RESEARCH REPORT

Mirror Neuron System and Mentalizing System connect during online social interaction

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Abstract Two sets of brain areas are repeatedly reported in neuroimaging studies on social cognition: the Mirror Neuron System and the Mentalizing System. The Mirror System is involved in goal understanding and has been associated with several emotional and cognitive functions central to social interaction, ranging from empathy to gestural communication and imitation. The Mentalizing System is recruited in tasks requiring cognitive processes such as self-reference and understanding of other's intentions. Although theoretical accounts for an interaction between the two systems have been proposed, little is known about their synergy during social exchanges. In order to explore this question, we have recorded brain activity by means of functional MRI during live social exchanges based on reciprocal imitation of hand gestures. Here, we investigate, using the method of psychophysiological interaction, the changes in functional connectivity of the Mirror System due to the conditions of interest (being imitated, imitating) compared with passive observation of hand gestures. We report a strong coupling between the Mirror System and the Mentalizing System during the imitative exchanges. Our findings suggest a complementary role of the two networks during social encounters. The Mirror System would engage in the preparation of own actions and the simulation of other's actions, while the Mentalizing System would engage in the anticipation of the other's intention and thus would participate to the co-regulation of reciprocal actions. Beyond a specific effect of imitation, the design used offers the opportunity to tackle the role of role-switching in an interpersonal account of social cognition.

Keywords Mirror Neuron System · Mentalizing System · Neuroimaging · Functional connectivity · Social interaction · Imitation

Introduction

The anticipation of others' actions and the understanding of others' intentions are two essential facets of a successful adaptation to the social world. But while motor anticipation can be found in a large variety of primates, the capacity to read minds is restricted to human species and, at some extent, to great apes. Whether these two distinct levels of predictive capacities correspond to related or independent brain networks are still a matter of debate. Thereby, the relationships between the "Mirror Neuron System" (MNS) and the "Mentalizing System" have become a focus of attention for social neuroscientists in the last years. Indeed both sets of brain regions contribute to social understanding, but there is no clear evidence of a cooperation and exchange of information between them.

The main nodes of the human MNS are the posterior part of the inferior frontal gyrus (pIFG) and the rostral part of the inferior parietal cortex (aIPS), though other regions

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such as the dorsal premotor cortex (dPMC) and the primary motor cortex (M1) show also mirror properties (Dushanova and Donoghue 2010; Gazzola and Keysers 2009). In humans, MNS regions have been reported to commonly code for action execution and perception (Iacoboni et al. 1999), with a distributed function: frontal regions tend to code for goals of actions and parietal regions tend to code for means (Iacoboni 2005). According to Hurley (2008), such functional distribution may explain why the human MNS allows us to imitate, i.e., match both means and goals (Iacoboni 2009; Rizzolatti and Craighero 2004, but see Molenberghs et al. 2009, 2010) while the monkey MNS enables just emulation (matching goals but not means). Beyond imitation, MNS has been proposed to provide a "first-person-grasp" of the other's motor goals and intentions during social interaction (Rizzolatti and Sinigaglia 2010). Empirical studies have shown that it underpins a series of functions central to social interaction ranging from empathy (Decety and Jackson 2004; Iacoboni 2009; Nummenmaa et al. 2008) to gestural symbolic communication (Schippers et al. 2009, 2010).

The Mentalizing System or theory of mind (ToM) system is not established to the same degree that the Mirror System as a coherent large-scale network with functional significance. However, it concerns regions that are all activated when we infer intentions referred to volitional or epistemic mental states. It includes the cortical midline structures (CMS) and the temporoparietal junction (TPJ) (Saxe et al. 2006; Spunt and Lieberman 2013; Uddin et al. 2007; Van Overwalle and Baetens 2009). CMS comprise the ventromedial part of the prefrontal cortex (vMPFC), the posterior cingulate cortex (PCC), and the precuneus, that are frequently activated during ToM tasks (Amodio and Frith 2006; Frith and Frith 2003; Van Overwalle and Baetens 2009; Wolf et al. 2010) and observation of social interactions (Iacoboni et al. 2004). TPJ is involved in mindreading (Frith and Frith 2001) and plays an important role in the attribution of external agency (David et al. 2007; Farrer and Frith 2002; Farrer et al. 2003; Fink et al. 1999; Nahab et al. 2011; Sperduti et al. 2011; Yomogida et al. 2010). Interestingly, this set of regions corresponds to the "default mode network" (DMN) that shows a sustained activity during self-referential processing (Lemogne et al. 2011; Martinelli et al. 2013; Northoff et al. 2006). Thus, the Mentalizing System appears to be involved both in the representation of others' mental states and in self-referential processes (Schilbach et al. 2008).

