Contents lists available at SciVerse ScienceDirect

NeuroImage

Social grasping: From mirroring to mentalizing

Cristina Becchio [a], Andrea Cavallo [a], Chiara Begliomini [b], Luisa Sartori [b], Giampietro Feltrin [c], Umberto Castiello [b],*

[a] *Centro di Scienza Cognitiva, Dipartimento di Psicologia, Università di Torino, Turin, Italy*
[b] *Dipartimento di Psicologia Generale, Università di Padova, Padova, Italy*
[c] *Dipartimento di Scienze Medico-Diagnostiche e Terapie Speciali, Università di Padova, Padova, Italy*

ARTICLE INFO

ABSTRACT

Because the way we grasp an object varies depending on the intention with which the object is grasped, monitoring the properties of prehensile movements may provide access to a person's intention. Here we investigate the role of visual kinematics in the implicit coding of intention, by using functional brain imaging while participants observed grasping movements performed with social versus individual intents. The results show that activation within the mirror system is stronger during the observation of socially intended movements relative to individual movements. Moreover, areas that form the mentalizing system are more active during social grasping movements. These findings demonstrate that, in the absence of context information, social information conveyed by action kinematics modulates intention processing, leading to a transition from mirroring to mentalizing.

Introduction

When we perform actions in daily life, these actions are usually driven by a prior intention. For instance, the action of grasping a cup might be performed with the intention to drink or to pass the cup to another person. Because different intentional actions are characterized by different movement profiles (Becchio et al., 2010), monitoring the properties of observed movements may convey information about the actor's intention. Does she intend to drink or to pass the cup to another person? By simply observing the initial phase of the action, observers can discriminate between movements performed with different intents. For example, by watching everyday actions such as lifting a box, they can easily tell whether the actor is trying to deceive them about the real weight of the box (Grezes et al., 2004; Runeson and Frykholm, 1983). Depending on their level of motor skill, they are able to determine whether a basketball player is about to throw a ball or mimic a throw (Sebanz and Shiffrar, 2009). Moreover, by observing an actor reaching towards an object and grasping it, they are able to discriminate correctly between prehensile movements directed at another agent and prehensile movements performed in isolation (Manera et al., 2011; Sartori et al., 2011). This suggests that, in the absence of contextual information, observers can use differences in visual kinematics to infer goals and intentions from an observed movement (Kilner et al., 2007). However, what mechanisms and neural processes mediate this ability to extract intention from body motion?

Two hypothetical systems have been proposed to contribute to intention understanding: the *mirror* system and the *mentalizing* system (Van Overwalle and Baetens, 2009; Grafton, 2009). It is commonly assumed that the mirror system enables the pre-reflective understanding of others' intentions by internally simulating their behaviors (Gallese and Goldman, 1998). Observing others' actions activates corresponding representations in the observer's motor system, and these representations might be used to generate predictions about the intentions of others by running internal simulations (Wolpert and Flanagan, 2001). Mirror areas are consequently defined as those areas of the brain recruited by both execution and observation of actions, namely the inferior frontal gyrus (IFG), the premotor cortex (PM), and the inferior parietal lobule (IPL). In contrast, the mentalizing system is recruited when people reflect on the intentionality of others in the absence of detailed information on biological motion, for example, when reading stories or watching cartoons implying goals, beliefs or morality (Van Overwalle and Baetens, 2009). At this level, inferences about the intentions of others are thought to be based on a set of rules used as a 'theory of mind' to predict others' behavior (Leslie et al., 2004). This process of mentalizing has been consistently related to regions along the temporo-parietal junction (TPJ), the medial prefrontal cortex (mPFC), and the posterior cingulated cortex (Frith and Frith, 2006; Saxe, 2006).

The mirror system and the mentalizing system are sometimes portrayed as mutually exclusive and even oppositional. Rather than reflect the functional independence of the two systems, this opposition, however, is likely to result from experimental paradigms designed to artificially isolate the processes of just one system (Grafton, 2009; Keysers and Gazzola, 2007; Schilbach, 2010; Thioux

* Corresponding author at: Dipartimento di Psicologia Generale, Università di Padova, 35131, Padova, Italy. Fax: +39 049 8276600.
E-mail address: umberto.castiello@unipd.it (U. Castiello).

et al., 2008): perceived motor behavior with little social content for testing the mirror system; more abstract descriptions in the absence of any motion for probing the mentalizing system (Van Overwalle and Baetens, 2009).

An unresolved issue is how *social intention* conveyed by body movement impact on the recruitment of the mirror and mentalizing systems. Both systems seem to favor intentions arising in the context of a social interaction as opposed to individual intentions (Centelles et al., 2011; Kourtis et al., 2010; Oberman et al., 2007; see also Ciaramidaro et al., 2007). Social interaction modulates activity within the mirror system (e.g., Kourtis et al., 2010) and can enhance and even reverse human mirror neurons activity (Catmur et al., 2007). However, it remains unclear to what extent the mirror areas are sensitive to kinematic cues to social intention. In other words, whether in the absence of context information, activation within the mirror system is stronger during the observation of socially intended movements than of non-social movements. A second, related issue is whether observing social movements might lead to the concurrent activation of the mentalizing system. During movement observation, the mentalizing system may become active when observers reflect on the intentionality of an observed action (e.g. Buccino et al., 2007; de Lange et al., 2008; Iacoboni et al., 2005). For example, when they are asked to judge whether the intention underlying an action is ordinary or non-ordinary (de Lange et al., 2008), and during observation of unusual actions performed in non-stereotypical contexts (e.g. someone operating a light switch with their knee when their hands are free; Brass et al., 2007; Liepelt et al., 2008). Because inferring the purpose of an unusual action and the reason why it is performed in an implausible context necessitates a great deal of active inferencing, these findings can be explained by assuming that under these circumstances the mirror system fails and the additional recruitment of the mentalizing system is required (Van Overwalle and Baetens, 2009). Situations involving social interactions generally trigger inferences regarding the contents of other people's minds (Frith and Frith, 2006), but is the observation of socially intended movements sufficient to recruit the mentalizing system? Social gaze shifts, i.e. gaze shift directed at the observer, have been shown to activate the mPFC as a function of personal involvement (Schilbach et al., 2006; see also, Bristow et al., 2006). Moreover, in gaze-based social interactions, increased activity in mPFC is observed when participants follow the gaze of another person to engage in joint attention (Schilbach et al., 2010). However, no study has so far elucidated the possibility that social information conveyed by movement kinematics may engage the mentalizing system.

