Mirroring others' emotions relates to empathy and interpersonal competence in children

Jennifer H. Pfeifer,[a,b] Marco Iacoboni,[a,b,c] John C. Mazziotta,[a,d,e] and Mirella Dapretto[a,b,c,*]

[a]*Ahmanson-Lovelace Brain Mapping Center, Jane and Terry Semel Institute for Neuroscience and Human Behavior at UCLA, Los Angeles, CA 90095-7085, USA*
[b]*FPR-UCLA Center for Culture, Brain, and Development, Los Angeles, CA 90095-1563, USA*
[c]*Department of Psychiatry and Biobehavioral Sciences, David Geffen School of Medicine at UCLA, Los Angeles, CA 90095-7085, USA*
[d]*Department of Neurology, David Geffen School of Medicine at UCLA, Los Angeles, CA 90095-1769, USA*
[e]*Department of Radiological Sciences and Pharmacology, David Geffen School of Medicine at UCLA, Los Angeles, CA 90095-1735, USA*

The mirror neuron system (MNS) has been proposed to play an important role in social cognition by providing a neural mechanism by which others' actions, intentions, and emotions can be understood. Here functional magnetic resonance imaging was used to directly examine the relationship between MNS activity and two distinct indicators of social functioning in typically-developing children (aged 10.1 years ± 7 months): empathy and interpersonal competence. Reliable activity in pars opercularis, the frontal component of the MNS, was elicited by observation and imitation of emotional expressions. Importantly, activity in this region (as well as in the anterior insula and amygdala) was significantly and positively correlated with established behavioral measures indexing children's empathic behavior (during both imitation and observation) and interpersonal skills (during imitation only). These findings suggest that simulation mechanisms and the MNS may indeed be relevant to social functioning in everyday life during typical human development.
© 2007 Elsevier Inc. All rights reserved.

The capacity to code the 'like me' analogy between self and others may represent a basic prerequisite for the development of social cognition (Meltzoff, 2005; Meltzoff and Brooks, 2001; Meltzoff and Moore, 1977), allowing for meaningful social bonds to be established between individuals. It has been proposed that the mirror neuron system (MNS) may be the neurophysiological mechanism at the basis of this self/other equivalence (Gallese et al., 2004). First described in the ventral premotor cortex (area F5) of the macaque brain but later also found in the inferior parietal lobule

(area PF), mirror neurons fire both when a monkey executes goal-related hand and mouth actions as well as when it observes the same actions being performed by others (Ferrari et al., 2003; Gallese et al., 1996; Umilta et al., 2001). This MNS is thus thought to constitute a neural substrate for understanding others' actions, as well as their intentions (Fogassi et al., 2005), via a 'simulation' mechanism whereby seeing the actions of others elicits neural activity in cells that are active when we perform those actions ourselves (Gallese and Goldman, 1998). The presence of an analogous neural system in the human brain – encompassing the pars opercularis of the inferior frontal gyrus and adjacent ventral premotor cortex, as well as the anterior inferior parietal lobule – has subsequently been demonstrated in several independent studies (for reviews, see Iacoboni and Dapretto, 2006; Rizzolatti and Craighero, 2004) of imitation (Buccino et al., 2004; Iacoboni et al., 1999; Koski et al., 2003, 2002; Leslie et al., 2004; Molnar-Szakacs et al., 2005), action observation (Buccino et al., 2001; Johnson-Frey et al., 2003; Leslie et al., 2004), and intention understanding (Iacoboni et al., 2005).

Relevant to the proposed role of the MNS in social cognition is evidence suggesting that – in concert with activity in the anterior insula and amygdala – the MNS may also be involved in decoding the emotional states of others (Carr et al., 2003; Dapretto et al., 2006; Leslie et al., 2004; Schulte-Ruther et al., 2007; van der Gaag et al., 2007). According to the embodied model of emotion understanding proposed by Carr et al. (2003), the configuration of facial muscles denoting a particular emotional expression (e.g., furrowed eyebrows, scrunched up nose, and pursed lips in the case of anger) is indeed an action associated with a motor plan which is activated – via the firing of mirror neurons – both when displaying a given facial expression oneself, and when observing that expression in another individual. As connected through the anterior insula (Augustine, 1996), the frontal component of the MNS (i.e., pars opercularis and adjacent ventral premotor cortex) would then modulate activity within the limbic system (i.e., the

* Corresponding author. UCLA Department of Psychiatry and Biobehavioral Sciences, Ahmanson-Lovelace Brain Mapping Center, Room 101, 660 Charles E. Young Drive South, Los Angeles, CA 90095-7085, USA. Fax: +1 310 794 7406.
E-mail address: mirella@loni.ucla.edu (M. Dapretto).

Available online on ScienceDirect (www.sciencedirect.com).

amygdala) where the emotion associated with a given facial expression is actually felt by the observer. In this model, the internal simulation of others' emotions via this mechanism is also thought to support our ability to empathize with others — particularly the affective ("I feel what you feel") aspects of empathy (for a distinction between emotional and cognitive perspective-taking components of empathy, see Baron-Cohen and Wheelwright, 2004; Davis, 1983; Jackson et al., 2005; Lawrence et al., 2006; for an additional distinction between emotional empathy and motor empathy, see Blair, 2005).

A number of recent studies have provided empirical evidence of a link between several different aspects of empathy and activity in the MNS system, narrowly defined as the pars opercularis and adjacent ventral premotor cortex, as well as the anterior inferior parietal lobule (i.e., the human homologues of areas F5 and PF in the monkey brain where mirror neurons were first discovered using single cell recordings). MNS activity in response to non-emotional stimuli has been associated with cognitive aspects of empathy, such as perspective-taking abilities (Gazzola et al., 2006), as well as with empathic concern (Kaplan and Iacoboni, 2006). With respect to emotionally-laden stimuli, personal distress (as well as perspective-taking, albeit to a lesser extent) has been associated with MNS activity in response to disgusted and pleased emotional expressions (Jabbi et al., 2007). Emotional empathy and empathic concern have also been linked to MNS activity in the right inferior frontal cortex while viewing angry and fearful facial expressions (Schulte-Ruther et al., 2007).

With regard to the role of the MNS in empathizing with others' pain, the evidence is less clear. Several studies have not reported significant activity within MNS regions in response to the perception of pain in others. Rather, both feeling pain and observing someone else experience pain have been consistently associated with robust activation in the anterior cingulate cortex and anterior insula (Botvinick et al., 2005; Jackson et al., 2006, 2005; Lamm et al., 2007; Saarela et al., 2006; Singer et al., 2004, 2006), with activity in this circuitry also shown to be related to several indicators of empathic tendencies (Lamm et al., 2007; Saarela et al., 2006; Singer et al., 2004, 2006). One study did find, however, that when perceiving pain from others' faces, various indices of affect sharing were positively correlated with activity in a cluster encompassing the anterior insula as well as the inferior frontal gyrus (though this appeared to involve the pars triangularis rather than the pars opercularis; Saarela et al., 2006). Furthermore, in another recent study relating neural activity associated with the observation of pain to several indicators of dispositional empathy (Lamm et al., 2007), significant correlations were found between emotional contagion and activity in both frontal and parietal MNS regions, although this activity was attributed to a general role of these areas in motor control, rather than to mirroring mechanisms.

