

Functional imaging of face and hand imitation: towards a motor theory of empathy

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Empathy requires the ability to map the feelings of others onto our own nervous system. Until recently, there was no plausible mechanism to explain how such a mapping might occur. The discovery of mirror neurons, however, suggests that the nervous system is capable of mapping the observed actions of others onto the premotor cortex of the self, at least for reaching and grasping movements. Is there a mirroring system for emotive actions, such as facial expression? Subjects ($N = 15$; all right-handed; eight men, seven women) watched movies of facial expressions (smile or frown) and hand movements (move index or middle finger) while brain activity was imaged using functional magnetic resonance imaging (fMRI). Subjects watched the movies under three different conditions: passive viewing, active imitation, and an active motor control. Subjects also performed a verb generation task to functionally identify language-processing areas. We found evidence for a common cortical imitation circuit for both face and hand imitation, consisting of Broca's area, bilateral dorsal and ventral premotor areas, right superior temporal gyrus (STG), supplementary motor area, posterior temporo-occipital cortex, and cerebellar areas. For faces, passive viewing led to significant activation in the right ventral premotor area, whereas imitation produced bilateral activation. This result is consistent with evidence for right hemisphere (RH) dominance for emotional processing, and suggests that there may be a right hemisphere mirroring system that could provide a neural substrate for empathy.

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Introduction

How do we understand the emotional experiences of others? Lipps (1903) proposed an “imitative drive” that leads us to automatically imitate the facial expression of another, retrieve the associated emotion, and attribute that emotion to the other individual. There is good evidence for the ubiquity of unconscious mimicry: measures of electromyographic (EMG) activity show that

people rapidly and unconsciously imitate the facial expressions of others, even when the presentation of these faces is not consciously perceived (Dimberg and Thunberg, 1998; Dimberg et al., 2000). Social psychological studies show that the mere perception of another's behavior seems to increase the likelihood of engaging in that behavior (Bargh et al., 1996). This phenomenon, dubbed the chameleon effect, refers to the unconscious tendency to mimic the postures, mannerisms, and facial expressions of one's interaction partners. Unconscious mimicry has even been shown to facilitate the smoothness of interactions and increase liking between interaction partners (Chartrand and Bargh, 1999). And people who are high-scorers on empathy tests are more likely to exhibit the chameleon effect (Chartrand and Bargh, 1999; Sonnyby-Borgström, 2002). Unconscious mimicry could lead to an empathic response by biasing the facial motor system, which has been shown to influence mood (Ekman et al., 1983; Levenson et al., 1990). Together, these results suggest that there may be a seamless integration among perception, socially relevant mimicry, emotional experience, and empathy.

The discovery of mirror neurons (Gallese et al., 1996; Rizzolatti et al., 1996) has led to new speculation regarding the neural basis of empathy (Carr et al., 2003; Preseton and de Waal, 2002). Mirror neurons were first identified in area F5c of the monkey brain and have the unusual property of firing during both action execution and action observation (this is known as motor resonance or mirroring; for a review, see Rizzolatti et al., 2002). Mirror neurons have been identified in monkeys in response to the production and observation of reaching and grasping relevant objects, such as food, with the hands (Gallese et al., 1996; Rizzolatti et al., 1996) and mouth (Ferrari et al., 2003). There is even evidence for mirror neuron activity associated with communicative mouth gestures in monkeys, that is, lip smacking (Ferrari et al., 2003). Mirror neurons also appear to be multimodal and respond to both the visual observation of an action as well as the sounds associated with specific actions, for example, tearing of paper (Kohler et al., 2002).