As briefly summarized above, the Mirror and the Mentalizing systems both participate in the anticipation and understanding of other's behaviors. One hypothesis would be that they are involved in different levels of representation of the other's mental states. A lower level would concern simple representation of the other's action goals during motor exchanges; a higher level would include meta-

representational inferences about the other's intentions (De Jaegher 2009). Within this framework, Uddin et al. (2007) have suggested that the Mirror System would enable physical simulation of actions and action goals, while the Mentalizing System would allow simulation of mental states. Similarly, Keysers and Gazzola (2007) have proposed a pre-reflective versus reflective simulation account of the two systems. Yet, only a few authors have focused on the two networks in their research, and concurrent activation has been rarely reported (Zaki and Ochsner 2009).

The paucity of data may be partly explained by the lack of live social designs compatible with fMRI recordings. To our knowledge, only three studies have used innovative designs in this direction. Schippers et al. (2010, 2011) used a game of charades in which a subject mimed objects (e.g., a pencil) or actions (e.g., painting) while the partner had to guess the object or the action gestured. They reported that the MNS of the gesturer predicts the activity in the MNS and in the ventral portion of MPFC (vMPFC) of the guesser. A connection between the two systems has also been reported in the context of emotion attribution (Spunt and Lieberman 2012b). Spunt and Lieberman (2012a) have recorded fMRI during the computation of the "why" and the "how" of observed actions presented as videos, or as verbal scripts. The same authors have reported a modulation of the Mentalizing System when a task with high cognitive load interfered with the inference of an actor's mental state. But, no such modulation was found in the Mirror System. To explain this dissociation, Spunt and Lieberman (2013) propose a dual-process model where the Mirror System supports automatic action understanding and the Mentalizing System supports controlled causal attribution. The authors call for future research that will analyze the conditions of involvement of the two systems.

Our suggestion here is that social interaction is the right condition for an exploration of the potential connection between the two systems. Indeed a critical component of any social interaction is a complementary contingent oscillation between social roles. Role switching requires the anticipation of the other's pending switch in role. Besides an understanding of the other's action, an inference of the other's intention is needed. A connection between the Mirror and the Mentalizing systems should account for this dynamics.

So far, little is known about the potential synergy of the Mirror and the Mentalizing systems during bilateral social exchanges. The neural correlates underpinning social interaction remain poorly studied and are still often confused with the correlates of social perception and lone social cognition. Social perception does not require any social response to the perceiver, and social cognition can consist in a solitary computation of the mental states of absent others. By contrast, social interaction requires the presence of real

partners co-operating so as to produce a coherent exchange. To explore the brain correlates of online social interaction, there is a strong need for novel designs. But, as Hari and Kujala (2009, p. 454) wrote "the current challenge for brain imaging is to bring everyday human interaction, occurring in a complex natural environment between two or more subjects, into the laboratory."

Looking for a solution to this problem, we designed a procedure based on the developmental research. A series of studies have shown that reciprocal imitation is a primary communicational system consisting in matching actions that are alternately proposed by one or the other partner as a way to switch roles between imitator and model (Nadel-Brulfert and Baudonnière 1982; Nadel and Butterworth 1999; Uzgiris et al. 1984). With our experimental platform, partners cannot speak to each other or watch their faces. They only see each other's hand gestures through a double video setup (Nadel et al. 1999) while their brain activities are recorded using fMRI (see Fig. 3a). They are asked to move continuously their hands, either performing their own gestures or imitating the other's gestures at will. This procedure contrasts with the classical procedure used in neuroimaging studies. In all previous studies, imitation was performed under instructions ("imitate what you see") by an individual alone. Here, the two unacquainted subjects are free to imitate or not, and they need to anticipate each other's intention in order to assure a harmonious role switching.

