



1 Functional imaging of face and hand imitation: towards a motor 2 theory of empathy

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

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34
35 *Keywords:* Empathy; Imitation; Facial expression; Mirror neurons
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38 Introduction

39 How do we understand the emotional experience of others?
40 Lipps (1903) proposed an “imitative drive” that leads us to
41 automatically imitate the facial expressions of others, retrieve the
42 associated emotion, and attribute that emotion to the other indi-
43 vidual. There is good evidence for the ubiquity of unconscious
44 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 inter-
action 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; Sonny-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 the 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., in press), 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 be the

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87 human homologue of monkey area F5 (Rizzolatti et al., 2002). The
 88 identification of a human mirroring system for affective facial
 89 expressions would have important implications for our understand-
 90 ing of the neurobiology of empathy. Preston and de Waal (2002)
 91 have suggested that a motor resonance system could play a vital
 92 role in a perception-action model (PAM) of empathy, and that
 93 empathy is part of a larger class of processes that depend on
 94 perception-action mechanisms. A more limited proposition of this
 95 general idea would be a motor theory of empathy, similar to the
 96 motor theory of speech (Lieberman and Mattingly, 1985; Lieberman
 97 and Wahlen, 2000; Lieberman et al., 1967). According to a motor
 98 theory of empathy, the same premotor neurons that are involved in
 99 the generation of facial expressions for the self-expression of
 100 emotion are also involved in recognizing that emotion in others,
 101 whether that emotion is conveyed by facial expression or other
 102 means. Hence, we are hypothesizing that there are multimodal
 103 mirror neurons for facial expression that play a key role in the
 104 experience of empathy. Brain areas that could play a role in a motor
 105 theory of empathy include the ventral premotor cortex (operation-
 106 ally defined as the precentral gyrus and sulcus rostral and inferior
 107 to the face area of motor cortex) and the adjacent inferior frontal
 108 cortex (Buccino et al., 2001; Carr et al. 2003; Iacoboni et al.,
 109 1999), encompassing Brodmann's areas 44 and 45, that is, Broca's
 110 area (Amunts et al., 1999).

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

126 Materials and methods

127 Subjects

129 Fifteen right-handed subjects (eight men and seven women)
 130 participated in the study. The average age of participants was 26
 131 years (with ages ranging from 19 to 37 years old). Handedness was
 132 evaluated using the Edinburgh Handedness Inventory (Oldfield,
 133 1971). After describing the study, all subjects gave written consent
 134 to participate in a research protocol approved by the Committee for
 135 the Protection of Human Subjects of Dartmouth College.

136 Magnetic resonance imaging

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

143 oxygenation-level-dependent (BOLD) contrast was used to ac-
 144 quire 25 slices per TR (4.5-mm thickness, 1-mm gap, in-plane
 145 resolution, 3.125×3.125 mm). The following parameters were
 146 used: TR = 2500 ms, TE = 35 ms, flip angle = 90° . The first four
 147 volumes of each functional run were discarded to allow longitu-
 148 dinal magnetization to approach equilibrium. A high-resolution,
 149 T1-weighted, axial fast spin echo sequence was used to acquire 25
 150 contiguous slices (4.5 mm slice thickness with 1.0 mm gap)
 151 coplanar to the BOLD images: TE = Min full, TR = 650 ms, Echo
 152 Train = 2, FOV = 24 cm. High resolution ($0.94 \times 0.94 \times 1.2$
 153 mm), whole brain, T1-weighted structural images were also
 154 acquired using a standard GE spoiled gradient recalled (SPGR)
 155 3D sequence.

