

Mirror Neuron System Differentially Activated by Facial Expressions and Social Hand Gestures: A Functional Magnetic Resonance Imaging Study

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Abstract

■ Facial expressions and hand gestures are utilized in nonverbal communication to convey socially relevant information. One key process that mediates nonverbal communication is simulation. The mirror neuron system (MNS), which maps observed actions onto the motor representations used when producing those actions, likely plays a role in simulation. Previous neuroimaging experiments have identified a putative human MNS that includes the inferior parietal lobule (IPL) and the frontal operculum. Although understanding nonverbal communication presumably involves the MNS, it is unknown whether these two forms of nonverbal social communication have distinct representations within that system. Here we report the results of a

functional magnetic resonance imaging experiment in which participants viewed, imitated, and produced facial expressions and social hand gestures. The observation and execution of facial expressions and social hand gestures activated the MNS, but the magnitude of response differed. Activation in the IPL was greater for social hand gestures, whereas activation in the frontal operculum was greater for viewing facial expressions. The locations of neural activity evoked by viewing facial expressions and social hand gestures in the frontal operculum were significantly different. These data argue that there are distinct representations of different types of social nonverbal communication in the MNS. ■

INTRODUCTION

In humans, the principal nonverbal gestures for conveying socially relevant information involve facial expressions and hand movements (Parr, Waller, & Fugate, 2005; Hobson, 1993). Investigators have argued that the understanding of actions of others is mediated by a common or overlapping representation for perception and action (Prinz, 1992; Bandura, 1977). A likely neural basis for the link between perception and action was discovered when mirror neurons, neurons that respond during both the observation and execution of an action, were found in the ventral premotor cortex (area F5) and the inferior parietal cortex of the macaque monkey (Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Cytoarchitectonic maps indicate that the likely human homologue for area F5 is the frontal operculum (Petrides & Pandya, 1994). Functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies suggest that the inferior parietal lobule (IPL) and the frontal operculum form a human mirror neuron system (MNS; Leslie, Johnson-Frey, & Grafton, 2004; Decety, Chaminade, Grezes, & Meltzoff, 2002; Iacoboni et al., 1999). Previous neurophysiological and neuroimaging studies have indicated that the superior temporal sulcus (STS) is involved in the perception of biological motion and, more broadly,

in the processing of social communication (Puce & Perrett, 2003; Allison, Puce, & McCarthy, 2000; Hoffman & Haxby, 2000; Perrett et al., 1985). There are direct anatomical connections between the STS and the IPL and between the IPL and F5, but not between the STS and area F5 (Rizzolatti, Fogassi, & Gallese, 2001). Thus, the STS, along with the MNS, forms a network of areas that play a central role in action understanding (Rizzolatti & Craighero, 2004; Bruce, Desimone, & Gross, 1981).

Previous microstimulation and single-unit recording studies demonstrated that area F5 contains both hand and mouth representations (Rizzolatti, Fadiga, Fogassi, & Gallese, 1999; Gentilucci et al., 1988; Rizzolatti et al., 1988; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981), but the representations are spatially distinct, with hand movement representations in dorsal F5 and mouth movement representations in ventral F5 (Rizzolatti et al., 1999). Previous mirror neuron studies only had found hand mirror neurons, but Ferrari and colleagues (2003) discovered mouth mirror neurons that responded during the observation and execution of mouth actions. Furthermore, a subset of these mouth mirror neurons were termed communicative mouth mirror neurons because they responded to the observation and execution of communicative actions, such as lip-smacking, that did not involve an object (Ferrari et al., 2003).

Humans use a wide range of facial expressions and social hand gestures to communicate and inform others

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of their mental states (Decety & Chaminade, 2003). Distinctions between the human MNS representation of facial expressions and social hand gestures are not well understood. Leslie et al. (2004) found more ventral activation in the frontal operculum for the imitation of facial expressions as compared to hand movements, but they did not find significant activation in the frontal operculum for the observation of either facial expressions or hand movements. Furthermore, other previous fMRI studies that have used facial expressions and nonsocial hand movements to investigate the MNS (Grosbras & Paus, 2006; Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003) did not examine social hand gestures or directly compare the representations of facial expressions and social hand gestures in the same participants.

We measured local hemodynamic responses with fMRI while participants viewed, imitated, and produced facial expressions and social hand gestures. We predicted that we would find significant responses in the MNS, but the representations of facial expressions and social hand gestures would be distinct, as indicated by differences in the distribution of neural activity in the MNS. In particular, we were interested in whether these two forms of social gestures have distinct representations in the frontal operculum, analogous to those found in the monkey (Rizzolatti & Craighero, 2004), as indicated by different locations of peak activity. The results confirmed this prediction.

METHODS

Participants

Twelve healthy participants (7 women), between 22 and 31 years of age, participated in the study. They gave

informed consent for participation in the study, which was approved by the Institutional Review Panel for Human Subjects of the Princeton University Research Board. The participants were paid for their participation. All participants were right-handed and had normal or corrected-to-normal vision.

