Social Neuroscience

Spatio-temporal Brain Dynamics of Understanding Social Versus Private Intentions: An Electrical Neuroimaging Study

Yiwen Wang*, Liang Huang*, Chongde Lin[†],
Zhen Zhang*, Fucheng Liang*, Deli Shen*

ABSTRACT

Although a growing body of research provides critical information about the spatio-temporal dynamic of the brain network mediating the understanding of causality between an action and its outcome at the individual level, little remains known about this cognitive process when the action outcome has a social connotation. To address this question, we recorded electrical brain activity from 16 healthy adults while they performed an intention understanding task including actions with three different types of causality; 1) private intentions by two agents acting independently from one another; 2) communicative intentions by two agents acting in an interactive way with one another; 3) physical causality among objects. Electrophysiological results showed differential electrical activity for private compared to communicative intentions within 400 ms post-stimulus. Brain source localization of the difference waves between communicative and private actions showed a generator located in the vicinity of middle cingulate cortex, which reinforces the role of this brain area in predicting social intentions.

Key Words: electrical brain imaging, intention understanding, theory of mind, ERP

Introduction

Understanding intentions of others based on the observation of their body language is a fundamental skill for behaving appropriately and efficiently in social settings (den Ouden *et al.*, 2005; Satpute *et al.*, 2005; Cacioppo *et al.*, 2010; Bara, 2007; Leslie, 1994; Premack and Woodruff, 1978;.Ekman, 1991; Wang *et al.*, 2010). Recent theories of embodied cognition (i.e., implicit understanding of others' actions through our own past motor experiences) suggest one understands intention of others by shaping one's understanding and anticipation of actions performed by others based on one's

own motor system (Jeannerod, 2001; Niedenthal, 2007; Grafton, 2009), which is a process that takes place in embodied cognition (Grafton, 2009; Rizzolatti & Sinigaglia, 2008; Jeannerod, 2000; Ortigue *et al.*, 2010, Grafton, 2009). As Jackson and Decety (2004) initially noted, the existence of a system matching executed and perceived actions offers a parsimonious explanation of how one recognizes other people's intended actions— i.e., by a direct mapping of the visual representation of the observed action onto one's own motor representation of the same action. Along these lines, several neurophysiological evidences suggest that the same neural representation is used for intending actions as well as understanding other people's motor intentions (Garbarini & Adenzato, 2004; Grafton, 2009; Niedenthal, 2007). In other words, the understanding of actions and intentions of other people is based, at least in part, on the same brain mechanisms

Corresponding authors: Deli Shen and Chongde Lin

Address: *****Academy of Psychology and Behavior, Tianjin Normal University, 300074, Tianjin 300074, PR China. **†**State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing 100875, PR China.

Phone: +86-22-23540114, Fax: +86-22-23540063

✉ wangeven@126.com; linchongde@263.net

than those underlying the formation of one's own motor intention (Frith, 2002; Rizzolatti and Sinigaglia, 2008). Along these lines, the understanding other people's behavior involves different steps, such as: i) to recognize a physical action, ii) to represent goal-directed actions, iii) to understand the causal relationship between an action and the intention that leads to that action, and iv) to re-experience/re-enact the perceptual, somato-visceral, and motor components of one's acts (Grafton, 2009; Niedenthal, 2007; Niedenthal et al., 2005; Frith and Frith, 1999).

Recent functional neuroimaging studies provide insights into people's ability to infer others' intentions by unraveling the neural bases of this mechanism (Aglioti et al., 2008; Grafton et al., 2008; Rizzolatti & Sinigaglia, 2008). Inferring intentions of other people from the observation of their actions recruits an inferior fronto-parietal action observation network (AON) as well as a putative social network (SN) that includes the posterior superior temporal sulcus (STS), the temporo-parietal junction (TPJ), the anterior paracingulate and also the cingulate cortex, a key prefrontal region subserving theory of mind (ToM). Furthermore, electrophysiological studies using high-density EEG recordings in healthy volunteers provide further information regarding the temporal dynamics between these two brain networks (AON and SN) for private intentions (Ortigue et al., 2009, 2010; Sabbagh et al., 2004a; Wang et al., 2008, 2010). For instance, Ortigue et al. recently showed the dynamic involvement of both the posterior superior temporal sulcus (pSTS) and inferior parietal lobe (IPL) at early stages of information processing for private intentions, and without a strict segregation between the AON and SN networks (Ortigue et al., 2009; 2010). In addition, Sabbagh et al. (2004a) reported that decoding another person's intentions from the observation of their eyes was associated with a specific ERP component (i.e., N270-400) over the inferior frontal and anterior temporal regions. Brain source estimation of this ERP component reinforced the recruitment of the orbito-frontal and medial temporal regions. Together, these studies demonstrate the possibility to characterize the dynamics of intention understanding across time and cortical regions in the early stages of information processing i.e., within the first 400 ms. In 2011, Proverbio and colleagues reinforced this early involvement of the AON and SN by recording brain activity from 35 university students while they were perceiving 260 pictures of cooperative (e.g., 2 people dragging a box) or affective (e.g., 2 people smiling and holding hands) interactions, and showing that the action's goal was automatically discriminated at about 150–170 ms, as reflected by occipito/temporal N170 response. The swLORETA inverse solution revealed the strongest sources in the right posterior cingulate cortex (CC) for affective actions and in the right pSTS for cooperative actions. In a later time window (200–250 ms) the processing of cooperative interactions activated the left post-central gyrus (BA3), the left parahippocampal gyrus, the left superior frontal gyrus (BA10), as well as the right premotor cortex (BA6; Proverbio et al., 2011). Although these findings did shed critical light on social intention understanding, they were not directly comparing private vs. communicative intentions. Thus, it remains unclear whether these findings would generalize to the decoding of communicative intentions (e.g., declarative pointing) observed in social settings. Communicative intentions allow one to express their intentions to share an object with another person. The study of this type of intentions is a question of particular interest in social and cognitive neuroscience as: i) communicative intentions constitute some of the most important signs for non-verbal communication (Bara, 2007), and ii) they may facilitate (or inhibit) the cooperation (or the competition) between individuals in daily life (Pierno et al., 2007). Accordingly, increasing attention focuses on communicative intention understanding in neuroscience. And a few fMRI studies start to unravel the neural bases sustaining the understanding of communicative intentions (Ciaramidaro et al., 2007; Walter et al., 2004; Brunet et al, 2000). For instance, in two separate fMRI experiments, Walter et al. (2004) have demonstrated that the anterior paracingulate cortex (PCC) is not necessarily involved in the understanding of other people's intentions per se, but primarily in the understanding of the intentions of people involved in social interaction.