156 Stimuli and experimental design

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

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

169 Verb generation task

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

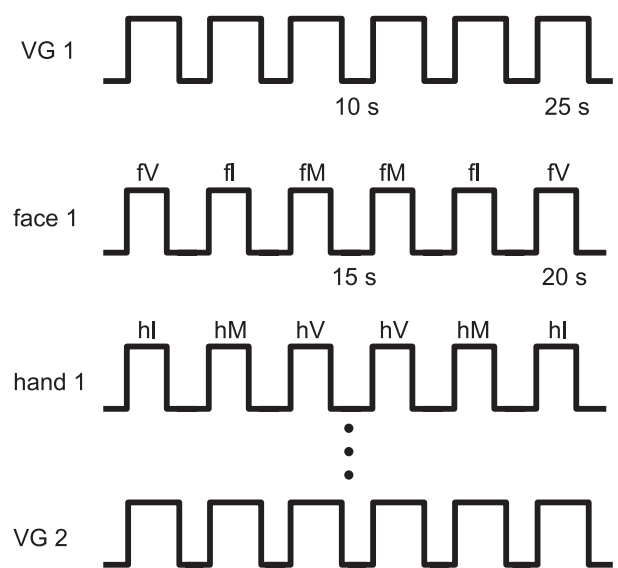


Fig. 1. There were two verb generation (VG) runs, and alternating face and hand runs (four each). Each face and hand run had two view (V), two imitate (I), and two move (M) conditions.

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

181 182 Face task

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

207 208 Hand task

209 The hand task was organized in the same way as the face task.
 210 Subjects watched short (2 s) movies of hand movements (see Fig.
 211 2). The subjects viewed the model's left hand, and the model
 212 moved either her index or middle finger up and then down. In the
 213 View condition, subjects were instructed to passively watch the
 214 movie. In the Imitate condition, subjects were instructed to mirror-
 215 imitate the action as best as possible, using their right hand. In the
 216 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

221 Structural and functional images were preprocessed and ana-
 222 lyzed using SPM99 (<http://www.fil.ion.ucl.ac.uk/spm>). Functional
 223 data for each individual subject were corrected for differences in
 224 time of slice acquisition and head motion. Realignment parameters
 225 demonstrated delta head translation under 1 mm and delta head
 226 rotation under 2°. Functional and structural images were coregis-
 227 tered and transformed into a standardized stereotaxic space. This
 228 resulted in 25 axial slices of isotropic, 3-mm³ voxels. Data were
 229 smoothed with a 9 mm full width at half maximum (FWHM)
 230 isotropic Gaussian kernel.

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

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

248 We also performed an exploratory analysis of facial mirror
 249 effects in cortical areas beyond the inferior frontal cortex. We
 250 hypothesized that a face mirroring system should be maximally
 251 active during face imitation and less active during passive face
 252 viewing. Hence, we created a mask of face imitation at the $P <$
 253 0.001 level ($t > 3.85$) and used the resultant mask to look for
 254 areas of common activity in the face viewing condition at the
 255 $P < 0.05$ level ($t > 1.76$). Results were converted to the
 256 standardized coordinate system used by the Talairach Atlas
 257 (Talairach and Tournoux, 1988) using a nonlinear transformation
 258 (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispac.html>). Loci
 259 were rendered with respect to cortical anatomy using the

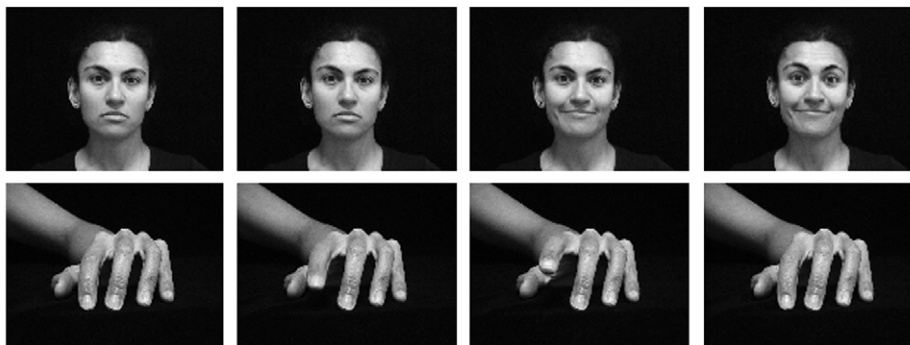


Fig. 2. Example of face and hand movies. Each movie was 2 s long. Subjects were asked to passively view, actively imitate, or perform a motor control in response to each movie.

