Reciprocal Imitation: Toward a Neural Basis of Social Interaction

Sophie Guionnet[1,2,3,4], Jacqueline Nadel[1], Eric Bertasi[2,3,5], Marco Sperduti[1], Pauline Delaveau[1,2] and Philippe Fossati[1,2,3,4]

[1]Centre Emotion, Centre National de la Recherche Scientifique Unité de Service et de Recherche 3246, 75651 Paris Cedex 13, France, [2]Centre de Recherche de l'Institut du Cerveau et de la Moelle épinière (CRICM), 75651 Paris Cedex 13, France, [3]Université Pierre et Marie Curie (UPMC), Paris VI, 75252 Paris Cedex 05, France, [4]Service de Psychiatrie d'Adultes, Groupe Hospitalier Pitié-Salpêtrière, Assistance Publique-Hôpitaux de Paris, France and [5]Centre de NeuroImagerie de Recherche (CENIR), 75651 Paris Cedex 13, France

Address correspondence to Sophie Guionnet, Centre Emotion, Centre National de la Recherche Scientifique USR 3246, Groupe Hospitalier Pitié-Salpêtrière, 47-83 Boulevard de l'hôpital, 75013 Paris, France. Email: soph.guionnet@gmail.com.

Social interaction is a coregulated coupling activity that involves at least 2 autonomous agents. Numerous methodological and technical challenges impede the production of natural social interaction within an Magnetic Resonance Imaging environment under controlled conditions. To overcome the obstacle, we chose a simple format of social interaction, namely "interactive imitation" through a double-video system. We registered blood oxygen level–dependent activity of 23 participants during 2 imitative conditions: free (F) and instructed (I) episodes of imitating (i) and of being imitated (bi). In addition to the areas classically reported in instructed imitation tasks, 2 activation patterns were found, which differentiate the subconditions. Firstly, brain areas involved during decisional and attentional processes (dorsolateral prefrontal cortex, dorsal part of anterior cingulate gyrus [dACC], pre-SMA) were activated during all conditions except for instructed imitation—classically used in neuroimaging studies of imitation. Second, a greater activation in dACC and insula combined with an increased deactivation in the default mode network was observed when subjects were imitated compared with when they imitated. We suggest that these 2 patterns reflect the anticipation of the other's behavior and the engagement with others required by social interaction.

Keywords: fMRI, imitation, social interaction

Introduction

Social interaction is a coregulated coupling activity that engages at least 2 autonomous agents (De Jaegher et al. 2010). It mostly involves social cognition as an underlying process by which humans understand, anticipate, or infer the intentional behavior of others. Moreover, social interaction is the place where social cognition most frequently occurs in everyday life. So far, neural correlates of social cognition have mainly been studied with approximate consideration of the interaction component. For instance, researches have explored the neural correlates underlying mental state attribution (Amodio and Frith 2006) or social perception (Carr et al. 2003; Ciaramidaro et al. 2007; Hasson et al. 2008) in the absence of an interactive partner. Other studies have used as an interactive context a virtual character gazing at the subject (Schilbach et al. 2006), a prerecorded partner playing charades (Schippers et al. 2010), or an invisible human partner playing an online game with designated rounds (Montague et al. 2002; Krueger et al. 2008). Socially relevant functions appear to be underpinned by several brain regions. A first line of research has demonstrated that observing others acting (Iacoboni et al. 1999; Fogassi et al. 2005) or experiencing emotions (Carr et al. 2003; Montgomery and Haxby 2008) engage the same brain regions as performing similar actions or experiencing similar states. Areas activated include not only the inferior frontal cortex and the inferior parietal lobule (IPL), the classic "mirror neuron system" (Rizzolatti and Craighero 2004), but also the limbic and sensorimotor areas. This "shared representations" system was suggested to enable the brains of 2 interacting individuals to "resonate" with each other (Gallese and Goldman 1998). A second line of research has consistently revealed activity in the medial prefrontal cortex and the temporoparietal junction during mentalizing (Amodio and Frith 2006) through inferential and reflective processes (Frith and Frith 2003). Again, such explorations of social cognition have been conducted in the absence of an interactive context.