The limited MNS involvement observed in these studies of empathy for pain may indicate that the sharing of affective responses can be achieved without relying on motor circuitry, as suggested by de Vignemont and Singer (2006; but see Avenanti et al., 2005, for evidence of sensorimotor involvement in empathy for pain). These seemingly discrepant findings, however, may also reflect the fact that the designs and stimuli used in these studies (e.g., the use of abstract cues to indicate that a person was in pain and/or the repeated presentation of the same emotional expression) might not have been suited to elicit significant MNS activity. Regardless, these findings suggest that the link between distinct aspects of empathy and MNS activity in response to a variety of emotionally-laden stimuli could benefit from additional examination. Furthermore, given that all previous studies were conducted in adults, it may be valuable to extend this investigation to a developmental population.

What about the more general hypothesis that MNS may also play a significant role in social cognition? This issue remains rather controversial in the field. Some have championed a simulation theory of 'mind reading' grounded on mirroring mechanisms (Gallese, 2006; Gallese and Goldman, 1998; Keysers and Gazzola, 2006), whereby we come to understand others by implicitly simulating their actions, intentions, and emotions (as well as sensations) in our minds — thus relying on our own mental states to inform our understanding of other individuals (for a discussion of different shared representation accounts of social cognition, see Decety and Grezes, 2006). Others, however, have been rather skeptical about the role played by mirroring mechanisms in social cognition (Jacob and Jeannerod, 2005), even arguing that mirror neurons may at best support the representation of "simple actions and some basic emotions (most plausibly, disgust and fear)" (Saxe, 2005, p. 174). At present, direct empirical evidence bearing on this broader issue is lacking, although numerous findings of MNS dysfunction in autism (for reviews, see Iacoboni and Dapretto, 2006, and Oberman and Ramachandran, 2007) are consistent with the hypothesis of MNS involvement in social cognition, given that social deficits are a hallmark of this disorder. Notably, in one study where MNS functioning in children with autism was directly related to symptom severity in the social domain, significant negative correlations were found between activity in the frontal component of the MNS and two independent measures of social impairment (Dapretto et al., 2006). However, it remains to be determined whether the relationship between MNS activity and interpersonal skills exist only in this clinical population, or whether the MNS can also explain individual variability in typically-developing children.

To summarize, the goals of this functional magnetic resonance imaging (fMRI) study were to further elucidate the role of the MNS with respect to two separate indices of social functioning – empathy and interpersonal competence – in a sample of typically-developing children. More specifically, using a paradigm previously shown to reliably activate the putative MNS in both adults and children (Carr et al., 2003; Dapretto et al., 2006), we examined whether activity elicited by imitation and observation of emotional expressions in the frontal component of the MNS would (i) correlate with children's tendencies to empathize with others, and (ii) also be related to children's interpersonal competence, thus supporting a more general role for the MNS in understanding others.

Materials and methods

Participants

Sixteen children (nine boys and seven girls) participated in the study (with no overlap between these participants and those of Dapretto et al., 2006). Their age ranged from 9.6 to 10.8 years ($M=10.2$, $SD=0.4$). Participants had no history of significant medical (e.g., complications during gestation or birth, systematic malignancies), psychiatric (e.g., ADHD, autism), or neurological (e.g., seizures, myotonic dystrophy) disorders based on parental reports on a medical questionnaire. All children exceeded an exclusionary criterion set for full scale IQ > 80 ($M=116$, $SD=13$). The sample was predominantly right-handed (14 right-, 1 mixed-,

and 1 left-handed; based on self-reported Stated Hand Preference and parent-reported Waterloo Handedness Questionnaire). Children also underwent a brief neurological screening (Quick Neurological Screening Test; Mutti et al., 1988), and no gross structural abnormalities were detected in participating children during scanning. The UCLA Institutional Review Board approved the study, and written informed consent was obtained from children and their parents.

fMRI tasks

Full-color, whole-face stimuli comprising an ethnically diverse set of 16 individuals (8 male, 8 female) expressing 5 different emotions (angry, fearful, happy, neutral, or sad) were selected from the MacBrain Face Stimulus Set (http://www.macbrain.org/faces/index.htm). During one scan (Imitation), children were asked to "imitate the expression on each face." During the other scan (Observation), children were asked to "just look at the expression on each face." The order of imitation and observation scans was counterbalanced between participants. Both imitation and observation scans consisted of 96 events lasting 3 s each. These events comprised the 80 whole-face stimuli described above (16 per emotion) and an additional 16 null events (fixation cross). The order of events was determined using Optimize Design 11 (Wager and Nichols, 2003) to maximize contrast detection efficiency. Similar observation–imitation paradigms have been used in prior imaging studies (Carr et al., 2003; Dapretto et al., 2006; Iacoboni et al., 1999; Leslie et al., 2004) to elicit mirror neuron activity. Since mirror neurons activate both when performing an action oneself and observing others perform that same action, asking participants to imitate an action they observed ensures a close match between the observed and executed action.

Behavioral measures

At least 1 day prior to the fMRI session, children filled out a modified version of the Interpersonal Reactivity Index (IRI; Davis, 1983), indicating to what extent short phrases described them on a 5-point scale (from "does not describe me at all" to "describes me very well"). This measure was chosen because it taps a variety of aspects of empathy, and is not limited to either emotional or cognitive components, although it does not directly address motoric aspects like mimicry. Sample items from each of the subscales include: "Sometimes I don't feel very sorry for other people when they are having problems" (empathic concern, reverse coded), "Being in a tense emotional situation scares me" (personal distress), "I sometimes try to understand my friends better by imagining how things look from their point of view" (perspective-taking), and "I really get involved with the feelings of the characters in a story" (fantasy). While this scale was developed to assess empathy in adults, the validity of a modified version of the IRI was demonstrated in a large-scale study of 478 children ranging in age from second to sixth grade (Litvack-Miller et al., 1997). This modified IRI was found to be a reliable assessment of empathy in children over repeated administrations and was significantly associated with a variety of objective measures of prosocial behaviors that clearly indicate dispositional empathy (including teacher ratings of each child's tendency to comfort, help, share, and cooperate). Hence, although in this study actual social behavior was not measured, the high correlations found between the IRI and assessments of prosocial behavior (even after

controlling for grade and gender) suggest the IRI is strongly indicative of predispositions towards real empathic behavior.

Children's parents also filled out the Interpersonal Competence Scale (ICS; Cairns et al., 1995) at least 1 day prior to the fMRI session, indicating the most appropriate rating for their child on a 7-point scale (e.g., from "always" or "very" to "never" or "not"). Sample items include: "Gets into trouble at school," "Shy," "Has lots of friends," and "Popular with boys/girls." The ICS has been extensively validated in ethnically and socio-economically diverse children across grades 1–12 and has been used to predict outcomes such as academic performance, motivational attributions, social relations, and loneliness (Bellmore et al., 2004; Estell et al., 2002; Mahoney and Cairns, 1997; Mahoney et al., 2005; Rodkin et al., 2000).

