

Electrophysiological correlates of social information processing for detecting agents in social interaction scenes: P200 and N250 components

Davide Crivelli

Research Unit in Affective and Social Neuroscience, Catholic University of the Sacred Heart, Milan, Italy

Department of Psychology, Catholic University of the Sacred Heart, Milan, Italy

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davide.crivelli@unicatt.it

ABSTRACT

According to interaction theories, the detection of situated agents and the understanding of their intentions and mental states are mediated by smart perceptual and embodied mechanisms. While the network supporting agency-attribution, action-understanding, and grasping of others' mental state is quite known, the actual mental chronometry of such social perception processes is still not clear. We then designed an exploratory study to investigate electrophysiological correlates (ERPs and source localization) of information-processing for the detection of potential agents in realistic interaction scenes. Morphological and statistical analyses of electrophysiological data highlighted that the manipulation the nature of a potential agent, the gesture it executed and the relative position of an interagent was differently associated to the modulation of specific relevant middle-latency ERP components, labelled as P200 and N250, and of their relative intra-cortical current density distribution within the first 300 ms from the appearance of the stimulus.

Keywords: Social perception; Agency; EEG/ERPs; Social interaction; eLORETA

1. INTRODUCTION

Agency – defined as the ability to intentionally exert an effect on our environment and to control our behaviour – is a pervasive and fundamental aspect of our lives: we are essentially active beings in a world full of objects to act with and subjects to interact with (Balconi, 2010). It being a defining feature for human beings, in the very moment we sense ourselves as intentional agents and, in particular, we consciously self-attribute that kind of stance, we have to assume that other people might be the same: we have to admit that they can be potential agents too.

As a consequence, to adequately act – and re-act – in a social context and to exert control on a social interaction, we need to be able to sense and judge the authorship of our behaviour and its outcomes, but we need also to do the same with every other potential interagent. An effective and efficient mechanism for the detection of agency then plays a crucial role both in case of individual actions, in case of dyadic interactions, and in case of collective actions. Further, it has been suggested that basic social perception processes such as the attribution of an agentive stance to other subjects in our environment are the necessary starting point for higher social understanding skills such as mind-reading (see: Gallagher & Meltzoff, 1996; Saxe, 2006), since the purposeful nature of behaviour is what ties the construct of agency to the construct of intentionality and what makes us think that other agents are guided by intentions that are informed by beliefs and implemented as means aiming at goals. Consistently, it has been suggested that such ability is at the basis even of the development of a sense of inter-agency, defined as the sense that we – me and you – are the ones that are generating an action and causing its effects by acting together (Crivelli & Balconi, 2010).

According to interaction theories (Gallagher, 2008), the detection of situated agents and the understanding of their intentions and mental states are mediated by smart perceptual and embodied mechanisms. Thus, even before we develop a complete ability to theorize, simulate, explain or predict others' mental states, direct perception mechanisms would mediate, for example, the preliminary but relevant parsing of our environment into potential agents and other “passive” entities. And that, in turn would be the first step of the process that allows us to grasp if someone is happy or sad, if someone is attending to us or not, or to identify someone as friendly or menacing.

Consistent with classic accounts suggesting that such smart social perception skills are innate (Meltzoff & Moore, 1977; Gallagher & Meltzoff, 1996), many subsequent evidences suggest that biological motion-specific perception, even for highly degraded stimuli, is hard-wired in human visual

system (Vaina, Solomon, Chowdhury, Sinha & Belliveau, 2001; Grossman & Blake, 2002; Servos, Osu, Santi & Kawato, 2002). Further, recent ample meta-analyses on the functional role of various structures thought to be involved in social understanding abilities (Van Overwalle, 2009; Van Overwalle & Baetens, 2009); highlighted that the network supporting detection and attribution of agency, action understanding, and grasping of others' mental state is widely distributed and largely interconnected, though research on the internal structure of such processes and on the spatiotemporal characteristics of related information-processing steps is still lacking.