Only a handful of brain explorations have focused on isolated features of social interaction, like social coordination (Tognoli et al. 2007), joint attention (Schilbach et al. 2009), and contingent responding (Redcay et al. 2010). In a hyperscanning study (Dumas et al. 2010), interbrain synchronies during an online imitative interaction between 2 partners were documented. Apart from these few examples, the brain correlates of social interaction remain an unexplored field of investigation. This paucity of research may be related to the methodological and technical difficulties involved in creating a natural social interaction within an Magnetic Resonance Imaging (MRI) environment. Indeed, social interaction is an autonomous system and therefore difficult to study under controlled conditions. In an attempt to overcome this obstacle, we opted for a simple format of social interaction that can be initiated in an functional Resonance Magnetic Imaging environment, namely reciprocal imitation. Reciprocal imitation is a primary communicational system in infancy (Nadel-Brulfert and Baudonnière 1982) and has been suggested to act as a pathway toward the construction of social cognition abilities (Meltzoff 1990; Meltzoff and Gopnik 1994). Even if it is no longer a primary means of interaction in adulthood, some socially powerful forms of imitation persist. For instance, the automatic tendency to adopt the postures, gestures, and mannerisms of a partner, also called the "chameleon effect," has been demonstrated to enhance the feeling of "smoothness" during a social interaction (Chartrand and Bargh 1999).

What we know about the brain correlates of imitation comes from neuroimaging studies of instructed imitation. A recent meta-analysis revealed that parietal and frontal regions extending beyond the classical mirror neuron network (including the superior parietal lobule, the IPL, and the dorsal premotor cortex) are crucial in imitation tasks (Molenberghs et al. 2009).

The neuroimaging focus on instructed imitation has yielded fruitful knowledge concerning the links between perception and action (Iacoboni et al. 1999; Decety et al. 2002; Carr et al. 2003). This differs from free imitation, which is unique in that it allows for an exploration of the brain mechanisms underpinning the link between imitation and social cognition, including "being imitated," the crucial social counterpart of imitation (Nadel-Brulfert and Baudonnière 1982). To our knowledge, the neural correlates of "being imitated" have only been studied by Decety et al. (2002) in a Positron Emission Topography experiment not allowing for interaction and by Kühn et al. (2010) in an fMRI experiment in which subjects had to take the perspective of an actor filmed while being imitated (in a mimicry paradigm).

The present study used imitation as a well-framed and repeatable paradigm of online social interaction where 2 individuals freely match their gestures and coregulate their turn-taking as imitator and model. This condition was compared with a condition whereby the participants were required to act as either a model or an imitator. The objective was to study the patterns of brain activation developed in a real social interaction and to specify the cerebral regions more specifically involved in a free social engagement with others.

Materials and Methods

Participants

Twenty-three dyads composed of 23 healthy right-handed women aged 18–30 years and an experimenter (a woman) as partner participated in the study. They were all volunteers enrolled by advertisements on campus and were prescreened via a phone interview. They had normal or corrected-to-normal vision. They gave informed written consent to participate. The study was approved by the local ethics committee (n° 31-08). Exclusion criteria were neurological and/or psychiatric history, psychotropic treatment, and axis I disorder (Diagnostic and Statistical Manual for Mental Disorders IV) assessed by Beck depression inventory (cutoff < 8) and Mini International Neuropsychiatrique Interview.
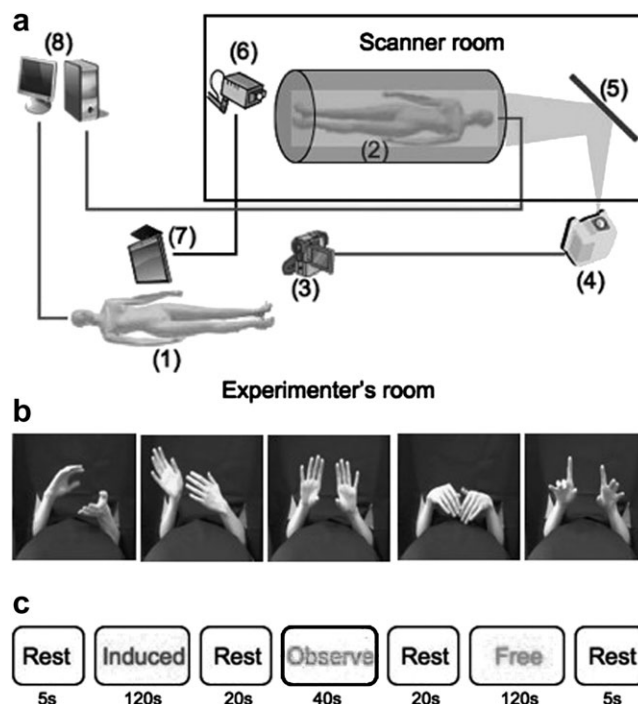
Experimental Setup

The setup was composed of a double-video system (Nadel et al. 1999) modified so as to allow for an interaction between a participant in the MRI scanner and the experimenter outside the scanner room. A compatible MRI video camera recorded the participants' hand movements that were then displayed on the experimenter's screen. Likewise, a digital camera projected the experimenter's hand movements onto a screen visible to the participant lying in the scanner (Fig. 1a). The experimenter was lying on the ground in a position similar to the position of the scanned participant.