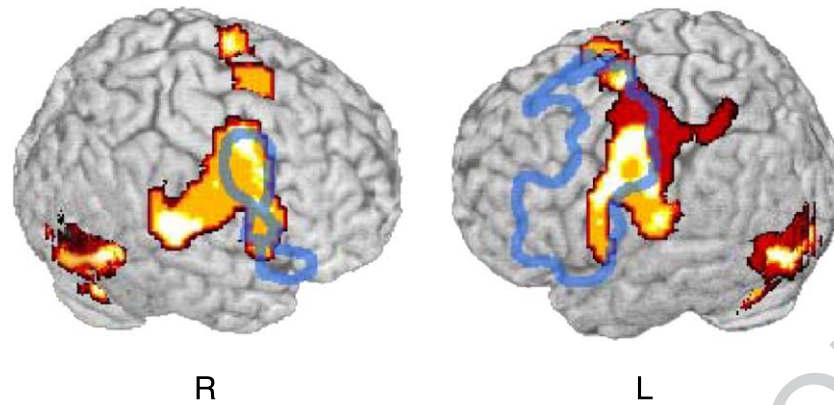


Fig. 3. Red shows areas of activation during hand imitation only, while orange shows areas of activation during face imitation only. White shows areas of common activation for both face and hand imitation (both at $P < 0.001$, uncorrected). Blue shows the areas of frontal activation during the verb-generation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

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

262 Results

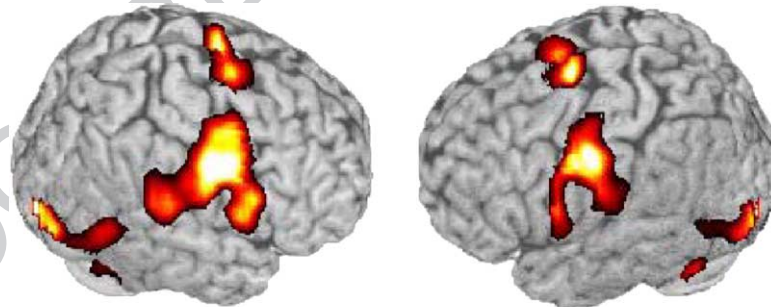
263 264 Common circuit for imitation of faces and hands

265 Is there a common imitation circuit that is independent of
266 modality? To answer this, we looked at the area of overlap between
267 face imitation and hand imitation at the $P < 0.001$ level. The area of
268 overlap generated from these two maps is shown in Fig. 3 in white.

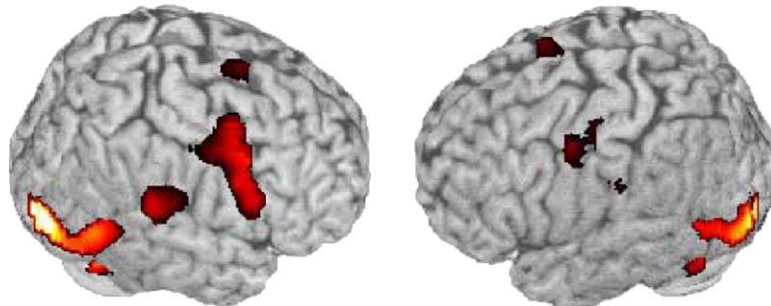
269 There is significant activation in the bilateral dorsal precentral
270 sulcus and adjacent superior frontal sulcus (dorsal premotor
271 cortex), ventral precentral sulcus (ventral premotor area), and
272 inferior frontal cortex including the superior aspect of the *pars*
273 *opercularis* (BA 44).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

277 Fig. 3 also demonstrates areas where face and hand imitations
278 differ. Face imitation recruited more right frontal cortex than hand
279 imitation. Hand imitation recruited more activity in the hand area
280 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.

281 whereas face imitation recruited activity in the more ventral motor
282 premotor and parietal cortex. Recruitment of bilateral *pars oper-*
283 *cularis* was more extensive with face imitation.