In particular, a network of brain areas that are able to perform unique computations – including the superior temporal sulcus, the fusiform gyrus, the premotor cortex, the amygdala, the orbitofrontal cortex, the inferior and posterior parietal cortex, and the cerebellum – has been found showing selective activity in response to human actions (Grossman, 2006), and it may constitute a specialized neural circuitry that mediate social perception processes and cooperate with other perceptual, cognitive and motor circuits to allow us to grasp other's intentional behaviour. Then it is plausible – in agreement with Puce and Perrett (2003) and Allison, Puce and McCarthy (2000) – that the coordinated activity of higher visual areas, superior temporal sulcus, prefrontal cortex, and inferior parietal regions fosters our ability to detect other agents, to understand their behaviour and, thus, to interact adequately.

Going down to specifics, specialized regions in the inferior temporal-occipital cortex – namely the fusiform face area (Kanwisher, McDermott & Chun, 1997), the fusiform body area (Peelen & Downing, 2005; Schwarzlose, Baker & Kanwisher, 2005), and the extrastriate body area (Downing, Jiang, Shuman & Kanwisher, 2001) – proved to be sensitive to human perceptual features concerning the shape and posture of faces and human body parts. Regions in the Superior Temporal Sulcus (STS), instead, are activated by dynamic representation of faces and body parts such as hands or mouth (Allison et al., 2000; Grossman & Blake, 2002; Wheaton, Thompson, Syngienotis, Abbott & Puce, 2004; Saygin, 2007) and animal studies showed that specific neural populations in the STS of non-human primates code selectively for intentional actions (Jellema, Baker, Wicker & Perrett, 2000). For those reasons, such structure is thought to be involved in early stages of the analysis of body movement, and to mediate biological movement perception. There are also empirical evidences of a kind of interplay between superior temporal, premotor and somatosensory structures for the representation of our and others' actions (Blakemore & Decety, 2001). And again, the posterior part of the Superior Temporal Sulcus (pSTS) seems to be involved even in processing abstract representations of intentional actions beyond

actual elaboration of biological movement schemata. pSTS has indeed been found to be more active in response to animations where simple geometric shapes mimicked complex social interactions than to animations depicting inanimate motion (Castelli, Happé, Frith & Frith, 2000; Schultz, Friston, O'Doherty, Wolpert & Frith, 2005).

Moving to higher-level areas, the medial Prefrontal Cortex (mPFC) is another crucial structure in social understanding and its involvement in thinking about others' mental states, in inferring their beliefs and desires, in meta-representation, and in evaluating long-term disposition is widely accepted (Amodio & Frith, 2006; Balconi & Bortolotti, 2012; Balconi, Falbo & Conte, 2012). The mPFC is thought to be one of the key regions of the mentalizing network together with posterior temporo-parietal regions, and should then build on previously processed perceptual information to mediate higher social cognition skills. Finally, cortical areas constituting the Temporo-Parietal Junction (TPJ) have been associated with taking someone else's perspective, both in space and from a psychological point of view (Saxe & Kanwisher, 2003). According to Barresi and Moore (2008), TPJ areas mediate the integration of first-person and third-person information deriving from interactions. In particular, the left TPJ might be associated to allocentric representations while the right TPJ might be associated to egocentric representations.

The integrated activity of above-mentioned structures may then allow us to perceive some entities as animate and acting according to a goal, and thus as showing agency. However, while their functional roles are quite known, the actual mental chronometry of their involvement and of social perception stages they mediate is still not clear. Electrophysiological methods and techniques seem to be the best candidates to try and clarify those points because of their excellent time-resolution and their notable sensitivity to even the slightest modulations of cognitive processes and relative information-processing steps. Up to now, however, research on electrophysiological markers of mental processes leading to agency perception focused on self-attribution of agency and on mechanisms that support such self-attribution, such as behaviour error-monitoring (see Balconi & Crivelli, 2009; 2010a; 2010b; Balconi & Scioli, 2012), thus leaving the electrophysiological signature of agency attribution to others and proper agents-detection processes unexplored.