Stimuli

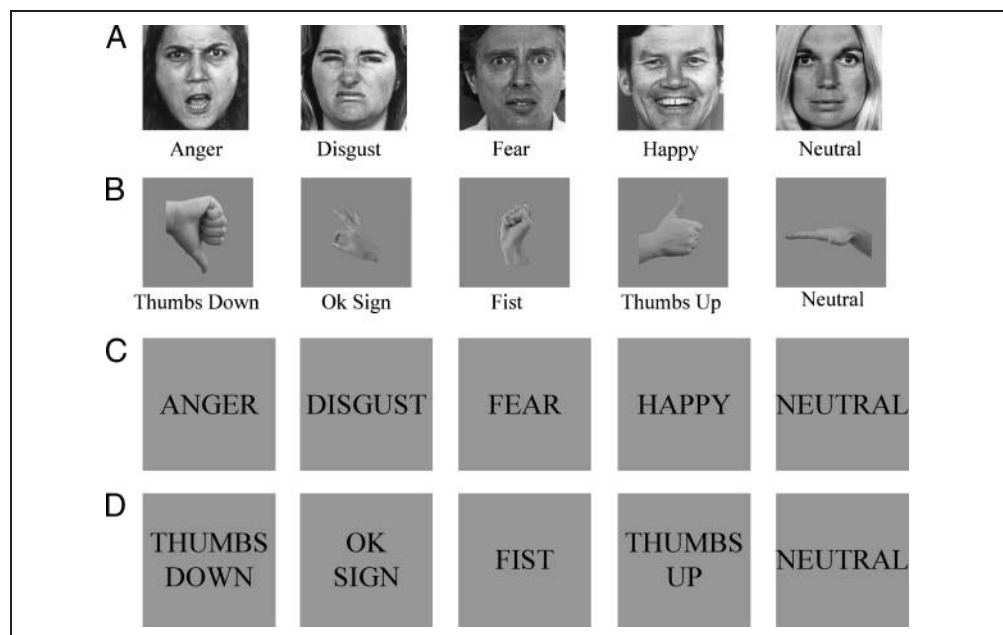
Stimuli were gray-scale pictures of facial expressions (anger, disgust, fear, happy, neutral), gray-scale pictures of social hand gestures (thumbs down, okay sign, fist, thumbs up, neutral), and word stimuli that described the facial expressions or social hand gestures (Figure 1). The facial expression stimuli were from 10 individuals (6 women) from the Pictures of Facial Affect (Ekman & Friesen, 1976). The social hand gesture stimuli were from 10 individuals (5 women) making the gestures with their right hand, cropped to show only the hand and the forearm. The word stimuli were presented as black text on a gray background. In total, there were 50 facial expression stimuli, 50 social hand gesture stimuli, and 10 word stimuli (5 to describe the facial expressions and 5 to describe the social hand gestures).

Stimuli were presented using SuperLab (Cedrus, San Pedro, CA) and were displayed to the participants in high resolution via an Epson 7250 LCD projector, projected through a wave guide into a small circular screen in the scanner bore. The participants viewed the images via a small mirror placed above their eyes.

Experimental Design

For each participant, we obtained 10 time series, 5 for facial expressions and 5 for social hand gestures. During

Figure 1. Facial expression and social hand gesture stimuli. (A) Examples of facial expression stimuli that show four emotions (anger, disgust, fear, happy) and a neutral expression. (B) Examples of social hand gesture stimuli that show four gestures (thumbs down, okay sign, fist, thumbs up) and a neutral hand position. (C) The five word stimuli that describe the facial expressions. (D) The five word stimuli that describe the social hand gestures.



each time series, there were three conditions: passive viewing of the facial expressions or social hand gestures, imitating the viewed facial expression or social hand gesture, and producing facial expressions or social hand gestures in response to a word stimulus that described the action. In the passive viewing condition, participants viewed the pictures of facial expressions or social hand gestures. During the imitation condition, participants would imitate the facial expression or social hand gesture seen in the observed picture. Finally, during the production condition, participants would see a word or phrase describing the facial expression or social hand gesture and would produce the action described. For the neutral facial expression and social hand gesture, the participants were instructed not to make a movement. In response to the neutral facial expression, participants maintained a neutral facial expression, and to the neutral social hand gesture, participants kept their hand at their side. Every time series had six blocks with two blocks for each condition. The blocks were 49.5 sec in duration and began with a 2-sec cue that indicated the condition type, followed by five items. Each item consisted of a 2-sec stimulus followed by a 7.5-sec period of a blank gray screen. During the imitation and production conditions, the participant performed the action during the 2-sec stimulus period and returned to a neutral, nonmoving position during the 7.5-sec pause between stimuli. Each time series began and ended with a 20-sec period of a blank gray screen. In addition, there were 10-sec periods of a blank gray screen between blocks. Each time series had a duration of 6 min and 27 sec. Both the order of blocks and of the time series were counterbalanced and pseudorandomized across participants. Due to a technical problem, only nine time series for one of the participants were analyzed.

During two of the three conditions, the participants made facial and hand movements during fMRI scanning, which could introduce changes in the magnetic field. Motion produces an immediate change to the magnetic field leading to signal changes, whereas the blood oxygenation level-dependent (BOLD) signal is delayed and peaks approximately 4 to 6 sec after stimulus presentation (Birn, Bandettini, Cox, & Shaker, 1999; Friston, Jezzard, & Turner, 1994). To distinguish BOLD MR signal changes from movement-related artifacts, each stimulus was followed by a 7.5-sec pause when the participant was not making any movement. Consequently, the fast changes in the magnetic field linked with brief movements could be distinguished from the slow hemodynamic responses related to brain activity.

Participants were trained before the scanning session to familiarize themselves with the conditions and stimuli and to ensure accurate performance.

Data Acquisition and Analyses

MRI scanning was performed using a 3-T head scanner (Allegra, Siemens, Erlangen, Germany) with a standard

birdcage head coil. Functional images were taken with a gradient-echo echo-planar imaging (EPI) sequence (TR = 2000 msec, TE = 30 msec, FoV = 192 mm, flip angle = 90°, 64 × 64 matrix). Thirty-two axial slices that covered most of the brain were obtained (thickness = 3 mm; gap = 1 mm; in-plane resolution = 3 × 3 mm). For each time series, a total of 188 EPI volume images were acquired. A high-resolution anatomical scan of the whole brain (T1-MP-RAGE, 256 × 256 matrix, TR = 2500 msec, TE = 4.3, flip angle = 8°) was acquired in the same session for anatomical localization and spatial normalization.