Functional imaging studies in humans, involving observation of hand actions (Grafton et al., 1996), hand–object interactions (Johnson-Frey et al., 2003), hand (Iacoboni et al., 1999), and now face imitation (Carr et al., 2003), suggest that the inferior frontal cortex, including Broca's area, may be a key component of a human imitation system. Broca's area is hypothesized to include

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the human homologue of monkey area F5 (Rizzolatti et al., 2002). The identification of a human mirroring system for affective facial expressions would have important implications for our understanding of the neurobiology of empathy. Preston and de Waal (2002) have suggested that a motor resonance system could play a vital role in a perception-action model (PAM) of empathy, and that empathy is part of a larger class of processes that depend on perception-action mechanisms. A more limited proposition of this general idea would be a motor theory of empathy, similar to the motor theory of speech (Liberman and Mattingly, 1985; Liberman and Wahlen, 2000; Liberman et al., 1967). According to a motor theory of empathy, the same premotor neurons that are involved in the generation of facial expressions for the self-expression of emotion are also involved in recognizing that emotion in others, whether that emotion is conveyed by facial expression or other means. Hence, we are hypothesizing that there are multimodal mirror neurons for facial expression that play a key role in the experience of empathy. Brain areas that could play a role in a motor theory of empathy include the ventral premotor cortex (operationally defined as the precentral gyrus and sulcus rostral and inferior to the face area of motor cortex) and the adjacent inferior frontal cortex (Buccino et al., 2001; Carr et al. 2003; Iacoboni et al., 1999), encompassing Brodmann's areas 44 and 45, that is, Broca's area (Amunts et al., 1999).

Is face imitation mediated by the same neural circuits as hand imitation? And is there a motor resonance system for emotive facial expressions? Brain activity was measured with functional magnetic resonance imaging (fMRI) as normal subjects watched movies of face and hand movements (smile or frown, and move index or middle finger). Subjects were asked to passively watch, actively imitate, or perform an active motor control. Real movies rather than static pictures were used in all conditions to approximate conditions under which unconscious mimicry might occur. Subjects also performed a verb generation task to functionally localize language production centers. It was hypothesized that the inferior frontal cortex should be activated during both face and hand imitation, with a special role for Broca's area. Passive viewing of faces was hypothesized to activate premotor face areas, consistent with a motor theory of empathy.

Materials and methods

Subjects

Fifteen right-handed subjects (eight men and seven women) participated in the study. The average age of participants was 26 years (with ages ranging from 19 to 37 years old). Handedness was evaluated using the Edinburgh Handedness Inventory (Oldfield, 1971). After describing the study, all subjects gave written consent to participate in a research protocol approved by the Committee for the Protection of Human Subjects of Dartmouth College.

Magnetic resonance imaging

Imaging was performed with a General Electric Horizon echospeed whole body 1.5 T MRI scanner using a standard birdcage head coil. Head movements were minimized by using a foam pillow and padding. For each functional run, an ultrafast echo planar gradient echo imaging sequence sensitive to blood-

oxygenation-level-dependent (BOLD) contrast was used to acquire 25 slices per TR (4.5-mm thickness, 1-mm gap, in-plane resolution, 3.125×3.125 mm). The following parameters were used: TR = 2500 ms, TE = 35 ms, flip angle = 90° . The first four volumes of each functional run were discarded to allow longitudinal magnetization to approach equilibrium. A high-resolution, T1-weighted, axial fast spin echo sequence was used to acquire 25 contiguous slices (4.5 mm slice thickness with 1.0 mm gap) coplanar to the BOLD images: TE = Min full, TR = 650 ms, Echo Train = 2, FOV = 24 cm. High resolution ($0.94 \times 0.94 \times 1.2$ mm), whole brain, T1-weighted structural images were also acquired using a standard GE spoiled gradient recalled (SPGR) 3D sequence.

Stimuli and experimental design

Each experiment began with a 2-min practice sequence presented during the acquisition of the coplanar image. During the practice sequence, subjects saw representative stimuli for the verb generation, hand, and face tasks. The practice word list for the verb generation task was “bench”, “lawn”, “ruler”, “church”, “key”, and “statue”.

Actual runs consisted of a verb generation run, followed by alternating hand and face runs (4 of each), and a final verb generation run, for a total of 10 runs (see Fig. 1). Half the subjects started with a face run, and half started with a hand run. Each run lasted for 222.5 s (i.e., a total of 89 TRs).