We then designed an exploratory study aimed at investigating the contribution of structures constituting the social perception network in information-processing for the detection of potential agents and intentional behaviour. We were in particular interested in investigating the information flow and processing stages of such process, and thus looked at the time course

and cortical generators of relevant event-related electroencephalographic responses (Event-Related Potentials, ERPs) during a social perception task involving realistic interaction scenes. Specifically, we focused on the elaboration of three main sources of information and perceivable cues concerning the nature of a potential agent, the gesture it executes and the relative position of an interagent, and we manipulated them to explore how and when they are processed.

Given the lack of relevant electrophysiological literature on the topic, this study had a mainly exploratory aim. Nonetheless, we hypothesised, first of all, that the manipulation of agent-related perceptual cues would have led to the modulation of posterior electrophysiological components generated by high-level visual and associative structures, such as superior temporal and inferior parietal areas. While first evidences on the sensitivity of an early ERP component associated to perceptual coding of human/biological entities to such manipulation have already been reported in Crivelli and Balconi (2015), we still expected that information on the agent nature would have affected later processing stages, thus resulting even in a modulation of later cognitive components rising after 200 ms from stimuli presentation. Secondly, we hypothesised that different categories of gestures, i.e. instrumental vs. relational ones, would have been associated to different spatio-temporal patterns of electrophysiological responses depending on their goal. Namely, we expected a greater involvement of affective prefrontal generators when participants had to process a relational gesture – i.e. gestures intended to influence the relationship. Thirdly, we hypothesised that interaction context cues would have been processed together with the other pieces of information we manipulated, thus modulating the influence of the other two experimental manipulation on ERP responses. According to this framing hypothesis, we expected potentially observed differences in ERP components in response to different agents (artificial vs human) and gestures (instrumental vs relational) to be greater when an interagent was present in the interaction scene with respect to when it was out of the scene. That because the perceivable presence of an interagent would have likely made the social interaction context more complex and would have induced a greater activation of the social understanding network.

2. METHODS

2.1. Sample

The experimental sample was constituted by twenty right-handed participants (12 women, 8 men; $range_{age} = 21-31$, $M_{age} = 25.11$, $SD_{age} = 2.66$). Handedness was checked by means of a brief structured interview including questions on participants' manual preference for a number of activities, like writing, cutting with a knife or throwing a ball. All participants had normal or corrected-to-normal sight; none of them reported history of neurological or psychiatric disorders. They gave their written informed consent for participating in the study and the research was approved by the Ethical Committee of the Catholic University of the Sacred Heart of Milan.

2.2. Procedure

Participants were asked to carefully observe realistic visual stimuli appearing on a 17" PC screen (distance ≈ 70 cm) and were told that each stimulus would have been preceded by a cue (a sound). The cue was introduced to keep a minimum level of vigilance. Going down to specifics, we presented participants with interaction scenes where a primary potential agent executes a simple meaningful gesture in the direction of a secondary human interagent. However, three sources of information for agency detection and social understanding have been manipulated to create experimental stimuli: stimulus features concerning the agent, features concerning its action, and relational context cues. In particular, the scenes differed in: the nature of the primary agent (human vs artificial); the kind of gesture that was executed (instrumental vs relational), and a context-related condition related to the position of the secondary interagent (out of the scene vs giving his/her back to the primary agent vs facing the primary agent). Stimuli were constituted by two static frames presented in close succession so to induce the perception of a movement in the absence of the movement itself. Such procedure and its advantages have been described also in Crivelli and Balconi (2015). All experimental conditions were completely balanced, thus resulting in twelve different kinds of scenes (see *Figure 1*). Twenty-eight different stimuli for each of the twelve kinds of scenes were randomly presented in seven experimental blocks (E-Prime2.0 software, Psychology Software Tools, Pittsburgh, PA).