Procedure and Design

Before the scanning session, a prerecorded library of intransitive hand movements, validated by 5 judges, was shown to the participant as an example of possible intransitive movements (Fig. 1b). The experiment was composed of 3 conditions (free imitation, instructed imitation, and observation) and a resting condition (Fig. 1c).

During the free (F) condition, the participants were told to either produce at will their own hand movements or imitate (Fi) the experimenter's hand movements "whenever they would like to." They were informed that they will be imitated (Fbi) sometimes by the experimenter. The experimenter followed a protocol requiring her to produce intransitive hand movements and to alternately imitate the participant initiating novel hand movements.

The instructed imitation (I) condition was externally triggered by 2 different auditory tones delivered every 20 s: A brief and deep tone meant "move your hands," while a long and high-pitched tone meant "imitate experimenter." The experimenter also received computer-monitored instructions. Auditory tones received by the participant or

Figure 1. (a) Experimental setup. Experimenter (1) and subjects (2) in the scanner laid in the same position. A standard video camera (3) recorded experimenter's hand movements and sent them to a projector (4) outside the scanner room. The video was projected to the subject by a mirror behind the scanner (5). A video camera compatible with MRI environment (6) recorded subjects' hand movements and fed them back to the experimenter via a monitor (7). A computer (8) automatically delivered auditory instructions to the experimenter and subjects. (b) Some examples of movements used during the experiment. (c) Schedule of one experimental session. The order of the 3 experimental conditions was counterbalanced between sessions and subjects.

the experimenter were not synchronized, nor did the participants hear the auditory tones of the experimenter. In order to preserve variety within instructed imitation blocks across runs, we used 6 different sequences of instructions (see Supplementary Fig. 1).

So, both free and instructed blocks of imitation included 2 subconditions: imitate and being imitated. During free episodes, imitate and being imitated (Fi and Fbi) emerged as a free alternation between matching the experimenter's gestures and doing one's own hand gestures (Fi and Fbi). By contrast, during instructed episodes, instructions generated imitate and being imitated (Ii and Ibi).

During the observation (O) condition, participants observed "online" the experimenter's hand movements without moving. In the rest condition, the participant stayed still, looking at the blank screen. A spoken word instruction informed participants about the experimental condition: "free imitation," "instructed imitation," "observation," or "rest."

fMRI Paradigm

After a practice run inside the scanner, a blocked fMRI design was used consisting of 6 scanning runs. Each run contained 3 blocks. Each block was associated with an activation condition (O, I, F). The free imitation and instructed imitation blocks each lasted 2 min. Each sequence of instructed imitation generated 40 s of "imitate" (Ii) and 40 s of "being imitated" (Ibi) per block. The 6 different sequences used in instructed imitation condition appeared with a randomized order for each subject. The observation block also lasted 40 s. Note that while the blocks were strictly timed, the within-block episodes of free imitation were not, but nevertheless subjects spent the major part of their time in imitation rounds.

Condition order was counterbalanced across runs and participants. Each of the 3 blocks was followed by a 20-s rest period (R). Each run started and ended with a rest period of 5 s (Fig. 1c).

fMRI Scanning

All data were acquired on a 3T scanner (Magnetom Trio A Tim System; Siemens). fMRI scans were performed using a T2* gradient-echoplanar sequence (repetition time: 2290 ms, echo time: 28 ms, flip angle: 75°, matrix: 96 × 96, field of view:192 × 192, slice thickness of 2 mm + a gap thickness of 1 mm). The slices covered the whole brain and were acquired parallel to the anterior–posterior commissure plane. Each run lasted 330 s resulting in 149 volumes. The first 3 volumes of each functional run were discarded in order to allow longitudinal magnetization to approach equilibrium.

High-resolution 3D T1-weighted images (3D fast gradient-echo inversion-recovery sequence, inversion time: 900 ms, repetition time: 2300 ms, echo time: 4.18 ms, field of view: 256 mm × 256 mm, matrix: 256 × 256, slice thickness: 1 mm, voxel size: 1 × 1 × 1) were acquired through the whole brain for anatomical localization.