However, the poor temporal resolution of fMRI neuroimaging limits the characterization of the temporal dynamics of communicative

NeuroQuantology | December 2012 | Volume 10 | Issue 4 | Page 733-743
Wang Y et al., Brain dynamics of understanding intentions

735

intention decoding (Ortigue *et al.*, 2009, 2010). Methods using millisecond temporal resolution, e.g., high-density surface EEG recordings, may provide critical information about the temporal dynamics of intention understanding (Liu *et al.*, 2009a, 2009b, 2004; Wang *et al.*, 2010, 2008; Sabbagh *et al.*, 2004a; Ortigue *et al.*, 2009).

The main aim of the present study was to extend recent fMRI findings on communicative versus private intentions by characterizing the spatio-temporal dynamics of this cognitive process using high-density EEG. Based on the above-described studies, we hypothesized that the spatio-temporal brain patterns for intention understanding would vary as a function of the type of intentions in the early stages of information processing (i.e., within 400 ms post-stimulus).

Materials and Method
Subjects
Sixteen undergraduates (ten females and six males, age range 19-23 years, mean age 19.93 years) without prior history of any neurological dysfunction completed the experiment. All of them were right-handed, and had normal or corrected-to-normal vision. The study was carried out according to the principles laid down in the Declaration of Helsinki. Informed written consent was obtained from all participants, conforming to the ethics committee's rules and procedures of the American Psychological Association (APA).

Stimuli and design
In the present study, we used similar stimuli than those used in previous studies on communicative intention understanding (Brunet *et al.*, 2000, 2003; Walter *et al.* 2004; Gallagher *et al.*, 2000; Bahnemann *et al.*, 2010). As in previous studies, stimuli included comic strips that depicted three different conditions: 1) private intentions by two agents acting independently from one another; 2) communicative intentions by two agents acting in an interactive way with one another; 3) physical causality among objects (i.e., non-intentional control condition). Each comic strip consisted of two pictures presented sequentially so they could create the visual illusion of a movement of the objects or agents. As in previous studies, the comic strips did not differ as a function of difficulty in

making a decision. The main difference between the three conditions was in the nature of the element that was causing the action. The comic strips for the physical condition included objects only, whereas the other two conditions included two individuals (who were either interacting with one another, or not). In the physical condition, the comic strips (N = 63) displayed several objects, such as, a ball running down a hill because of gravity, and breaking a wooden barrier on its way (see Figure 1a). In the private condition (N = 63), the two agents acted independently without any interaction between them, either facing each other or not (e.g., an agent was doing her homework by herself, while the other agent was playing with a ball by himself; see Figure 1b). In the communicative condition (N = 63), there was an interaction between the two agents (e.g., an agent was pointing to a ringing phone to request the other agent to answer the phone; see Figure 1c).

A total of 188 trials were used in the present experiment. Like in Gallagher *et al.* (2000) and Walter *et al.*'s (2004) studies, all comic strips were drawn by a postgraduate artist to control for uniform physical details, and size (i.e., 9.98 cm in width, 7.51 cm in height) of each cartoon. Each cartoon was 283×213 pixels. All stimuli matched in luminance, contrast, color saturation and spatial frequency spectrum level, as ascertained with Adobe Photoshop 7.0 software. All stimuli were presented in a monochrome color with a black background.

Experimental procedure
Figure 1 illustrates the experimental procedure. First, a 500-ms fixation sign (+) was presented in the center of the screen as a prompt to indicate the start of each trial. Then, a 1500-ms picture was presented followed by a 400-600 ms black screen. Finally, a second picture was presented for 1500 ms. The inter-trials intervals (ITI) among trials were randomized between 400-600 ms with 10 ms increments.

Participants' instruction
As in Gallagher *et al.*, (2000), participants were asked to look at each comic strip and think about the intention illustrated in the pictures. Then, participants were asked to indicate, as quickly and as accurately as possible, whether each intention was private,

NeuroQuantology | December 2012 | Volume 10 | Issue 4 | Page 733-743
Wang Y et al., Brain dynamics of understanding intentions

736

communicative or physical. Participants were required to answer before the disappearance of the second picture (i.e., within 1500 ms after the onset of the second picture), forcing them to make rapid judgments with understanding the agents' intentions. Participants were required to use their right hand and press one of the assigned keys (key #1: physical intentions; key #2 private intentions; and key #3: communicative intentions) on a three-button pad. The key response assignment was counterbalanced between participants in order to avoid any key sequence effects. Prior the intention understanding task, participants received a training session with eight comic strips to ensure they fully understood the procedure and instruction. None of the comic strips, presented during the practice session, was presented during the experiment. A debriefing session, performed at the end of the experiment, confirmed that the participants did not subjectively consider one condition harder than another condition in terms of categorization.
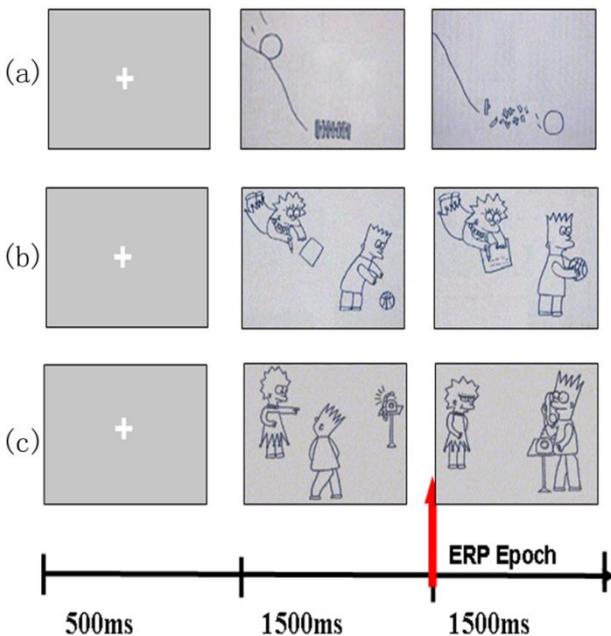

Figure 1. Illustration of the task setup Note: (a) physical condition, a running ball because of gravity knocks over and breaks the wooden barrier; (b) private condition, an agent is doing homework and another agent is playing a ball; (c) communicative condition, an agent pointing to the ringing phone to request another one to answer it.