To address these issues we measured brain activity while participants observed isolated prehensile movements performed with different social and non-social intents. Participants viewed video clips showing a human arm reaching towards a wooden block and grasping it. Depending on condition, this action was performed with the intent to compete against an opponent as to put first the block in the middle of the working surface (competition), to cooperate with a partner in building a tower (cooperation), or to perform an individual action at a fast (individual fast) or slow speed (individual slow). Occlusion at the moment of contact between the fingers and the object ensured that neither the second part of the movement nor the interacting partner was made visually available. Apart from the visual properties of the grasping movement, the action sequences were therefore identical (see Figs. 1A and B). Note that, at the behavioral level, Sartori et al. (2011) demonstrated that observers are attuned to movement information and can rely on early differences in visual kinematics to discriminate between social and non-social intentions. We therefore reasoned that if the mirror system favors social kinematics, then mirror areas should be more strongly activated during the observation of competitive and cooperative reach-to-grasp movements relative to individual movements performed at fast and slow speed. Furthermore, we expected that, as mentalizing is essential for successful interaction, observing cooperative and competitive

movements relative to individual movements would lead to a transition from the mirror to the mentalizing system.

Methods

Participants

Sixteen volunteers (9 women and 7 men) aged 19–36 years (mean 23.3) participated in the study. All were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971) and none had a history of neurological, major medical, or psychiatric disorders. Before the study participants gave their written informed consent. Specific information about the study was provided after the experimental session. Experimental procedures and scanning protocols were approved by the University of Padova Ethics Committee and conducted in accordance with the 1964 Declaration of Helsinki. None of the individuals taking part in the experiment experienced discomfort during fMRI acquisition.

Experimental stimuli

To create the stimulus material, we filmed four types of action sequence:

Competitive (i.e., social fast)
Two models seated opposite to each other. They were requested to reach towards and grasp their respective objects and to compete as to put first the respective object in the middle of the working surface.

Cooperative (i.e., social slow)
This action sequence was similar to the cooperative sequence, except that the models had to cooperate in order to build a tower in the middle of the working surface.
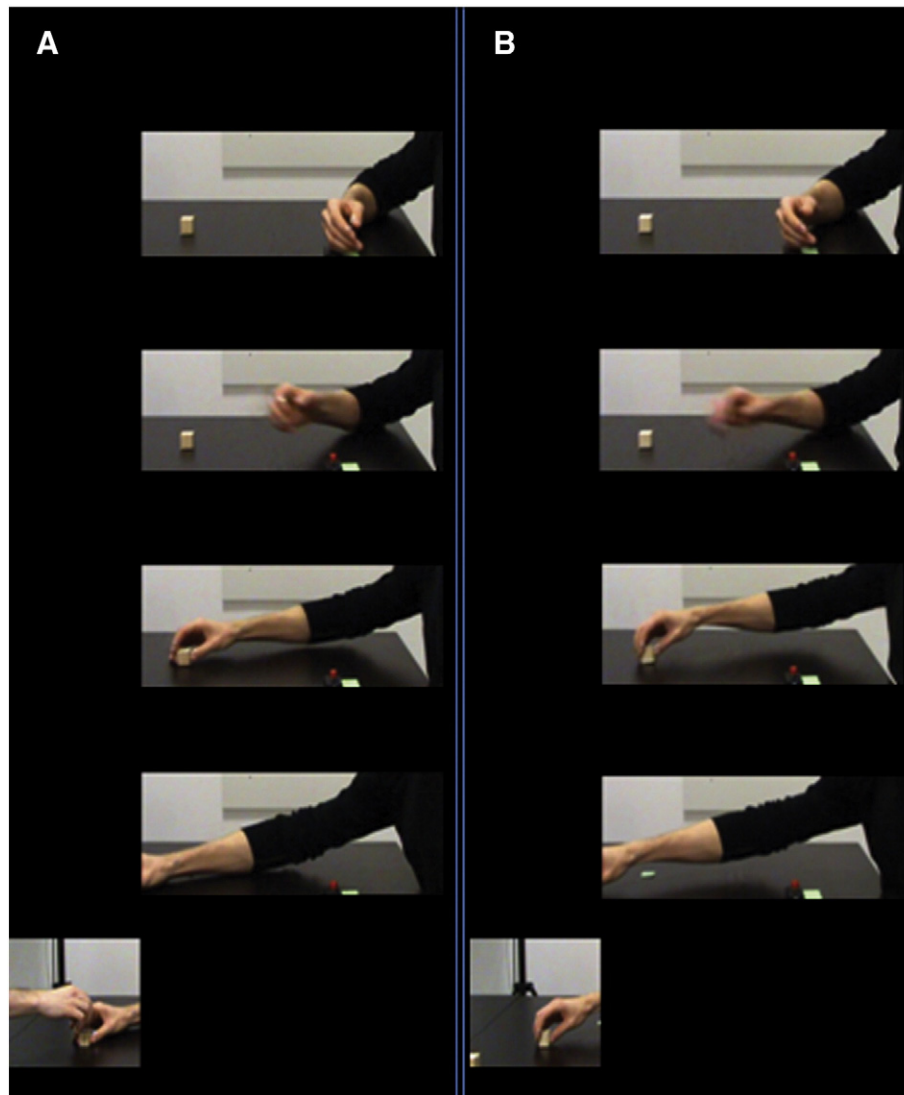
Individual fast
The model was requested to reach for and grasp the stimulus in front of his/her right hand as fast as possible and to put it quickly in the middle of the working surface.

Individual slow
The model was requested to reach and grasp the stimulus in front of his/her right hand at a natural speed and to put it in the middle of the working surface.

Each model performed 10 trials for each type of action. This resulted in 80 trials per type of action. The models were filmed from a lateral perspective using a digital video camera and recorded using a SMART-D motion analysis system (Bioengineering Technology & Systems, B|T|S|). Reflective passive markers (diameter 0.25 cm) were attached to the wrist, index finger, and thumb of each model's right hand; the wrist marker was used to measure the reaching component of the action, while the markers positioned on the index finger and thumb were used to measure the grasp component of the action. Six infrared cameras (sampling rate 140 Hz) placed around the table captured the movement of the markers in 3D space.

Out of 320 trials, 30 representative trials for each type of action were selected. The videos corresponding to the selected trials provided the raw material used to create experimental stimuli. 120 unique video clips, 30 for each type of action sequence, were edited using a video editing software package (Adobe Premiere pro; .avi format, disabled audio, 25 frames/s, resolution 720×576 pixels, duration 3000 ms, subtended region $22.62° \times 33.40°$). Each video clip started with the model resting his/her right hand on a starting pad and ended immediately after the model had placed the object in its final position. To reduce movement onset predictability, hand action started randomly 10, 18 or 25 frames after the video clip began.