Behavioral Data Analyses

The digitalized video recordings of the free imitation blocks were coded frame-by-frame, using Grynspan's revised version of the ELAN software (http//:www.lat-mpi.eu/tools/elan). This software allows a simultaneous presentation of the frames of the 2 partners on the ELAN window and a recording of time (latency, duration) and occurrence of behavioral events (imitate, being imitated, no imitation). Latency was used to determine who was the initiator and who was the follower of an imitated hand gesture. Imitation was defined according to 2 parameters: morphological and directional similarity of hand movements. A second coder blind to the aim of the study coded 25% of all blocks. We assessed the reliability of our fine-grained analysis of free imitation blocks using Cohen's kappa coefficient. Interobserver's kappa agreement was 0.90 for imitation and 0.92 for the roles of imitator and model (who imitates whom).

fMRI Data Analysis

Data were processed using SPM5 software (Statistical Parametric Mapping 5; Wellcome Department of Cognitive Neurology, University College London, UK).

Preprocessing

EchoPlanar Imaging (EPI) volumes were corrected for slice timing, realigned to the first image, coregistered with the high-resolution T_1-weighted image, and normalized into a standard stereotaxic space. The normalization used the Montreal Neurological Institute (MNI) template and the rigid transformations computed during the segmentation of the high-resolution T_1-weighted image. Finally, the normalized EPI volumes were smoothed using an isotropic Gaussian kernel filter of 8 mm full-width half-maximum.

Analyses

For each subject, General Linear Model was used to estimate the parameters for each experimental condition (O, Ii, Ibi, Fi, Fbi, and R). Six parameters of movement were also included in the model as regressors of no interest. Whole-brain t-tests were computed to estimate contrasts of interest for each subject. Contrasts of interest were as follows: O versus R, Ii versus R, Ibi versus R, Fi versus R, and Fbi versus R.

Contrasts for each individual were then used for 2 second-level analyses in order to estimate which clusters were significantly activated at group level. First, to explore brain areas involved in each imitation subcondition, we compared brain activity during each condition (Ii, Ibi, Fi, Fbi, O) and baseline (R) by means of a one-sample t-test. To investigate structures commonly activated between conditions of interest, we fed these contrasts in a second-level repeated-measure analysis of variance (ANOVA) and we then computed a conjunction analysis, using the conjunction null hypothesis (Nichols et al. 2005), between activation reported in Ii, Ibi, Fi, and Fbi when contrasted to O.

Secondly, to compare brain activity between conditions, we used a 2 × 2 ANOVA with imitation condition (F and I) and imitation type (i and bi) as factors. Contrasts were corrected for multiple comparisons using the familywise error correction with a threshold of $P < 0.05$.

Results

Behavioral Results

A frame-by-frame analysis of the participants' behavior during free imitation blocks was conducted (see Supplementary Video) allowing us to define the exact timing of free imitation (Fi) and freely being imitated (Fbi) for further fMRI data analysis. For the 2-min blocks, we found a mean duration of 43.6 s for Fi and 49.5 s for Fbi (Fig. 2a), thus giving 75% mean time of imitation. Of course, the average number of role switching between model and imitator and the average length of the sequences (i and bi) differed from one dyad to another, as Figure 2b shows.

Brain Activity during Imitating and Being Imitated

Comparisons between each subcondition (instructed imitation, Ii; being imitated in instructed condition, Ibi; free imitation, Fi; freely being imitated, Fbi) and baseline are shown in Figure 3. The conjunction analysis revealed a partly common set of cortical and subcortical activations (see Supplementary Table 1) consistent with results by Decety et al. (2002).
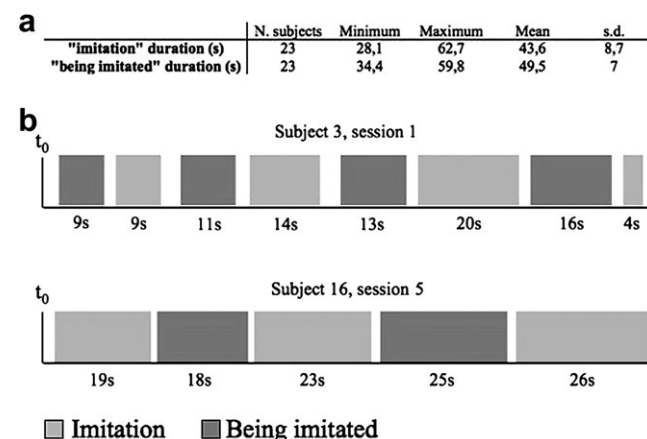
Figure 2. Behavioral analysis. (a) Duration of "imitation" and "being imitated" for "free imitation" block. (b) Example of a free imitation block for 2 subjects after behavioral analysis (i, imitation; bi, being imitated; T, time).
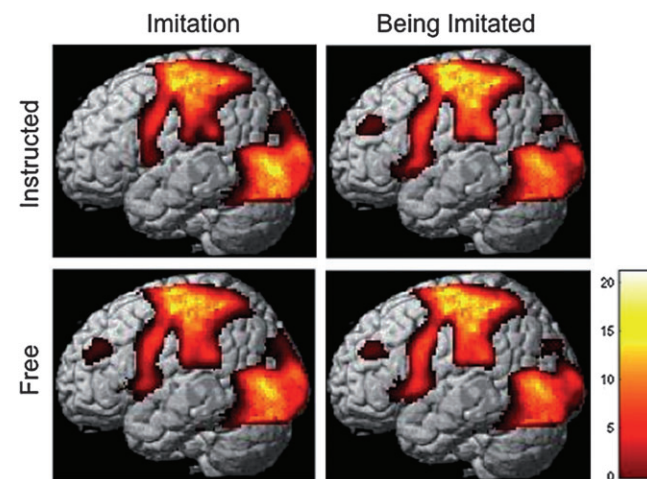
Figure 3. Statistical maps for each experimental subcondition compared with baseline superimposed to a rendered template. The statistical threshold corrected for multiple comparisons (FWE) was set at $P < 0.05$, $k = 10$. FWE, familywise error.

