



Review

Is the mirror neuron system involved in imitation? A short review and meta-analysis

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ABSTRACT

It has been suggested that the mirror neuron system provides an important neural substrate for humans' ability to imitate. Mirror neurons have been found during single-cell recordings in monkeys in area F5 and PF. It is believed that the human equivalent of this mirror system in humans is the pars opercularis of the inferior frontal gyrus (area 44) and the rostral part of the inferior parietal lobule. This article critically reviews published fMRI studies that examined the role of frontal and parietal brain regions in imitation. A meta-analysis using activation likelihood estimation (ALE) revealed that the superior parietal lobule, inferior parietal lobule, and the dorsal premotor cortex but not the inferior frontal gyrus, are all commonly involved in imitation. An additional meta-analysis using a label-based review confirmed that in the frontal lobe, the premotor cortex rather than the inferior frontal gyrus is consistently active in studies investigating imitation. In the parietal region the superior and inferior parietal lobules are equally activated during imitation. Our results suggest that parietal and frontal regions which extend beyond the classical mirror neuron network are crucial for imitation.

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1. Introduction

Imitation is the copying of body movements that we observe (Brass and Heyes, 2005). A fundamental question with imitation is the correspondence problem: “How does the observer’s motor system ‘know’ which muscle activations will lead to the observed movement if the observer does not see the underlying muscle activation in the actor?” (Brass and Heyes, 2005). It has been suggested that so-called ‘mirror neurons’ resolve this correspondence problem by automatically mapping observed movements onto a motor program, thus leading to the widely held view that the mirror neuron system is crucial for imitation (Heyes, 2001; Rizzolatti et al., 2001; Buccino et al., 2004; Rizzolatti and Craighero, 2004; Brass and Heyes, 2005; Iacoboni, 2005; Rizzolatti, 2005; Iacoboni and Dapretto, 2006).

Mirror neurons are visuomotor neurons that fire both when an action is performed, and when a similar or identical action is passively observed (Rizzolatti and Craighero, 2004). Mirror neurons were first observed using microelectrode recordings of single neurons in area F5 of the monkey premotor cortex (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996) and later also in the PF/PFG complex within the inferior parietal cortex (Gallese et al., 2002; Fogassi et al., 2005; Fogassi and Luppino, 2005).

Several studies have claimed to provide evidence for an analogous frontoparietal mirror system in humans, but there are currently no published studies of recordings from single neurons within putative human mirror areas. Thus, direct evidence for the existence of mirror neurons in humans is lacking (Rizzolatti and Craighero, 2004; Dinstein et al., 2008; Turella et al., 2009). There is, however, a considerable amount of indirect evidence suggesting that a mirror neuron system does exist in humans. Data from fMRI studies, for example, have shown that there are brain areas in humans that exhibit overlapping activation for observed and executed actions (Chong et al., 2008; Dinstein et al., 2007). It is widely believed that the pars opercularis of the posterior inferior frontal gyrus (Brodmann area 44) is the human equivalent of monkey area F5; and that the rostral inferior parietal lobule (IPL) is the human equivalent of area PF/PFG (for reviews, see Rizzolatti et al., 2001; Rizzolatti, 2005; Rizzolatti and Craighero, 2004; Iacoboni and Dapretto, 2006; Fabbri-Destro and Rizzolatti, 2008; but see Turella et al., 2009; Keyers and Fadiga, 2008; Gazzola and Keyers, 2008 for a critical review on additional regions associated with the human mirror system).

Here, for the first time, we review human fMRI studies that have studied imitation of hand and finger movements. We used a quantitative meta-analysis (Laird et al., 2005) to critically investigate, in an unbiased manner, the frontal and parietal regions – both of which have been identified as containing classically defined mirror neurons in monkeys – that are reliably involved in imitation.

2. Materials and methods

2.1. Literature selection

We searched (November 1, 2008) the Web of Science database (<http://apps.isiknowledge.com>) using the keywords ‘fMRI’ and ‘imitation’. This revealed 129 papers. The inclusion criteria for this review are listed as follows:

1. Studies that used fMRI in healthy subjects were included and studies that used only other techniques (PET, SPECT, TMS, MEG, behavioural studies and review articles) were excluded. We only included fMRI studies because we wanted to have approximately comparable spatial and temporal resolution. Seventy-one of the 129 papers found met this criterion.
2. Studies that used an imitation condition (e.g., showing a static picture or movie of an action that participants were later

required to execute) were included. Studies that did not include an imitation condition (e.g., those that included only execution or imagery or observation) were excluded. Twenty-six of the remaining 71 papers met this criterion.