ERP recording and analysis

We measured brain electric activity from 64 channels with the averaged bilateral mastoid reference and a forehead-ground using a modified 10-20 system electrode cap (Neuroscan Inc.). The vertical EOG was recorded with electrodes placed above and below the left eye, and horizontal EOG was recorded with the electrodes placed the outboard of both eyes. All inter-electrode impedance was maintained below 5kΩ. EEG and EOG were amplified using a 0.05-100 Hz band pass and continuously sampled at 1000 Hz/channel for off-line analysis. Eye blink artifacts were removed automatically using Scan software (Neuroscan Inc.). EEG contaminated with artifacts due to amplifier clipping, bursts of electromyographic (EMG) activity, or peak-to-peak deflection exceeding ±100 μV were also excluded from trials. In present study, the ERP waveforms were time-locked to the onset of the second picture. The averaged epoch for ERP was 1000 ms including a 200 ms pre-stimuli baseline. To obtain the ERP waves under each of the three conditions, the EEGs associated with correct responses were averaged for each condition. After artifact rejection, the mean numbers of valid trials for each condition were 47 (private), 50 (communicative), and 53 (physical), respectively.

The peak amplitudes (baseline to peak) of visual N170 and N2 waves were measured in 100-200 ms and 200-300 ms time windows, respectively. The mean amplitudes of the late positive component (LPC) were measured in 100 ms intervals over 300-1000 ms. As in previous studies (Wang, *et al.* 2010; Liu *et al.* 2004; 2009a), the following specific nine electrode sites were chosen for statistical analysis: F3/Fz/F4, C3/Cz/C4, and TP7/Pz/TP8. The ERP data were analyzed using three-way repeated measures analysis of variance (ANOVA). The ANOVA factors were 3 (conditions: private, communicative, and physical), 3 (laterality: left, midline and right) and 3 (caudality: frontal, central, and parietal areas). The *p*- values of all main and interaction effects were corrected using the Greenhouse-Geisser method for repeated-measures effects.

ERP brain source analysis

The N2 and LPC difference waves were obtained through subtracting (private condition minus the control physical condition, and communicative condition minus the control physical condition). Brain source estimations were performed on the

NeuroQuantology | December 2012 | Volume 10 | Issue 4 | Page 733-743
Wang Y et al., Brain dynamics of understanding intentions

737

difference waves, using BESA V5.0 (Brain Electrical Source Analysis program: Megis Software). Grand ERP data of 64 channels were merged with MRI data of a standard head. Principal component analysis (PCA) was then used to identify the amount of the dipoles. The dipoles were freely fitted for location and orientation while aiming for the smallest possible residual variance (RV). We tentatively reconstructed the sources in a four-shell ellipsoidal head model using dipole fits method. Genetic algorithm and dipole modeling were applied in source analysis.Talairach and Tournoux (1988) system, and the 3D coordinates of the dipole were, then determined on the MRI with respect to the Talairach space.

Results
Behavioral performance
Table 1 shows the accuracies and reaction times (RTs) for the three conditions.

Table1. The accuracy (%) and reaction times (ms) for the three conditions (*n*=16).

Conditions	Accuracy (M±SD)	Reaction time (M±SD)
Physical	86.90±28.96	665.37±203.31
Private	83.52±9.76	836.51±158.93
Communicative	91.90±6.26	718.86±111.99

Accuracy
On average, accuracy was 83.52% for the private condition (SD = 9.76), 91.90% for the communicative condition (SD = 6.26), and 86.90% for the physical condition (SD = 28.96). A one-way ANOVA revealed that there was no significant difference between the three conditions (F(2, 45) = 0.88, p = 0.424). The absence of behavioral difference confirmed that there were no significant differences in task difficulty.
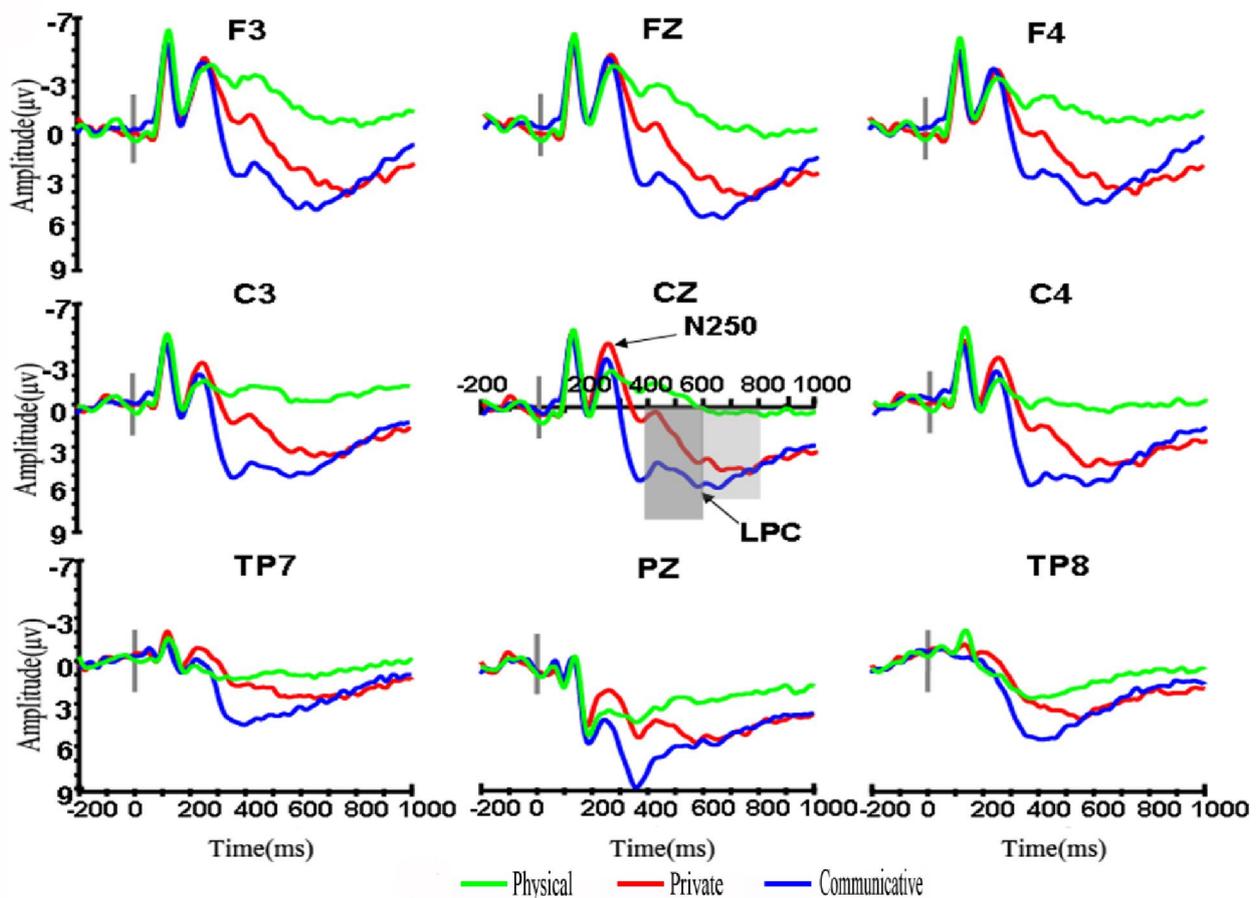