Data were analyzed using AFNI (Cox, 1996). Prior to statistical analysis, images were motion corrected to the fifth volume of the first EPI time series and smoothed with a 6-mm full-width half-maximum 3-D Gaussian filter. The first four images of each time series were excluded from analysis. Images were analyzed using a voxelwise multiple regression with square wave functions reflecting each condition (facial expression view, imitate, do; social hand gesture view, imitate, do), which were convolved with a Gamma function model of the hemodynamic response to reflect the time course of the BOLD signal. In addition, unconvolved square wave functions for each condition were included as regressors of noninterest to account for changes in the magnetic field associated with the hand or face movements (see Supplementary Figure 1 for an illustration of the predicted nonoverlapping signal changes that were modeled by the regressors that modeled the changes in magnetic field and the condition regressors). Additional regressors of noninterest were used to factor out variance due to overall motion of the participant between time series, as well as regressors accounting for mean, linear, and quadratic trends within the time series. Thus, the multiple regression analysis models included six regressors of interest, six regressors to account for changes in the magnetic field introduced by the execution of face and hand movements, a regressor for the condition cue, six regressors for head movement (roll, pitch, yaw, x , y , and z) from the motion correction program, and 30 regressors that accounted for mean, linear, and quadratic trends. The multiple regression model results identified the areas that were activated for each condition compared to baseline. The beta coefficients for each regressor of interest were normalized to the mean baseline response, which was found by calculating the mean activity for the baseline periods between each condition, and converted to percent signal change maps. The percent signal change maps for each individual participant were converted into Talairach space for group analysis (Talairach & Tournoux, 1988). A mixed effects analysis of variance (ANOVA) was performed to obtain group results. Regions that were activated significantly by the perception and production of actions were identified based on the response during imitation, using a threshold of $p < .001$ (uncorrected)

and a cluster size of 20 voxels (540 mm³) (Tables 1 and 2). To examine activity during observation or execution alone, we tested the significance of the response during the view and do conditions in the peak voxel for the imitate condition.

For the analyses of mean responses, we used the significantly responsive voxels in anatomically defined volumes of interest (VOIs) that were drawn on high-resolution structural images. We drew VOIs to identify the three areas for which we had specific hypotheses: the STS, the IPL, and the frontal operculum (Supplemental Figure 2). The STS VOI included the STS and the superior temporal gyrus (BA 22) and extended from 60 to 10 mm posterior to the anterior commissure in Talairach and Tournoux (1988) brain atlas coordinates. The VOI for the IPL extended from 60 to 24 mm posterior to the anterior commissure and included the intraparietal sulcus and supramarginal gyrus (BA 40). The VOI for the frontal operculum extended from 8 to 32 mm anterior to the anterior commissure and included the pars opercularis and pars triangularis (BA 44 and BA 45). The VOIs were transformed into each participant's native

space and voxels within these VOIs that were significantly responsive to any of the experimental conditions determined by an omnibus general linear test at $p < .0001$ were identified in each individual.

Mean responses in all activated voxels within a given VOI in each individual participant were computed by averaging across the condition blocks of motion corrected, detrended raw time signals. The average number of activated voxels (1 mm³) was 158 ($SE = 36$) in the bilateral STS, 472 ($SE = 100$) in the bilateral IPL, and 191 ($SE = 44$) in the bilateral frontal operculum. The magnitudes were computed as the average response from 2 to 8 sec (3 time points) after stimulus onset. Thus, the data acquisition window was centered on the 5-sec poststimulus onset period after excluding the first 2 sec, which included the motion artifact. ANOVAs were performed to determine whether there was a main effect of stimulus type (facial expressions and social hand gestures) in each of the three VOIs. ANOVAs also were performed to test whether there was a main effect of task (view, imitate, and do) for each stimulus type independently in each of the three VOIs.

Table 1. Coordinates and Statistics for Activation Evoked during Viewing, Imitating, and Producing Facial Expressions

<i>Brain Region</i>	<i>Talairach Coordinates</i>	<i>t Value for View</i>	<i>t Value for Imitate</i>	<i>t Value for Do</i>
Primary motor cortex, BA 4	RH: 49, -8, 41	2.37*	6.23***	5.72***
	LH: -51, -8, 40	2.38*	6.65***	4.47***
Primary somatosensory cortex, BA 3	RH: 47, -19, 42	2.66*	3.33**	3.54**
	LH: -45, -19, 39	4.16**	6.57***	5.01***
Premotor cortex, BA 6	RH: 46, 2, 30	3.30**	6.16***	5.89***
	LH: -51, 3, 25	2.42*	5.98***	5.75***
Frontal operculum, BA 44	RH: 44, 15, 7	2.99*	6.95***	6.94***
	LH: -45, 15, 7	2.87*	7.05***	6.79***
Inferior parietal lobe, BA 40	RH: 45, -40, 41	2.42*	5.78***	4.92***
	LH: -33, -49, 41	2.49*	5.82***	3.34**
Superior temporal sulcus, BA 22	RH: 53, -37, 5	4.44***	6.87***	6.19***
	LH: -52, -51, 4	2.29*	3.76**	3.94**
Fusiform gyrus, BA 37	RH: 36, -51, -17	10.67***	10.67***	5.93***
	LH: -37, -66, -15	5.91***	5.50***	5.08***
Middle occipital gyrus, BA 19/37	RH: 43, -69, 5	3.90**	4.70***	5.23***
	LH: -48, -69, 3	3.58**	4.62***	4.66***
Insula	RH: 35, 3, 9	<i>ns</i>	4.76***	4.70***
	LH: -38, 4, 10	<i>ns</i>	6.15***	6.44***

BA = Brodmann's area; RH = right hemisphere; LH = left hemisphere; *ns* = not significant.

* $p < .05$.