Converging with studies of instructed imitation (Iacoboni 2005; Molenberghs et al. 2009; Molenberghs et al. 2010), we found a strong recruitment of parietofrontal regions regardless of the condition (free or instructed imitation) and of the subcondition (imitate or being imitated). In particular, activated clusters were found in primary sensorimotor cortex, premotor and supplementary motor areas, left inferior frontal gyrus (areas 44, 9), left IPL, and left insula.

Pars opercularis of the inferior frontal gyrus (area 44) and the rostral part of the IPL are ascribed to the original mirror neuron system (MNs), supposed to mediate a shared motor and perceptual representation for action (Rizzolatti and Craighero 2004; Brass and Heyes 2005).

Basal ganglia and cerebellum are classically reported as activated during motor activities and motor control (Grezes and Decety 2001; Lehericy et al. 2006).

In all but instructed imitation (Ii) subcondition, we also found activation of the dACC and the pre-SMA, along with a more rostral part of the left dorsolateral prefrontal cortex (DLPFC).

To further investigate this difference and since the principal aim of the study was to examine the neural correlates of free interactive imitation, we carried out a supplementary analysis to assess the differential activation between subconditions. Results are reported below.

Differential Activations between Imitate and Being Imitated

To test for differential activations between subconditions, we used a 2 × 2 ANOVA with imitation condition (free and instructed) and imitation type (imitate or being imitated) as factors. There was no significant main effect of imitation condition but a main effect of imitation type and a significant interaction between the 2 factors.

Being Imitated > Imitate

Post hoc tests revealed an increased activity in the dorsal part of anterior cingulate gyrus (dACC, area 32 and area 24), in the pre-supplementary motor area (pre-SMA), in the DLPFC (area 46), and in the dorsal part of the left anterior insular cortex (left dAIC) during "bi" subconditions compared with "i" (Fig. 4; see Supplementary Table 2).

Imitate > Being Imitated

This comparison showed greater activation notably of visual areas, medial frontal cortex, posterior cingulate gyrus, precuneus, bilateral IPL, parahippocampus, and hippocampus (Fig. 4; see Supplementary Table 3). With the exception of the visual areas, regions known to be part of the default mode network (DMN) (Raichle et al. 2001; Spreng et al. 2009) were actually more deactivated in Fbi and Ibi than Fi and Ii. We also note a significant DMN deactivation in the contrast between Fi and Fbi.

Interaction

We found a significant interaction in 3 regions: bilateral DLPFC (Brodmann Area [BA] 9/10), dACC (area 32), and pre-SMA, (Fig. 5a; see Supplementary Table 4). This effect was due to the fact that the activity in these areas during Ii was lower than in all other subconditions (Fig. 5b).

Discussion

Via a double-video system with an MRI-compatible camera, our protocol enabled us to record 23 spontaneous imitative exchanges, to assess their associated brain correlates, and to compare them with the brain correlates of the same subjects involved in an instructed task of imitation. To our knowledge, it is the first brain-imaging study that investigates the brain activations related to a truly free interaction via "imitating" and "being imitated." Beyond similarities with previous findings regarding the imitative network, our study revealed a pattern of activation involving the DLPFC, dACC, and pre-SMA for "free imitation" and "be imitated" subconditions but not for "instructed imitation," which questions the use of "instructed imitation" as a relevant paradigm to explore the neural correlates of all kinds of imitation. We also found a pattern of activation (dACC and left insula)–deactivation (DMN) in "bi" subconditions compared with "i" subconditions. This result leads us to stress the importance of "being imitated" and to discuss the role of this often overlooked facet of imitation.