The IRI and ICS were not significantly correlated with each other ($r = 0.32$, *ns*). This does not contradict the results of the study validating the use of the IRI in children (Litvack-Miller et al., 1997), which related empathy to various prosocial behaviors, because that study had a sample size nearly 30 times larger than in the present investigation. For example, the unique relationship between empathic concern and cooperation found in that study was small but nevertheless significant ($r = 0.13$, calculated from the *t* value of a beta weight in a multiple regression). Thus, previous findings and our own both indicate that, while not unrelated, empathy and interpersonal competence are not interchangeable and represent different psychological constructs.

fMRI data acquisition

Data were acquired using a Siemens Allegra 3.0 T MRI scanner. A 2D spin-echo scout (TR = 4000 ms, TE = 40 ms, matrix size 256 by 256, 4-mm thick, 1-mm gap) was acquired in the sagittal plane to allow prescription of the slices to be obtained in the remaining scans. Each imitate or observe scan lasted 4 min and 54 s (gradient-echo, TR = 3000 ms, TE = 25 ms, flip angle = 90°, matrix size 64 by 64, FOV = 20 cm, 36 slices, 3.125-mm in-plane resolution, 3-mm thick). For each participant, a high-resolution structural T2-weighted echo-planar imaging volume (spin-echo, TR = 5000 ms, TE = 33 ms, matrix size 128 by 128, FOV = 20 cm, 36 slices, 1.56-mm in-plane resolution, 3-mm thick) was acquired coplanar with the functional scans. Stimuli were presented to participants through high-resolution magnet-compatible goggles (Resonance Technology, Inc.).

fMRI data analysis

Using Automated Image Registration (Woods et al., 1998a,b), all functional images were a) realigned to correct for head motion and co-registered to their respective high-resolution structural images using a 6-parameter rigid body transformation model, b) spatially normalized into a Talairach-compatible MR atlas (Woods et al., 1999) using polynomial non-linear warping, and c) smoothed using a 6-mm FWHM isotropic Gaussian kernel.

Statistical analyses were implemented in SPM99 (Wellcome Department of Cognitive Neurology, London, UK; http://www.fil.ion.ucl.ac.uk/spm/) and MarsBaR (http://marsbar.sourceforge.net/), a region of interest (ROI) toolbox for SPM99. For each subject, condition effects were estimated according to the general linear model, using a canonical hemodynamic response function, high-pass filtering, and no global scaling. Linear contrasts were employed to assess comparisons of interest within individual participants

(i.e., all expressions vs. null events). Although this contrast was used to maintain consistency with previously published literature in the field (Carr et al., 2003; Dapretto et al., 2006; Iacoboni et al., 1999; Leslie et al., 2004), when the reported analyses were re-run comparing emotional expressions vs. neutral expressions, the same patterns remained.

Random effects analyses were computed using the contrast images generated for each subject. For the Imitation scan (Table 1), activity was considered reliable if it survived $p < 0.001$ at the voxel level (magnitude) as well as correction for multiple comparisons at the cluster level ($p < 0.05$). The observation of emotional expressions was expected to result in reduced activity relative to imitation based on prior findings in the neuroimaging literature in humans (Carr et al., 2003; Dapretto et al., 2006; Iacoboni et al., 1999; Leslie et al., 2004), as well as results from single-cell recording in monkeys. That is, mirror neurons have often been shown to fire at a higher rate when the monkey executes an action itself than when it observes that same action being performed by others; further, only a small percentage of neurons (10–20%) that respond during action execution also respond during observation (e.g., Ferrari et al., 2003; Gallese et al., 1996; Keysers et al., 2003; Kohler et al., 2002). Accordingly, a more liberal threshold was set for the Observation scan, $p < 0.01$ at the voxel level, though activity still needed to survive correction for multiple comparisons at the cluster level ($p < 0.05$) in order to be deemed reliable. Small-volume corrections were applied in some instances to a priori regions of interest constituting the nodes of the network proposed in previously published literature (i.e., pars opercularis in posterior inferior frontal gyrus, insula, and amygdala; see Table 1).

To explore whether brain activity was related to empathy and interpersonal competence, separate simple regression analyses were conducted within the brain regions significantly activated during imitation or observation (Table 2). Significance levels for these analyses were also set at $p < 0.01$ at the voxel level, with correction for multiple comparisons at the cluster level ($p < 0.05$). Again, small-volume corrections were applied in some instances to the a priori regions of interest specified above. When these regression analyses were repeated with age entered as a covariate, a virtually identical pattern of results was observed, likely due to the minimal age variation in the sample.

Results

As expected, given the nature of the stimuli and the motor task, reliable activation during imitation was seen in primary somato-motor and visual cortices, as well as in extrastriate visual areas. Importantly, imitation of facial emotional expressions was also associated with reliable activation of the MNS (bilateral pars opercularis, adjacent ventral premotor cortex, and rostral inferior parietal lobule), insula, and amygdala (see Table 1, Figs. 1A and 4). The frontal MNS–insula–amygdala circuit was also reliably activated during observation of facial emotional expressions, albeit to a lesser extent — indeed, all regions activated when observing emotional expressions (except for the hippocampus) were also activated when imitating facial expressions. (see Table 1, Figs. 1B and 4). This pattern of activity closely resembles that previously observed in adults (Carr et al., 2003) and, in an independent sample, replicates the first demonstration of mirror neuron-like

Table 1
Peaks of activity during imitation and observation of emotional expressions

Anatomical region	BA	H	Imitation				Observation			
			x	y	z	t	x	y	z	t
Central sulcus	4	L	−46	−16	36	7.23				
	4	R	56	−10	30	10.38				
Precentral gyrus	6	L	−40	2	32	5.57				
	6	R	54	0	30	6.66				
Medial frontal gyrus	6	R	4	0	58	10.39				
Inferior frontal gyrus	44	L	−42	16	8	4.08	−54	4	26	3.99
	44	R	50	6	18	5.46	40	24	18	1.86*
Insula		L	−32	12	10	5.91	−42	−6	6	3.80
		R	36	10	12	4.18	36	4	14	2.25*
Postcentral gyrus	2	L	−48	−18	42	6.34				
	3	R	42	−14	22	4.51				
Inferior parietal lobule	40	L	−52	−34	34	4.72				
	40	R	56	−38	36	4.43				
Fusiform gyrus	37	L	−38	−58	−12	6.43	−44	−56	−10	5.78
	37	R	34	−60	−12	4.50	30	−46	−12	4.56
Lingual gyrus	18	L	−6	−84	2	9.62	−8	−82	0	6.79
	18	R	8	−78	2	6.29	10	−84	4	9.72
Amygdala		L	−24	−6	−10	6.33				
		R	18	−6	−6	8.44	24	−6	−12	3.08*
Hippocampus		L					−28	−20	−6	3.86
Putamen		L	−24	−2	−2	8.73				
		R	30	−4	0	4.82				

For Imitation: $p < 0.001$ (magnitude), corrected for multiple comparisons at the cluster level ($p < 0.05$).
For Observation: $p < 0.01$ (magnitude), corrected for multiple comparisons at the cluster level ($p < 0.05$); * small volume correction for a priori regions of interest.
BA refers to putative Brodmann Area; L and R refer to left and right hemispheres; x, y, and z refer to the Talairach coordinates corresponding to the left–right, anterior–posterior, and inferior–superior axes, respectively; t refers to the highest t score within a region.