** $p < .01$.

*** $p < .001$.

Table 2. Coordinates and Statistics for Activation Evoked during Viewing, Imitating, and Producing Social Hand Gestures

<i>Brain Region</i>	<i>Talairach Coordinates</i>	<i>t Value for View</i>	<i>t Value for Imitate</i>	<i>t Value for Do</i>
Primary motor cortex, BA 4	LH: -32, -22, 64	<i>ns</i>	7.07***	6.97***
Primary somatosensory cortex, BA 3	LH: -37, -31, 58	<i>ns</i>	7.74***	7.44***
Premotor cortex, BA 6	RH: 50, 3, 32	2.41*	5.83***	4.61***
	LH: -54, 2, 30	<i>ns</i>	4.96***	4.64***
Frontal operculum, BA 44	RH: 51, 6, 13	2.26*	6.22***	6.00***
	LH: -52, 3, 15	2.25*	6.34***	6.60***
Inferior parietal lobe, BA 40	RH: 50, -40, 45	2.58*	6.08***	5.53***
	LH: -35, -40, 46	2.51*	8.83***	7.96***
Superior temporal sulcus, BA 22	RH: 46, -44, 3	3.41**	6.28***	6.05***
	LH: -52, -48, 6	2.51*	4.20**	4.57***
Fusiform gyrus, BA 37	RH: 42, -59, -11	7.78***	6.41***	5.62***
	LH: -44, -51, -14	5.17***	5.74***	4.21**
Middle occipital gyrus, BA 19/37	RH: 43, -69, 2	6.65***	6.81***	5.54***
	LH: -49, -69, 3	5.21***	6.64***	5.39***
Insula	RH: 39, 3, 7	<i>ns</i>	6.54***	5.84***
	LH: -38, 4, 10	<i>ns</i>	5.63***	7.15***

BA = Brodmann's area; RH = right hemisphere; LH = left hemisphere; *ns* = not significant.

* $p < .05$.

** $p < .01$.

*** $p < .001$.

Individual comparisons from significant main effects were tested with matched paired t tests. In addition, a comparison was performed between viewing facial expressions and social expressions due to an a priori hypothesis.

To test whether the locations of peak responses in the three regions were significantly different for facial expressions and social hand gestures, we found the locations of the peak responses to the viewing condition in the STS, IPL, and frontal operculum in each individual participant. In all cases, the voxel with the most significant response during the viewing condition also was activated during imitation and production, the conditions of execution. The viewing condition was selected to ensure that the individual peak selected reflected a voxel that was activated during observation and execution, instead of a voxel only activated during the execution conditions. Differences in location in the x , y , z dimensions were evaluated by t tests.

RESULTS

We found significant activations in the STS, IPL, and frontal operculum in all conditions (Figure 2; Tables 1 and 2).

Differences in Magnitude of Response

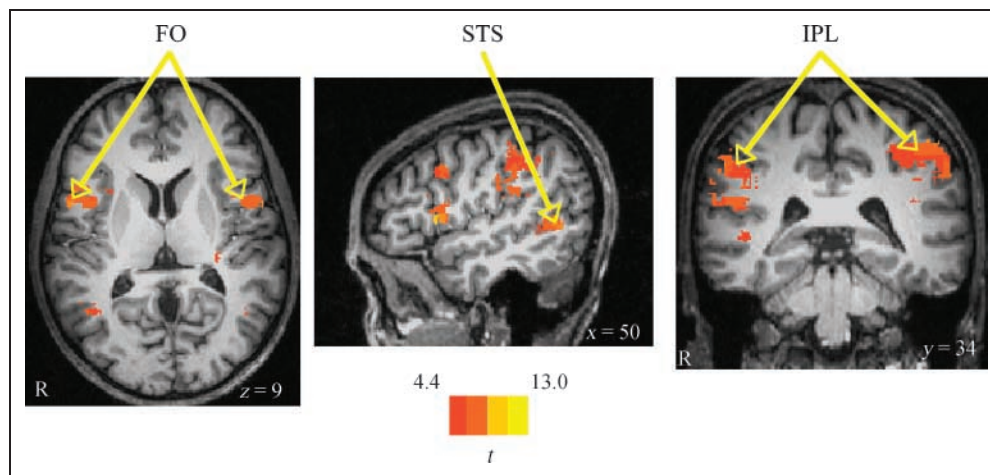
STS Activity

We did find significant differences between the responses in the STS to facial expressions and social hand gestures for the conditions based on the analysis of mean responses of individual responses [$F(1, 107) = 6.80, p < .05$] (Figure 3). There was a significant effect for task for facial expressions [$F(2, 35) = 6.65, p < .01$] and social hand gestures [$F(2, 35) = 3.37, p < .05$]. For facial expressions, there was a significantly greater response for imitating and producing than for viewing ($p < .01$). We did not find any significant differences between the imitation and production conditions. For social hand gestures, there was a significantly greater response for producing than viewing and imitating ($p < .05$). We did not find any significant differences between the view and imitation conditions. The regional analysis revealed a right hemisphere advantage with a larger volume of activated voxels (110 vs. 59) in the right STS as compared to the left ($p < .05$).

IPL Activity

There was a significant difference between the responses in the IPL to social hand gestures and facial expressions [$F(1, 107) = 11.57, p < .001$] (Figure 3). There was a

Figure 2. Significant activity in the MNS during imitation of facial expressions and social hand gestures as compared to baseline activity. Group data ($n = 12$) from a mixed effects ANOVA has been overlaid on a single participant's high-resolution anatomical scan. Significance was determined to be at a level of $p < .001$, uncorrected for multiple comparisons and a cluster size of 20 voxels (540 mm^3). The locations of activation in the STS, IPL, and frontal operculum (FO) are indicated.



significant effect for task for facial expressions [$F(2, 35) = 5.53, p < .01$] and social hand gestures [$F(2, 35) = 13.35, p < .001$]. For facial expressions and social hand gestures, there was a significantly greater response for imitating and producing than for viewing, but imitating and producing were not significantly different from one another ($p < .01$). Although small, however, even the response to viewing facial expressions was significantly greater than baseline activity, as defined by average activity to the periods of gray blank screen ($p < .01$) (Figure 3). The regional analysis revealed a left hemisphere advantage with a large volume of activated voxels (348 vs. 257) ($p < .05$).