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

292

293 *Dissociation between viewing and imitation for faces*

294 Previous work suggests that a cortical motor resonance (i.e.,
295 mirroring) system defined by fMRI should be maximally active
296 during active imitation and less active during action viewing
297 (Iacoboni et al., 1999; Koski et al., 2003). We first identified brain
298 regions that were activated during face imitation (df: 17, $t > 3.85$, P
299 < 0.001) and used this to generate a mask of areas of interest to
300 examine during passive viewing. Passive face viewing was then
301 examined at the $P < 0.05$ level ($t > 1.76$, df:17) after the application
302 of this mask. An examination of the distribution of cortical
303 activations rendered onto the surface anatomy of the brain (see
304 Fig. 4) reveals a dissociation between passive viewing and active
305 imitation: passive viewing yielded largely right hemisphere (RH)
306 activation in premotor areas, whereas active imitation led to
307 bilateral activation. The face imitation task resulted in broad
308 activation extending from the face area of the sensorimotor cortex
309 to the adjacent precentral sulcus (ventral premotor cortex). The
310 activity incorporated bilateral *pars opercularis* (BA 44) and
311 adjacent inferior precentral sulcus (BA 6) near the lateral fissure.
312 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 right superior
temporal sulcus extending dorsally into the right 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

t1.1 Table 1
t1.2 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

t1.3 Hemisphere	t1.4 Location	t1.5 BA	t1.6 Talairach coordinates			t1.7 t values	
			t1.8 x	t1.9 y	t1.10 z	t1.11 Face imitation	t1.12 Face view
t1.13 R	t1.14 Precentral sulcus, <i>Dorsal Premotor</i>	t1.15 6	t1.16 50	t1.17 8	t1.18 47	t1.19 8.03	t1.20 4.76
t1.13 R	t1.14 Precentral sulcus, <i>Mid Premotor</i>	t1.15 6	t1.16 48	t1.17 10	t1.18 24	t1.19 4.27	t1.20 4.43
t1.13 R	t1.14 Precentral sulcus, <i>Ventral Premotor</i>	t1.15 6	t1.16 53	t1.17 15	t1.18 16	t1.19 5.68	t1.20 4.48
t1.13 R	t1.14 Precentral sulcus, <i>Ventral Premotor</i>	t1.15 6	t1.16 59	t1.17 13	t1.18 19	t1.19 8.77	t1.20 3.69
t1.13 L	t1.14 Precentral sulcus, <i>Mid Premotor</i>	t1.15 6	t1.16 -56	t1.17 -1	t1.18 39	t1.19 10.47	t1.20 2.18
t1.13 L	t1.14 Precentral sulcus, <i>Ventral Premotor</i>	t1.15 6	t1.16 -59	t1.17 7	t1.18 19	t1.19 6.53	t1.20 -
t1.13 L	t1.14 Pars opercularis, <i>Broca's area</i>	t1.15 6, 44	t1.16 -48	t1.17 3	t1.18 3	t1.19 5.63	t1.20 -
t1.13 R	t1.14 Mesial superior frontal gyrus, <i>SMA</i>	t1.15 6	t1.16 9	t1.17 6	t1.18 58	t1.19 8.80	t1.20 2.13
t1.13 L	t1.14 Mesial superior frontal gyrus, <i>SMA</i>	t1.15 6	t1.16 -9	t1.17 0	t1.18 61	t1.19 10.96	t1.20 -
t1.13 R	t1.14 Precentral gyrus, <i>mouth motor area</i>	t1.15 4	t1.16 53	t1.17 -7	t1.18 36	t1.19 11.97	t1.20 -
t1.13 L	t1.14 Precentral gyrus, <i>mouth motor area</i>	t1.15 4	t1.16 -42	t1.17 -7	t1.18 36	t1.19 15.27	t1.20 -
t1.13 R	t1.14 Superior temporal gyrus	t1.15 22	t1.16 56	t1.17 -28	t1.18 18	t1.19 7.46	t1.20 2.75
t1.13 R	t1.14 Superior temporal gyrus	t1.15 22	t1.16 62	t1.17 -37	t1.18 21	t1.19 6.69	t1.20 4.34
t1.13 L	t1.14 Parietal operculum, <i>SII</i>	t1.15 40	t1.16 -56	t1.17 -16	t1.18 23	t1.19 5.37	t1.20 -
t1.13 L	t1.14 Parietal operculum, <i>SII</i>	t1.15 40	t1.16 -56	t1.17 -25	t1.18 26	t1.19 4.46	t1.20 2.11
t1.13 R	t1.14 Inferior temporal gyrus	t1.15 37	t1.16 48	t1.17 -61	t1.18 -2	t1.19 6.00	t1.20 5.86
t1.13 R	t1.14 Inferior temporal gyrus	t1.15 37	t1.16 48	t1.17 -61	t1.18 1	t1.19 5.91	t1.20 6.15
t1.13 L	t1.14 Inferior temporal gyrus	t1.15 19	t1.16 -45	t1.17 -67	t1.18 -2	t1.19 4.34	t1.20 4.08
t1.13 R	t1.14 Fusiform gyrus	t1.15 18	t1.16 30	t1.17 -88	t1.18 -3	t1.19 8.24	t1.20 13.81
t1.13 L	t1.14 Fusiform gyrus	t1.15 18	t1.16 -21	t1.17 -94	t1.18 -5	t1.19 9.92	t1.20 11.89
t1.13 R	t1.14 Cerebellum	t1.15 42	t1.16 -51	t1.17 -20	t1.18 20	t1.19 5.54	t1.20 4.82
t1.13 L	t1.14 Cerebellum	t1.15 42	t1.16 -18	t1.17 -62	t1.18 -25	t1.19 6.92	t1.20 -
t1.13 L	t1.14 Cerebellum	t1.15 42	t1.16 -39	t1.17 -68	t1.18 -19	t1.19 3.96	t1.20 4.45