Figure 2. Overall average ERP waveforms under physical (in green), private (in red) and communicative (in blue) conditions, measured from the 9 electrodes on the scalp.

NeuroQuantology | December 2012 | Volume 10 | Issue 4 | Page 733-743
Wang Y et al., Brain dynamics of understanding intentions

738

Reaction times (RTs)

On average, RTs were 837 ms for the private condition (SD = 159), 719 ms for the communicative condition (SD = 112), and 665 ms for the physical condition (SD = 203). A one-way ANOVA revealed a significant difference between the three conditions, $F(2, 45) = 4.65$, $p = 0.015$, suggesting significantly slower RTs for private intentions compared to communicative intentions ($p = 0.046$), or physical intentions ($p = 0.005$). No significant difference was found between communicative and physical intentions ($p = 0.357$).

ERPs data

Figure 2 shows the overall average ERP waveforms from the 16 subjects for the three types of intentions, The average ERPs revealed conventional components in response to the three conditions (private, communicative, and physical) i.e., N170, N2 and LPC. The analyses performed for each component are described below.

N170 (100-200 ms)

The ANOVA performed on the N170 mean amplitude values revealed no significant main effect of the intention type; $F(2, 30) = 0.13$, $p = 0.807$, $MSE = 18.71$. There was no other significant effect. Because of the absence of any significant differences, no further brain source localization analysis was performed for this time period.

Parietal N2 (200-300 ms)

The ANOVA performed on the N2 mean amplitude values revealed a significant interaction between condition, laterality and caudality, $F(8, 120) = 45.76$, $p = 0.034$, $MSE = 1.27$. At 238 ms post-stimulus onset, N2 reached its maximum amplitude (3.13 ± 0.85 µV) at parietal sites (Pz) for communicative intentions versus private intentions (0.66 ± 0.87 µV), $p = 0.001$. The inverse solution performed on the difference between the private condition and the communicative condition suggested a brain generator in the middle cingulate cortex (red location: x = 10.3, y = -24.5, z = 40.5; RV = 19.75%; see Figure 5b). There was no significant main effect of the intention type, $F(2, 30) = 2.34$, $p = 0.130$, $MSE = 19.77$.

Statistical analysis also showed greater amplitude in response to private intentions (-1.69 ± 0.47 µV) versus physical intention (-0.52 ± 0.56 µV), $p < 0.001$) at the left temporo-parietal site (TP7), and at the central parietal site (C4; $p = 0.020$). he dipole source analysis performed on the difference wave between private and physical intentions during this time period, showed that the processing of private intention was associated with activity in the medial frontal cortex (red location: x = 9.1, y = 1.8, z = 48.8) and occipital cortex (blue location: x = -1.1, y = -92.9, z = 5.4; RV = 19.60%; see Figure 5(a)). There was no significant difference between communicative and physical conditions at the level of the left temporo-parietal site ($p = 0.220$), or posterior parietal site ($p = 0.152$), or central parietal site ($p = 0.718$).
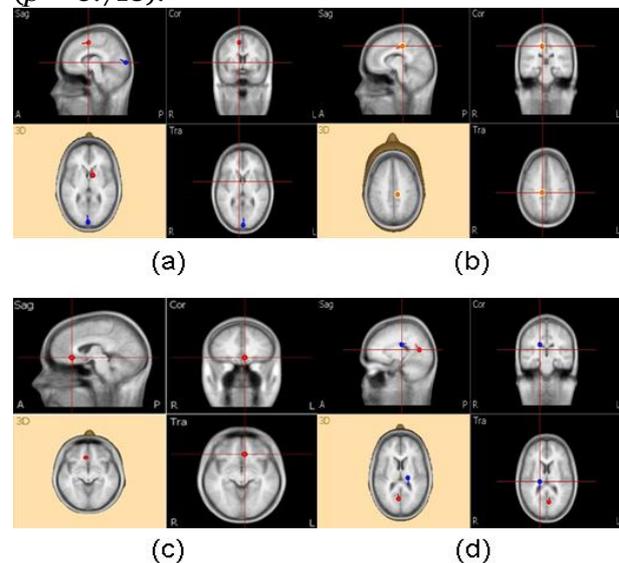

(a)   (b)

(c)   (d)

Figure 5. (a) Two dipoles of a best-fit solution of the difference wave of N250 (private minus physical); (b) The single dipole of a best-fit solution of the difference wave of N250 (communicative minus private) (c) The single dipole of a best-fit solution of the difference wave (private minus physical) during 400-600 ms; (d) Two dipoles of a best-fit solution of the difference wave (communicative minus private) during 400-600 ms.