Fig. 1. Exemplar schematic representation of event sequencing during a (A) competitive or (B) individual fast action sequences. Video clips were temporally occluded short after the point of contact between the fingers and the object, so that neither the second part of the movement nor the interacting partner (when present) was visible. A trial started with a video clip depicting the model's arm and forearm reaching towards and grasping for an object (3000 ms). The last visible frame of each clip showed the model's hand disappearing behind a black screen after the reach-to-grasp movement. Then a test picture (see small inset on left bottom of each column) showing the model's hand placing the object in its final position was presented. Participants were instructed to decide whether the test picture was a continuation of the action.

Digital video editing was used to reveal only the arm and forearm of the model's body. The face was deliberately not shown, in order to focus the participants' attention on the reach-to-grasp movements. Furthermore, the video clips were temporally occluded short after the point of contact between the fingers and the object so that the last visible frame showed the model's hand disappearing behind a black screen after grasping (see Fig. 1). We used this procedure to ensure that only advance information gained during the viewing of the reach-to-grasp phase of the action was made available to observer. Neither the final part of the movement nor the interacting model was visible in the video clips. Stimuli were projected via magnet-compatible video goggles at an 800×600 pixel resolution. E-prime software (Psychology Software Tools Inc., Pittsburgh, USA) was used for experimental control (stimulus presentation and response collection).

Procedure and design

The four types of action sequence were embedded in a 2×2 factorial design, in which the factors were the type of intention (*social* versus *individual*) and the speed of the observed action (*fast* versus *slow*).

A trial started with a video clip depicting the reach-to-grasp action sequence (3000 ms). Then a test picture showing the model's hand placing the object in its final position was presented. For congruent trials, the picture showed the continuation of the action in the video clip; for incongruent trials, the continuation of a different type of action sequence (individual test picture for social action sequence; social test picture for individual action sequence) was shown. Participants were instructed to decide whether the test picture was a continuation of the action and to indicate their decision by pressing a key with the index or middle finger of their right hand. They were instructed to respond as quickly as possible while keeping the number of errors low. The test picture was presented for at most 3000 ms, or until response. The intertrial interval (ITI) was determined by a 'long exponential' probability distribution (Hagberg et al., 2001), with a mean ITI of 2766 ms and a range of 1000–6000 ms. After a practice session outside the scanner, each participant underwent 6 functional runs, each run containing 60 trials and lasting approximately 9 min. The whole experimental session comprised 360 trials: 30 trials for each type of action sequence (competitive, cooperative, individual fast, and individual slow) by 3 repetitions. The congruent–incongruent judgment task ensured

that participants directed their attention to the specific kinematic features of the observed movement.

fMRI data acquisition

The experiment was carried out on a whole body 1.5 T scanner (Siemens Avanto) equipped with a standard Siemens 8 channels coil. Functional images were acquired with a gradient-echo, echo-planar (EPI) T2*-weighted sequence in order to measure blood oxygenation level-dependent (BOLD) contrast throughout the whole brain (37 contiguous axial slices acquired with descending interleaved sequence, 56×64 voxels, $3.5 \times 3.5 \times 4.0$ mm resolution, FOV = 196×224 mm, flip angle = 90°, TE = 49 ms). Volumes were acquired continuously with a repetition time (TR) of 3 s; 178 volumes were collected in each single scanning run. High-resolution T1-weighted images were acquired for each subject (3D MP-RAGE, 176 axial slices, no interslice gap, data matrix 256×256, 1 mm isotropic voxels, TR = 1900 ms, TE = 2.91 ms, flip angle = 15°).

fMRI analysis

Data preprocessing and statistical analyses were conducted using SPM5 (Statistical Parametric Mapping, Wellcome Institute of Cognitive Neurology, London, UK) implemented in MATLAB 7.5.0 environment (MathWorks, Natick, MA, USA). For each participant, the first two volumes of each fMRI run were discarded to allow for stabilization of magnetization. Images underwent motion correction in order to estimate head movements, and a two-pass procedure was used in order to register the images to the mean of the images after the first realignment. The mean of all functional images was then co-registered to the anatomical scan, previously corrected for variations in intensity. EPI images were normalized adopting the MNI152 template, supplied by the Montreal Neurological Institute (http://www.mni.mcgill.ca/) and distributed with the SPM software. Finally, all images were spatially smoothed using a $7 \times 7 \times 8$-mm full-width-at-half-maximum (FWHM) Gaussian kernel. High-pass filtering (cutoff period 128 s) was also applied to remove low-frequency drifts in signal.

A random effects analysis was conducted on the data. The variance in the BOLD was first decomposed in a first-level model. Separate regressors were defined based on the timing of presentation of each of the four experimental conditions (competitive, cooperative, individual fast, and individual slow), and these functions were convolved with a canonical, synthetic hemodynamic response function (HRF) to produce the individual models. Each trial was modeled as a 3 s duration event, starting at the onset of the video. To exclude that evaluation of conflicting information might interfere with encoding of intention (e.g., Botvinick et al., 2004), test pictures, together with trials in which responses were incorrect (33%), were modeled as two further separate event types and differentiated from experimental conditions. For each participant, all regressors were incorporated into a General Linear Model (GLM), together with six regressors of no interest comprising the estimated head motion calculated during the realignment stage of pre-processing. Individual models were separately estimated and contrasts were defined in order to pick out the main effects of each experimental condition. These contrasts were then entered into a second-level analysis in which participants served as a random effect in a within-subjects ANOVA allowing for non-sphericity. Contrasts for the main effect of type of intention and the main effect of speed of observed action were obtained for the whole brain (p<.001 uncorrected, extend threshold: 10 voxels). To constrain the search space for interaction effects (Friston et al., 2006), the statistical map resulting from the F-contrast testing for main effect of type of intention (social versus individual) was used as searching area for the Small Volume Correction (SVC, Worsley et al., 1996). This mask was adopted to test the interaction between type of intention and speed of the observed action (extent cluster size of $k \geq 10$, height threshold of p<0.05, FDR corrected — Genovese et al., 2002). In

order to detect differential effects specifically driven by competitive and cooperative movements, we calculated the following simple contrasts: competitive > cooperative, cooperative > competitive, competitive > individual fast, and cooperative > individual slow.

