children find movements which cross the body midline difficult? *Q J Exp Psychol* 28: 571–582, 1976.

Seltzer B and Pandya DN. Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: a retrograde tracer study. *J Comp Neurol* 343: 445–463, 1994.

Shipp S, Blanton M, and Zeki S. A visuo-somatomotor pathway through superior parietal cortex in the macaque monkey: cortical connections of areas V6 and V6A. *Eur J Neurosci* 10: 3171–3193, 1998.

Sirigu A, Daprati E, Pradat-Diehl P, Franck N, and Jeannerod M. Perception of self-generated movement following left parietal lesion. *Brain* 122: 1867–1874, 1999.

Sirigu A, Duhamel J-R, Cohen L, Pillon B, Dubois B, and Agid Y. The mental representation of hand movements after parietal cortex damage. *Science* 273: 1564–1568, 1996.

Sperry RW. Neural basis of the spontaneous optokinetic response produced by visual inversion. *J Comp Physiol Psychol* 43: 482–489, 1950.

Stephan KM., Fink GR, Passingham RE, Silbersweig D, Ceballos-Baumann AO, Frith CD, and Frackowiak RS. Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J Neurophysiol* 73: 373–386, 1995.

Strafella AP, Paus T, Barrett J, and Dagher A. Repetitive transcranial magnetic stimulation of the human prefrontal cortex induces dopamine release in the caudate nucleus. *J Neurosci* 21: RC157, 2001.

Talairach J and Tournoux P. *Co-Planar Stereotaxic Atlas of the Human Brain.* New York: Thieme, 1988.

Tomaiuolo F, MacDonald JD, Caramanos Z, Posner G, Chiavaras M, Evans AC, and Petrides M. Morphology, morphometry and probability mapping of the pars opercularis of the inferior frontal gyrus: an in vivo MRI analysis. *Eur J Neurosci* 11: 3033–3046, 1999.

Tootell RB and Taylor JB. Anatomical evidence for MT and additional cortical visual areas in humans. *Cereb Cortex* 5: 39–55, 1995.

vvon Bonin G and Bailey P. *The Neocortex of Macaca Mulatta.* Urbana, IL: The University of Illinois Press, 1947.

Vorobiev V, Govoni P, Rizzolatti G, Matelli M, and Luppino G. Parcellation of human mesial area 6: cytoarchitectonic evidence for three separate areas. *Eur J Neurosci* 10: 2199–2203, 1998.

Wapner S and Cirillo L. Imitation of a model's hand movements: age changes in transposition of left-right relations. *Child Dev* 39: 887–894, 1968.

Watson JD., Myers R, Frackowiak RS, Hajnal JV, Woods RP, Mazziotta JC, Shipp S, and Zeki S. Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cereb Cortex* 3: 79–94, 1993.

Williams JH, Whiten A, Suddendorf T, and Perrett DI. Imitation, mirror neurons and autism. *Neurosci Biobehav Rev* 25: 287–295, 2001.

Woods RP, Dapretto M, Sicotte NL, Toga AW, and Mazziotta JC. Creation and use of a Talairach-compatible atlas for accurate, automated, nonlinear intersubject registration, and analysis of functional imaging data. *Hum Brain Map* 8: 73–79, 1999.

Woods RP, Grafton ST, Holmes CJ, Cherry SR, and Mazziotta JC. Automated image registration. I. General methods and intrasubject, intramodality validation. *J Comput Assist Tomogr* 22: 139–152, 1998a.

Woods RP, Grafton ST, Watson JD, Sicotte NL, and Mazziotta JC. Automated image registration. II. Intersubject validation of linear and nonlinear models. *J Comput Assist Tomogr* 22: 153–165, 1998b.

Woods RP, Iacoboni M, Grafton ST, and Mazziotta JC. Improved analysis of functional activation studies involving within-subject replications using a three-way ANOVA model. In: *Quantification of Brain Function Using PET*, edited by Myers R, Cunningham V, Bailey D, and Jones T. San Diego, CA: Academic, 1996, p. 353–358.