Table 2
Relation between empathy and observation, as well as interpersonal competence and imitation

Anatomical region	BA	H	Empathy and observation					Interpersonal competence and imitation				
			x	y	z	t	$p<$	x	y	z	t	$p<$
Inferior Frontal Gyrus	44	R	48	16	22	5.21	0.00001	48	14	12	3.88	0.0001
Precentral Gyrus and Inferior Frontal Gyrus	6/44	L	−54	8	32	4.49	0.0001					
Insula		L						−44	10	4	2.58	0.01
		R	24	24	12	2.87*	0.01	40	10	6	4.43	0.0001
Periamygdala		L	−16	−4	−2	4.10*	0.0001	−26	−10	−14	3.84	0.0001
Fusiform Gyrus	37	L	−34	−62	−10	4.29	0.0001					

$p<0.01$ (magnitude), corrected for multiple comparisons at the cluster level ($p<0.05$); *small volume correction for *a priori* regions of interest.
BA refers to putative Brodmann Area; L and R refer to left and right hemispheres; x, y, and z refer to the Talairach coordinates corresponding to the left–right, anterior–posterior, and inferior–superior axes, respectively; t refers to the highest t score within a region; $p<$ refers to the p value associated with the relevant t score.

responses in classical mirror areas during the observation and imitation of facial emotional expressions in children (Dapretto et al., 2006).

Given that activity in human cortical areas considered to contain mirror neurons was reliably elicited by the observation and imitation task as predicted, the first critical aspect of this investigation was to examine the possible links between MNS activity and empathy in children. Consistent with the hypothesis that the MNS – together with anterior insula and amygdala – may provide a neural substrate for empathy (Carr et al., 2003), activity in these regions varied as a function of the children's scores on the Interpersonal Reactivity Index (IRI; see Table 2, Figs. 2 and 4). Specifically, during the observation of facial emotional expres-

sions, the greater the child's empathic tendencies, the greater the activity in bilateral inferior frontal gyrus and adjacent ventral premotor cortex. In addition, significant correlations were observed

Fig. 2. Relationship between mirror neuron system activity and empathy. Panel A shows that during observation of emotional expressions, activity in MNS regions, insula, amygdala, and fusiform gyrus was positively correlated with children's tendency to empathize. Scatterplots depicting the correlation in right IFG with the overall score on the IRI and the three subscales which also produced significant correlations in this region (personal distress, empathic concern, and fantasy) are shown in panel B, with IRI scores along the ordinate and parameter estimates along the abscissa (for display purposes, the imaging data are thresholded at $t>1.76$, $p<0.05$, corrected for multiple comparisons at the cluster level, $p<0.05$, with a small volume correction for the amygdala in panel A). x, y, and z refer to the Talairach coordinates corresponding to the left–right, anterior–posterior, and inferior–superior axes, respectively.
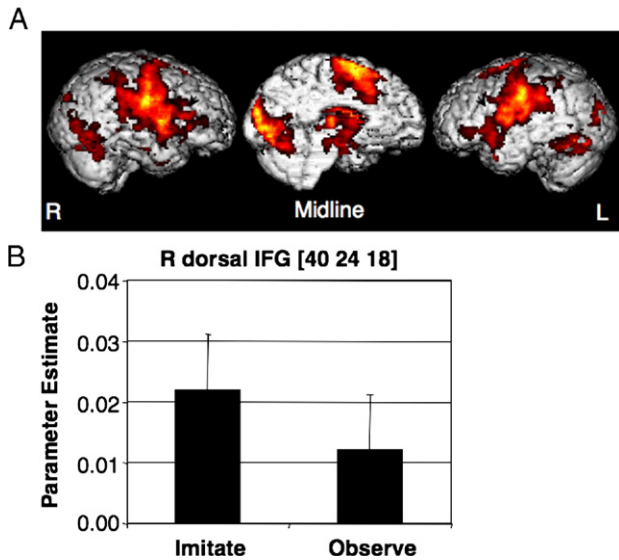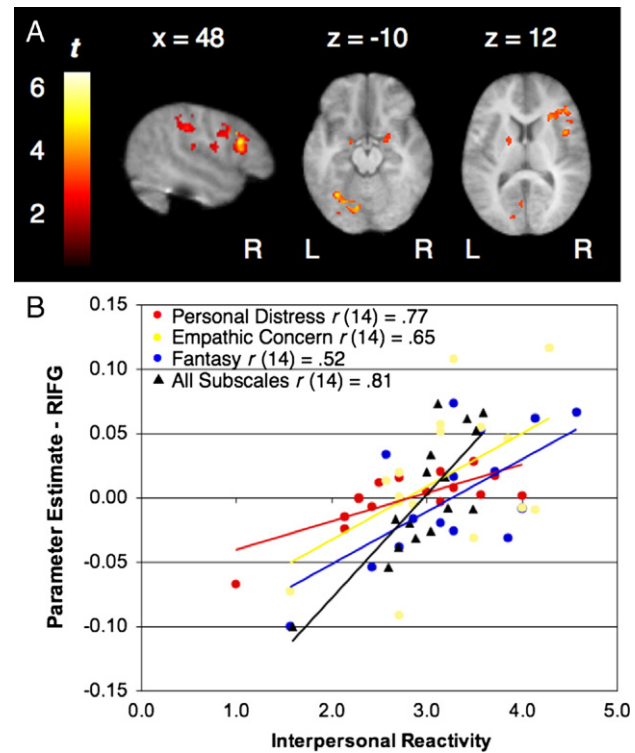
Fig. 1. Mirror neuron system activity in children. Panel A shows increased activity in mirror neuron areas, including pars opercularis, as well as rostral inferior parietal lobule, during imitation of facial expressions compared to null events (for display purposes, the imaging data were thresholded at $t>2.60$, $p<0.01$, corrected for multiple comparisons at the cluster level, $p<0.05$). Also shown are activations in ventral premotor, primary motor, and somatosensory cortex, supplementary motor area, visual cortices, as well as the limbic system including the amygdala. Panel B compares activity in right pars opercularis during imitation and observation of facial emotional expressions.

in the right insula, left amygdala, and left fusiform gyrus. To determine if these results held for the different aspects of empathy tapped by the IRI, separate regression analyses were also conducted with each of the four IRI subscales (see Table 3). For the empathic concern, personal distress, and fantasy subscales, significant correlations were again found in the right inferior frontal gyrus (IFG) and left fusiform gyrus. Significant correlations were also observed in the left IFG as well as in right insular and/or left periamygdalar regions for the empathic concern and personal distress subscales only. For the perspective-taking subscale, no significant correlations were observed. Children's overall scores on the IRI were also significantly correlated with activity during imitation in the right inferior frontal gyrus ([48 2 12], $t=6.48$), right insula ([32 10 8], $t=4.76$), and left FG ([−34 −64 −12], $t=3.40$). Qualitatively speaking, for both observation and imitation the correlations were highest in the pars opercularis, which was the only region for which the clusters survived a more stringent statistical threshold for magnitude ($p<0.001$). Direct tests of the difference in the strength of the reported correlations showed that the correlation between empathy and activity in this region was significantly stronger than those in the right insula (during observation, $t=1.75$, $p=0.05$) and the fusiform gyrus (during imitation, $t=1.81$, $p<0.05$).