The "Core Circuit" of Imitation

Our results revealed similar activations of the imitation network that has been previously evidenced (Decety et al. 2002; Iacoboni 2005; Molenberghs et al. 2009; Molenberghs et al. 2010). We found activations not only in the left pars opercularis (the core circuit of imitation described by Iacoboni 2005) but also in the primary sensorimotor cortex, ventral and dorsal premotor areas, supplementary motor areas, inferior frontal gyrus (BA 9), left IPL, and left insula. We notice that Molenberghs et al. (2009) did not identify inferior frontal gyrus as activated in their meta-analysis of hand and finger movements. Makuuchi (2005) suggested that BA 44 is more involved in execution timing than in imitation. Spontaneous synchronization of hand movements during free imitation may require timing to be taken into account in order to coordinate tempo, as instructed imitation of finger movements does in the paradigm of Iacoboni et al. (1999).

Why Is Instructed Imitation So Different?

For free imitation and be imitated (Fi, Fbi, and Ibi), all 3 activated the DLPFC (BA 9/10/46), the dACC (area 32), and the pre-SMA, but instructed imitation did not. It has been shown that free selection of an action involves BA10 (Soon et al. 2008) and pre-SMA (Lau et al. 2004). The dACC (BA 32) has been shown to be involved in conflict monitoring and adjustments in control (Kerns et al. 2004). Such brain activations are likely to reflect here the anticipation (Fi) or monitoring (Fbi and Ibi) of the partner's motor behavior. Indeed, during free imitation, the subjects had to anticipate the trajectory of the gesture to act in synchrony and to freely decide when to start, to continue, and to stop imitating. When imitated (Fbi and Ibi), they had to freely choose subsequent movements in order to influence the partner's motor behavior. Conversely, during instructed imitation, no decision making was necessary since the subjects had to follow an auditory signal to start and stop imitating. This result demonstrates that instructed imitation does not activate brain networks involved in self-managing a natural interaction.

Note that we found no significant main effect of imitation condition (free vs. instructed). This result is probably due to a similarity of activation in the 2 "bi" subconditions. Though different in context (free vs. instructed), it is probable that at the end, the subject experienced our 2 subconditions "bi" quite similarly.
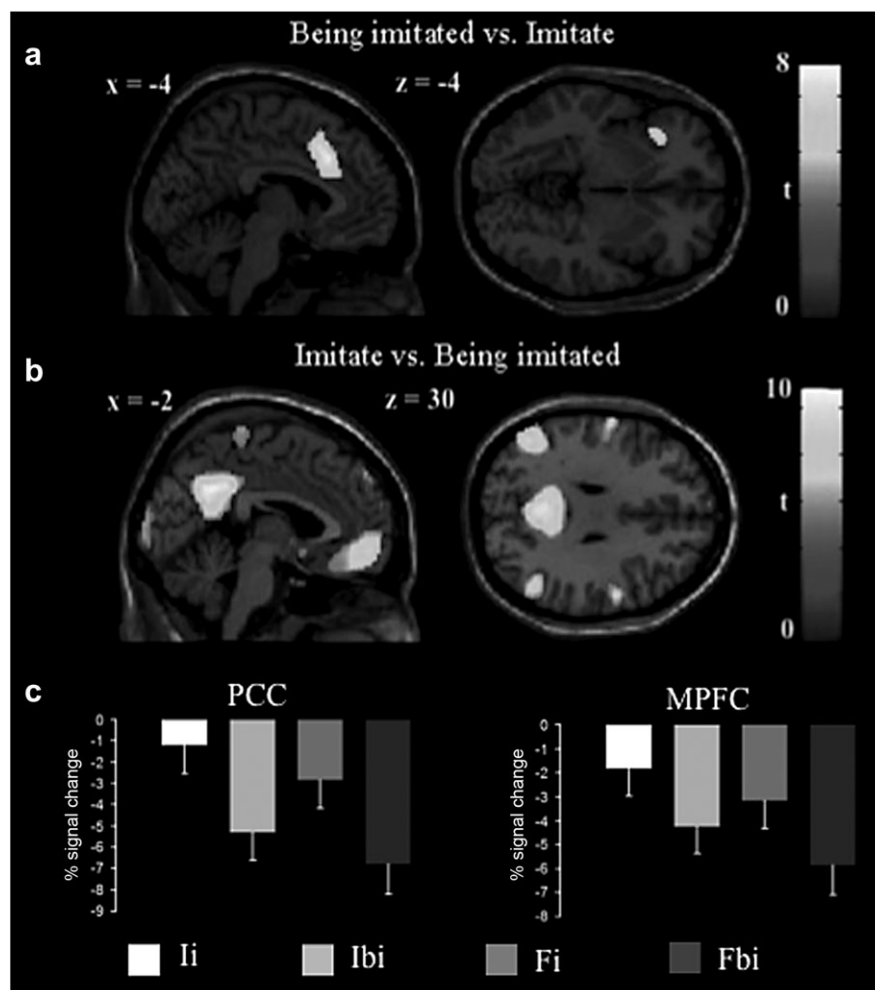
Figure 4. Post hoc comparisons between "be imitated versus imitate" and "imitate vs. be imitated" in the upper and lower part of the figure respectively. Statistical maps were superimposed to an MNI T1 template. The statistical threshold corrected for multiple comparisons (FWE) was set at $P < 0.05$, $k = 1$. (*a*) In "be imitated versus imitate," activations were found in dACC (brodmann area 32: $x, y, z = -2, 22, 38$; $T = 9.24$; brodmann area 24: $x, y, z = 6, 24, 28$; $T = 7.68$) and in the dorsal part of left anterior insula ($x, y, z = -38, 18, 0$; $T = 5.52$). (*b*) In "imitate versus be imitated," activations were found especially in Posterior Cingulate Cortex ($x, y, z = -2, -44, 34$; $T = 10.62$), MPFC (BA 10/11/25, $x, y, z = 2, 60, -4$; $T = 8.51$), right IPL, and left IPL ($x, y, z = 52, -62, 38$; $T = 8.73$; $x, y, z = -54, -58, 30$; $T = 8.07$). (*c*) Percentage signal change for peak activation voxels in the Posterior Cingulate Cortex and in the MPFC, error bars are the SDs. FWE, familywise error; MPFC, medial prefrontal cortex; MNI, Montreal Neurological Institute; SD, standard deviation.