Frontal Operculum Activity

The responses in the frontal operculum were significantly different for facial expressions and social hand gestures [$F(1, 107) = 6.62, p < .05$] (Figure 3). There was a significant effect for task for facial expressions [$F(2, 35) = 12.31, p < .001$] and social hand gestures [$F(2, 35) = 11.87, p < .001$]. The response during viewing social hand gestures was small, but nonetheless, significantly greater than baseline activity, as defined by average activity to the periods of gray blank screen in both the voxelwise analysis (Table 2) and the mean response analysis (Figure 3) ($p < .05$, in both cases). For facial expressions, there were significant differences among all conditions ($p < .05$). For social hand gestures, the response in the frontal operculum during viewing was significantly less than the responses during both imitating and producing ($p < .001$), but imitating and producing were not significantly different from each other. The volumes of activated voxels in the right and left frontal operculum were not significantly different.

Differences in Peak Location

We found significant differences in the peak locations for viewing facial expressions and social hand gestures in the IPL and in the frontal operculum.

Superior Temporal Sulcus

There were no significant differences in the location of peak responses in the STS for viewing facial expressions and social hand gestures (Table 3).

Inferior Parietal Lobule

We found small differences in the locations for the peak responses for viewing facial expressions and social hand gestures in the IPL (Table 3). For the observation of social hand gestures, one participant did not have significant activation in the IPL. The mean peak location for viewing facial expressions in the left IPL was more inferior to the location of the peak response for viewing social hand gestures ($p < .05$) (Table 3). The mean peak location for viewing facial expressions in the right IPL was significantly more medial than the location of the peak response for viewing social hand gestures ($p < .05$).

Frontal Operculum

We found consistent differences in the locations of the peak responses for facial expressions and social hand gestures in the frontal operculum. The location of the peak response for the facial expressions was more anterior and inferior to the location of the peak response for the social hand gestures in both the left and right frontal operculum (Figure 4 and Table 3). For viewing of facial expressions, two participants only had unilateral responses that reached significance. For viewing of social hand gestures, one of those participants with unilateral response for viewing facial expressions, along with another participant, did not have significant activation in the frontal operculum. The location of the mean peak for viewing facial expressions in the left hemisphere was significantly more medial, anterior, and inferior than the location of the peak response for viewing social hand gestures ($p < .05$, in all dimensions) (Table 3). The

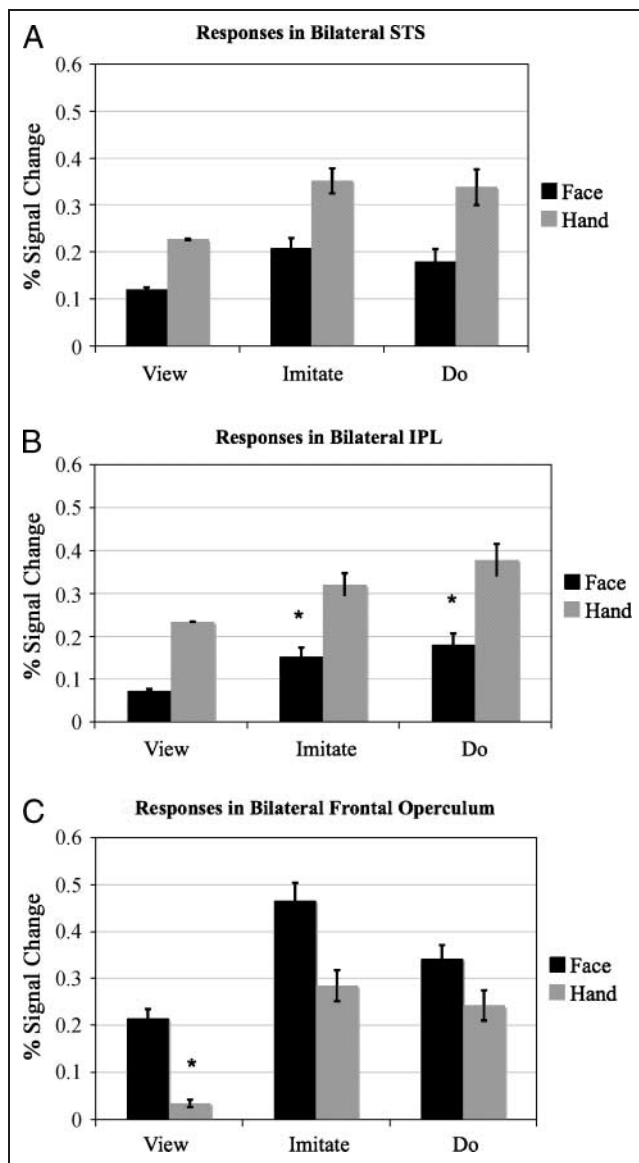


Figure 3. Mean responses in the MNS. (A). Mean responses in the bilateral STS. For facial expressions, there was a significant difference between viewing and imitating and viewing and producing ($p < .01$), but no significant difference between imitating and producing. For social hand gestures, there was a significant difference between producing and imitating and producing and viewing ($p < .05$), but no significant difference between viewing and imitating. (B). Mean responses in the bilateral IPL. For facial expressions and social hand gestures, there was a significant difference between viewing and imitating and viewing and producing ($p < .01$), but no difference in response between imitating and producing. There were significant differences in the responses between facial expressions and social hand gestures in the imitation condition ($p < .01$). (C). Mean responses in the bilateral frontal operculum. For facial expressions, there was a significant differential response for all conditions ($p < .05$). For social hand gestures, there was a significant difference between viewing and imitating and viewing and producing ($p < .001$), but no significant difference between imitating and producing. There were significant differences in the responses between facial expressions and social hand gestures in the viewing condition ($p < .05$).