The second aim of the study was to assess whether MNS activity would be associated with children's interpersonal competence. In line with the hypothesis that the MNS plays an important role in social behavior, the greater a child's interpersonal skills (as indexed by parental reports on the Interpersonal Competence Scale (ICS)), the greater the activity during imitation in the mirror neuron area in the right inferior frontal gyrus, as well as in the left amygdala, and bilateral insula (see Table 2, Figs. 3 and 4). Just as in the correlations with empathy, the highest correlation was observed in the cluster extending from the right inferior frontal gyrus to the anterior insula, but this correlation was not significantly stronger than those observed in the other regions. Children's scores on the ICS did not significantly correlate with activity during observation.

Finally, for the reader's convenience, we display the overlap between our various results in our primary regions of interest (i.e., the IFG, insular, and amygdalar regions). Fig. 4 illustrates this via color overlays created for both activation conditions (imitation and observation) as well as for the main correlations (with the IRI and the ICS).

Discussion

Our findings confirm that, in children just as in adults, the observation and imitation of emotional expressions elicit significant activity in putative mirror neuron areas in inferior frontal cortex, as well as anterior insula and the amygdala. Further, they indicate a link between activity in these regions and two distinct social cognitive capacities: empathy and interpersonal competence. These results then suggest that even in children, shared neural representations of our own and others' emotions may be readily evoked by simply viewing a variety of emotional expressions and, perhaps more importantly, that inter-individual variability in the extent to which these processes are engaged is significantly associated with abilities that are critical to social development (e.g., Eisenberg, 2004).

Consistent with prior research findings (Botvinick et al., 2005; Carr et al., 2003; Dapretto et al., 2006; Lamm et al., 2007; Leslie et al., 2004; Jabbi et al., 2007; Jackson et al., 2006, 2005; Saarela et al., 2006; Singer et al., 2004, 2006; van der Gaag et al., 2007; Wicker et al., 2003) and the model of emotion understanding via action representation proposed by Carr et al. (2003), significant activity was also observed in the anterior insula, an area known to be involved in the internal representation of subjective feeling states (Craig, 2002, 2003; Critchley et al., 2004), as well as in the amygdala, a region known to be implicated in the generation of affective responses to emotional stimuli (for reviews, see Phelps and LeDoux, 2005; Phillips et al., 2003). In line with the hypothesis that the MNS – specifically its input onto limbic networks of emotion representation – may provide a neural substrate for the ability to empathize with others' emotions (Carr et al., 2003; Leslie et al., 2004), activity in these regions was also found to be significantly correlated with children's tendency to empathize (for similar hypotheses about the relation between shared neural representations and empathy, see also Lamm et al., 2007; Jabbi et al., 2007; Saarela et al., 2006; Singer et al., 2004, 2006).

Of critical importance to the first aim of the present study – namely, to further examine the relationship between the MNS and empathy in typically-developing children – a significant correlation between children's empathy scores and activity during the observation (and imitation) of emotional faces was also found in the putative mirror neuron area in the right pars opercularis of the inferior frontal gyrus. This suggests that the neural mirroring of the

Table 3
Relation between IRI Subscales and Observation

Anatomical region	BA	H	Empathic concern					Personal distress					Fantasy				
			x	y	z	t	$p<$	x	y	z	t	$p<$	x	y	z	t	$p<$
Inferior Frontal Gyrus	44	R	50	18	22	3.57	0.002	44	6	32	4.50	0.0003	48	18	16	2.95	0.005
								50	12	28	4.13	0.001					
Precentral Gyrus and Inferior Frontal Gyrus	6/44	L	−50	0	26	3.70	0.001	−50	2	26	3.33	0.002					
Insula		R						30	22	12	4.17	0.0005					
Periamygdala		L	−18	−4	−8	3.37*	0.002	−18	−6	−2	2.93*	0.005					
Fusiform Gyrus	19/37	L	−28	−68	−10	4.05	0.001	−30	−62	−12	2.90	0.006	−34	−62	−10	2.90	0.006

$p<0.01$ (magnitude), corrected for multiple comparisons at the cluster level ($p<0.05$); *small volume correction for *a priori* regions of interest.
BA refers to putative Brodmann Area; L and R refer to left and right hemispheres; x, y, and z refer to the Talairach coordinates corresponding to the left–right, anterior–posterior, and inferior–superior axes, respectively; t refers to the highest t score within a region; $p<$ refers to the p value associated with the relevant t score.
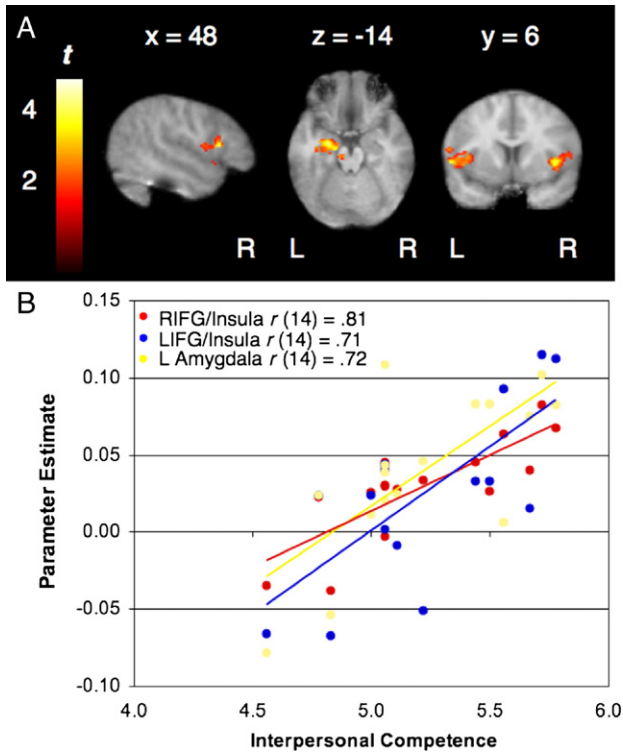
Fig. 3. Relationship between mirror neuron system activity and interpersonal competence. Panel A shows that during imitation of emotional expressions, activity in MNS regions, insula, and amygdala was positively correlated with children's social abilities. Scatterplots depicting the correlation in these three regions with the ICS are shown in panel B, with interpersonal competence scores along the ordinate and parameter estimates along the abscissa (for display purposes, the imaging data are thresholded at $t > 1.76$, $p < 0.05$, corrected for multiple comparisons at the cluster level, $p < 0.05$). x, y, and z refer to the Talairach coordinates corresponding to the left–right, anterior–posterior, and inferior–superior axes, respectively.

emotions displayed by others may play an important role in allowing us not only to 'read' the emotional states of others but also to feel what others feel, consistent with developmental psychologists' conception of empathy as the affective reaction to an emotion displayed by another individual that is virtually identical to what one feels (Eisenberg, 2004; Eisenberg and Fabes, 1998; Hatfield et al., 1994; see de Vignemont and Singer, 2006, for alternative definitions of empathy). Interestingly, while cognitive aspects of empathy (indexed by the perspective-taking subscale of the IRI; Davis, 1983) have been associated with putative MNS responses to non-emotional stimuli (Gazzola et al., 2006), we only observed significant correlations between the more affect-laden subscales of the IRI (particularly empathic concern and personal distress) and activity in the IFG, insula, and amygdala.