Verb generation task

For the verb generation task, subjects viewed concrete nouns, for example, “bench”, “lawn”, “key”. Subjects were instructed to think of a verb associated with each noun, for example, “sit”, “mow”, and “turn”. Words in each run were shown in random order, and chosen from one of two lists (see Appendix A). These

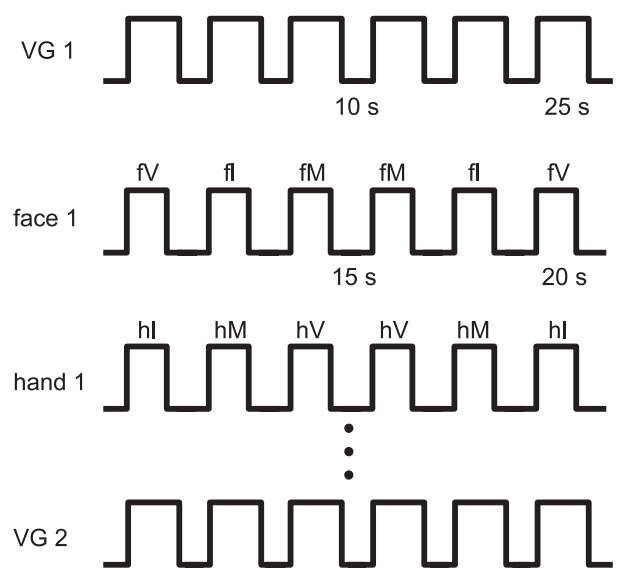


Fig. 1. There were two verb generation (VG) runs, and alternating face and hand runs (four each). Each face and hand run had two view (V), two imitate (I), and two move (M) conditions.

lists were adapted from Seger et al. (1997), with the addition of other concrete nouns, for a total of 60 words per list. Each word was shown only once. Each word was displayed for 500 ms, with 2 s of black screen displayed among words. Words were shown in 10 word blocks, with 10 s of rest among blocks.

Face task

For the face task, subjects viewed short movies of a model either smiling or frowning (see Fig. 2). Each movie was 2 s long, with 0.5 s of black screen shown between movies. Each face run consisted of three different conditions: View, Imitate, and Move. In the View condition, subjects were instructed to passively watch the movie, and not perform any action. In the Imitate condition, subjects were instructed to imitate the facial movement made by the model (either smiling or frowning), as well as possible, and not subvocalize. Both the smiling and frowning movements involved eyebrow and mouth movements, with the mouth always closed so as to minimize scanning artifacts due to changes of air volume in the oral cavity. For the Move condition, subjects were instructed to always smile or always frown, irrespective of the model's expression, but with the same timing. A brief instruction appeared before the start of each block, either: "View", "Imitate", or "Move" = "Smile" or "Move" = "Frown". There were two View, two Imitate, and two counter-balanced Move blocks per run. Each block consisted of four smile and four frown movies presented in random order. Blocks were presented in a pseudo-random order, that is, random order for the first three blocks, and then in reverse order, for example, "View", "Imitate", "Move" = "Smile", "Move" = "Frown", "Imitate", "View". Presentation order was counterbalanced for each subject.

Hand task

The hand task was organized in the same way as the face task. Subjects watched short (2 s) movies of hand movements (see Fig. 2). The subjects viewed the model's left hand, and the model moved either her index or middle finger up and then down. In the View condition, subjects were instructed to passively watch the movie. In the Imitate condition, subjects were instructed to mirror-imitate the action as best as possible, using their right hand. In the Move condition, subjects were instructed to always move either the

index or middle finger, regardless of the stimulus shown (but with the same timing).

Image processing

Structural and functional images were preprocessed and analyzed using SPM99 (<http://www.fil.ion.ucl.ac.uk/spm>). Functional data for each individual subject were corrected for head motion. Realignment parameters demonstrated delta head translation under 1 mm and delta head rotation under 2°. Functional and structural images were coregistered and transformed into a standardized stereotaxic space. This resulted in 25 axial slices of isotropic, 3-mm³ voxels. Data were smoothed with a 9 mm full width at half maximum (FWHM) isotropic Gaussian kernel.

Fixed effects analyses were performed on individual subject's data, with session as the random variable. Both linear and quadratic regressors were included as additional factors to account for within run drift of scanner sensitivity. Similarly, the parameter estimates (translation and rotation in x , y , and z) resulting from motion correction were included as regressors in our statistical model to account for any residual effects of head motion.