3. Only studies with imitation of hand and/or finger movements were included, because the original descriptions of mirror neurons in monkeys were based upon single-cell recordings made while monkeys were doing these movements. Studies that did not use these conditions (e.g., imitation of facial expressions or foot actions only) were excluded. Twenty of the 26 remaining papers met this criterion.
4. To date, mirror neurons have only been reported in frontal and parietal regions in monkeys. Moreover, some human fMRI studies (Iacoboni et al., 1999; Williams et al., 2006) of imitation only analyzed activity within frontal and parietal areas, or only reported on voxels in these regions. Thus, we included studies that analyzed frontal and parietal regions alone, or the whole brain, and that reported all the significant voxels in the relevant areas. Studies that did not report all the significant voxels in the frontal and parietal regions were excluded. Sixteen of the 20 remaining papers met this criterion.

An additional search in PubMed (<http://www.ncbi.nlm.nih.gov/pubmed>) with the same keywords found two extra papers (Iacoboni et al., 1999; Koski et al., 2003). Additionally, two papers (Grèzes et al., 2003; Cunnington et al., 2006) not found in the databases but known to the authors that matched the criteria were included. Twenty studies matched all the criteria. Table 1 lists the studies that were included in the meta-analysis.

2.2. Selection of contrasts

The contrasts used in the original studies to determine brain regions crucial for imitation and the mirror system were also applied in the current meta-analysis here. These contrasts yielded one of five outcomes: (1) an increase in activation in the imitation condition compared with execution and/or an observation-alone condition (Iacoboni et al., 1999; Koski et al., 2003; Buccino et al., 2004; Chaminade et al., 2005; Cunnington et al., 2006; Makuuchi, 2005; Makuuchi et al., 2005; Jackson et al., 2006; Williams et al., 2006, 2007; Jonas et al., 2007; Rocca et al., 2008); (2) common activation across imitation, execution and observation conditions (Grèzes et al., 2003; Aziz-Zadeh et al., 2006; Montgomery et al., 2007; Montgomery and Haxby, 2007; Vogt et al., 2007); (3) greater activation for imitating novel vs. known finger configurations (Tanaka et al., 2001); (4) greater activation for imitating goal-directed actions vs. non-goal-directed actions (Koski et al., 2002); or (5) greater activity for imitating variable (16 different) gestures vs. stereotyped (2 different) gestures (Mühlau et al., 2005).

2.3. Selection of foci

From the 20 studies we included all voxels located within the frontal or parietal lobes that survived the FWE, $p < 0.05$ threshold corrected for the whole brain. If the study did not report this threshold we used a Z-value of 4.5 (which corresponds approximately to a FWE, $p < 0.05$ threshold corrected for the whole brain). If only a T-value was given in the paper, we transformed the T-value to a Z-value in Matlab (Mathworks Inc., USA) using the `spm_t2z` algorithm implemented in SPM5 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London; <http://www.fil.ion.ucl.ac.uk/spm>) and corrected for the degrees of freedom used in the study. This strategy was used to make the inclusion criteria identical for each study. As noted above, we were only interested in foci located in the frontal or parietal cortex because these are the only regions in monkeys within which mirror neurons for hand or

Table 1

Overview of the 20 studies that matched all the inclusion (see Section 2) criteria. Comparison = crucial comparison used in the study. Voxels = voxels located in the frontal and parietal lobe in the study that survived the FWE corrected for whole brain analysis threshold of $p < 0.05$, or Z-value of 4.5 in the comparison. ns = no suprathreshold voxels in parietal or frontal regions.