The Weight of "Being Imitated"

We evidenced an interesting difference between "be imitated" and "imitate." In particular, in both "bi" subconditions (Fbi and Ibi), we observed an activation of dACC (area 32 and 24), DLPFC (BA 46), and the left dAIC. Furthermore, we noticed a greater deactivation of the DMN for "be imitated" compared with "imitate."

Unlike "imitate," "be imitated" requires a choice of movement: Sensitive to contingency and responsive to their partner (Reddy and Morris 2004), subjects tend to produce attractive gestures likely to maintain the other's imitation. BA 46 is known to play a significant role in working memory (Smith and Jonides 1999) and especially in attention during the selection of action (Pochon et al. 2001). We have already pointed the activation of dACC in conflict monitoring and adjustment.

The dAIC has been involved in a multitude of different studies (Craig 2009). Kurth et al. (2010) suggest that this region could have an integrative function of own perceptions, feelings, thoughts, and planning. The left insula is activated by the parasympathetic system (Oppenheimer et al. 1992; Craig

2005), a system involved in nourishment, safety, positive affects, and approach behavior (Craig 2005). This is also consistent with the involvement of left forebrain activity in social engagement (Schmidt and Fox 1994). According to some studies, the left insula might share this parasympathetic function with the left anterior cingulate cortex (ACC; Critchley et al. 2003; Matthews et al. 2004). Seeley et al. (2007) have suggested that both the ACC and the frontoinsular cortex are core regions of a "salient network." According to these authors, by integrating sensory data with visceral, autonomic, and hedonic markers, this network could allow an organism in a natural context to decide what to do or not to do.