Results of the individual subject analyses were then submitted to a second-level, random effects analysis, with subjects as the random variable. Statistical activation maps were constructed based on differences among trial types using a t statistic. Clusters consisting of at least five voxels, separated by a minimum of 9 mm, and having t values equal to or greater than 3.85 ($P < 0.001$, uncorrected for multiple comparisons), were considered statistically significant. Correction for multiple comparisons across the whole brain was not employed because of our a priori hypothesis testing for activation within the bilateral inferior frontal cortex.

We also performed an exploratory analysis of facial mirror effects in cortical areas beyond the inferior frontal cortex. We hypothesized that a face mirroring system should be maximally active during face imitation and less active during passive face viewing. Hence, we created a mask of face imitation at the $P < 0.001$ level ($t > 3.85$) and used the resultant mask to look for areas of common activity in the face viewing condition at the $P < 0.05$ level ($t > 1.76$). Results were converted to the standardized coordinate system used by the Talairach Atlas (Talairach and Tournoux, 1988) using a nonlinear transformation (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispac.html>). Loci were rendered with respect to cortical anatomy using the

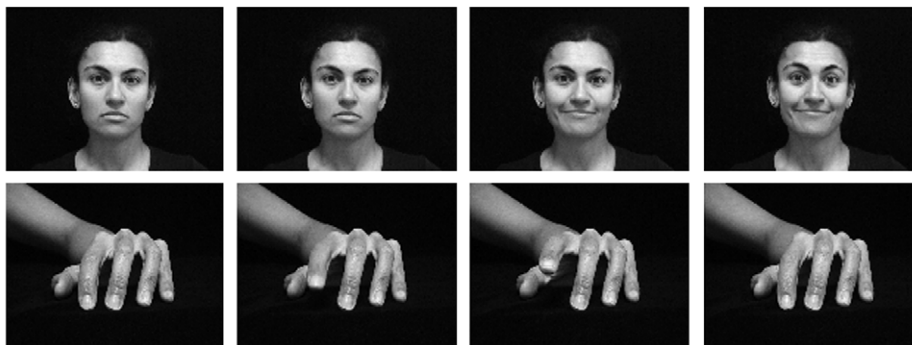


Fig. 2. Example of face and hand movies. Each movie was 2 s long. Subjects were asked to passively view, actively imitate, or perform a motor control in response to each movie.

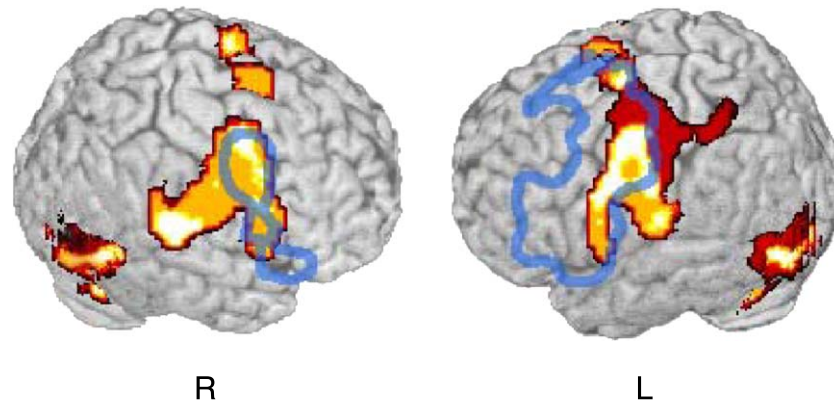


Fig. 3. Red shows areas of activation during hand imitation only, while orange shows areas of activation during face imitation only. White shows areas of common activation for both face and hand imitation (both at $P < 0.001$, uncorrected). Blue outlines the areas of frontal activation during the verb-generation task ($P < 0.05$).

software MRICro (<http://www.psychology.nottingham.ac.uk/staff/cr1/mricro.html>).