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

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

359
 360 *Face mirroring system*

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

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

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

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

purposefully make a face out of his left hemisphere, but not out of
 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.

Uncited references

Blonder et al., 1991
 Zilles et al., 2001

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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.

References

- Adolphs, R., Damasio, H., Tranel, D., Damasio, A.R., 1996. Cortical sys-
 tems for the recognition of emotion in facial expressions. *J. Neurosci.*
 16 (23), 7678–7687.
 Adolphs, R., Damasio, H., Tranel, D., Cooper, G., Damasio, R., 2000. A
 Role for the somatosensory cortices in the visual recognition of emotion
 as revealed by three-dimensional lesion mapping. *J. Neurosci.* 20 (7),
 2683–2690.
 Amunts, K., Schleicher, A., Bürgel, U., Mohlberg, H., Uylings, H.B.M.,
 Zilles, K., 1999. Broca's region revisited: cytoarchitecture and intersub-
 ject variability. *J. Comp. Neurol.* 412, 319–341.
 Bargh, J.A., Chen, M., Burrows, L., 1996. Automativity of social behavior:
 direct effects of trait construct and stereotype activation on action. *J.*
Pers. Soc. Psychol. 71 (2), 230–244.
 Beauchamp, M.S., Lee, K.E., Haxby, J.V., Martin, A., 2002. Parallel visual
 motion processing streams for manipulable objects and human move-
 ments. *Neuron* 34, 149–159.