Study	Comparison	Voxels: x, y, z (Z-value)
Iacoboni et al. (1999)	Imitation > execution > observation	–50, 12, 12 (5.05); 37, –40, 57 (5.07); 58, –24, 32 (5.95)
Tanaka et al. (2001)	Novel non-symbolic vs. symbolic finger configurations	No suprathreshold voxels in the frontal or parietal lobe
Koski et al. (2002)	Goal-directed vs. non-goal-directed	–16, 0, 64 (4.8); 13, –4, 62 (4.9)
Grèzes et al. (2003)	Conjunction: gesture towards and object (OGO-OB and EGO-EB)	40, 0, 52 (6.2); 32, –52, 58 (inf); –34, –52, 58 (5.9); 60, –32, 24 (4.6)
Koski et al. (2003)	Specular imitation vs. control motor task	5, –22, 64 (4.8); –14, 16, 52 (5.0); –4, –50, 58 (4.7); 32, –82, 34 (4.5)
Buccino et al. (2004)	IMI-3 vs. non-IMI-3 and IMI-3 vs. EXE-3	No suprathreshold voxels in the frontal or parietal lobe
Chaminade et al. (2005)	Imitating (identical action with the same limb) vs. different action with the other limb	No suprathreshold voxels in the frontal or parietal lobe
Cunnington et al. (2006)	Imitation vs. self-selection	52, –29, 29 (4.86); 30, –53, 50 (4.58); –35, –39, 59 (4.62)
Makuuchi (2005)	Imitation vs. symbolic instruction	No suprathreshold voxels in the frontal or parietal lobe
Makuuchi et al. (2005)	Imitation > execution (masked by imitation vs. rest)	–29, –69, 22 (4.77)
Mühlau et al. (2005)	Conjunction of all gestures (variable vs. stereotyped)	10, –65, 57 (>7); –8, –69, 51 (>7); –4, –63, 57 (>7); –55, –25, 34 (>7); –50, –33, 33 (>7); –36, –41, 37 (>7); 57, –21, 40 (6.7); 63, –26, 29 (5.9); 46, –38, 57 (6.4); –42, 5, 24 (>7); 50, 11, 6 (6.6); –22, 5, 53 (>7); –16, –6, 68 (6.6); 26, 5, 62 (>7)
Aziz-Zadeh et al. (2006)	Left and right visual field presentation (observation, execution and imitation) vs. rest	–41, 10, 34 (4.7); 39, –14, 56 (5.1); 36, –4, 56 (5.3); 54, 7, 26 (4.6); 38, 0, 54 (4.9); 28, –56, 50 (4.5); 12, 2, 66 (5.3); 1, 6, 52 (4.9); –16, 0, 64 (4.8); –46, 2, 48 (4.7); –30, –5, 60 (5.3); –33, –22, 62 (5.3); –27, –52, 56 (5.0)
Jackson et al. (2006)	Imitation vs. observation	–24, –16, 69 (5.2); –6, –22, 72 (5.4); –6, –38, 71 (5.2)
Williams et al. (2006)	Imitation vs. action execution	59, –26, 27 (4.73)
Jonas et al. (2007)	Imitative finger movements vs. control cues	No suprathreshold voxels in the frontal or parietal lobe
Montgomery et al. (2007)	Significantly active during viewing, imitating and execution in communicative or goal-directed hand gestures	No suprathreshold voxels in the frontal or parietal lobe
Montgomery and Haxby (2007)	Significantly active during viewing, imitating and execution of social hand gestures	No suprathreshold voxels in the frontal or parietal lobe
Vogt et al. (2007)	Conjunction between observation, preparation and imitative execution	–41, –41, 39 (inf); –41, –47, 49 (inf); –15, –63, 57 (6.0); –51, 1, 36 (4.7); –22, –11, 64 (6.6); –24, –14, 53 (5.9); 35, –43, 39 (7.8); 35, –47, 47 (7.7); 13, –63, 56 (5.9); 22, –11, 54 (5.6)
Williams et al. (2007)	Imitation condition vs. incongruous action	No suprathreshold voxels in the frontal or parietal lobe
Rocca et al. (2008)	Mirror neuron system vs. simple task activations in healthy volunteers	No suprathreshold voxels in the frontal or parietal lobe

finger movements have been found. If the voxels reported in the original study were reported in MNI space we transformed them to Talairach space using the icbm2tal algorithm (Lancaster et al., 2007) used in the Ginger ALE software (Laird et al., 2005).