Results

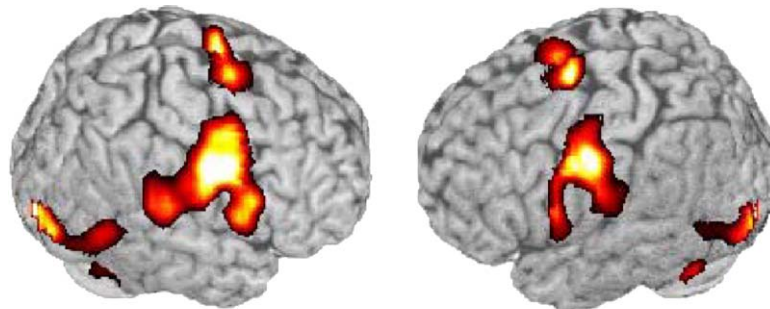
Common circuit for imitation of faces and hands

Is there a common imitation circuit that is independent of response modality? To answer this, we looked at the area of overlap between face imitation and hand imitation at the $P < 0.001$ level. The area of overlap generated from these two maps is

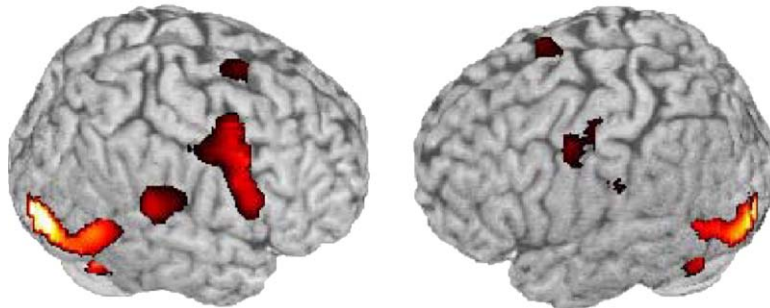
shown in Fig. 3 in white. There is significant activation in the bilateral dorsal precentral sulcus and adjacent superior frontal sulcus (dorsal premotor cortex), ventral precentral sulcus (ventral premotor area), and inferior frontal cortex including the superior aspect of the *pars opercularis* (BA 44). Common activations also include the medial wall of the superior frontal gyrus (SMA) in both hemispheres, right superior temporal gyrus (STG), and bilateral posterior temporo-occipital cortex.

Fig. 3 also demonstrates areas where face and hand imitation differ. Face imitation recruited more right frontal cortex than hand imitation. Hand imitation recruited more activity in the hand area of the left motor cortex and adjacent premotor and parietal cortex,

Face Imitate



Face View



RH

LH

Fig. 4. Parametric maps (t statistic) of face imitation ($P < 0.001$) and face view ($P < 0.05$). The imitation map was used to mask the view condition.

whereas face imitation recruited activity in the more ventral motor premotor and parietal cortex. Recruitment of bilateral *pars opercularis* was more extensive with face imitation.

Frontal areas involved in language were functionally identified using the verb-generation task. An outline of the bilateral frontal areas of activation from the verb-generation task is also shown in Fig. 3 in blue at the $P < 0.05$ level ($t > 1.76$). The activation during hand and face imitation in the *pars opercularis* falls within the posterior aspect of the inferior frontal area functionally and anatomically defined as Broca's area in the left inferior frontal cortex (Amunts et al., 1999; Tomaiuolo et al., 1999).

Dissociation between viewing and imitation for faces

Previous work suggests that a cortical motor resonance (i.e., mirroring) system defined by fMRI should be maximally active during imitation and less active during action viewing (Iacoboni et al., 1999; Koski et al., 2003). We first identified brain regions that were activated during face imitation (df: 14, $t > 3.85$, $P < 0.001$) and used this to generate a mask of areas of interest to examine during passive viewing. Passive face viewing was then examined at the $P < 0.05$ level ($t > 1.76$, df:14) after the application of this mask. An examination of the distribution of cortical activations rendered onto the surface anatomy of the brain (see Fig. 4) reveals a dissociation between passive viewing and active imitation: passive viewing yielded largely right hemisphere (RH) activation in premotor areas, whereas active imitation led to bilateral activation. The face imitation task resulted in broad activation extending from the face area of the sensorimotor cortex to the adjacent precentral sulcus (ventral premotor cortex). The activity incorporated bilateral *pars opercularis* (BA 44) and adjacent inferior precentral sulcus (BA 6) near the lateral fissure. Activations were greater in magnitude in the right hemisphere for all of these sites.