- 452 Blonder, L.E., Bowers, D., Heilman, K.M., 1991. The role of the right
453 hemisphere in emotional communication. *Brain* 114 (Pt 3), 1115–1127.
- 454 Borod, J.C., Haywood, C.S., Koff, E., 1997. Neuropsychological aspects of
455 facial asymmetry during emotional expression: a review of the normal
456 adult literature. *Neuropsychol. Rev.* 7 (1), 41–60.
- 457 Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V.,
458 Seitz, R.J., Zilles, K., Rizzolatti, G., Freund, H.-J., 2001. Action ob-
459 servation activates premotor and parietal areas in a somatotopic manner:
460 an fMRI study. *Eur. J. Neurosci.* 13, 400–404.
- 461 Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J.C., Lenzi, G.L., 2003.
462 Neural mechanisms of empathy in humans: a relay from neural systems
463 for imitation to limbic areas. *PNAS*, Published April 7, 2003 online,
464 10.1073/pnas.0935845100.
- 465 Chartrand, T.L., Bargh, J.A., 1999. The chameleon effect: the perception-
466 behavior link and social interaction. *J. Pers. Soc. Psychol.* 76 (6),
467 893–910.
- 468 Dimberg, U., Petterson, M., 2000. Facial reactions to happy and angry
469 facial expressions: evidence for right hemisphere dominance. *Psycho-*
470 *physiology* 37 (5), 693–696.
- 471 Dimberg, U., Thunberg, M., 1998. Rapid facial reactions to emotional
472 facial expressions. *Scand. J. Psychol.* 39, 39–45.
- 473 Dimberg, U., Thunberg, M., Elmehed, K., 2000. Unconscious facial reac-
474 tions to emotional facial expressions. *Psychol. Sci.* 11 (1), 86–89.
- 475 Ekman, P., Friesen, W.V., 1976. *Pictures of Facial Affect*. Consulting Psy-
476 chologist Press, Palo Alto, CA.
- 477 Ekman, P., Levenson, R.W., Friesen, W.V., 1983. Autonomic nervous system
478 activity distinguishes among emotions. *Science* 221 (4616), 1208–1210.
- 479 Ferrari, P.F., Gallese, V., Rizzolatti, G., Fogassi, L., 2003. Mirror neurons
480 responding to the observation of ingestive and communicative mouth
481 actions in the monkey ventral premotor cortex. *Eur. J. Neurosci.* 17,
482 1703–1714.
- 483 Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition
484 in the premotor cortex. *Brain* 119 (Pt 2), 593–609.
- 485 Gazzaniga, M.S., Smylie, C.S., 1990. Hemispheric mechanisms controlling
486 voluntary and spontaneous mechanisms. *Ann. Neurol.* 13, 536–540.
- 487 Grafton, S.T., et al., 1996. Localization of grasp representations in humans
488 by positron emission tomography. 2. Observation compared with imag-
489 ination. *Exp. Brain Res.* 112 (1), 103–111.
- 490 Iacoboni, M., in press. Understanding others: imitation, language, empathy.
491 In: Hurley, S., Chater, N. (Eds.), *Perspectives on imitation: from cog-
492 nitive neuroscience to social science*. Cambridge, MA: MIT Press.
- 493 Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C.,
494 Rizzolatti, G., 1999. Cortical mechanisms of human imitation. *Science*
495 286, 2526–2528.
- 496 Johnson-Frey, S.H., Maloof, F.R., Newman-Norlund, R., Farrer, C., Inati,
497 S., Grafton, S.G., in press. Actions or hand–object interactions? Human
498 inferior frontal cortex and action observation. *Neuron*.
- 499 Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area:
500 a module in human extrastriate cortex specialized for face perception. *J.*
501 *Neurosci.* 17 (11), 4302–4311.
- 502 Kohler, E., Keysers, C., Umiltà, M.A., Fogassi, L., Gallese, V., Rizzolatti,
503 G., 2002. Hearing sounds, understanding actions: action representation
504 in mirror neurons. *Science* 297 (5582), 846–848.
- 505 Koski, L., Iacoboni, M., Dubeau, M.C., Woods, R.P., Mazziotta, J.J., 2003.