2.4. Activation likelihood estimation

To identify regions of consistent activation in the frontal and parietal cortex, we performed an activation likelihood estimation (ALE) analysis (Turkeltaub et al., 2002; Laird et al., 2005). ALE is a quantitative method for estimating consistent activation across different imaging studies (Grosbras et al., 2005; Sörös et al., 2008; Chan et al., 2009). The ALE analysis was conducted using the standard settings in the Ginger ALE software (Laird et al., 2005). ALE maps of the foci were created using a full-width half-maximum (FWHM) of 10 mm. Statistical significance was determined using a permutation test of randomly generated foci. Five thousand permutations were computed using the same FWHM value, and the same number of foci was used in computing the ALE values. The test was corrected for multiple comparisons using the false discovery rate (FDR) method with $p < 0.05$, and a standard minimum volume of 250 mm³ voxels was used to define a cluster. The maps of the ALE values were superimposed on a colin.nii (Laird et al., 2005) atlas using MRIcron software (<http://www.mricron.com/mricron/install.html>).

2.5. Label-based reviews

We conducted an additional label-based review by importing the voxels reported in Table 1 into the Talairach Daemon software

(<http://www.talairach.org/daemon.html>; Lancaster et al., 2000) using the 'search for nearest gray matter' function. We defined Brodmann areas for each voxel and calculated the following values per Brodmann area:

- (1) How many significant voxels in total were reported for the area. For the frontal lobe, we were specifically interested in any difference between Brodmann area 6 (premotor cortex) and Brodmann area 44 (Broca's area and the suggested human homologue of monkey F5 mirror region). For the parietal lobe we were interested in differences between Brodmann area 7 (superior parietal lobule) and Brodmann area 40 (inferior parietal lobule and suggested human homologue of the PF/PFG mirror region in monkeys).
- (2) To ensure that any difference found in step (1) was not simply a reflection of the influence of just a few studies, we also investigated how many studies contributed a significant voxel in the relevant area.

3. Results

3.1. Activation likelihood estimation

The ALE meta-analysis revealed 11 significant clusters in total (see Fig. 1).

3.2. Frontal lobe

The ALE meta-analysis revealed 3 significant clusters in the frontal lobe. All clusters were centred in the dorsal part of