At the behavioral level, the situation generated frequent periods of imitation including role switching between imitator and model, as found earlier with young children. At the brain level, it induced the involvement of mirror areas classically described as the *core circuit of imitation* (Iacoboni 2005), to which was added the activation of structures such as dLPFC and pre-SMA, concerned with free selection, planning, anticipation, and monitoring of action (Guionnet et al. 2011). To explore to which extent a connection between the Mirror and the Mentalizing systems should account for this complex set of brain activation, we studied the functional coupling of the Mirror System using the method of psychophysiological interaction (PPI) (Friston et al. 1997); we explored the changes of connectivity due to the conditions of interest: model (i.e., initiating and monitoring actions) and imitator (i.e., anticipating and adjusting actions) compared to passive observation of hand gestures that also elicits activity in the Mirror System.

Materials and methods

Participants

Twenty-three right-handed subjects (18–30 years) participated in the study. As the partner/experimenter was a female, they were all females, to avoid a possible confounding factor of gender hand incongruence within the dyad. They all had normal or corrected-to-normal vision. They were enrolled by advertisements on campus and were pre-screened via a phone interview. They gave their informed written consent to participate in the study that was approved by the local ethic committee. Exclusion criteria were neurological and/or psychiatric history, psychotropic treatment, and axis I disorder (DSM IV) assessed by Beck depression inventory (BDI, cut-off <8) and mini international neuropsychiatric interview (MINI).

Experimental paradigm

The setup was composed of an fMRI-compatible double video system adapted from Nadel et al. (1999). The lag between the two video systems could not exceed one frame (i.e., 40 ms). The system allowed the female participant lying in the MRI scanner, and the female experimenter lying outside the scanner room to see each other's forearms and hands through online dual video recordings. A schematic representation of the experimental setting is given Fig. 1.

Before the scanning session, the experimenter explained the task to the subjects without informing them about the fact that she will be the partner. As only the hands and the forearms were videotaped, the subjects could not identify the experimenter as their partner. The experiment was composed of three conditions: an observation condition, a condition of free *online* imitation, and a condition of instructed imitation. In this report, we only focused on the interactive part of the experiment, namely the free *online* imitation condition composed of episodes of imitating and being imitated (for a detailed description of the whole experiment, see Guionnet et al. 2011). For this part of the experiment, subjects were simply proposed to produce continuously hand gestures or to imitate the partner/experimenter's gestures whenever they would like it (imitating condition). They were informed that they could be imitated by the partner/experimenter (being imitated condition). Thus, the experimental condition here was an open situation, as is any situation of social interaction: the subjects did not know what the partner (experimenter) will do; they had to compute the other's intention. The experimenter followed a computerized experimental protocol (sounds) informing her to do hand gestures of her own or to imitate the subject. From this setting, a dyadic organization emerged, which was previously described in adults during a dual behavioral and hyperscanning EEG study (Dumas et al. 2010, 2012).

fMRI design

A blocked fMRI design composed of 6 scanning runs was used. A run consisted in 3 blocks, each associated with an