In the passive face viewing condition, these activations were largely attenuated, with significant activity still present in the right precentral sulcus (ventral premotor cortex).

Peak areas of all cortical activations for face viewing and imitation are summarized in Table 1. Both face conditions were also associated with strong activations in the fusiform gyrus and right superior temporal gyrus. Previous research confirms that viewing faces activate the fusiform gyrus (Kanwisher et al., 1997), while dynamic human motion activates the superior temporal sulcus extending dorsally into the superior temporal gyrus (Beauchamp et al., 2002).

Discussion

Common imitation circuit

We reasoned that a common imitation circuit would be active during both face and hand imitation. We found common activation in several areas consistent with this hypothesis, including: left *pars opercularis* (Broca's area), bilateral premotor areas, right STG, and bilateral SMA, posterior temporo-occipital, and cerebellar areas (see Fig. 3). These findings are consistent with previous studies (Iacoboni et al., 1999; Carr et al., 2003), and indicate that the *pars opercularis* is involved in the imitation of multiple body parts.

We did not see any left *pars opercularis* activity during passive viewing of either faces or hands, even when we reduced the P level down to $P < 0.05$. Both Carr et al. (2003) and Iacoboni et al. (1999) have reported Broca's area activation during passive viewing, although they acknowledge that this is a less robust effect. Our inability to replicate this specific finding may be due to the limitations of our 1.5 T scanner (e.g., we may have had more success with a 3 T scanner: see Krasnow et al., 2003), susceptibility

Table 1

Significant cortical and cerebellar activations for face imitation ($P < 0.001$, $t > 3.85$) and face view ($P < 0.05$, $t > 1.76$) subjected to a face imitation mask

Hemisphere	Location	BA	Talairach coordinates			t values	
			x	y	z	Face imitation	Face view
R	Precentral sulcus, <i>Dorsal Premotor</i>	6	50	8	47	8.03	4.76
R	Precentral sulcus, <i>Mid Premotor</i>	6	48	10	24	4.27	4.43
R	Precentral sulcus, <i>Ventral Premotor</i>	6	53	15	16	5.68	4.48
R	Precentral sulcus, <i>Ventral Premotor</i>	6	59	13	19	8.77	3.69
L	Precentral sulcus, <i>Mid Premotor</i>	6	-56	-1	39	10.47	2.18
L	Precentral sulcus, <i>Ventral Premotor</i>	6	-59	7	19	6.53	-
L	Pars opercularis, <i>Broca's area</i>	6, 44	-48	3	3	5.63	-
R	Mesial superior frontal gyrus, <i>SMA</i>	6	9	6	58	8.80	2.13
L	Mesial superior frontal gyrus, <i>SMA</i>	6	-9	0	61	10.96	-
R	Precentral gyrus, <i>mouth motor area</i>	4	53	-7	36	11.97	-
L	Precentral gyrus, <i>mouth motor area</i>	4	-42	-7	36	15.27	-
R	Superior temporal gyrus	22	56	-28	18	7.46	2.75
R	Superior temporal gyrus	22	62	-37	21	6.69	4.34
L	Parietal operculum, <i>SII</i>	40	-56	-16	23	5.37	-
L	Parietal operculum, <i>SII</i>	40	-56	-25	26	4.46	2.11
R	Inferior temporal gyrus	37	48	-61	-2	6.00	5.86
R	Inferior temporal gyrus	37	48	-61	1	5.91	6.15
L	Inferior temporal gyrus	19	-45	-67	-2	4.34	4.08
R	Fusiform gyrus	18	30	-88	-3	8.24	13.81
L	Fusiform gyrus	18	-21	-94	-5	9.92	11.89
R	Cerebellum		42	-51	-20	5.54	4.82
L	Cerebellum		-18	-62	-25	6.92	-
L	Cerebellum		-39	-68	-19	3.96	4.45

effects in inferior frontal areas, or a weak effect of the stimuli. However, previous work with our system has detected activations here in association with observation of hand–object interactions (Johnson-Frey et al., 2003).