How might these findings contribute to our understanding of the neural basis of empathy? Blair (2005) has argued that while motoric empathy may rely upon the MNS, emotional empathy recruits limbic/paralimbic and somatosensory areas. At a more basic level, Keysers and Gazzola (2006) have suggested that whereas action understanding is achieved by shared representations in action-relevant circuitries, emotions are understood by reactivation of emotion-relevant circuitries (e.g., anterior insula, amygdala, secondary sensory cortices). Our findings of strong correlations between empathy and activity in pars opercularis, anterior insula,

and amygdala suggest that *both* the MNS and emotion-relevant circuitries may actually subserve emotional empathy. While corroborating the importance of the anterior insula and amygdala in the affective aspects of empathy, our results also add to an increasing body of evidence suggesting that the MNS may indeed be implicated in more than just action observation, mimicry, and emotional contagion (Gazzola et al., 2006; Kaplan and Iacoboni, 2006; Schulte-Ruther et al., 2007). Interestingly, a very recent study in which participants were asked to concentrate on their own and others' emotional states found that while activity elicited in the frontal component of the MNS was associated with emotional empathy, no correlations emerged in the anterior insula or amygdala (Schulte-Ruther et al., 2007). This suggests that during explicit attribution of emotional states, the involvement of the anterior insula and/or amygdala may be downregulated, consistent with previous studies where amygdalar activity was reduced during affect labeling (Hariri et al., 2000; Lieberman et al., 2007). Future research using connectivity analyses may help to further elucidate the complex interactions amongst the many brain regions that are involved in emotion understanding and empathy.

The ability to understand and empathize with how others feel is integral to successfully navigating social interactions. However, *overtly* mirroring the emotions displayed by others – hence communicating we understand them – is also likely to play a critical role in interpersonal exchanges (just imagine how you
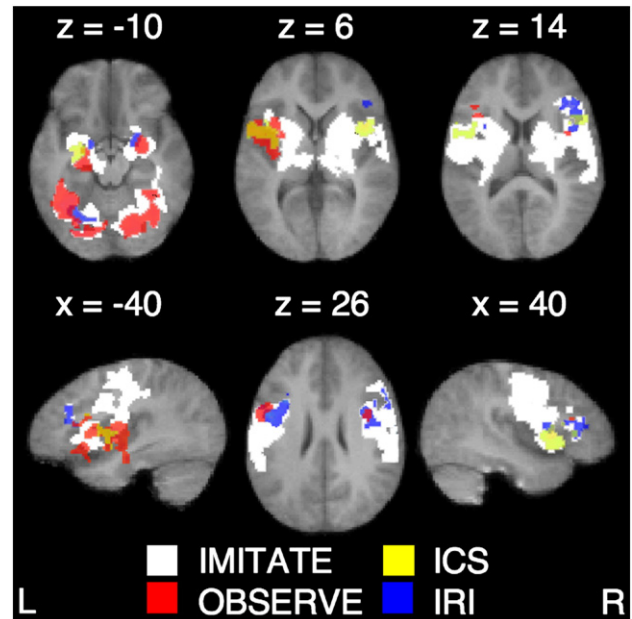

Fig. 4. Overlap Between Imitation, Observation, and Correlations with Empathy and Interpersonal Competence. Regions active during the imitation and observation of emotional expressions (vs. null events) are shown in white and red, respectively. Areas that were more active during imitation in children with greater interpersonal competence are shown in yellow, while those more active during observation in children with greater empathic tendencies are shown in blue. Color overlays are shown at reduced opacity to demonstrate regions of overlap between analyses. For display purposes, all activations were thresholded at $p < 0.05$ for magnitude, corrected for multiple comparisons at the cluster level, $p < 0.05$ (with small volume correction in a priori regions of interests as shown in Tables 1–3). x and z refer to the Talairach coordinates in the left–right and superior–inferior dimensions, respectively. L and R refer to the left and right hemispheres, respectively.

would feel if your display of deep sorrow or intense happiness was met by others displaying a stone face). Indeed, it has been observed that empathy is often associated with imitation (i.e., the nonconscious behavioral mimicry also known as the 'chameleon effect'), which facilitates social interactions by coordinating behaviors and emotions between interacting partners (Bavelas et al., 1996; Chartrand and Bargh, 1999). Thus, a link between interpersonal competence and MNS activity during overt imitation might be expected because of the communicative function that imitative displays of emotion serve (Bavelas et al., 1996). While MNS activity during spontaneous imitation of others' emotional expressions cannot easily be assessed in the context of an fMRI study, reliable correlations were found between children's interpersonal skills and activity in frontal mirror, insular, and amygdalar areas during the intentional imitation of facial emotional expressions. These robust correlations between children's social abilities and activity in the circuitry previously found to be involved during the observation and execution of facial expressions (Carr et al., 2003; Leslie et al., 2004) lend further empirical support to the notion that the MNS – and its interface with the amygdala via the anterior insula – plays a significant role in social interaction by establishing a direct link between others' actions, intentions, and emotions and one's own (Gallese et al., 2004).

Obviously, additional means of discerning others' mental states, ranging from conscious simulation to reasoning based on naïve psychological theories (for discussion, see Adolphs, 2006; Frith and Frith, 2006; Mitchell, 2005) – and the neural systems supporting these functions (such as the superior temporal sulcus, the temporo-parietal junction, and the middle prefrontal cortex; see Frith and Frith, 2006, for a review) – are also important in social cognition and development. As suggested by others (Keysers and Gazzola, 2007; Singer, 2006), future research should explore how these processes may build upon and interact with mirroring and simulation mechanisms to support mentalizing. Together with growing evidence of MNS abnormalities in autism (Bernier et al., 2007; Dapretto et al., 2006; Hadjikhani et al., 2006; Nishitani et al., 2004; Oberman et al., 2005; Theoret et al., 2005; Williams et al., 2006), a disorder characterized by marked impairments in social interaction and theory of mind, the present findings further strengthen the link between the MNS and social functioning.

References

Adolphs, R., 2006. How do we know the minds of others? Domain-specificity, simulation, and enactive social cognition. Brain Res. 1079, 25–35.

Augustine, J.R., 1996. Circuitry and functional aspects of the insular lobe in primates including humans. Brain Res. Rev. 22, 229–244.

Avenanti, A., Bueti, D., Galati, G., Aglioti, S.M., 2005. Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. Nat. Neurosci. 8, 955–960.

Baron-Cohen, S., Wheelwright, S., 2004. The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. J. Autism Dev. Disord. 34, 163–175.

Bavelas, J.B., Black, A., Lemery, C.R., Mullett, J., 1996. "I show you how you feel": Motor mimicry as a communicative act. J. Pers. Soc. Psychol. 50, 322–329.