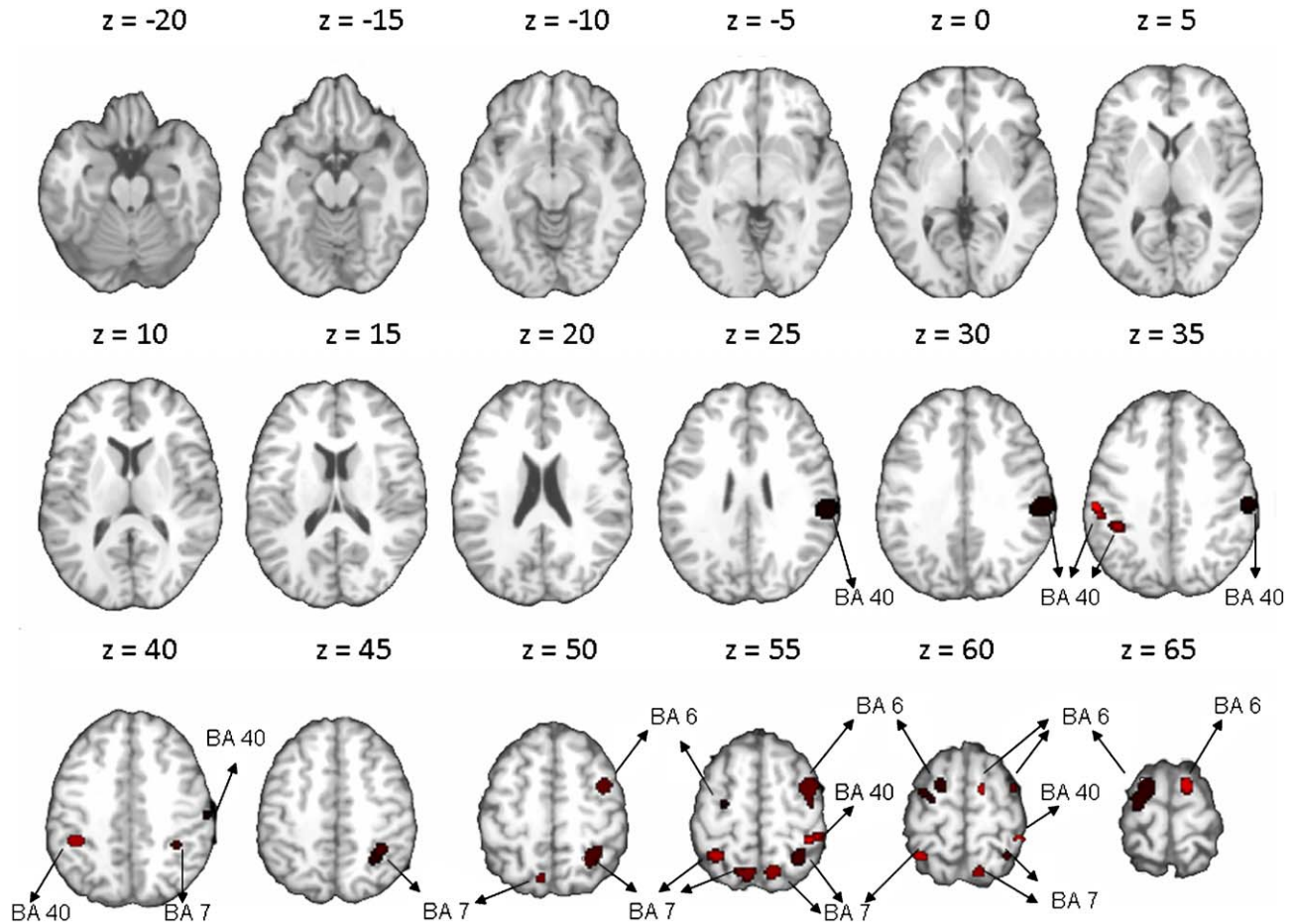


Fig. 1. Results from the activation likelihood estimation. Display of the significant clusters in frontal and parietal cortex (corrected for multiple comparisons using the false discovery rate (FDR) method of $p < 0.05$). Arrows indicate the Brodmann area (BA) corresponding to the center of the cluster.

premotor cortex (BA 6, see Fig. 1), with two clusters lying along the posterior part of the superior frontal gyrus (cluster 1 (left SFG): including 2444 mm³ voxels, centered at: $x = -19$, $y = -6$, $z = 64$; cluster 2 (right SFG): 520 mm³ voxels, $x = 13$, $y = -1$, $z = 64$) and the third cluster along the posterior part of the right middle frontal gyrus (cluster 3: 1448 mm³ voxels, $x = 38$, $y = -2$, $z = 54$).

3.3. Parietal lobe

The ALE meta-analysis revealed 8 significant clusters in the parietal lobe. Four clusters included Brodmann area 40. Two were located in the right inferior parietal lobule (cluster 1: 2512 mm³ voxels, $x = 59$, $y = -26$, $z = 29$; cluster 2: 384 mm³ voxels, $x = 41$, $y = -39$, $z = 57$) and two were located in the left inferior parietal lobule (cluster 3: 608 mm³ voxels, $x = -39$, $y = -41$, $z = 38$; cluster 4: 320 mm³ voxels, $x = -53$, $y = -29$, $z = 34$). The remaining four clusters included Brodmann area 7. Two clusters were located in the right superior parietal lobule (cluster 1: 1840 mm³ voxels, $x = 31$, $y = -51$, $z = 50$; cluster 2: 656 mm³ voxels, $x = 11$, $y = -64$, $z = 56$) and two were located in the left superior parietal lobule (cluster 3: 664 mm³, $x = -8$, $y = -65$, $z = 55$; cluster 4: 552 mm³, $x = -31$, $y = -52$, $z = 57$).

3.4. Label-based review

3.4.1. Total number of significant voxels per region

Fifty-eight voxels survived the threshold, as shown in Table 1.