Results

Kinematic analysis of the observed reach-to-grasp movements

To characterize the kinematic profiles for the observed reach-to-grasp movements, we considered key reach-to-grasp kinematic landmarks, which are known to vary depending on movement speed and the type of intention (for details, see Georgiou et al., 2007; Becchio et al., 2008a, 2008b; Sartori et al., 2009). This is a fundamental aspect of the study, given that no information other than the visual kinematics of the observed movements was provided to discriminate between intentions.

In line with previous studies (e.g. Becchio et al., 2008b), we found statistically significant differences among competitive, cooperative, and individual movements performed at fast or slow speed for nine kinematic parameters concerned with both the reaching and the grasping component of the action (see Table 1). To uncover the structure of the possible differences related to the kinematics underlying the selected reach-to-grasp actions (30 representative trials for each type of action), we submitted the nine kinematic parameters to a principal components analysis (PCA). The results indicated that the first three components accounted for 79% of the variance (54%, 15%, and 10%, respectively). As they provided a good characterization of the data, they were retained and subjected to oblique rotation (direct oblimin). The weights of the kinematic parameters for the first three components are reported in Table 1. The three components were positively correlated with each another (r_s from .21 to .32). The first component had positive weights ($\geq$.30) for the movement time, the time of peak wrist deceleration, and the amplitude of peak grip closing velocity, and negative weights for the amplitude of peak wrist velocity, the amplitude of maximum grip aperture, and the amplitude of peak grip opening velocity. This suggests that this component can be interpreted as a *global* descriptor of combined reaching and grasping kinematics. The time of peak grip-opening velocity and the time of peak grip-closing velocity weighted substantially on the second component,

Table 1
Weights of the kinematic parameters for the first three components.

	Component 1	Component 2	Component 3
Movement time (ms)	.721	.286	.203
Maximum wrist velocity (mm/s)	−.776	−.113	−.132
Maximum wrist deceleration (mm/s²)	.016	−.100	.977
Time of maximum wrist deceleration (ms)	.707	.276	.212
Maximum grip aperture (mm)	−.889	.161	.292
Maximum grip opening velocity (mm/s)	−.810	−.122	−.155
Time of maximum grip opening velocity (ms)	.187	.722	.097
Maximum grip closing velocity (mm/s)	.869	−.109	−.025
Time of maximum grip closing velocity (%)	−.071	.930	−.137

Notes. Weights of the kinematic parameters for the first three components of the principal component analysis (PCA). Significant differences among competitive, cooperative, individual fast and slow reach-to-grasp movements were observed for the following: movement time; maximum wrist velocity: the amplitude of wrist peak velocity during reaching; maximum wrist deceleration: the amplitude of wrist peak deceleration during reaching; time of maximum wrist deceleration: the time at which peak wrist deceleration occurred; maximum grip aperture: the maximal distance between the two markers positioned on the index finger and thumb; maximum grip opening velocity: the amplitude of peak grip opening velocity; time of maximum grip opening velocity: the time at which the fingers reached the maximum velocity during hand opening; maximum grip closing velocity: the amplitude of peak grip closing velocity; time of maximum grip closing velocity: the time at which the fingers reached the maximum velocity during hand closing.

suggesting that it can be interpreted as a *grip timing* component. Finally, the third component showed only one large weight related to the amplitude of peak *wrist deceleration*. Univariate ANOVAs (followed by Tukey HSD post-hoc tests) were used to compare the different types of action (competitive, cooperative, individual fast, and individual slow) with respect to the three kinematic components. The effect of the type of action was significant for all three components (see Table 2). For the global component, all pairwise comparisons were significant. For the grip timing component, post-hoc comparisons showed significant differences between competitive and cooperative, and between individual fast and slow movements. This indicates that this component has the ability to discriminate between movements performed at different speeds. Finally, for the wrist deceleration component, pairwise comparisons revealed significant differences between individual fast movements and slow movements, and between competitive and individual fast movements. Because only the global kinematic component discriminated between cooperative and individual slow movements, it can be suggested that the kinematic profiles for cooperative versus slow movements were more similar compared to those for both competitive versus cooperative movements (discriminated by the global component and the grip timing component) and competitive versus individual fast movements (discriminated by the global component and the wrist deceleration component). Linear discriminant analysis on the component scores provided further support to this interpretation. Whereas 92% of the competitive trials were correctly classified based on the three kinematic components, only 59% of the cooperative trials were correctly classified as cooperative. Indeed, 30% of the cooperative trials were misclassified as slow trials, and 7% as competitive trials.

fMRI results

The peak of activity and stereotaxic coordinates for activations are listed in Table 3.

Main effect of type of intention

Observing reach-to-grasp movements performed with a *social* intent relative to reach-to-grasp movements performed with an *individual* intent [(competition + cooperation) > (individual fast + individual slow)] increased activity bilaterally in the posterior portion of the middle frontal gyrus (BA 46) and in the adjacent left IFG (BA 9) (Fig. 2A). Within the left hemisphere, differential activations were also observed in the inferior parietal cortex, within the supramarginal gyrus (BA 40), extending inferiorly to encompass the TPJ. Additional loci of increased activity were found within the right middle temporal gyrus (BA 21) and the dorsal sector of the mPFC (BA 8). As can be seen in Figs. 2B and C, the main effect of type of intention in the mPFC and in the left TPJ was mainly driven by the observation of competitive reach-to-grasp movements. Observing *individual* reach-to-grasp movements relative to *social* reach-to-grasp movements [(individual fast + individual slow) > (competition + cooperation)] revealed no differential activation.

Table 3
Peak activity and stereotaxic coordinates for activations.

	BA	Coordinates (x,y, z)			T	Z	Cluster size
Main effect of type of intention							
Social > individual							
Middle temporal gyrus	21	63	−32	−12	5.09	4.50	17
Inferior parietal lobule (IPL)	40	−60	−46	40	5.08	4.49	53
Temporo-parietal junction (TPJ)	40	−60	−53	28	4.81	4.29	
Middle frontal gyrus	46	42	18	20	4.52	4.08	60
Inferior frontal gyrus (IFG)	9	−42	11	24	4.28	3.90	54
Medial frontal gyrus (mPFC)	8	0	28	40	3.97	3.66	16
Individual > social	NS						
Main effect of speed							
Slow > fast							
Middle occipital gyrus	19	−46	−81	−4	8.06	6.31	352
Middle occipital gyrus	37	42	−67	0	7.82	6.18	181
Cuneus	18	−21	−88	24	5.16	4.55	352
Insula	13	−42	−35	24	4.94	4.39	28
Inferior parietal lobule (IPL)	40	−39	−35	48	4.74	4.25	23
Superior temporal gyrus	41	49	−39	12	4.30	3.92	13
Fast > slow	NS						
Interaction type of intention by speed							
Temporo-parietal junction (TPJ)	40	−60	−46	28	5.53	4.81	33
Competitive > cooperative							
Temporo-parietal junction (TPJ)	40	−60	−46	28	4.50	4.06	18
Medial frontal gyrus (mPFC)	8	4	28	44	3.41	3.20	10
Cooperative > competitive	NS						
Competitive > individual fast							
Temporo-parietal junction (TPJ)	40	−60	−46	28	6.83	5.63	36
Inferior parietal lobule (IPL)	40	−60	−46	40	6.00	5.12	
Middle temporal gyrus	21	63	−32	−12	5.84	5.01	14
Inferior frontal gyrus (IFG)	45	49	18	24	4.66	4.18	38
Medial frontal gyrus (mPFC)	8	0	28	44	4.71	4.22	10
Inferior frontal gyrus (IFG)	45	−53	18	20	4.17	3.81	27
Individual fast > competitive	NS						