Bellmore, A.D., Witkow, M.R., Graham, S., Juvonen, J., 2004. Beyond the individual: the impact of ethnic context and classroom behavioral norms on victims' adjustment. Dev. Psychol. 40, 1159–1172.

Bernier, R., Dawson, G., Webb, S., Murias, M., 2007. EEG mu rhythm and imitation impairments in individuals with autism spectrum disorder. Brain Cogn. 64, 228–237.

Blair, R.J.R., 2005. Responding to the emotions of others: dissociating forms of empathy through the study of typical and psychiatric populations. Conscious. Cogn. 14, 698.

Botvinick, M., Jha, A.P., Bylsma, L.M., Fabian, S.A., Solomon, P.E., Prkachin, K.M., 2005. Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. NeuroImage 25, 312–319.

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

Buccino, G., Vogt, S., Ritzl, A., Fink, G.R., Zilles, K., Freund, H.J., Rizzolatti, G., 2004. Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. Neuron 42, 323–334.

Cairns, R.B., Leung, M.-C., Gest, S.D., Cairns, B.D., 1995. A brief method for assessing social development: structure, reliability, stability, and developmental validity of the interpersonal Competence Scale. Behav. Res. Ther. 33, 725–736.

Carr, L., Iacoboni, M., Dubeau, M.C., Mazziotta, J.C., Lenzi, G.L., 2003. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. Proc. Natl. Acad. Sci. U. S. A. 100, 5497–5502.

Chartrand, T.L., Bargh, J.A., 1999. The chameleon effect: the perception-behavior link and social interaction. J. Pers. Soc. Psychol. 76, 893–910.

Craig, A.D., 2002. How do you feel? Interoception: the sense of the physiological condition of the body. Nat. Rev., Neurosci. 3, 655–666.

Craig, A.D., 2003. Interoception: the sense of the physiological condition of the body. Curr. Opin. Neurobiol. 13, 500.

Critchley, H.D., Wiens, S., Rotshtein, P., Ohman, A., Dolan, R.J., 2004. Neural systems supporting interoceptive awareness. Nat. Neurosci. 7, 189–195.

Dapretto, M., Davies, M.S., Pfeifer, J.H., Scott, A.A., Sigman, M., Bookheimer, S.Y., Iacoboni, M., 2006. Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. Nat. Neurosci. 9, 28–30.

Davis, M.H., 1983. Measuring individual differences in empathy: evidence for a multidimensional approach. J. Pers. Soc. Psychol. 44, 113–126.

Decety, J., Grezes, J., 2006. The power of simulation: imagining one's own and other's behavior. Brain Res. 1079, 4–14.

de Vignemont, F., Singer, T., 2006. The empathic brain: how, when and why? Trends Cogn. Sci. 10, 435–441.

Eisenberg, N., 2004. Emotion, regulation, and moral development. Annu. Rev. Psychol. 51, 665–697.

Eisenberg, N., Fabes, R.A., 1998. Prosocial development. In: Damon, W., Eisenberg, N. (Eds.), Handbook of Child Psychology, Social, Emotional, and Personality Development. Wiley and Sons, New York, NY, pp. 701–778.

Estell, D.B., Farmer, T.W., Cairns, R.B., Cairns, B.D., 2002. Social relations and academic achievement in inner-city early elementary classrooms. Int. J. Behav. Dev. 26, 518–528.

Ferrari, P.F., Gallese, V., Rizzolatti, G., Fogassi, L., 2003. Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. Eur. J. Neurosci. 17, 1703–1714.

Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., Rizzolatti, G., 2005. Parietal lobe: from action organization to intention understanding. Science 308, 662–667.

Frith, C.D., Frith, U., 2006. The neural basis of mentalizing. Neuron 50, 531–534.

Gallese, V., 2006. Intentional attunement: a neurophysiological perspective on social cognition and its disruption in autism. Brain Res. 1079, 15–24.

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

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

Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn. Sci. 8, 396–403.

Gazzola, V., Aziz-Zadeh, L., Keysers, C., 2006. Empathy and the somatotopic auditory mirror system in humans. Curr. Biol. 16, 1824–1829.

Hadjikhani, N., Joseph, R.M., Snyder, J., Tager-Flusberg, H., 2006. Anatomical differences in the mirror neuron system and social cognition network in autism. Cereb. Cortex 16, 1276–1282.

Hariri, A.R., Bookheimer, S.Y., Mazziotta, J.C., 2000. Modulating emotional responses: effects of a neocortical network on the limbic system. NeuroReport 11, 43–48.

Hatfield, E., Cacioppo, J.T., Rapson, R.L., 1994. Emotional contagion. Cambridge Univ. Press, Paris.

Iacoboni, M., Dapretto, M., 2006. The mirror neuron system and the consequences of its dysfunction. Nat. Rev., Neurosci. 7, 942–951.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science 286, 2526–2528.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G., 2005. Grasping the intentions of others with one's own mirror neuron system. PLoS Biol. 3, e79.

Jabbi, M., Swart, M., Keysers, C., 2007. Empathy for positive and negative emotions in the gustatory cortex. NeuroImage 34, 1744–1753.

Jackson, P.L., Meltzoff, A.N., Decety, J., 2005. How do we perceive the pain of others? A window into the neural processes involved in empathy. NeuroImage 24, 771–779.

Jackson, P.L., Brunet, E., Meltzoff, A.N., Decety, J., 2006. Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain. Neuropsychologia 44, 752–761.

Jacob, P., Jeannerod, M., 2005. The motor theory of social cognition: a critique. Trends Cogn. Sci. 9, 21–25.

Johnson-Frey, S.H., Maloof, F.R., Newman-Norlund, R., Farrer, C., Inati, S., Grafton, S.T., 2003. Actions or hand–object interactions? Human inferior frontal cortex and action observation. Neuron 39, 1053–1058.

Kaplan, J.T., Iacoboni, M., 2006. Getting a grip on other minds: mirror neurons, intention understanding and cognitive empathy. Soc. Neurosci. 1, 175–183.

Keysers, C., Gazzola, V., 2006. Towards a unifying neural theory of social cognition. Prog. Brain Res. 156, 379–401.

Keysers, C., Gazzola, V., 2007. Integrating simulation and theory of mind: from self to social cognition. Trends Cogn. Sci. 11, 194–196.

Keysers, C., Kohler, E., Umilta, M.A., Nanetti, L., Fogassi, L., Gallese, V., 2003. Audiovisual mirror neurons and action recognition. Exp. Brain Res. 153, 628–636.

Kohler, E., Keysers, C., Umilta, M.A., Fogassi, L., Gallese, V., Rizzolatti, G., 2002. Hearing sounds, understanding actions: action representation in mirror neurons. Science 297, 846–848.

Koski, L., Wohlschlager, A., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C., Iacoboni, M., 2002. Modulation of motor and premotor activity during imitation of target-directed actions. Cereb. Cortex 12, 847–855.

Koski, L., Iacoboni, M., Dubeau, M.C., Woods, R.P., Mazziotta, J.C., 2003. Modulation of cortical activity during different imitative behaviors. J. Neurophysiol. 89, 460–471.