Late Positive component (300-1000 ms)

Late Positive Component (LPC) was recorded at the frontal and central sites (F3/Fz/F4, C3/Cz/C4), and more posterior sites (TP7/Pz/TP8). ANOVA analysis showed a main effect of intention, indicating a progressive stepwise-effect of ERP enhancement from physical, to private, to communicative conditions. Results are shown in Table 2 and Figures 3a and 4.

NeuroQuantology | December 2012 | Volume 10 | Issue 4 | Page 733-743
Wang Y et al., Brain dynamics of understanding intentions

739

Table2. ANOVA of the LPC amplitudes measured at 100 ms intervals during the 300-1000 ms period.

Time window (ms)	Condition Main Effects F (2, 30)	Condition*Caudality Interaction Effects F (4, 60)	M±SE (amplitudes, µV)			Post hoc test
			Physical	Private	Communicative	
300-400	45.76***	20.98***	-0.21±0.73	0.84±0.61	4.20±0.74	1-2, 2-3***, 1-3***
400-500	33.42***	9.37***	-0.40±0.66	1.80±0.67	4.41±0.69	1-2**,2-3***,1-3***
500-600	31.43***	11.00***	0.05±0.80	3.39±0.64	4.92±0.57	1-2***,2-3**,1-3***
600-700	25.27***	9.09***	0.47±0.68	3.80±0.66	4.83±0.48	1-2***, 2-3, 1-3***
700-800	18.28***	5.76**	0.31±0.63	3.88±0.67	3.84±0.57	1-2***, 2-3, 1-3***
800-900	9.78**	2.60	0.23±0.65	3.20±0.66	2.85±0.59	1-2**, 2-3, 1-3***
900-1000	7.04**	2.16	0.04±0.69	2.76±0.73	2.03±0.54	1-2**, 2-3, 1-3**

Note: In the post hoc test, the number 1 denotes PC, 2 denotes PIC, and 3 denotes CIC. (*** $P<0.001$, ** $P<0.01$, * $P<0.05$)
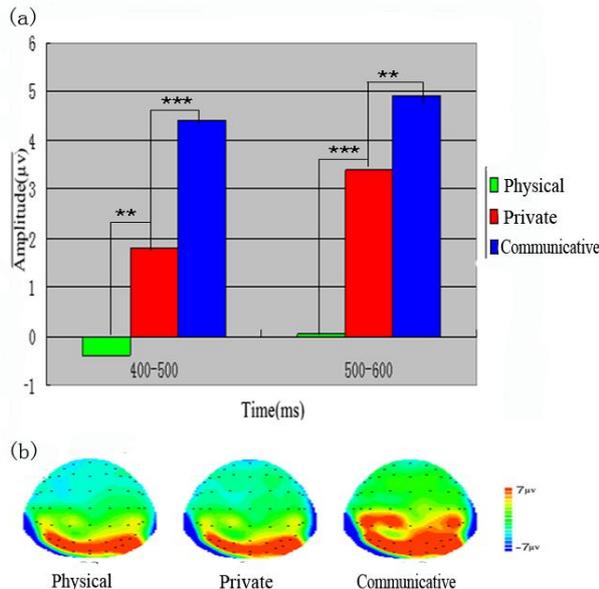

Figure 3. (a) The mean amplitudes of LPC elicited under three conditions during 400-600ms periods. (b) Topographic voltage maps of scalp electrical activity of the LPC from 400-600ms. ** indicates p<0.01, *** indicates p<0.001.

Post-hoc analysis revealed significant amplitude differences between conditions during the 400-to-600ms time window showed that LPC amplitude was of greater amplitude for communicative intentions than private intentions at the frontal and central sites (F3/Fz/F4, C3/Cz/C4) and at more posterior sites (TP7/Pz/TP8). The dipole source analysis showed a generator located in the vicinity of posterior cingulate cortex (red location: x = -6.1, y = -66.2, z = 14.2; see Figure 5(d)). No significant difference was observed between communicative and private conditions from 600 to 1000 ms.

During this 400-600 ms time window, LPC amplitude was also of greater amplitude for the private intentions versus the physical intentions at the frontal and central sites (F3/Fz/F4, C3/Cz/C4), although no significance was found between private and

physical condition at the posterior sites (TP7/Pz/TP8). We computed the LPC difference waves using the grand-average waves elicited under the private condition subtracting those elicited under the physical condition, which was associated with simple action intention understanding. The difference wave between private and physical intention is shown in the Figure 4. The dipole source analysis of this difference wave showed a generator located in the vicinity of anterior cingulated cortex (red location: x = -5.1, y = 29.6, z = -6.3; RV = 18.75%; Figure 5c).
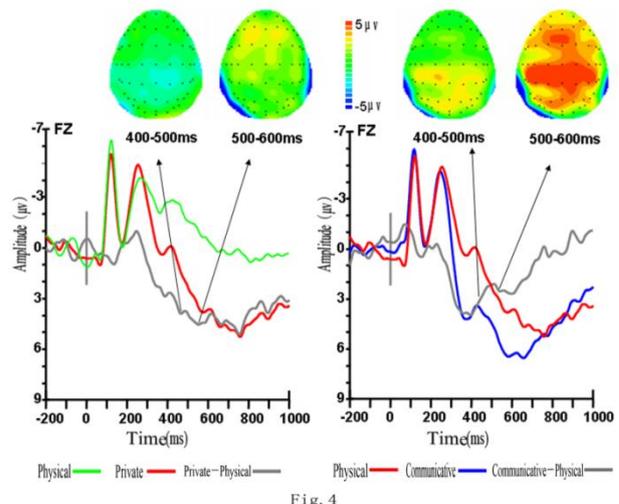

Fig. 4

Figure 4. The difference waves and its topographic voltage maps of scalp electrical activity from 400-600ms.