Fig. 1 Experimental setting. **a** Schematic representation of the experimental setting: a video camera recorded experimenter's hands movements (*blue box*) and projected them, via a mirror, to a screen visible by subjects in the scanner (*red box*). Similarly, an armored camera compatible with the MRI environment recorded subjects' movements and sent them to a monitor visible by the experimenter. **b** An example of an imitative exchange between the experimenter (*blue box*) and a subject (*red box*) (color figure online)
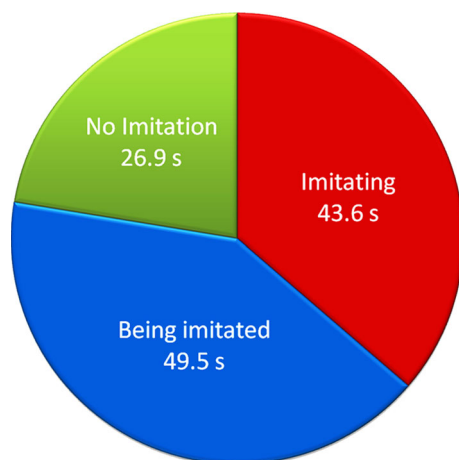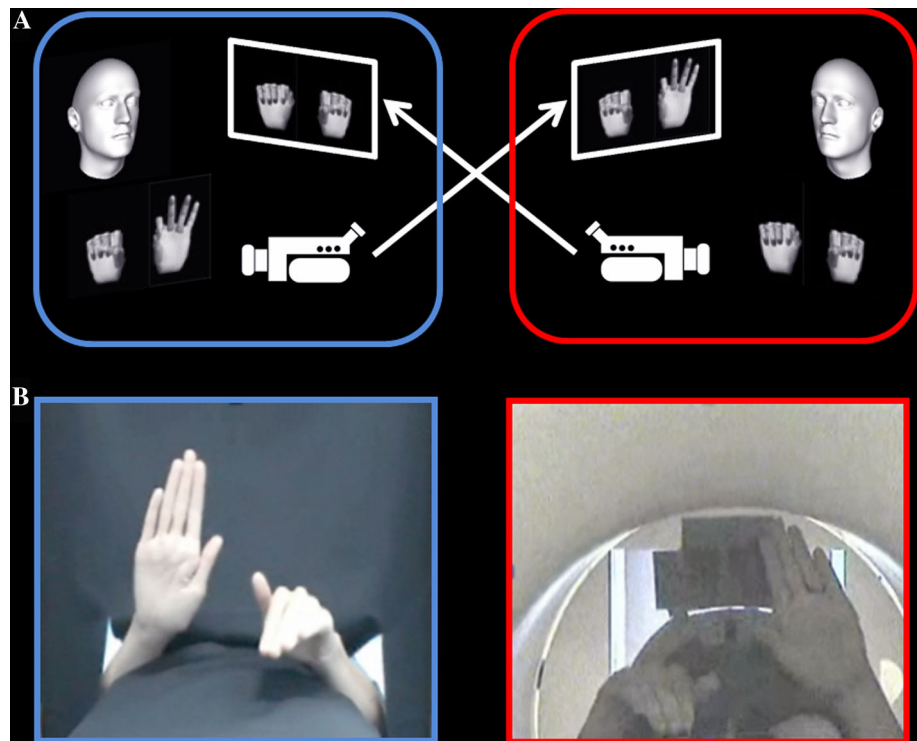

Fig. 2 Mean time subjects spent imitating and being imitated during 2-min blocks of free imitation

activation condition (observation, free imitation, and induced imitation). The free imitation and instructed imitation conditions lasted 120 s. The 6 sequences were presented in a randomized order for each subject. The observation condition lasted 40 s. The order of condition was counterbalanced across runs and participants. Each run started and ended with a 5 s rest. Each block was followed by a 20 s rest. Note that the blocks were strictly timed, but the within-block episodes of free imitation were not. Nevertheless, subjects spent the major part of their time in imitation episodes; Fig. 2 presents the mean time of imitation episodes across all blocks of free imitation.

fMRI data acquisition

Images were acquired on a 3-T scanner (Siemens, Magnetom Trio A Tim System). Functional MRI scans were performed using a T2* gradient-echoplanar sequence (repetition time: 2,290 ms, echo time: 28 ms, flip angle: 75°, matrix: 96 × 96, field of view: 192 × 192, slice thickness of 2 mm, 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 three-dimensional T1-weighted images (3D fast gradient echo inversion recovery sequence, inversion time: 900 ms, repetition time: 2,300 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 analysis

The two video recordings of hand movements during the condition of free imitation were digitized. Then, the LED signal recorded on the two videos at the beginning of each session was used to synchronize the frames of the two partners. The videos were coded frame-by-frame using a revised version (Grynszpan 2006) of the fine-grained

ELAN software that offers a simultaneous presentation of two frames from different sources on the ELAN window. This software allows an analysis of the behavioral frames on separate channels of the window and a recording of the time (latency, duration) and occurrence of behavioral events. Two main events were analyzed in each run: imitation and synchrony of hand movements. Synchrony was assessed when the hands of the two participants started and ended a movement at the same frame, thus showing a coordinated rhythm. The criterion of simultaneity used was the co-occurrence of two gestural movements within the same video frame. Imitation was assessed when the hand movements of the two partners showed a similar morphology (tracing a circle, waving, swinging …) and a similar direction (up, down, right, left…). For each imitative episode, the individual who started a hand movement followed by the partner was labelled the model, and the follower was labelled the imitator.

Onsets and duration of each condition were extracted to be used for fMRI data analysis. A second coder blind to the aim of the study coded 25 % of all blocks. Inter-observers' κ agreement was 0.90.

fMRI data analysis

Preprocessing

The data were processed using SPM5 (Statistical Parametric Mapping 5, Welcome Dept. Cognitive Neurology, UK). EchoPlanar Imaging (EPI) volumes were corrected for slice timing, realigned to the first image, co-registered with the high-resolution T1-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 T1-weighted image. Finally, the normalized EPI volumes were smoothed using an isotropic Gaussian kernel filter of 8-mm full-width half-maximum.