location of the mean peak for viewing facial expressions in the right hemisphere was significantly more anterior and inferior than the location of the peak response for viewing social hand gestures ($p < .001$, in both dimensions). Additionally, there was a trend in the right hemisphere for the location of the mean peak location for viewing facial expressions to be more medial than the location of the peak response for viewing social hand gestures ($p = .06$). The distinct representations for facial expressions and social hand gestures in the frontal operculum also are reflected during imitation in the group data (Tables 1 and 2).

Activation Outside the Mirror Neuron System

We also examined differences between the responses to facial expressions and social hand gestures outside the VOIs.

Insula

We found significant activation in the insula during the imitation and production of both facial expressions and social hand gestures (Tables 1 and 2). There was no significant difference in activation in the insula across stimuli type ($p = .21$).

Perceptual Areas

In perceptual areas, we found a stronger response to facial expressions than to social hand gestures in the fusiform gyrus (30, -56, -19 and -36, -56, -18), close to the coordinates reported for the fusiform face area (FFA) (Kanwisher, McDermott, & Chun, 1997) and, by contrast, a stronger response to social hand gestures than facial expressions in the lateral occipito-temporal cortex (48, -60, 1 and -50, -67, 5), close to the coordinates reported for the extrastriate body area (EBA) (Downing, Jiang, Shuman, & Kanwisher, 2001). Both types of stimuli resulted in significant activations in these regions, but the response in the fusiform gyrus was greater for viewing and imitating facial expressions as compared to social hand gestures, and the response in the lateral occipito-temporal cortex was greater for viewing and imitating social hand gestures as compared to facial expressions (Figure 5). When participants produced the facial expressions or social hand gestures without seeing them, there was significant activation in these regions, but the difference between facial expressions and social hand gestures was not significant.

Primary Motor Areas

We also found greater activity for the facial expressions in the face/mouth region of the bilateral precentral gyrus and greater activity for the social hand gestures in the

Table 3. Mean (*SEM*) Locations of Peak Responses for Facial Expressions and Social Hand Gestures in the Mirror Neuron System

Area	Facial Expressions	Social Hand Gestures
Frontal operculum	RH: 47 (1), 18 (1), 7 (0.3) LH: -52 (1), 13 (1), 7 (0.5)	RH: 51 (1), 7 (1), 12 (1) LH: -55 (1), 7 (1), 12 (1)
Inferior parietal lobe	RH: 37 (2), -49 (3), 41 (1) LH: -39 (2), -50 (2), 40 (1)	RH: 39 (2), -39 (9), 44 (0.5) LH: -40 (3), -50 (3), 42 (1)
Superior temporal sulcus	RH: 53 (1), -37 (2), 3 (1) LH: -52 (1), -43 (2), 5 (1)	RH: 42 (9), -37 (2), 3 (1) LH: -52 (1), -40 (2), 3 (2)

RH = right hemisphere; LH = left hemisphere.

hand region of the left precentral gyrus (Figure 5). Significant activation in the precentral gyrus was found both when participants imitated the facial expressions and social hand gestures and when participants produced the facial expressions and social hand gestures without viewing them. Significant activation was found when the participants viewed facial expressions, but not when participants viewed social hand gestures.

DISCUSSION

We investigated the differences in the representation of facial expressions and social hand gestures in the STS and MNS by examining the distribution of neural activity evoked by the perception and performance of these actions. We found greater responses in the IPL for social hand gestures as compared to facial expressions and

greater responses in the frontal operculum for viewing facial expressions as compared to social hand gestures; responses in the STS were equivalent for facial expressions and social hand gestures. Additionally, we found significant differences in the locations of the peak responses for facial expressions and social hand gestures in the frontal operculum, suggesting distinct representations.

The STS was significantly activated during viewing, imitation, and production of facial expressions and social hand gestures. Both neurophysiological and neuroimaging studies have suggested that the STS is involved in the perception of biological movement, including facial and hand movements (Puce & Perrett, 2003; Allison et al., 2000; Jellema, Baker, Wicker, & Perrett, 2000; Perrett et al., 1985). We found bilateral STS activity that was stronger in the right hemisphere, which is consistent with previous findings on the perception of biological motion (Pelphrey et al., 2003).

We found significant STS activity during the production of facial expressions and social hand gestures without the perception of the actions. This finding raises the question of whether the STS is involved only in the visual perception of action or in both the perception and execution of action. To our knowledge, there are no reports from single-unit recordings in monkey cortex of STS neurons that respond to an action when the monkey cannot see the action that is being produced. Neuroimaging results suggest that the STS responds to the imagery of biological motion (Grossman & Blake, 2001). STS activity during the production of facial expressions and social hand gestures, therefore, may be due to imagery of the movements that are being produced. However, if the response during execution alone was due to imagery, we would expect that response to be smaller than the response for viewing or imitating because studies of imagery have found a weaker response for imagery than for perception (Ishai, Haxby, & Ungerleider, 2002; O'Craven & Kanwisher, 2000). In our experiment, however, the response during production was stronger than the response during perception, which suggests that imagery, by itself, is an unlikely explanation for this activity. Another possible explanation