Discussion
The aim of the present study was to better understand the temporal brain dynamics of the understanding of communicative intentions compared to private intentions within an interpersonal context, by means of comic strips. First of all, our behavioral results suggest that participants take longer to understand intentional causality that involves individuals compared to objects, which reinforce previous studies, such as Walter *et*

NeuroQuantology | December 2012 | Volume 10 | Issue 4 | Page 733-743
Wang Y et al., Brain dynamics of understanding intentions

740

al.'s. These results are also in line with developmental studies showing a gradient of difficulty from physical to communicative to private intentions (Leslie, 1982; Spelke *et al.*, 1992; Wellman *et al.*, 2001; Wang and Zhang, 2002). Then, our behavioral results show that participants take more time to decode two persons' minds without communication (i.e., private intentions) than two integrated minds (i.e., communicative intentions). These results are also consistent with previous studies on communicative intention understanding (Walter *et al.*, 2004).

Our electrophysiological results extend these behavioral results by unraveling the spatio-temporal time course of private intention vs. communicative and physical intentions. The N2 data provided evidence of an early (~238ms) processing of social scene intent. Indeed, the brain response was of greater amplitude in response to communicative stimuli compared to private stimuli between 200–300 ms, a time period that was interpreted as the stage of intention understanding in previous studies (Ortigue *et al.*, 2010). This finding agrees with many studies in the literature supporting an early coding of intention understanding. For instance, the present N2 findings are, to some extent, consistent with Proverbio *et al.*'s results, which compared ERP waveforms for highly ecological pictures representing human cooperative versus affective actions, and showed that a centro-parietal response (N160–280) was the first component that displayed a larger potential to cooperative actions compared to affective actions (Proverbio *et al.*, 2011). The present results thus reinforce the assumption that individuals can detect the intentional causality at an early post-stimulus stage. This reinforces also the assumption suggesting a potential re-activation, at a pre-conscious level, of a brain network storing templates of previously encoded actions and intentions (Ortigue *et al.*, 2009, 2010). This is in line with a growing body of visual-evoked potential studies (VEPs) studies on intention understanding. For instance, Van der Cruyssen *et al.* showed that goals can be inferred rapidly and automatically i.e., at the level of 225-300 ms after stimulus onset (Van der Cruyssen *et al.* 2009). Sabbagh *et al.* (2004a) also showed that decoding mental states from the picture of eyes was associated with an early N270-400 over the right inferior and anterior temporal brain regions.

Interestingly, in our study, the inverse solution performed on the difference between private and communicative stimuli identified a strong focus of activation in the cingulate cortex (which is known to provide the affective connotation to visual coding). It is known that the cingulate cortex is involved in emotion processing in the subjective evaluation of events, and for understanding intentions in social interactions (Walter *et al.*, 2004), thus supporting our finding of a greater activation of the cingulate in response to communicative vs. private actions. It is also interesting to note that a fMRI study (Walter *et al.*, 2004) performed with similar stimuli, but on different subjects, provided similar evidence of a neural activation in the cingulate region for predicting intentional social interaction. Going further with the time course of information processing within the 250–350 ms time window, a late positive component had greater amplitude for communicative intentions than private intentions at the frontal and central sites and posterior sites. The dipole source analysis showed a generator located in the vicinity of posterior cingulate cortex. This result is compatible with the evidence from previous neuroimaging studies of theory of mind demonstrating a role of the cingulate cortex (Wang *et al.*, 2008; Gallagher *et al.*, 2000). For instance, Wang et. al (2008) found a single-dipole generator at the middle cingulate cortex during a ToM reasoning task on false beliefs. Addressing the issue of whether taking a self-perspective or modeling others' mind recruits similar neural networks, Vogeley *et al.* (2001) found that ToM reasoning specifically increased neural activity in the anterior cingulate cortex and left temporo-polar cortex. Similarly, Decety *et al.* (2004) showed recruitment of the medial prefrontal and para-cingulate cortex when one had to monitor others' minds in order to perform a cognitive task i.e., competitive games. McCabe *et al.* (2001) also found activation in the anterior paracingulate cortex in association with cooperation, i.e., a task that requires the ability to infer each other's mental states. Using positron emission tomography (PET), Gallagher *et al.* (2002) investigated the intentional stance in a competitive game of 'stone, paper, scissors'. The main comparison of the mentalizing condition vs. rule solving

showed only one region of significant activation – the bilateral anterior paracingulate cortex (PCC). Together these findings reveal that the cingulate cortex play an important role in social intention understanding and ToM processing. Interestingly, this brain region also showed specific activation when a represented intention implied social interaction that had not yet actually occurred, suggesting that the anterior PCC is also involved in one's ability to predict future intentional social interaction, based on an isolated agent's behavior.

Limitations and future perspective

It should be noted that the present study contains a number of limitations. First of all, the communicative condition may differ from the private condition in terms of its emotional content, or simply the arousal that it elicits (Krämer *et al.* 2010; Anokhin *et al.* 2006). For example, the stimuli in the communicative condition appear more humorously than those of the private condition. Second of all, the gender difference (Proverbio *et al.*, 2010) in processing the intention cannot be considered adequately here due to the gender proportion of participants. Further studies need to be done to address these questions to better understand the modulation of communicative vs. private intention, as a function of gender differences and arousal or emotional content. Then, the slight differences one might notice between the present study and previous neuroimaging studies on communicative intentions might be due to different methodology, such as a variation of the participants' instruction across the different experiments. For instance, in previous experiments, Brunet *et al.* (2000) and Walter *et al.* (2004) instructed their participants to look at the comic strips, and to choose the logic ending of the story without telling them to use any attribution of intention and physical reasoning response strategies. Finally, the ecological validity of the stimuli is low in the present study. Although comic strips have been proven to be efficient stimuli to investigate mentalizing ability regarding the understanding of intentions performed by other people stimuli like photos approximating real-life situation might provide another dimension that might be worth investigate in further studies.