Notes. Anatomical and Brodmann Areas (BA) and MNI coordinates of the maxima within each cluster. Main effects are significant at p<.001 (uncorrected). Interaction effect and additional simple contrasts (cooperative > competitive, competitive > cooperative, cooperative > individual slow, competitive > individual fast) are significant at p<0.05 (corrected for multiple comparisons using FDR). Extent cluster size of k = 10. Positive coordinates' values on the x axis indicate right lateralization, negative values indicate left lateralization.

Main effect of speed of observed action

Observing *fast* movements relative to *slow* movements [(competitive + individual fast) > (cooperative + individual slow)] revealed no differential activation. *Slow* movements relative to *fast* movements [(cooperative + individual slow) > (competitive + individual fast)] were associated with an increase of activation in visual regions, including the middle occipital gyrus (BA 19/37), the left inferior occipital gyrus (BA 18), and the left cuneus (BA 18). Outside these regions, two small clusters of activation were observed in the right superior

Table 2
Kinematic differences across types of actions (average component scores).

	Omnibus ANOVA	Natural-speed vs. fast-speed	Cooperative vs. competitive	Competitive vs. fast-speed	Cooperative vs. natural-speed
Component 1 Global	$F_{(3,101)} = 118.764$ p<0.001 $\eta^2_p = 0.77$	1.203 vs. −.651 p<.001**	.564 vs. −1.008 p<.001**	−1.008 vs. −.651 p = .035*	.564 vs. 1.203 p<.001**
Component 2 Grip timing	$F_{(3,101)} = 5.629$ p = 0.001 $\eta^2_p = 0.118$	.320 vs. −.380 p = .040*	.442 vs. −.345 p = .017*	−.345 vs. −.380 p = .999	.442 vs. .320 p = .967
Component Wrist deceleration	$F_{(3,101)} = 48.052$ p<0.001 $\eta^2_p = 0.576$	.364 vs. −1.210 p<.001**	.311 vs. .718 p = .117	.718 vs. −1.210 p<.001**	.311 vs. .364 p = .992

Notes. **p<.001; *p<.05.

Fig. 2. Areas of increased signal for the main effect of type of intention [(competitive + cooperative) > (individual fast + individual slow)]. Observing reach-to-grasp movements performed with a social intent increased activity in (A) left IFG (BA 9), (B) dorsal sector of the mPFC (BA 8/32), and (C) within the supramarginal gyrus (BA 40), extending inferiorly to encompass the TPJ. As can be seen, the main effect of type of intention was mainly due to the observation of competitive reach-to-grasp movements.

temporal gyrus (BA 41) and in the left posterior insular cortex (BA 13), a multisensory area involved in the integration of sensory and motor information (e.g. Farrer et al., 2003).

Interaction type of intention by speed of observed action

The within-subjects ANOVA revealed a significant interaction between type of intention and speed of the observed action [(competitive > cooperative) > (individual fast > individual slow)] within the left TPJ (Fig. 3).
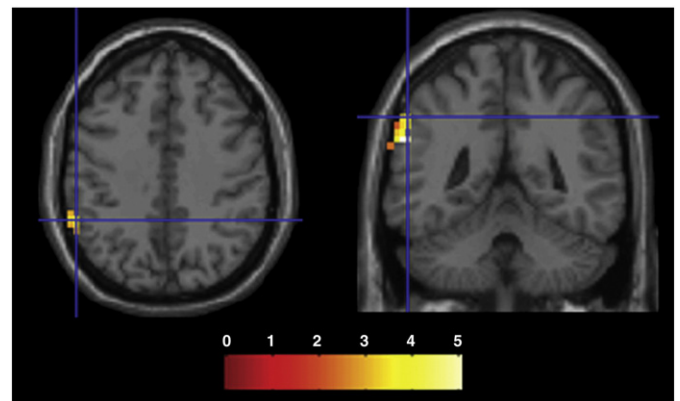
Type of social movement: competitive versus cooperative

Competitive reach-to-grasp movements, as compared to cooperative movements (competitive > cooperative), were associated with foci of enhanced activity in the left TPJ, and bilaterally in the mPFC (BA 8). Peaks of activity were found in regions very near to those activated by the comparison between social and non-social types of movements (see Table 3). The inverse contrast (cooperative > competitive) failed to reveal any differential peak of activation.

Fast movements: competitive versus individual fast

Observing competitive movements relative to individual fast movements (competitive > individual fast) was associated with a bilateral increase of activity in the IFG (BA 45). Enhanced activity was also

observed in the right middle temporal gyrus (BA 21), the left inferior parietal lobule (BA 40) extending to the TPJ, and the dorsal mPFC (BA 8). This pattern of activations largely overlapped with that associated with socially intended movements (social > individual).

Fig. 3. Temporo-parietal junction activation from the interaction between type of intention by speed of observed action [(competitive > cooperative) > (individual fast > individual slow)].

Slow movements: cooperative versus individual slow

Observing cooperative reach-to-grasp movements relative to individual slow movements (cooperative > individual slow) revealed no differential pattern of activation.

Discussion

In our daily life, we continuously monitor other people's actions and infer what they are intending to do. Here we investigated whether action understanding processes are sensitive to social information conveyed by movement kinematics.

The mirror system responds to social kinematics

When comparing observation of social movements with non-social movements, we found increased activation within mirror areas, including the IFG and the IPL (Molenberghs et al., 2012). In line with previous studies (Vingerhoets et al., 2010), this finding demonstrates that areas within the mirror system are sensitive to very subtle differences in the kinematics of the observed action. Most importantly, it suggests that mirror areas are more responsive to socially intended movements than to non-social movements.