"Imitation binds people" (Hari and Kujala 2009); could "be imitated" serve as a first step toward this binding? Data from behavioral studies have pointed out the social "connectedness effect" of "being imitated." Some evidence suggests that nonconscious mimicry enhances liking, rapport, affiliation, and prosocial behavior from the subject who is imitated (Chartrand and Bargh 1999; van Baaren et al. 2004). Drawing from these findings, Lakin and Chartrand (2003) propose that
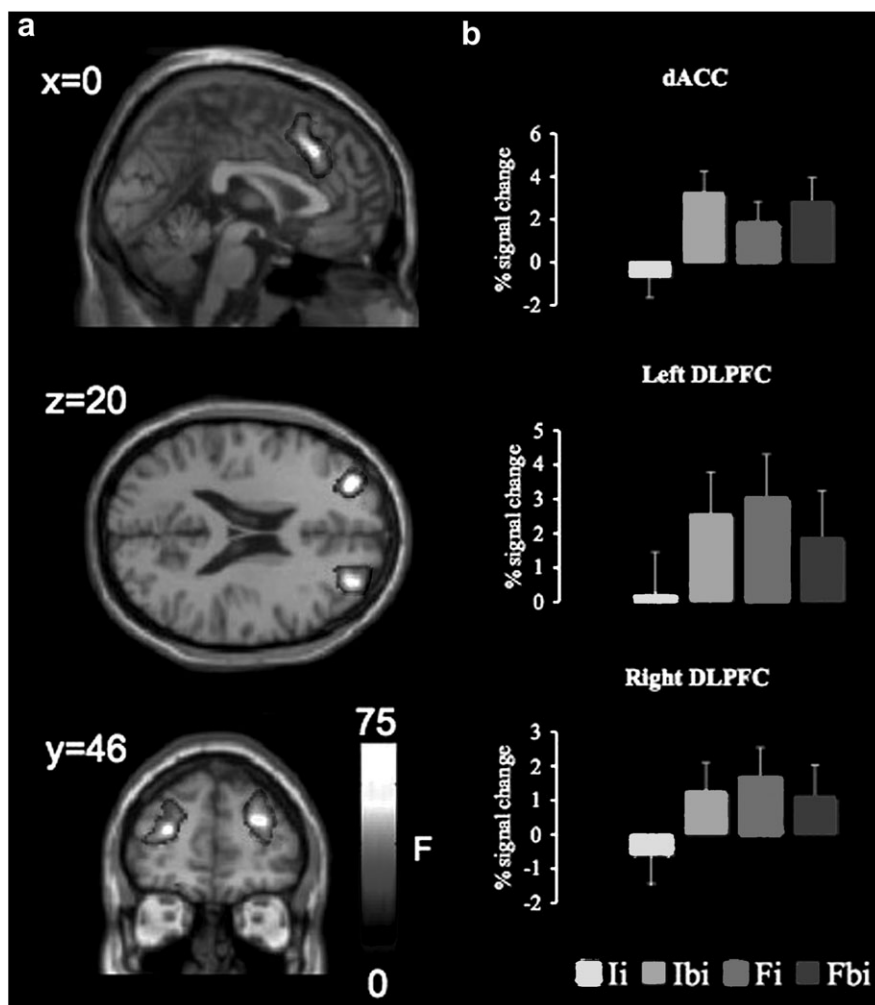
Figure 5. Interaction effect between the 2 factors imitation condition and imitation type. (*a*) Statistical maps were superimposed to an MNI T1 template. The statistical threshold corrected for multiple comparisons (FWE) was set at $P < 0.05$, $k = 10$. (*b*) Percentage signal change for peak activation voxels in the dACC (x, y, $z = -4$, 26, 36; $F = 63.93$), left DLPFC (x, y, $z = -30$, 54, 18; $F = 61.49$), and right DLPFC (x, y, $z = 26$, 44, 26; $F = 61.95$), error bars are the SDs. FWE, familywise error; MNI, Montreal Neurological Institute; SD, standard deviation.

the chameleon effect acts as "social glue." This echoes with evidence from a large number of studies showing that infants look at and smile more to adults acting like them (Meltzoff 1990) and that children with autism also are attracted toward their imitator (Field et al. 2001; Nadel 2002). We suggest that the joint left dAIC and dACC activation in "bi" subconditions could reflect the feeling of "visceral connectedness" to other people (Hari and Kujala 2009).

Medial frontal cortex, posterior cingulate gyrus, precuneus, bilateral IPL, parahippocampus, and hippocampus, all regions known to be part of the DMN (Raichle et al. 2001) and often reported in studies on self-referential processing (Fossati et al. 2003; Spreng et al. 2009), are significantly more deactivated during be imitated than during imitation subconditions. The DMN is usually more activated at rest than during externally oriented tasks (Gusnard et al. 2001). During an externally oriented task, the DMN can be more deactivated when the task requires a greater cognitive effort (Fox et al. 2005). Such deactivation is then anticorrelated with the activation of the dorsolateral prefrontal network (Pochon et al. 2002). When imitated, subjects experience monitoring the other's behavior,

controlling the matching, and trying to maintain their mastery via the use of attractive gestures. Anticipation of the other's response and significant external engagement are then in the forefront.

To conclude, using our free imitation design in an fMRI study does not result in exploring the whole of the subtle brain variations probably involved in a social exchange. Electroencephalography or magnetoencephalography techniques are certainly more suitable to this end since they operate on time scales following natural dyadic interaction. Nonetheless, our innovative design and multidisciplinary approach allowed us to define some neural correlates of the core of social interaction. Even if these results call for further assessment, they hopefully could be seen as an encouraging track for an exploration of the neural correlates underlying natural social interaction.

Supplementary Material

Supplementary Tables 1–4, Figure 1, and Video can be found at: http://www.cercor.oxfordjournals.org/.

Notes

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