Conclusion

Using high-density EEG, the present study helps to better understand the spatio-temporal dynamics of the understanding of communicative intentions versus other types of intentions (e.g., private). Notably, our results show that decoding communicative intentions occurs in the early stage of information processing and characterized by an activation in the cingulate cortex. The specific recruitment of this brain area, that is known to be a crucial node of the SN network, emphasizes the automatic re-activation of social templates (rather than basic principles of action observation) during the decoding of social intentions. These findings may be useful to better understand the interacting mind in social settings.

References

Aglioti SM, Cesari P, Romani M, Urgesi C. Action anticipation and motor resonance in elite basketball players. Nat Neurosci 2008; 11: 1109-1116.

Anokhin AP, Golosheykin S, Sirevaag E, Kristjansson S, Rohrbaugh JW, Heath AC. Rapid discrimination of visual scene content in the human brain. Brain Res 2006; 1903: 167-177.

Bahnemann M, Dziobek I, Prehn K, Wolf I, Heekeren HR. Sociology in the temporoparietal cortex: common versus distinct process. Soc Cogn Affect Neurosci 2010; 5: 48-58.

Bara BG. Cognitive Pragmatics: Mental processes of communication. MIT Press, Boston MA 2007.

Baron-Cohen S, Leslie AM, Frith U. Mechanical behavioral and intentional understanding of picture stories in autistic children. Br J Dev Psychol 1986; 4: 113-125.

Blakemore SJ, Decety J. From the perception of action to the understanding of intention. Nat Rev 2001; 2: 561-567.

Blakemore SJ, Winston J, Frith U. Social cognitive neuroscience: where are we heading? Trends Cogn Sci 2004; 8: 216-222.

Blakemore SJ, den Ouden H, Choudhury S, Frith C. Adolescent development of the neural circuitry for thinking about intentions. Soc Cogn Affect Neurosci 2007; 2: 130-139.

Boria S, Fabbrio-Destro M, Cattaneo L, Sparaci L, Sinigaglia C, Santelli E, Cossu G, Rizzaolatti G. Intention understanding in Austim. Plos One 2009; 4: e5596.

Brass M, Schmitt RM, Spengler S, Gergely G. Investing action understanding: inferential process versus action simulation. Curr Biol 2007; 17: 2117-2121.

Brunet E, Sarfatti Y, Hardy-Baylé MC. Reasoning about physical causality and other's intentions in schizophrenia. Cogn Neuropsychiatry 2003; 8: 129-139.

Brunet E, Sarfatti Y, Hardy-Baylé MC, Decety J. A PET Investigation of the Attribution of Intentions with a Nonverbal Task. NeuroImage 2000; 11: 157-166.

Ciaramidaro A, Adenzato M, Enrici I, Erk S, Pia L, Bara BG, Walter H. The intentional network: How the brain reads varieties of intentions. Neuropsychologia 2007; 45: 3105-3113.

Corcoran R, Cahill C, Frith CD. The appreciation of visual jokes in people with schizophrenia: a study of "mentalising" ability. Schizophr Res 1997; 24: 319–327.

Decety J, Jackson PL, Sommerville JA. The neural bases of cooperation and competition: An fMRI investigation. NeuroImage 2004; 23: 744-751.

de Lange FP, Sporonk M, Willems RM, Toni I, Bekkering H. Complementary Systems for Understanding Action Intentions. Curr Biol 2008; 18: 454-457.

de Vignemont F. Drawing the boundary between low-level and high-level mindreading. Philos Stud 2009; 14: 457-466.

den Ouden HEM, Frith U, Frith C, Blakemore SJ. Thinking about intentions. NeuroImage 2005; 28: 787-796.

Frith C. Attention to action and awareness of other minds. Conscious Cogn 2002; 11: 481-487.

Frith CD, Frith U. Interacting minds-a biological basis. Science 1999; 286: 1692-1695.

Frith CD, Frith U. How we predict other people are going to do. Brain Res 2006a; 1079: 36-46.

Frith CD, Frith U. The neural basis of mentalizing. Neuron 2006b; 50: 531-534.

Gallagher HL, Happé F, Brunswick N, Fletcher PC, Frith U, Frith CD. Reading the mind in cartoons and stories: An fMRI study of 'theory of the mind' in verbal and nonverbal tasks. Neuropsychologia 2000; 38: 11-21.

Gallagher HL, Jack AI, Roepstorff A, Frith CD. Imaging the intentional stance in a competitive game. Neuroimage 2002; 16: 814-821.

Grafton ST. Embodied cognition and the simulation of action to understand others. Ann N Y Acad Sci 2009; 1156: 97-117.

Grafton ST, Schmitt P, Van Horn J, Diedrichsen J. Neural substrates of visuomotor learning based on improved feedback control and prediction. Neuroimage 2008; 39: 1383-95.

Garbarini F, Adenzato M. At the root of embodied cognition: cognitive science meets neurophysiology. Brain Cogn 2004; 56: 100-106.

Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. Grasping the intentions of others with one's own mirror neuron system. Plos Biology 2005; 3: e79.

Jackson PL, Decety J. Motor cognition: a new paradigm to study self-other interactions. Curr Opin Neurobiol 2004; 14: 259-63

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

Krämer UM, Mohanmmadi B, Doñamayor N, Samii A, Münte TF. Emotional and cognitive aspects of empathy and their relation to social cognition-an fMRI study. Brain Res 2010; 1311: 110-120.

Leslie AM. The perception of causality in infants. Perception 1982; 11: 173-186.

Leslie AM. Pretending and believing: issues in the theory of tomm. Cognition 1994; 50: 211-238.

Lestou V, Pollick FE, Kourtzi Z. Neural substrates for action understanding at different description levels in the human brain. J Cogn Neurosci 2008; 20: 324-341.

Lingnau A, Gesierich B, Caramazza A. Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. Proc Natl Acad Sci 2009; 106: 9925-9930.

Liu D, Meltzoff AN, Wellman HM. Neural correlates of belief- and desire-reasoning. Child Dev 2009a; 80: 1163-1171.

Liu D, Sabbag MA, Gehring WJ, Wellman HM. Decoupling beliefs from reality in the brain: an ERP study of theory of mind. NeuroReport 2004; 15: 991-995.