As compared to non-social actions, social actions have been shown to elicit an increased level of activation within the mirror system (Oberman et al., 2007; Perry et al., 2010; Centelles et al., 2011; Kourtis et al., 2010). For example, mu wave suppression – an index of mirror neuron activity – has been shown to be greater for social interactive actions than for non-social actions (Oberman et al., 2007). Similarly, anticipatory activation of motor areas pertaining to the mirror system has been reported to be stronger during observation of actions performed by an interacting partner than for the actions a person performs alone (Kourtis et al., 2010). These findings have been interpreted as evidence of *top-modulation* modulations of the mirror system by social interaction. In this interpretation, activity changes in brain regions of the mirror system during social actions would result from the interaction of brain regions relevant to motor preparation/execution and brain regions that have been shown to be involved in processing the mental states of others (Gangopadhyay and Schilbach, in press; see also Csibra, 2007).

Our result showing differential activation within the IFG and the IPL as a function of movement kinematics (social versus individual) extends the proposed sensitivity of mirror areas to social stimuli, suggesting that increased activity within mirror areas might as well be *bottom-up* driven by socially salient kinematic features. Consistently with this view, we noted differential activation within IFG and IPL during observation of competitive movements in comparison to individual fast movements. For cooperative movements compared with individual slow movements, we did not find any differential activation. At first sight, this finding seems to contradict the hypothesis that the mirror system is sensitive to socially salient movement features. A crucial difference in the kinematic features of cooperative and competitive movements might, however, be responsible for this negative finding. Whereas linear discriminant analysis correctly classified 92% of the competitive trials based on the identified kinematic components, only 59% of the cooperative trials were correctly classified as cooperative. As many as 30% of the cooperative trials were misclassified as individual slow movements. This indicates that, in comparison to competitive versus individual fast movements, the kinematic profiles of cooperative and individual slow movements were more similar and thus more difficult to identify. As no cues, other than differences in the visual kinematics were provided to discriminate between movements performed with different intents, it is not surprising that no differential activation was noted when comparing the observation of cooperative and individual slow movements.

According to the most popular conception, action mirroring implements a simulation function in the motor system (Gallese et al., 2004; Rizzolatti and Sinigaglia, 2010). An alternative account is that mirror neurons process associations between observed and executed movements, and that both imitative and non-imitative associations may derive from this function (Hayes, 2010). Evidence favoring this hypothesis comes from experiments showing that laboratory training (e.g., Catmur et al., 2007) and context (Newman-Norlund et al., 2007; Van Schie et al., 2008) can reverse mirror activity. For example, Newman-Norlund et al. (2007) demonstrated that, following the observation of an action, activation in the right IFG and bilateral IPL is greater during preparation of complementary than of imitative actions. Although speculative, one intriguing hypothesis is that increased activation during observation of social actions reflects the activation of a complementary action sequence. As social actions (but not individual actions) are likely to evoke in the observer a complementary response, this might explain why in the present study we found stronger activation within mirror areas during observation of social actions in comparison to individual actions. A decisive test for this hypothesis could be the preferential activation of mirror areas for social actions evoking a complementary response relative to social actions evoking an imitative response.

The transition from mirroring to mentalizing

When comparing social reach-to-grasp movements with non-social movements, we also found differential activation within the left TPJ and the dorsal mPFC. Whereas it has been proposed that TPJ is specifically responsible for the attribution of goals and intentions within the mentalizing system (e.g. Saxe and Powell, 2006; Liepelt et al., 2008), activity within the mPFC has been linked to a variety of mentalizing tasks requiring reflective reasoning about actions and judgments (Van Overwalle, 2009). Modulation of dorsal regions within the mPFC has been reported, for example, during mentalizing about dissimilar others (Mitchell et al., 2006), thinking about friends (Kumaran and Maguire, 2005), and reasoning about false beliefs (e.g. Sommer et al., 2007). During action observation, activation of the TPJ and the mPFC is noted when observers are explicitly instructed to identify the intentions of the actors (e.g. de Lange et al., 2008; Centelles et al., 2011; Iacoboni et al., 2005; Spunt et al., 2010, 2011) or the actions themselves are atypical (e.g. Brass et al., 2007). Under these circumstances – it has been proposed – a deliberative focus is triggered either by the attentional focus of the perceiver (exogenous to the stimulus) or by the inconsistency of the action (endogenous to the stimulus) and the mentalizing areas are activated (Van Overwalle and Baetens, 2009). These findings support the idea that mentalizing regions contribute to analyze other people's actions when the viewer decides to reflect upon their goals, intentions and beliefs (Keysers and Gazzola, 2007; Thioux et al., 2008). Our data point to a further reason for why the mentalizing system might be recruited during observation of moving body parts: social intention, conveyed by action kinematics, might automatically engage brain regions that are part of the mentalizing system.

Anatomically our mPFC cortex activation ($x = 0$, $y = 28$, $z = 40$) was more posterior as compared to activations typically associated with thinking about mental states (e.g., Mitchell et al., 2006; $x = -9$, $y = 45$, $z = 42$). According to Amodio and Frith (2006), whereas the anterior region of the mPFC is associated with meta-cognitive representations that enable us "thinking about thinking", the more posterior region of the mPFC is involved in representing and continuously updating possible future actions in order to regulate behavior. Walton et al. (2004), for example, reported activity in this area ($x = 1$, $y = 24$, $z = 33$) when participants monitored the outcome of actions that were self-selected, but not when they monitored the outcome of externally-guided actions. Iacoboni et al. (2005) observed a similar activation ($x = -7$, $y = 34$, $z = 44$) during observation of grasping actions when participants were explicitly told to try to figure out the intention motivating the action. Because anticipating the sensory consequences of others' movements is essential to understand their intentions, this might suggest a special role of the posterior mPFC in monitoring both

self- and other-executed actions. In this interpretation, our activation in the dorsal mPFC might reflect the monitoring of observed actions rather than more abstract processes involved in mentalizing the underlying intentions.