Lamm, C., Batson, C.D., Decety, J., 2007. The neural substrate of human empathy: effects of perspective-taking and cognitive appraisal. J. Cogn. Neurosci. 19, 42–58.

Lawrence, E.J., Shaw, P., Giampietro, V.P., Surguladze, S., Brammer, M.J., David, A.S., 2006. The role of 'shared representations' in social perception and empathy: an fMRI study. NeuroImage 29, 1173–1184.

Leslie, K.R., Johnson-Frey, S.H., Grafton, S.T., 2004. Functional imaging of face and hand imitation: towards a motor theory of empathy. NeuroImage 21, 601–607.

Lieberman, M.D., Eisenberger, N.I., Crockett, M.J., Tom, S.M., Pfeifer, J.H., Way, B.M., 2007. Putting feelings into words: affect labeling disrupts amygdala activity in response to affective stimuli. Psychol. Sci. 18, 421–428.

Litvack-Miller, W., McDougall, D., Romney, D.M., 1997. The structure of empathy during middle childhood and its relationship to prosocial behavior. Genet. Soc. Gen. Psychol. Monogr. 123, 303–324.

Mahoney, J.L., Cairns, R.B., 1997. Do extracurricular activities protect against early school dropout? Dev. Psychol. 33, 241–253.

Mahoney, J.L., Lord, H., Carryl, E., 2005. An ecological analysis of after-school program participation and the development of academic performance and motivational attributes for disadvantaged children. Child Dev. 76, 811–825.

Meltzoff, A.N., 2005. Imitation and other minds: The "like me" hypothesis. In: Hurley, S., Chater, N. (Eds.), Perspectives on Imitation: From neuroscience to social science. MIT Press, Cambridge, MA, pp. 55–77.

Meltzoff, A.N., Brooks, R., 2001. "Like me" as a building block for understanding other minds: Bodily acts, attention, and intention. In: Malle, B.F., Moses, L.J., Baldwin, D.A. (Eds.), Intentions and intentionality: Foundations of social cognition. MIT Press, Cambridge, MA, pp. 171–192.

Meltzoff, A.N., Moore, M.K., 1977. Imitation of facial and manual gestures by human neonates. Science 198, 74–78.

Mitchell, J.P., 2005. The false dichotomy between simulation and theory-theory: the argument's error. Trends Cogn. Sci. 9, 174–179.

Molnar-Szakacs, I., Iacoboni, M., Koski, L., Mazziotta, J.C., 2005. Functional segregation within pars opercularis of the inferior frontal gyrus: evidence from fMRI studies of imitation and action observation. Cereb. Cortex 15, 986–994.

Mutti, M., Sterling, H., Martin, N., Spalding, N., 1988. Quick Neurological Screening Test II. Academic Therapy Publications, Novato, CA.

Nishitani, N., Avikainen, S., Hari, R., 2004. Abnormal imitation-related cortical activation sequences in Asperger's syndrome. Ann. Neurol. 55, 558–562.

Oberman, L.M., Ramachandran, V.S., 2007. The simulating social mind: the role of the mirror neuron system and simulation in the social and communicative deficits of autism spectrum disorders. Psychol. Bull. 133, 310–327.

Oberman, L.M., Hubbard, E.M., McCleery, J.P., Altschuler, E.L., Ramachandran, V.S., Pineda, J.A., 2005. EEG evidence for mirror neuron dysfunction in autism spectrum disorders. Brain Res. Cogn Brain Res. 24, 190–198.

Phelps, E.A., LeDoux, J.E., 2005. Contributions of the amygdala to emotion processing: from animal models to human behavior. Neuron 48, 175–187.

Phillips, M.L., Drevets, W.C., Rauch, S.L., Lane, R., 2003. Neurobiology of emotion perception I: the neural basis of normal emotion perception. Biol. Psychiatry 54, 504.

Rizzolatti, G., Craighero, L., 2004. The Mirror-Neuron System. Annu. Rev. Neurosci. 27, 169–192.

Rodkin, P.C., Farmer, T.W., Pearl, R., Van Acker, R., 2000. Heterogeneity of popular boys: antisocial and prosocial configurations. Dev. Psychol. 36, 14–24.

Saarela, M.V., Hlushchuk, Y., Williams, A.C., Schurmann, M., Kalso, E., Hari, R., 2006. The compassionate brain: humans detect intensity of pain from another's face. Cereb. Cortex 17, 230–237.

Saxe, R., 2005. Against simulation: the argument from error. Trends Cogn. Sci. 9, 174–179.

Schulte-Ruther, M., Markowitsch, H.J., Fink, G.R., Piefke, M., 2007. Mirror neuron and theory of mind mechanisms involved in face-to-face interactions: a functional magnetic resonance imaging approach to empathy. J. Cogn. Neurosci. 19, 1354.

Singer, T., 2006. The neuronal basis and ontogeny of empathy and mind reading: review of literature and implications for future research. Neurosci. Biobehav. Rev. 30, 855–863.

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R.J., Frith, C.D., 2004. Empathy for pain involves the affective but not sensory components of pain. Science 303, 1157–1162.

Singer, T., Seymour, B., O'Doherty, J.P., Stephan, K.E., Dolan, R.J., Frith, C.D., 2006. Empathic neural responses are modulated by the perceived fairness of others. Nature 439, 466–469.

Theoret, H., Halligan, E., Kobayashi, M., Fregni, F., Tager-Flusberg, H., Pascual-Leone, A., 2005. Impaired motor facilitation during action observation in individuals with autism spectrum disorder. Curr. Biol. 15, R84–R85.

Umilta, M.A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., Rizzolatti, G., 2001. I know what you are doing: a neurophysiological study. Neuron 31, 155–165.

van der Gaag, C., Minderaa, R.B., Keysers, C., 2007. Facial expressions: what the mirror neuron system can and cannot tell us. Soc. Neurosci. 2, 179–222.

Wager, T.D., Nichols, T.E., 2003. Optimization of experimental design in fMRI: a general framework using a genetic algorithm. NeuroImage 18, 293–309.

Williams, J.H., Waiter, G.D., Gilchrist, A., Perrett, D.I., Murray, A.D., Whiten, A., 2006. Neural mechanisms of imitation and 'mirror neuron' functioning in autistic spectrum disorder. Neuropsychologia 44, 610–621.

Woods, R.P., Grafton, S.T., Holmes, C.J., Cherry, S.R., Mazziotta, J.C., 1998a. Automated image registration: I. General methods and intrasubject, intramodality validation. J. Comput. Assist. Tomogr. 22, 139–152.

Woods, R.P., Grafton, S.T., Watson, J.D., Sicotte, N.L., Mazziotta, J.C., 1998b. Automated image registration: II. Intersubject validation of linear and nonlinear models. J. Comput. Assist. Tomogr. 22, 153–165.

Woods, R.P., Dapretto, M., Sicotte, N.L., Toga, A.W., Mazziotta, J.C., 1999. Creation and use of a Talairach-compatible atlas for accurate, automated, nonlinear intersubject registration, and analysis of functional imaging data. Hum. Brain. Mapp. 8, 73–79.