General linear model (GLM)

For each subject, the general linear model (GLM) was used to estimate the parameters for each experimental condition (imitating, being imitated and observation). The six movement parameters 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: imitating versus rest, being imitated versus rest, and observation versus rest. Contrast images from the first-level analysis were then fed into a second-level random-effect model. Contrasts were corrected for multiple comparisons using the familywise error rate (FWE) correction with a threshold of $p < 0.05$.

Psychophysiological interaction (PPI)

To assess for changes in functional connectivity of the MNS due to the experimental conditions, we used the PPI method (Friston et al. 1997). This method tests the changes in coherence or modulation of a seed region over a sink region due to a contextual or a psychological factor. A significant effect of PPI means that the regression slope between the seed and sink regions in the condition of interest is significantly higher than that in the control condition. Compared with other techniques assessing connectivity, such as structural equation modeling (SEM; Büchel and Friston 1997) or dynamic causal modeling (DCM; Friston et al. 2003), the advantage of PPI is that it does not require an a priori anatomical model: In fact, it computes the differences in regression slope of activity between a seed region and any other voxel in the brain. Nevertheless, PPI contrary to the aforementioned techniques does not give information about the causal or the driving role of the activity of one region over another one. Results of PPI analysis should be interpreted more in terms of changes of the modulatory effect of the seed region over the sink region or in terms of functional integration between these regions due to the contextual condition.

Mirror neuron areas to be used as seed regions in our analysis were identified using a conjunction analysis between the three experimental conditions. We restricted our analysis, using WFU_PickAtlas toolbox (Lancaster et al. 2000; Maldjian et al. 2003), to brain regions classically reported as belonging to the Mirror System: the inferior parietal lobule (IPL) and the inferior frontal gyrus (IFG). Since conjunction was computed on a priori ROIs, we used a more lenient threshold of $p < 0.05$ corrected for multiple comparison with the false discovery rate (FDR).

To localize seed regions in each subject, we used structural and functional criteria. Firstly, we localized the maxima of activation at group level for the conjunction analysis described above in the IPL (60, 32, 24) and IFG (50, 14, 18). Secondly, we looked, in each subject, for activations in the two a priori ROIs, IPL and IFG, as defined above. To refine our choice of individual coordinates for each ROI, we then localized for all subjects who showed activation in these anatomically defined ROIs the nearest local maxima to the group activation maxima. Finally, we used these individual coordinates to extract the mean corrected time series for each seed region within a sphere of 10 mm radius. All but two subjects showed activity in the two regions of interest, so results reported refer to 21 subjects.

The PPI term was calculated, for each seed separately, as the product of the extracted time series and a vector representing the comparison of interest. The parameters computed with the PPI for each seed and each condition (PPI term, condition term, and seed time series) were then
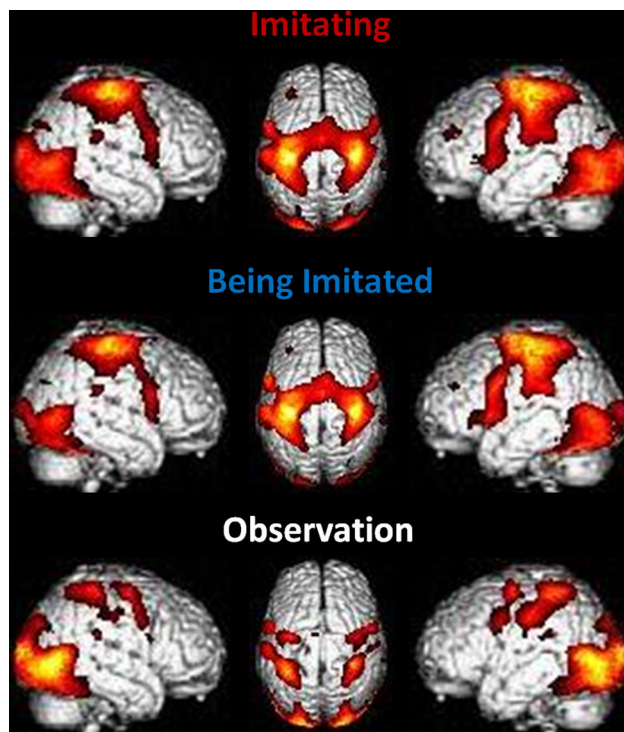
Fig. 3 General linear model results. Areas recruited during imitating, being imitated, and observation compared to rest. Results are superimposed to a single subject rendering and are significant at a threshold of $p < 0.05$ corrected for multiple comparison using the familywise error rate (FWE)