An alternative hypothesis is that the Broca's area in humans may not be specifically involved in mirroring, but may instead be important for action execution. Much of the literature on mirror neurons in humans has made the implicit assumption that imitation and mirroring (motor resonance) are the same thing. We would suggest that imitation involves the activation of both a mirroring system and a goal-planning and motor-execution system. One possible interpretation of our results is that the left hemisphere *pars opercularis* (classic Broca's area) is involved in conscious goal-directed movements, whereas the mirroring involved in unconscious mimicry and empathy is mediated by the right hemisphere ventral premotor cortex.

Face mirroring system

Mirroring and imitation are two related but separate concepts: Iacoboni (in press) has argued that a motor resonance system should be active during both action observation and action execution, and that this activity sums additively during imitation. We found a strong dissociation between passive viewing and imitation of facial expressions: viewing yielded significant activation in the right ventral premotor area, while imitation produced bilateral activation. This result is consistent with a face mirroring system in the right hemisphere (RH), in agreement with evidence for RH dominance in emotional understanding.

There is ample evidence that the RH plays a special role in understanding the emotional expressions of others. There is a RH superiority in the recognition of emotional valence in facial expression, with improved performance by subjects with presentation to the left visual field (Natale et al., 1983). Patients with damage to the right hemisphere are impaired in the recognition of a range of basic emotional expressions (Adolphs et al., 1996, 2000; Kucharska-Pietura et al., 2003). There is even evidence that the RH may play an important role in the generation of facial expressions: it is well known that the left side of the face, which is innervated by the RH, is more emotionally expressive than the right side of the face (Borod et al., 1997; Dimberg and Petterson, 2000; Sackeim et al., 1978). Our results suggest that the RH premotor cortex may play a role in both the generation and the perception of emotionally expressive faces, consistent with a motor theory of empathy.

A recent study on face imitation by Carr et al. (2003) found similar premotor activation in the right hemisphere, as well as activation of the insula and amygdala during observation and imitation of static Ekman faces (Ekman and Friesen, 1976), a canonical set of emotive faces. We did not find significant activation of either the insula or amygdala in response to our dynamic faces of smiling and frowning. This is not surprising, given that the insula is known to respond specifically to expressions of disgust and the amygdala to expressions of fear (Phillips et al., 1998; Sprengelmeyer et al., 1998), expressions we did not use.

Finally, is conscious goal-directed imitation of faces the same as the unconscious mimicry of faces that we think underlies empathy? Based on our results, we would argue that these are different and dissociable phenomena. Our results show that the goal-directed imitation of faces involves strong bilateral activation, with an important role for the left *pars opercularis*. Work by Gazzaniga and Smylie (1990) showed that a split-brain patient was able to

purposefully make facial expressions using his left hemisphere, but not his right. This suggests that there may be a conscious left hemisphere mediated control of the facial musculature that is different from the processes involved in unconscious mimicry. Hence, conscious imitation may have more in common with “putting on a face,” or even masking one's intentions, than with empathy.

Passive viewing, on the other hand, may involve more empathic processes: the literature suggests that passive viewing involves some measure of unconscious mimicry, and our results show strong RH activation of the ventral premotor cortex. We suggest that this RH activity may be important for unconscious mimicry, and that the RH ventral premotor cortex may contain mirror neurons that play a role in a motor theory of empathy.

Acknowledgments

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Appendix A. Verb generation stimuli

List 1: aisle, arm, baby, balloon, basket, bed, beer, blanket, bomb, broom, bucket, cane, cat, chair, choir, cigar, cloud, crayon, disease, dog, dollar, egg, finger, fist, food, fork, gift, grass, guest, gun, hose, ice, jet, joke, knife, lake, lens, lollipop, match, milk, money, movie, mustard, needle, orange, paper, pencil, pill, pool, purse, razor, school, shirt, soap, song, star, stove, towel, tree, zipper.

List 2: apple, army, ball, bank, baton, bee, bell, bird, boat, book, brick, bubble, bullet, car, cave, chalk, clock, coin, diamond, doctor, doll, door, eye, fire, flag, foot, frog, glove, grave, gum, hair, horn, house, itch, job, ladder, law, lemon, letter, map, menu, mirror, mouth, mud, nail, oar, oven, pen, phone, plane, pool, radio, scale, seed, shovel, soap, soup, tax, toy, zoo.

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