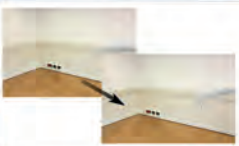
		INTERAGENT FACING TOWARDS	INTERAGENT FACING BACKWARDS	INTERAGENT OUT OF THE SCENE
INSTRUMENTAL	HUMAN			
	ARTIFICIAL			
RELATIONAL	HUMAN			
	ARTIFICIAL			

Figure 1. Main experimental variables and examples of interaction scenes from the set of final stimuli

2.3. EEG recording and reduction

EEG activity was recorded by means of a 32-channels SynAmps system (DC amplifier) and Scan4.2 Acquire software (Compumedics Neuroscan Inc., Charlotte, NC). The recording montage was constituted by 28 sintered Ag/AgCl electrodes – Fp1, Fp2, F7, F3, Fz, F4, F8, FT9, FC5, FCz, FC6, FT10, T5, C3, Cz, C4, T6, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, O1, O2 – referenced to linked earlobes and placed according the 10-10 International System (Chatrian, Lettich & Nelson, 1985; 1988). Electrodes impedance was kept under 5 k Ω and vEOG was recorded in order to keep track of ocular artifacts for subsequent correction and rejection. Data were sampled at 1000 Hz. The input filter was set as a 0.01-100 Hz bandpass with an additional 50 Hz notch filter.

EEG data were then filtered offline by an IIR 0.1-30 Hz bandpass filter with a gentle 12db/octave slope so to avoid excessive distortion of data in the time domain (Vision Analyser 2.0 software, Brain Product GmbH, Gilching, DE). We then applied a semiautomatic ICA-based artifact correction (Makeig, Jung, Bell, Ghahremani & Sejnowski, 1997; Jung et al., 2000). The outcomes of the correction algorithm were manually verified by visually checking the morphology and localization of the identified independent components so to avoid unwanted attenuation of relevant portions of EEG signal. EEG was then segmented (epochs length = 1000 ms; pre-stimulus baseline = 200 ms) with respect to the presentation of dynamic stimuli. Finally, epochs still affected by residual muscular, ocular or movement artifacts were manually rejected and artifact-free epochs were used to compute individual averages.

2.4. ERP signal source localization

Signal source localization was computed for relevant ERP deflections that showed to be sensitive to experimental manipulations in order to investigate potential differences in estimated signal generators. Intra-cortical distribution of current density associated to scalp recorded event-related electric potential distribution was computed by applying the exact Low Resolution Brain Electromagnetic Tomography (eLORETA) method and algorithm (Pascual-Marqui, 2007; 2009). Such method is a discrete, 3D distributed, linear, weighted minimum norm inverse solution. The particular weights used in eLORETA allow for the exact localization of signal sources even though with low spatial resolution, and the related computations allow for creating a map of the exact magnitude of estimated voxel-specific current density. As for the version of eLORETA algorithm we used, computations were made in a realistic head model (Fuchs, Kastner, Wagner, Hawes & Ebersole, 2002) and the three-dimensional solution space was restricted to cortical gray matter, as determined by the probabilistic Talairach atlas (Lancaster et al., 2000). The head model was based on the MNI152 template (Mazziotta et al., 2001) with superimposed standard electrode positions (Oostenveld & Praamstra, 2001; Jurcak, Tsuzuki & Dan, 2007). The cortical volume is partitioned in 6239 voxels (resolution = 5 mm).

3. RESULTS

Morphological analyses of event-related EEG waveforms firstly guided us in the selection of relevant ERP components, defined as deflections that consistently and systematically come out of background electrophysiological activity and that was modulated by our manipulated experimental conditions. We then identified two middle-latency components – P200 and N250 – rising between 200 and 300 ms from stimuli onset in addition to a previously reported early N150 component (Crivelli & Balconi, 2015).