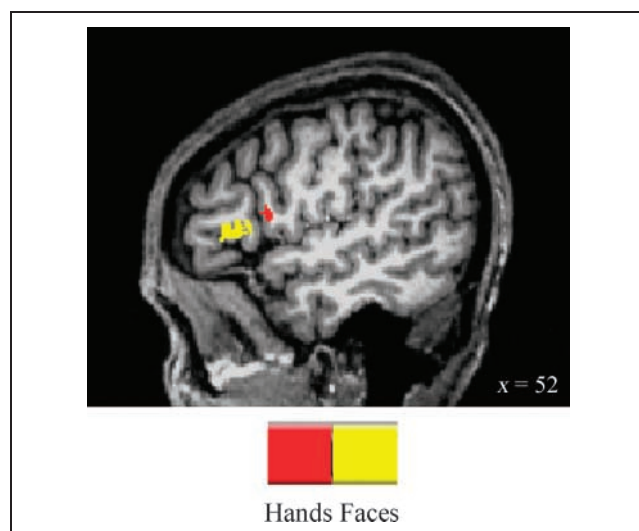


Figure 4. Significant difference in the locations for the peak response during viewing facial expressions and social hand gestures in the frontal operculum. In the frontal operculum, the location of the peak response for viewing facial expressions was anterior and inferior to the location of the peak response for viewing social hand gestures. The difference was found in both hemispheres, but the right hemisphere is shown.

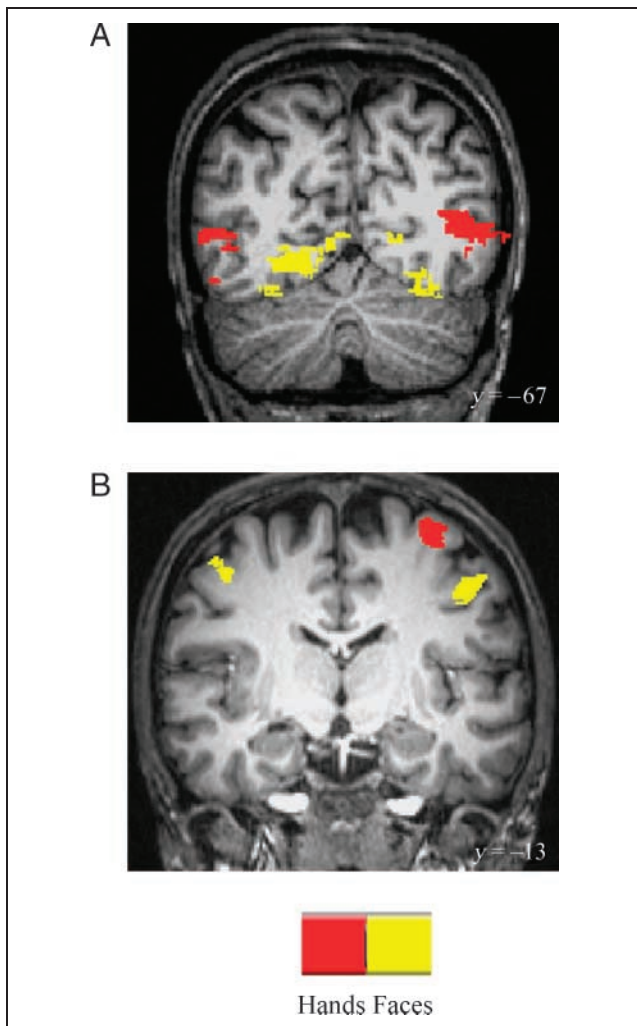


Figure 5. Differential responses outside of the MNS. (A). Differential activation in perceptual areas during viewing facial expressions and social hand gestures. In coordinates close to that of the FFA, there was a larger response for viewing facial expressions compared to social hand gestures seen in yellow ($p < .01$, uncorrected). In coordinates close to that of the EBA, there was a larger response for viewing social hand gestures compared to facial expressions illustrated in red ($p < .01$, uncorrected). (B). Differential activation in the precentral gyrus during imitation of facial expressions and social hand gestures. There was greater activity in the face/mouth region of the bilateral precentral gyrus for facial expressions seen in yellow and a more dorsal, hand region of the left precentral gyrus for social hand gestures seen in red ($p < .005$, uncorrected).

is that STS activity could be driven by the MNS, which is connected to the STS (Rizzolatti et al., 2001). We found greater activation in the STS while imitating actions as compared to viewing actions, suggesting augmentation by feedback derived from motor-related activity. Iacoboni et al. (2001) also found stronger activation in the STS during the imitation of actions as compared to the viewing of actions. If the response in the production condition were due only to feedback, however, we would expect the response to be smaller than in the imitation condition, which contains the perceptual re-

sponse along with feedback related activity. Because the production response is equal to that of imitation, it is unlikely that it is due solely to imagery or feedback, but may reflect both.

There was significant bilateral IPL activity during viewing, imitating, and producing facial expressions and social hand gestures. The significant response in the IPL to the observation and execution of action is consistent with the finding of mirror neurons in the posterior parietal lobe and with previous neuroimaging reports finding IPL activity during imitation tasks (Montgomery, Isenberg, & Haxby, 2007; Fogassi et al., 2005; Buccino et al., 2004; Decety et al., 2002; Iacoboni et al., 1999). We found greater responses in the bilateral IPL to social hand gestures than to facial expressions in all conditions. The stronger IPL activation to social hand gestures is consistent with the patient literature linking parietal damage, typically left hemisphere damage, to hand and finger imitation deficits (Goldenberg & Hermsdorfer, 2002; Goldenberg, 1999) and with previous neuroimaging studies that found less activation in the IPL for face stimuli (Dapretto et al., 2006; Carr et al., 2003). Activity in the IPL was stronger in the left hemisphere, which agrees with the patient literature and with a recent fMRI study investigating gesture imitation, which concluded that activity in the IPL was strongly left lateralized (Muhlau et al., 2005). One hypothesis for the role of the IPL in the MNS is that the IPL may be part of a route from visual perception to motor action where perceptual information about the action is coded according to the body parts needed to produce the action (Goldenberg & Hermsdorfer, 2002). Our results are in agreement with this hypothesis and with previous evidence suggesting that the IPL is an integral part of the MNS.