Modulation of cortical activity during different imitative behaviors. *J.*
Neurophysiol. 89, 460–471. 506
- Krasnow, B., Tamm, L., Greicius, M.D., Yang, T.T., Glover, G.H., Reiss,
507 A.L., Menon, V., 2003. Comparison of fMRI activation at 3 and 1.5 T
508 during perceptual, cognitive, and affective processing. *NeuroImage* 18,
509 813–826. 510
- Kucharska-Pietura, K., Phillips, M.L., Gernand, W., David, A.S., 2003.
511 Perception of emotions from faces and voices following unilateral brain
512 damage. *Neuropsychologia* 41, 1082–1090. 513
- Levenson, R.W., Ekman, P., Friesen, W.V., 1990. Voluntary facial action
514 generates emotion-specific autonomic nervous system activity. *Psycho-*
515 *physiology* 27 (4), 363–384. 516
- Lieberman, A.M., Mattingly, I.G., 1985. The motor theory of speech per-
517 ception revised. *Cognition* 21, 1–36. 518
- Lieberman, A.M., Wahlen, D.H., 2000. On the relation of speech to lan-
519 guage. *Trends Cogn. Neurosci.* 4, 187–196. 520
- Lieberman, A.M., Cooper, F.S., Shankweiler, D.P., Stuart-Kennedy, M.,
521 1967. Perception of the speech code. *Psychol. Rev.* 74, 431–461. 522
- Lipps, T., 1903. Einfühlung, innere Nachahmung und Organempfindung.
523 *Arch. Gesamte Psychol.* 1, 465–519. 524
- Natale, M., Gur, R.E., Gur, R.C., 1983. Hemispheric asymmetries in pro-
525 cessing emotional expressions. *Neuropsychologia* 21 (5), 555–565. 526
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the
527 Edinburgh inventory. *Neuropsychologia* 9 (1), 97–113. 528
- Phillips, M.L., Young, A.W., Scott, S.K., Calder, A.J., Andrew, C., Giam-
529 pietro, V., Williams, S.C., Bullmore, E.T., Brammer, M., Gray, J.A.,
530 1998. Neural responses to facial and vocal expressions of fear and
531 disgust. *Proc. R. Soc. Lond., B Biol. Sci.* 265 (1408), 1809–1817. 532
- Preston, S.D., de Waal, F.B., 2002. Empathy: it's ultimate and proximate
533 bases. *Behav. Brain Sci.* 25 (1), 1–20. 534
- Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex
535 and the recognition of motor actions. *Brain Res., Cogn. Brain Res.* 3
536 (2), 131–141. 537
- Rizzolatti, G., Fogassi, L., Gallese, V., 2002. Motor and cognitive functions
538 of the ventral premotor cortex. *Curr. Opin. Neurobiol.* 12 (2), 149–154. 539
- Sackeim, H.A., Gur, R.C., Saucy, M.C., 1978. Emotions are expressed
540 more intensely on the left side of the face. *Science* 202, 434–436. 541
- Seger, C.A., Rabin, L.A., Zarella, M., Gabrieli, J.D., 1997. Preserved verb
542 generation priming in global amnesia. *Neuropsychologia* 35 (8),
543 1069–1074. 544
- Sonnby-Borgström, M., 2002. Automatic mimicry reactions as related to
545 differences in emotional empathy. *Scand. J. Psychol.* 43, 433–443. 546
- Sprengelmeyer, R., Rausch, M., Eysel, U.T., Przuntek, H., 1998. Neural
547 structures associated with recognition of facial expressions of basic
548 emotions. *Proc. R. Soc. Lond., B Biol. Sci.* 265 (1409), 1927–1931. 549
- Talairach, J., Tournoux, P., 1988. *Co-Planar Stereotaxic Atlas of the Human*
550 *Brain*. Thieme Medical Publishers Inc., New York. 551
- Tomaiuolo, F., MacDonald, J.D., Caramanos, Z., Posner, G., Chiavaras, M.,
552 Evans, A.C., Petrides, M., 1999. Morphology, morphometry and prob-
553 ability mapping of the pars opercularis of the inferior frontal gyrus: an
554 in vivo MRI analysis. *Eur. J. Neurosci.* 11, 3033–3046. 555
- Zilles, K., Rizzolatti, G., Freund, H.-J., 2001. Action observation activates
556 premotor and parietal areas in a somatotopic manner: an fMRI study.
557 *Eur. J. Neurosci.* 13, 400–404. 558