As is apparent from Fig. 2, increased activation in the mPFC and the TPJ was mainly driven by observation of competitive reach-to-grasp movements; cooperative movements had little if any effect compared to individual movements. This was further supported by the finding of a significant effect of interaction between the type of intention and the speed of the observed action within the TPJ. Inspection of activity specifically related to competitive movements relative to individual fast movements revealed differential activation within the left TPJ and the dorsal sector of the mPFC. In contrast, no significant effect of cooperative relative to individual slow movements was observed. This pattern might be ascribable to differences in the kinematic profile of competitive and cooperative movements relative to individual movements. Because reflecting on the intention of an agent performing an action necessarily involves processing *what* she is doing and *how* she is doing it, activation within mentalizing areas interacting with the mirror system might be expected to vary as a function of intention-related information conveyed by kinematic features. Van Overwalle (2009) has suggested the TPJ as the most likely candidate for such a mentalizing area that might interact with the mirror system. This idea is supported by both the selective involvement of TPJ in goal inferences and its spatial proximity to IPL regions displaying mirror properties (Liepelt et al., 2008).

An alternative but not mutually exclusive explanation invokes the varying mentalizing demands of cooperation and competition. With cooperation, the intention of the interacting partner is known and her action can therefore easily be predicted. With competition, the opponent's next action is less predictable and might need to be inferred. In line with this, Decety et al. (2004) found that dorsal mPFC involvement during social interactions was specific to competition. In this fMRI study, participants played a computer game either in cooperation or in competition with another person. Distinct regions were found to be selectively associated with cooperation and competition: the orbitofrontal cortex specifically for cooperation ($x = -12$, $y = 36$, $z = -12$), and the dorsal mPFC for competition ($x = -2$, $y = 36$, $z = 40$). In the context of these findings, the observed increase of activity within the dorsal mPFC for competitive movements might imply that watching a competitive movement requires a higher mentalizing demand compared to watching a cooperative movement. A decisive test for this hypothesis could be the activation of mentalizing areas for actions performed in competitive contexts relative to kinematically identical actions performed in cooperative contexts.

General conclusions

Whereas most studies in mirror research focus on perceived body movements, immediate goals and actions embedded in a context, studies revealing the working of the mentalizing system typically involve tasks of a higher complexity and abstractness than the mere movement of body parts. Little is known regarding how the mirror and the mentalizing systems do integrate as to decode intention during real-world interactions. The current experiment was designed to explore the role of visual kinematics in the implicit coding of social intention. Our results demonstrate that, in the absence of contextual information, activation within the mirror system is stronger during the observation of socially intended reach-to-grasp movements than non-social movements. Moreover, areas involved in mentalizing are more active during social than non-social grasping movements. These findings show that the mirror and the mentalizing systems work in concert as to code for others' social intentions. Examining how the decoding of intentions is modulated by the degree to which human observers perceive themselves as participants of an ongoing interaction is an important future direction. In the present study participants observed social movements directed at

another agent. An extension of the current paradigm could consist in recording brain activity while participants observe self-directed and other-directed socially intended movements. Based on the assumption that social cognition is fundamentally different when an individual is actively and directly interacting with others (Schilbach, 2010), a further extension could consist in developing experimental paradigms that allow participants to be part of a social interaction in the constrained fMRI setting. Such paradigms may help to shed light on the putatively complementary roles of mirror neurons and mentalizing networks in situations that better approximate those encountered in daily life.

Appendix A. Supplementary material

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2012.03.013.

References

Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7, 268–277.
Becchio, C., Sartori, L., Bulgheroni, M., Castiello, U., 2008a. Both your intention and mine are reflected in the kinematics of my reach-to-grasp movement. Cognition 106, 894–912.
Becchio, C., Sartori, L., Bulgheroni, M., Castiello, U., 2008b. The case of Dr. Jekyll and Mr. Hyde: a kinematic study on social intention. Conscious. Cogn. 17, 557–564.
Becchio, C., Sartori, L., Castiello, U., 2010. Toward you: the social side of actions. Curr. Dir. Psychol. Sci. 19, 183–188.
Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: an update. Trends Cogn. Sci. 8, 539–546.
Brass, M., Schmitt, R.M., Spengler, S., Gergely, G., 2007. Investigating action understanding: inferential processes versus action simulation. Curr. Biol. 17, 2117–2121.
Bristow, D., Rees, G., Frith, C.D., 2006. Social interaction modifies neural response to gaze shifts. Soc. Cogn. Affect. Neurosci. 2, 52–61.
Buccino, G., Baumgaertner, A., Colle, L., Buechel, C., Rizzolatti, G., Binkofski, F., 2007. The neural basis for understanding non-intended actions. NeuroImage 36, T119–T127.
Catmur, C., Walsh, V., Heyes, C., 2007. Sensorimotor learning configures the human mirror system. Curr. Biol. 17, 1527–1531.
Centelles, L., Assaiante, C., Nazarian, B., Anton, J.L., Schmitz, C., 2011. Recruitment of both the mirror and the mentalizing networks when observing social interactions depicted by point-lights: a neuroimaging study. PLoS One 6, e15749.
Ciaramidaro, A., Adenzato, M., Enrici, I., Erk, S., Pia, L., Bara, B.G., Walter, H., 2007. The intentional network: how the brain reads varieties of intentions. Neuropsychologia 45, 3105–3113.
Csibra, G., 2007. Action mirroring and action interpretation: An alternative account. In: Haggard, P., Rosetti, Y., Kawato, M. (Eds.), Sensorimotor Foundations of Higher Cognition. : Attention and Performance XXII. Oxford University Press, Oxford, pp. 435–459.
de Lange, F.P., Spronk, M., Willems, R.M., Toni, I., Bekkering, H., 2008. Complementary systems for understanding action intentions. Curr. Biol. 18, 454–457.
Decety, J., Jackson, P.L., Sommerville, J.A., Chaminade, T., Meltzoff, A.N., 2004. The neural bases of cooperation and competition: an fMRI investigation. NeuroImage 23, 744–751.
Farrer, C., Franck, N., Georgieff, N., Frith, C.D., Decety, J., Jeannerod, M., 2003. Modulating the experience of agency: a positron emission tomography study. NeuroImage 18, 324–333.
Friston, K.J., Rotshtein, P., Geng, J.J., Sterzer, P., Henson, R.N., 2006. A critique of functional localisers. NeuroImage 30, 1077–1087.
Frith, C.D., Frith, U., 2006. The neural basis of mentalizing. Neuron 50, 531–534.
Gallese, V., Goldman, A., 1998. Mirror neurons and the simulation theory of mind-reading. Trends Cogn. Sci. 2, 493–501.
Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn. Sci. 8, 396–403.
Gangopadhyay, N., Schilbach, L., in press. Seeing Minds: A neurophilosophical investigation of the role of perception-action coupling in social perception. Soc. Neurosci. the article is in press: 2011 Nov 7. [Epub ahead of print]. doi:10.1080/17470919.2011.633754
Genovese, C.R., Lazar, N.A., Nichols, T., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. NeuroImage 15, 870–878.
Georgiou, I., Becchio, C., Glover, S., Castiello, U., 2007. Different action patterns for cooperative and competitive behaviour. Cognition 102, 415–433.
Grafton, S.T., 2009. Embodied cognition and the simulation of action to understand others. Ann. N. Y. Acad. Sci. 1156, 97–117.