Table 1 Coordinates of local maxima activation for the three conditions of interest: imitating, being imitated, and observation

Label	MNI			k	t
	x	y	z		
Imitating					
L precentral gyrus	−36	−24	62	20,507	24.50
R precentral gyrus	36	−24	62		23.03
L cerebellum	−16	−52	−22	17,275	18.16
R cerebellum	20	−50	−20		16.25
L thalamus	−14	−20	8	2,384	10.91
R thalamus	16	−20	8		10.56
R inf. par.	60	−32	24	141	6.75
L mid. front.	−26	38	24	220	6.22
Being imitated					
L precentral gyrus	−36	−24	62	19,180	20.50
	−36	−22	54		20.08
R precentral gyrus	36	−24	62		19.10
L cerebellum	16	−52	22	11,161	15.46
R cerebellum	20	−50	−20		14.05
Precuneus	−2	−62	−16		13.66
R thalamus	16	−18	10	502	8.16
R inf. par.	62	−32	24	107	6.59
L mid. front.	−32	40	28	52	5.80
R mid. occ.	30	−76	32	18	5.74
Observation					
R mid. occ.	48	−74	0	13,844	20.52
L mid. occ.	−42	−80	0		18.67
R sup. par.	34	−36	54	1,778	15.21
L inf. par.	−36	−36	54	2,553	14.80
R precentral gyrus	42	−6	62	815	12.09
R mid. front.	54	2	46		9.04
R sup. front.	30	−8	58		7.66
L precentral gyrus	−38	−6	58	640	9.96
R inf. par.	60	−32	24	75	6.95
SMA	−4	−4	58	89	6.77
L thalamus	−10	−20	10	37	5.69
R inf. front.	46	12	20	19	5.56
L inf. par.	−52	−38	24	42	5.52

Results are significant at p(FWE) < 0.05

R right, *L* left, *SMA* supplementary motor area, *mid.* middle, *sup.* superior, *inf.* inferior, *occ.* occipital, *front.* frontal, *par.* parietal

entered as regressors in separate first-level general lineal models (GLM). To test for brain areas showing greater coupling with each seed during imitating versus observation, being imitated versus observation and imitating versus being imitated, we computed separate t tests, in the corresponding model, with 1 for the PPI term and 0 elsewhere.

In order to test for changes in connectivity at group level, we then computed a one-sample t test for each region of interest and each condition, using individual contrasts. Statistical maps were thresholded at p(FDR) < 0.001, if not otherwise specified.

Results

General linear model (GLM)

Results from contrasts of interest revealed that imitating and being imitated were associated with activations in a widespread bilateral network encompassing the primary motor area, dorsal and ventral premotor areas, and left dorsolateral prefrontal cortex. In addition, these conditions recruited the inferior parietal cortex and occipital regions. During observation, the most pronounced activation, not surprisingly, was found in the bilateral occipital regions, but importantly this condition was also correlated with activity in IPL and IFG. Activation clusters for the three conditions are shown in Fig. 3; coordinates of local maxima are reported in Table 1.

Psychophysiological interaction (PPI)

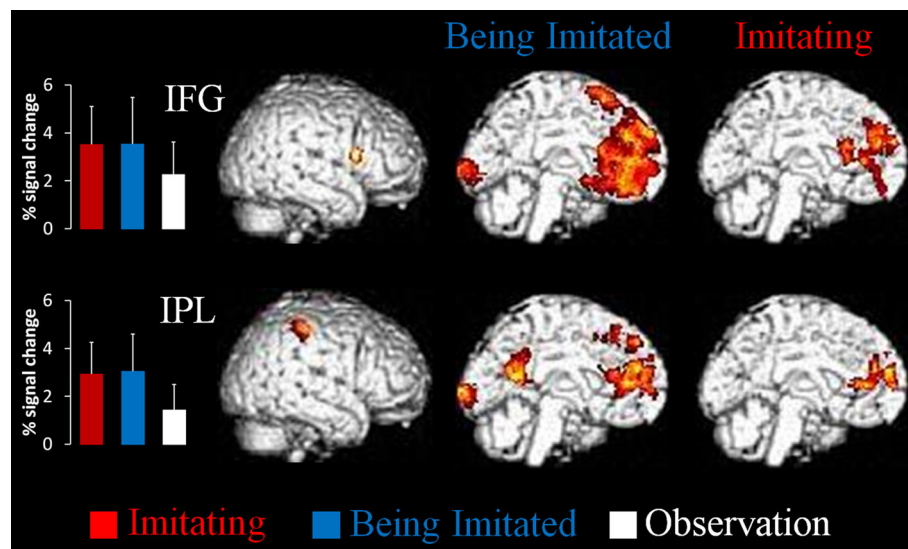From PPI analysis, it appeared that both IFG and IPL showed a greater coupling with areas of the Mentalizing