Liu D, Sabbagh MA, Gehring KW, Wellman HM. Neural correlates of children's theory of mind development. Child Dev 2009b; 80: 318-326.

McCabe K, Houser D, Ryan L, Smith V, Trouard T. A functional imaging study of cooperation in two-person reciprocal exchange. Proc Natl Acad Sci 2001; 98: 11832-11835

Niedenthal PM. Embodying emotion. Science 2007; 316: 1002-1005.

Niedenthal PM, Barsalou LW, Winkielman P, Krauth-Gruber S, Ric F. Embodiment in attitudes, social perception, and emotion. Pers Soc Psychol Rev 2005; 9: 184-211.

Ortigue S, Thompson JC, Parasuraman R, Grafton ST. Spatio-Temporal Dynamics of Human Intention Understanding in Temporo-Parietal Cortex: A

Combined EEG/fMRI Repetition Suppression Paradigm. Plos One 2009a; 4: e6962.

Ortigue S, King D, Gazzaniga M, Miller M, Grfton S. Right hemisphere dominance for understanding the intentions of others: evidence from a split-brain patient. BMJ Case Reports 2009b; [doi:10.1136/bcr.07.2008.0593].

Ortigue S, Sinigaglia C, Rizzolatti G, Grafton ST. Understanding actions of others: The electrodynamics of the left and right hemispheres. A high-density EEG neuroimaging study. Plos One 2010; 5: e12160.

Pelphrey KA, Morris JP, McCarthy G. Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. J Cogn Neurosci 2004; 16: 1706-1716.

Pierno AC, Ansuini C, Castiello U. Motor intention versus social intention: One system or multiple systems? Psyche 2007; 13: 1-10.

Pineda JA, Hecht E. Mirroring and mu rhythm involvement in social cognition: Are there dissociable subcomponents of theory of mind? Biol Psych 2009; 80: 306-314.

Premack D, Woodruff G. Does the chimpanzee have a theory of mind? Behav Brain Sci 1978; 4: 515-526.

Proverbio AM, Riva F, Zani A. When mirrors do not mirror the agent's intentions: Sex differences in neural coding of goal-directed actions. Neuropsychologia 2010; 48: 1454-1463.

Proverbio AM, Riva F. RP and N400 ERP components reflect semantic violations in visual processing of human actions. Neurosci Lett 2009; 459: 142-146.

Redcay E. The superior temporal sulcus performs a common function for social and speech perception: implications for the emergence of autism. Neurosci Biobehav Rev 2008; 32: 123–42.

Rizzolatti G, Sinigaglia C. Further reflections on how we interpret the actions of others. Nature 2008; 455: 589.

Sabbagh MA. Understanding orbitofrontal contributions to theory-of-mind reasoning: Implications for autism. Brain Cogn 2004a; 55: 209-219.

Sabbagh MA, Moulson MC, Harkness KL. Neural correlates of mental state decoding in human adults: an event-related potential study. J Cogn Neurosci 2004b; 16: 415-426.

Satpute AB, Fenker DB, Waldmann MR, Tabibnia G, Holyoak KJ, Lieberman MD. An fMRI study of causal judgments. Eur J Neurosci 2005; 22: 1233-1238.

Saxe R, Wexler A. Making sense of another mind: the role of the right temporo-parietal junction. Neuropsychologia 2005; 43: 1391-1399.

Saxe R, Xiao DK, Kovacs G, Perrett DI, Kanwisher N. A region of right posterior superior temporal sulcus responds to observed intentional actions. Neuropsychologia 2004; 42: 1435-1446.

Spelke ES, Breinlinger K, Macomber J, Jacobson K. Origins of knowledge. Psychol Rev 1992; 99: 605-632.

Tager-Flusberg H, Sullivan K. A componential view of theory of mind: evidence from Williams syndrome. Cognition 2000; 76: 59-89.

Talairach J, Tournoux P. Co-planar stereotaxic atlas of the human brain. New York. Thieme 1998.

Turella L, Pierno A, Tubaldi F, Castiello U. Mirror neurons in humans: Consisting or confounding evidence? Brain Lang 2009; 108: 10-21.

Van der Cruyssen L, Van Duynslaeger M, Cortoos A, Van Overwalle F. ERP time course and brain areas of spontaneous and intentional goal inferences. Soc Neurosci 2009; 4: 165-184.

Van Overwalle F, Baetens K. Understanding others' actions and goals by mirror and mentalizing system: A meta-analysis. Neuroimage 2009; 48: 564-584.

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

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happé, F., Falkai, P., Maier, W., Shah, N.J., Fink, G.R., Zilles, K., 2001. Mind reading: Neural mechanisms of theory of mind and self-perspective. NeuroImage 14, 170-181.

Walter H, Adenzato M, Ciaramidaro A, Enrici I, Pia L, Bara BG. Understanding Intentions in Social Interaction: The Role of the Anterior Paracingulate Cortex. J Cogn Neurosci 2004; 16: 1854-1863.

Walter H, Ciaramidaro A, Adenzato M, Vasic N, Ardito RB, Erk S, Bara BG. Dysfunction of the social brain in schizophrenia is modulated by intention type: An fMRI study. Soc Cogn Affect Neurosci 2009; 4: 166-176.

Wang YW, Zhang WX. Development of theory-of-mind of 3-6 years old children. Psychological Development and Education 2008; 18: 11-16.

Wang YW, Ling CD, Yuan B, Huang L, Shen DL. Person perception precedes theory of mind: an event related potential analysis. Neuroscience 2010; 170: 238-246.

Wang YW, Liu Y, Gao YX, Chen J, Zhang WX, Lin CD. False belief reasoning in the brain: An ERP study. Science China life sciences 2008; 51: 72-79.

Wang YW, Zheng YW, Lin CD, Wu J, Shen DL. Electrophysiological correlates of reading the single- and interactive-mind. Front Hum Neurosci 2001; 5: 64.

Wellman HM, Cross D, Waston J. Meta-analysis of theory-of-mind development: the truth about false belief. Child Dev 2001; 72: 655-684.