We found significant activity in the frontal operculum during all conditions, consistent with previous work (Montgomery et al., 2007; Iacoboni et al., 1999; Gallese et al., 1996). We found a greater response during viewing facial expressions than viewing social hand gestures. Faces are one of the most salient visual stimuli for people, and facial expressions elicit automatic mimicry (Dimberg, Thunberg, & Elmehed, 2000). Additionally, this difference in observation activation may be due to the increased emotional intensity of the facial expression stimuli as compared to the social hand gesture stimuli. Lotze et al. (2006) found significantly more activation in the frontal operculum for the observation of expressive gestures as compared to isolated hand actions or body referred actions. Our results suggest that facial expression stimuli may be more effective in recruiting the MNS than still pictures of social hand gestures, but further research is needed to understand the role that emotion intensity may play.

In the frontal operculum, we found significant differences in the locations of peak responses for facial expression and social hand gestures suggesting distinct

representations. Our results are consistent with the finding that mirror neurons that respond to hand and mouth actions are in different locations of area F5 in the macaque monkey (Rizzolatti & Craighero, 2004). Previous neuroimaging experiments have suggested somatotopic organization in premotor and parietal areas as indicated by activity evoked by viewing mouth, hand, and foot movements (Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004; Buccino et al., 2001), by listening to sentences describing actions made with the mouth, hand, or foot (Tettamanti et al., 2005), or by viewing neutral and angry hand and face actions (Grosbras & Paus, 2006). Our findings, however, suggest distinct representations within the frontal operculum, which is more consistent with studies in nonhuman primates that found different populations of mirror neurons for processing hand and mouth actions within area F5 (Rizzolatti & Craighero, 2004). Previous fMRI studies have described distinctions within the premotor cortex (Brodmann's area 6) (Buccino et al., 2001), but not within the frontal operculum (Brodmann's area 44).

Outside of the MNS, we found significant activation in the insula for imitation and production of facial expressions and social hand gestures and perceptual areas that showed different responses to face and hand stimuli. Carr et al. (2003) previously reported significant activation in the insula during the observation and imitation of facial expressions. In this study, we found significant activation in the insula during the imitation and production conditions of facial expressions and social hand gestures, but did not find significant activation in the insula to the observation of either facial expressions or social hand gestures. Although Carr and colleagues found significant activation during observation, the activation during imitation was much stronger. Our finding supports the hypothesis that the insula might be an important connection between action and emotion areas during action, but more studies are needed to understand the role of the insula as a relay between action and emotion areas during observation of actions.

Previous neuroimaging experiments have suggested that areas in the ventral visual stream respond differentially to object categories (Downing et al., 2001; Haxby et al., 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher et al., 1997). In this experiment, we found greater activity in the fusiform gyrus, close to the coordinates reported for the FFA (Kanwisher et al., 1997), during the observation and imitation of facial expressions as compared to social hand gestures. Although weaker, the finding of significant activation in the FFA for hand gesture stimuli is consistent with previous neuroimaging studies (Kanwisher et al., 1997). Additionally, we found stronger activity in a region in the human lateral occipito-temporal cortex, close to the coordinates reported for the EBA (Downing et al., 2001), for the observation and imitation of social hand gestures as compared to facial expressions. We found an

increase of activation in the EBA during the execution of actions, not just the perception, which is in agreement with an fMRI report that found that the EBA responded during both the perception and the execution of limb movements (Astafiev, Stanley, Shulman, & Corbetta, 2004).

In the precentral gyrus, we found bilateral activation in the ventral precentral gyrus when participants imitated and produced facial expressions and in a more dorsal location in the left precentral gyrus when participants imitated and produced social hand gestures. These differences agree with the classic somatotopic organization of the motor cortex (Penfield & Rasmussen, 1950). At a lower threshold, we did find significant primary motor activation for viewing of facial expressions, but not for viewing social hand gestures. The lack of primary motor activation while viewing social hand gestures could be due to the use of static stimuli.

We found significant activation in the STS and the MNS during the observation, imitation, and execution of facial expressions and social hand gestures supporting the hypothesis that this action understanding network in the human brain plays a role in social nonverbal communication. Although the MNS responds to actions conveying social nonverbal communication, there are differences in both the magnitudes and locations of responses depending on whether the social nonverbal communication is conveyed by a facial expression or social hand gesture. It has been argued that mirror neurons are the neural mechanism that underlies action understanding (Rizzolatti & Craighero, 2004). Because humans are social beings, action understanding plays a crucial role in social communication. Whether the MNS is critical for effective social communication and social skills more broadly has not been established, but recent studies have suggested that autism, a neurodevelopmental disorder characterized by marked dysfunction in social communication, is associated with a deficit in the MNS (Oberman & Ramachandran, 2007; Dapretto et al., 2006; Hadjikhani, Joseph, Snyder, & Tager-Flusberg, 2006; Iacoboni & Dapretto, 2006; Isenberg, Montgomery, Neuberger, & Haxby, 2005; Oberman et al., 2005; Theoret et al., 2005).

Acknowledgments

We thank A. D. Engell, M. I. Gobbini, N. Isenberg, S. Kastner, and M. A. Pinsk for valuable discussions, and S. T. Fiske, J. Kirkland, S. Klockner, and M. W. Roche for comments on versions of the manuscript. This study was supported by Princeton University and a National Alliance for Autism Research (NAAR) predoctoral fellowship to K. J. M., and an American Association of University Women (AAUW) dissertation fellowship to K. J. M.

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