Fig. 4 PPI results. The first column shows parameters estimates for the two ROIs, IFG and IPL, in the three conditions: imitating (*red*), being imitated (*blue*) and observation (*white*). The second column represents the location of ROIs used as seed regions for the PPI analysis: IFG and IPL are, respectively, showed in the *upper* and the *lower* part of the figure. The *third* and *fourth* column represent areas showing greater coupling with IFG and IPL during being imitated and imitating conditions when compared to observation. Results are superimposed to a single subject rendering and are significant at a threshold of $p < 0.001$ corrected for multiple comparison using the false discovery rate (FDR). Connectivity for the IPL in imitating condition was significant at a slightly more lenient threshold of $p(\text{FDR}) < 0.003$ (color figure online)

System during the two experimental conditions of interest (imitating and being imitated) compared with observation. Areas showing greater coupling with IFG during imitating were located in the medial wall of the frontal lobe encompassing dorsal and ventral medial prefrontal cortex (MPFC) and anterior cingulate cortex (ACC). In addition to frontal structures, posterior regions in the occipital lobe showed a greater coupling during being imitated. Concerning IPL, the same pattern of connectivity was found with medial frontal structures, ACC and MPFC during imitating, and an additional posterior region comprising the precuneus during being imitated (Fig. 4). Table 2 details the complete list of areas that showed a modulation of connectivity with the two seeds. No area showed significantly greater coupling with both seeds when imitating and being imitated conditions were directly compared or when observation was compared to the imitation conditions.

Discussion

It has recently been argued that the Mirror System and the Mentalizing System, though involved in different social functions, could interact directly when self-other representations are concerned. Mirror System would allow to relate self to other at the motor level via simulation of other's actions, while the Mentalizing System would be involved at a meta-cognitive level in computation of self and other's mental states (Uddin et al. 2007). With this option in mind, Uddin et al. (2007) have called for paradigms designed to understand how and under what conditions these two networks may interact.

Our proposal was that an imitative interaction represents a test situation in this direction. Indeed, imitation offers the opportunity to go beyond simulation and to physically produce the action while seeing it. MNS would then work as an observation action coupling between two persons and allow synchronization of their actions. On the other hand, producing similarity is not sufficient to structure an interaction (Dumas et al. 2012). Any social interaction commands a contingent oscillation between social roles (here, model and imitator). Such oscillation is the by-product of a continuous negotiation requiring in each partner the anticipation and the mutual understanding of the other's intentions (here, who will be the model and who the imitator) and should thus involve the Mentalizing System.

Our online interactive context was expected to reveal the emergence of a coupling between the Mirror and the Mentalizing systems; indeed, imitating and being imitated modulated significantly the connectivity between the two systems, when compared to passive observation. In particular, the IFG showed greater coupling with the dorsal and ventral MPFC and ACC during imitating and being imitated conditions. The same regions showed greater coupling with the IPL (posterior component of the MNS) during imitation, while the modulation of activity extended to the PCC and the precuneus, another major node of the

Table 2 Coordinates of local maxima showing greater coupling with the two seed regions, IFG and IPL, in imitating and being imitated conditions