Grezes, J., Frith, C., Passingham, R.E., 2004. Brain mechanisms for inferring deceit in the actions of others. J. Neurosci. 24, 5500–5505.

Hagberg, G.E., Zito, G., Patria, F., Sanes, J.N., 2001. Improved detection of event-related functional MRI signals using probability functions. NeuroImage 14, 1193–1205.

Hayes, C., 2010. Mesmerising mirror neurons. NeuroImage 51, 789–791.

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, 529–535.

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

Kilner, J.M., Friston, K.J., Frith, C.D., 2007. The mirror neuron system: a Bayesian perspective. Neuroreport 18, 619–623.

Kourtis, D., Sebanz, N., Knoblich, G., 2010. Favouritism in the motor system: social interaction modulates action simulation. Biol. Lett. 6, 758–761.

Kumaran, D., Maguire, E.A., 2005. The human hippocampus: cognitive maps or relational memory? J. Neurosci. 25, 7254–7259.

Leslie, A.M., Friedman, O., German, T.P., 2004. Core mechanisms in 'theory of mind'. Trends Cogn. Sci. 8, 528–533.

Liepelt, R., Cramon, D.Y., Brass, M., 2008. What is matched in direct matching? Intention attribution modulates motor priming. J. Exp. Psychol. Hum. Percept. Perform. 34, 578–591.

Manera, V., Becchio, C., Cavallo, A., Sartori, L., Castiello, U., 2011. Cooperation or competition? Discriminating between social intentions by observing prehensile movements. Exp. Brain Res. 3–4, 547–556.

Mitchell, J.P., Macrae, C.N., Banaji, M.R., 2006. Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. Neuron 50, 655–663.

Molenberghs, P., Cunnington, R., Mattingley, J.B., 2012. Brain regions with mirror properties: a meta-analysis of 125 human fMRI studies. Neurosci. Biobehav. Rev 36, 314–349.

Newman-Norlund, R.D., van Schie, H.T., van Zuijlen, A., Bekkering, H., 2007. The mirror neuron system is more active during complementary compared with imitative action. Nat. Neurosci. 10, 817–818.

Oberman, L.M., Pineda, J.A., Ramachandran, V.S., 2007. The human mirror neuron system: a link between action observation and social skills. Soc. Cogn. Affect. Neurosci. 2, 62–66.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.

Perry, A., Troje, N.F., Bentin, S., 2010. Exploring motor system contributions to the perception of social information: evidence from EEG activity in the mu/alpha frequency range. Soc. Neurosci. 5, 272–284.

Rizzolatti, G., Sinigaglia, C., 2010. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. Nat. Rev. Neurosci. 11, 264–274.

Runeson, S., Frykholm, G., 1983. Kinematic specification of dynamics as an informational basis for person-and-action perception: expectation, gender recognition, and deceptive intention. J. Exp. Psychol. Gen. 112, 585–615.

Sartori, L., Becchio, C., Bara, B.G., Castiello, U., 2009. Does the intention to communicate affect action kinematics? Conscious. Cogn. 18, 766–772.

Sartori, L., Becchio, C., Castiello, U., 2011. Cues to intention: the role of movement information. Cognition 119, 242–252.

Saxe, R., 2006. Why and how to study theory of mind with fMRI. Brain Res. 1079, 57–65.

Saxe, R., Powell, L.J., 2006. It's the thought that counts: specific brain regions for one component of theory of mind. Psychol. Sci. 17, 692–699.

Schilbach, L., 2010. A second-person approach to other minds. Nat. Rev. Neurosci. 11, 449.

Schilbach, L., Wohlschlaeger, A.M., Kraemer, N.C., Newen, A., Shah, N.J., Fink, G.R., et al., 2006. Being with virtual others: neural correlates of social interaction. Neuropsychologia 44, 718–730.

Schilbach, L., Wilms, M., Eickhoff, S.B., Romanzetti, S., Tepest, R., Bente, G.B., Shah, N.J., Fink, G.R., Vogeley, K., 2010. Minds made for sharing. Initiating joint attention recruits reward-related neurocircuitry. J. Cogn. Neurosci. 22, 2702–2715.

Sebanz, N., Shiffrar, M., 2009. Detecting deception in a bluffing body: the role of expertise. Psychon. Bull. Rev. 16, 170–175.

Sommer, M., Dohnel, K., Sodian, B., Meinhardt, J., Thoermer, C., Hajak, G., 2007. Neural correlates of true and false belief reasoning. NeuroImage 35, 1378–1384.

Spunt, R.P., Falk, E., Lieberman, M.D., 2010. Dissociable neural systems support retrieval of "how" and "why" action knowledge. Psychol. Sci. 21, 1593–1598.

Spunt, R.P., Satpute, A.B., Lieberman, M.D., 2011. Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. J. Cogn. Neurosci. 23, 63–74.

Thioux, M., Gazzola, V., Keysers, C., 2008. Action understanding: how, what and why. Curr. Biol. 18, R431–R434.

Van Overwalle, F., 2009. Social cognition and the brain: a meta-analysis. Hum. Brain Mapp. 30, 829–858.

Van Overwalle, F., Baetens, K., 2009. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. NeuroImage 48, 564–584.

Van Schie, H.T., vanWaterschoot, B.M., Bekkering, H., 2008. Understanding action beyond imitation: reversed compatibility effects of action observation in imitation and joint action. J. Exp. Psychol. Hum. Percept. Perform. 34, 1493–1500.

Vingerhoets, G., Honore, P., Vandekerckhove, E., Nys, J., Vandemaele, P., Achten, E., 2010. Multifocal intraparietal activation during discrimination of action intention in observed tool grasping. Neuroscience 169, 1158–1167.

Walton, M.E., Devlin, J.T., Rushworth, M.F., 2004. Interactions between decision making and performance monitoring within prefrontal cortex. Nat. Neurosci. 7, 1259–1265.

Wolpert, D.M., Flanagan, J.R., 2001. Motor prediction. Curr. Biol. 11, R729–R732.

Worsley, K.J., Marrett, S., Neelin, P., Vandal, A.C., Friston, K.J., Evans, A.C., 1996. A unified statistical approach for determining significant signals in images of cerebral activation. Hum. Brain Mapp. 4, 58–73.