3.4.2. Frontal lobe

Brodmann area 6 (see Fig. 2A) included significantly more of the suprathreshold voxels (21 out of 58 voxels) than Brodmann area 44 (2 out of 58 voxels), $\chi^2(1, N = 58) = 19.58$, $p < 0.0001$. We adjusted for the size difference between BA44 and BA6 by combining BA 44 with two other adjacent areas associated with the human mirror system (BA45 and the ventral part of BA6 (BA6 voxels with a z-coordinate equal to or below 45)) and comparing this region with the dorsal part of BA6 (z-coordinate above 45). The latter area still had significantly more of the suprathreshold voxels (20 out of 58 voxels) than the three other areas combined (3 out of 58 voxels), $\chi^2(1, N = 58) = 15.67$, $p < 0.0001$.

3.4.3. Parietal lobe

There was no difference in significant voxels (see Fig. 2A) between Brodmann area 7 (11 out of 58 voxels) and Brodmann area 40 (14 out of 58 voxels), $\chi^2(1, N = 58) = 0.46$, $p > 0.25$.

3.4.4. Total number of studies with a significant voxel per region

Eleven out of the 20 studies showed at least one significant voxel in the frontal or the parietal lobe.

3.4.5. Frontal lobe

Activation in Brodmann area 6 was reported in significantly more studies (6 out of 11 studies with a significant voxel) than activation in Brodmann area 44 (2 out of 11 studies), $\chi^2(1, N = 11) = 3.14$, $p = 0.038$ (see Fig. 2B).

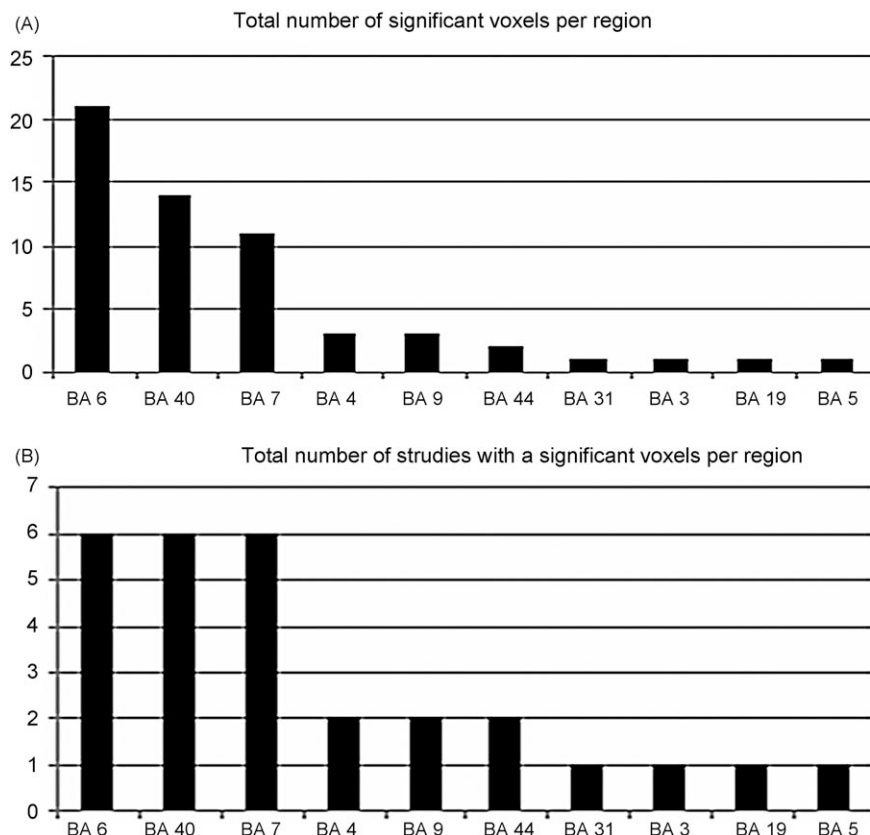


Fig. 2. Label-based review of the studies that showed one or more significant voxels. (A) Overview of the total number of significant voxels per Brodmann area. (B) Overview of the total number of studies with a significant voxel per Brodmann area.

3.4.6. Parietal lobe

There was no significant difference in the number of studies that reported activity in Brodmann area 7 (6 out of 11 studies) compared with Brodmann area 40 (6 out of 11 studies), $\chi^2(1, N = 11) = 0.0, p > 1$ (see Fig. 2B).