Label	MNI			k	t
	x	y	z		
Imitating—IFG					
ACC	−8	22	22	1,403	8.64
sgACC	−2	22	8		8.52
MPFC	−8	54	−18		8.12
Being imitated—IFG					
SMA	−8	16	66	6,339	9.97
ACC	−2	30	12		9.53
sgACC	6	24	−2		9.30
L mid. occ.	−20	−86	0	1,123	9.91
L inf. occ.	−32	−90	−6		7.28
L insula	−26	12	−14	1,015	8.19
L inf. front.	−38	22	−14		8.06
L mid. front.	−28	36	−18		7.23
R mid. occ.	26	−84	2	640	7.61
R mid. temp.	36	−64	−2		7.44
L ang. gyr.	−44	−70	30	323	7.05
L mid. temp.	−42	−64	24		6.58
L sup. occ.	−28	−74	42		5.15
*Imitating—IPL**					
ACC	−12	40	8	893	7.11
MPFC	8	60	14		6.30
Being imitated—IPL					
L mid. occ.	−16	−98	0	786	8.36
L inf. occ.	−26	−88	−4		7.66
Precuneus	−16	−54	30	858	8.00
R ang. gyr.	48	−62	28	412	7.80
R mid. occ.	38	−72	38		5.49
ACC	16	46	8	1,921	7.67
MPFC	−8	46	24		7.66
ACC	−10	40	8		7.59
L mid. occ.	−38	−72	36	449	6.90
L ang. gyr.	−40	−52	26		6.68
L mid. temp.	−44	−64	24		6.52
L sup. front.	−16	44	42	348	6.71
MPFC	8	42	44		6.53
R sup. front.	18	38	54		5.97
L mid. front.	−26	34	48	259	5.84

Results are significant at p(FDR) < 0.001; * p(FDR) < 0.003

R right, *L* left, *ACC* dorsal anterior cingulate cortex, *sgACC* subgenual anterior cingulate cortex, *MPFC* medial prefrontal cortex, *SMA* supplementary motor area, *mid.* middle, *sup.* superior, *inf.* inferior, *occ.* occipital, *front.* frontal, *temp.* temporal, *ang. gyr.* angular gyrus

Mentalizing System (Saxe et al. 2006), during being imitated. Our PPI results showed that when an imitative interaction is involved, the Mirror System modulates the activity of regions belonging to the Mentalizing System, in particular the vMPFC.

While most previous studies investigating social cognition have mainly addressed the functional specialization of the two systems, we addressed the question of their functional integration. Our results extend previous findings concerning the connection of the two systems (Spunt and Lieberman 2012a, b; Schippers and Keysers 2011; Schippers et al. 2010). For instance, Schippers et al. (2010) showed that the mirror activity of a gesturer predicts the mirror and vMPFC activity of the guesser during a game of charades; moreover, the prediction was higher during active guessing than during passive observation. When studying, on the same dataset, intra-brain connectivity in the guesser, the posterior flow of information (from premotor to parietal to middle temporal gyrus) was greater for active guessing than for passive observation (Schippers and Keysers 2011). Yet, the nature of the task used in this study elicited specifically mentalizing processes. Moreover, the task did not allow real social interaction between partners, as the guesser did not influence the gesturer. A dual behavioral paradigm is needed to explore embodied and participatory aspects of social understanding (De Jaegher et al. 2010). To our knowledge, our study has been the first to use a real online context in the MRI environment to explore a concurrent connection between the MNS and the Mentalizing System. Our findings suggest that while MNS is engaged on a small timescale in the preparation of one's own action in regard to the other's action, the Mentalizing System subserves higher cognitive processes such as the computation of the other's intention to switch role. In this sense, the anticipation of a motor response of the partner goes hand in hand with the prediction of the other's mental state.

Conclusion

The neural exploration of social interaction is an open challenge, as it is the objective of moving toward a two-person neuroscience (Hari and Kujala 2009). This new field indeed has rapidly revealed how difficult it is to "let humans interact socially while probing their brain activity", as said by Montague et al. (2002). Our choice has been to design an online procedure based on imitation. Free imitation requires both an understanding of the other's action to act in synchrony and the anticipation of the other's intention to switch role. As a paradigm, free imitation offers a double advantage. Firstly, the brain areas of instructed imitation are already delineated by previous research. Secondly, we can add new data related to the context of social interaction.

Our PPI results suggest that the sophisticated aspects of an ongoing social interaction involve both the Mirror and the Mentalizing systems. Close to Spunt and Lieberman (2013)'s dual-process model, a proposal will be that the Mirror System allows us to understand and anticipate action schemes but cannot account alone for the dynamic of role switching which involves an understanding of the other's intention. The Mentalizing System is required to achieve a fine-grained strategy of readiness to initiate and willingness to follow.

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