4. Discussion

We critically reviewed 20 published fMRI studies that examined the role of frontal and parietal brain regions in imitation. Our ALE meta-analysis shows that in the frontal lobe, the dorsal premotor cortex rather than the inferior frontal gyrus is consistently active in fMRI studies that have investigated imitation of hand and finger gestures. This effect was not driven by a single study: in the label-based review both the total number of significant voxels per region, and the total number of studies with a significant voxel per region, was encountered significantly more often in the premotor cortex (BA 6) than the pars opercularis of the inferior frontal gyrus (BA 44). It is also clear from Fig. 1 that the significant clusters were localized more within the dorsal segment of Brodmann area 6 (dorsal premotor cortex and supplementary motor area) than in its ventral part (ventral premotor cortex). In the parietal lobe, the superior parietal lobule, intraparietal sulcus and inferior parietal lobule were all consistently activated (see Fig. 1). There were no significant differences in reported activations between the superior parietal lobule (BA 7) and inferior parietal lobule (BA 40) (see Fig. 2).

The first fMRI study on imitation (Iacoboni et al., 1999), which used a fixed-effects analysis on data from 12 subjects, found more activation in the pars opercularis of the inferior frontal gyrus (BA 44) during imitation of simple repetitive hand movements compared with execution and passive observation. On the basis

of this finding, it has been suggested that the mirror neuron system is involved in imitation (Heyes, 2001; Rizzolatti et al., 2001; Buccino et al., 2004; Rizzolatti and Craighero, 2004; Brass and Heyes, 2005; Iacoboni, 2005; Rizzolatti, 2005; Iacoboni and Dapretto, 2006). Indeed, several subsequent studies of imitation have used a region of interest approach (Koski et al., 2002, 2003; Grèzes et al., 2003; Aziz-Zadeh et al., 2006; Montgomery and Haxby, 2007) to target specifically the posterior inferior frontal gyrus (IFG), plus the adjacent ventral premotor cortex (PMC). This a priori focus on a certain region can lead to a common belief that this mirror region is crucially involved in imitation. But a recent replication of the Iacoboni et al. (1999) study showed no evidence of increased activation in the inferior frontal gyrus or adjacent ventral prefrontal region during imitation compared with execution, even when the threshold was lowered to $p = 0.05$ uncorrected (Williams et al., 2006; see also Jonas et al., 2007 for similar results). TMS stimulation of the left and right pars opercularis, on the other hand, did show an increase in the absolute error rate during an imitation task compared with a control task (Heiser et al., 2003). Makuuchi (2005) suggests that area 44 is more involved in execution timing than imitation. Evidence that monkeys appear to be relatively poor imitators (Whiten and Ham, 1992; Visalberghi and Fragaszy, 2001) also calls into question the crucial role of the mirror neuron system in imitation.

Iacoboni and Dapretto (2006) have suggested a 'core circuit' for imitation that includes three regions. Two of these regions form part of the mirror neuron network: the posterior inferior frontal gyrus (IFG) plus adjacent ventral premotor cortex (PMC), and the rostral part of the inferior parietal lobule (IPL). The third region, the posterior part of the superior temporal sulcus (STS), is outside the classically defined mirror neuron system. Our meta-analysis suggests that in the frontal lobe the dorsal part of the premotor

cortex, rather than the posterior IFG plus adjacent ventral premotor cortex, are consistently activated in fMRI studies of imitation. In the parietal lobe, our findings implicate both the inferior and superior parietal lobule in imitation of hand and finger actions. Because the human homologue of monkey area F5 is believed to be the pars opercularis of the IFG (Brodmann area 44; Rizzolatti and Craighero, 2004), our meta-analytic results suggest that at least the frontal node of the mirror neuron network is not necessary for imitation.

In conclusion, for the first time, our critical meta-analysis shows which frontal and parietal regions are most consistently involved during imitation in fMRI studies. The superior parietal lobule, inferior parietal lobule, and the dorsal part of the premotor cortex are all commonly involved in imitation. Our results question the crucial role of the frontal mirror neuron area, the pars opercularis of the IFG, during imitation and suggest that parietal and frontal regions which extend beyond the classical mirror neuron network are crucial for imitation.

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