Subsequently, peak amplitude data for the two relevant ERPs have been analysed by repeated-measures ANOVA models. The models included the three experimental manipulations and the recording site as factors (Context x Gesture x Agent x Electrode). They aimed at testing overall specificities in scalp distribution of electrophysiological components and modulations due to experimental conditions. Type-I Errors due to inhomogeneity of variances have been controlled by applying Greenhouse-Geisser or Huynh-Feldt corrections to degrees of freedom, respectively when the estimate of sphericity (ϵ) was lower than 0.75 or greater than 0.75. All pair-wise comparisons (t tests) have been Bonferroni corrected.

Statistically significant interaction effects highlighted by ANOVA models on amplitude and latency data have been further investigated by computing statistical comparisons of intra-cerebral current density distributions (Statistical non-Parametric Mapping, SnPM). Current density data have been analysed by a non-parametric approach based on estimating, via randomization, the empirical probability distribution for the max-statistic (in our case t values), under the null hypothesis. This methodology corrects for multiple testing biases due to the series of tests performed for all voxels and for all time samples and do not rely on any assumption of Gaussianity. See Nichols and Holmes (2002) for a clear and complete presentation of the approach. Statistical non-parametric mapping was computed on the basis of the maximum t value distribution across all voxels. The significance threshold was set to $p \leq 0.05$ and based on a permutation test with 5000 permutations. No variance smoothing factor was applied to the computation and no normalization has been applied to eLORETA localization data in order to avoid the possible flattening of differences in activity amplitude.

3.1. P200 component

The analysis of variance model including all electrodes revealed significant amplitude differences across electrode positions ($F[27, 513] = 34.394$; $p < 0.001$; $\eta^2 = 0.644$), and significant interaction effects for electrode position and context-related manipulation ($F[54, 1026] = 4.126$; $p < 0.001$; $\eta^2 = 0.178$) and for electrode position and agent-related manipulation ($F[27, 513] = 3.761$; $p = 0.007$; $\eta^2 = 0.165$). The amplitude of P200 increased gradually moving from frontal sites to posterior ones and reached the maximum over right parietal-occipital areas. Going down to specifics, scenes where the interagent is present and can see the gestures elicited lower deflections over right inferior frontal-central-temporal areas (F8, FCz, FC6, C4, FT10 and T8), while the same condition elicited ampler deflections over posterior areas (P7, P8, O1 and O2), especially on the right (all $p < 0.05$, see *Figure 2*). A similar bipolar distribution seems to emerge also from pair-wise comparisons analysis of scenes with human and artificial agents. The amplitude of P200 component at Fz, F8, FCz, FC6, FT10, Cz, CP2, CP6 and C4 was significantly greater in response to scenes depicting human agents than to scenes depicting artificial agents, while at P7 the deflection was ampler in response to scene depicting artificial agents than to the other ones (all $p < 0.05$, see *Figure 3*).

Source localization applied to the P200 deflection (time window = 200-230 ms) showed that the main signal source was in the right parahippocampal gyrus (BA30; MNI: X = 25, Y = -55, Z = 0; Mean value = $6.66E^{-3}$ A/m²; see *Figure 4*). Non-parametric analyses of estimated intra-cerebral current density distribution related to P200 deflection as a function of interaction context manipulation reported some significant differences. In particular, scenes including an interagent that can see the gestures elicited significantly greater activity than those without interagent in correspondence to the right paracentral lobule and the precuneus (all $p < 0.05$). The comparison between scenes where the interagent was facing towards the gestures and those where it was facing backward showed significant differences primarily in correspondence to the left parahippocampal gyrus (all $p < 0.05$). Non-parametric analyses of estimated intra-cerebral current density distribution related to P200 deflection as a function of agent's nature manipulation reported some significant differences. Scenes depicting human agents elicited greater activity than scenes depicting artificial gesturing arms primarily in correspondence to the left lingual gyrus and the right precuneus (all $p < 0.05$).

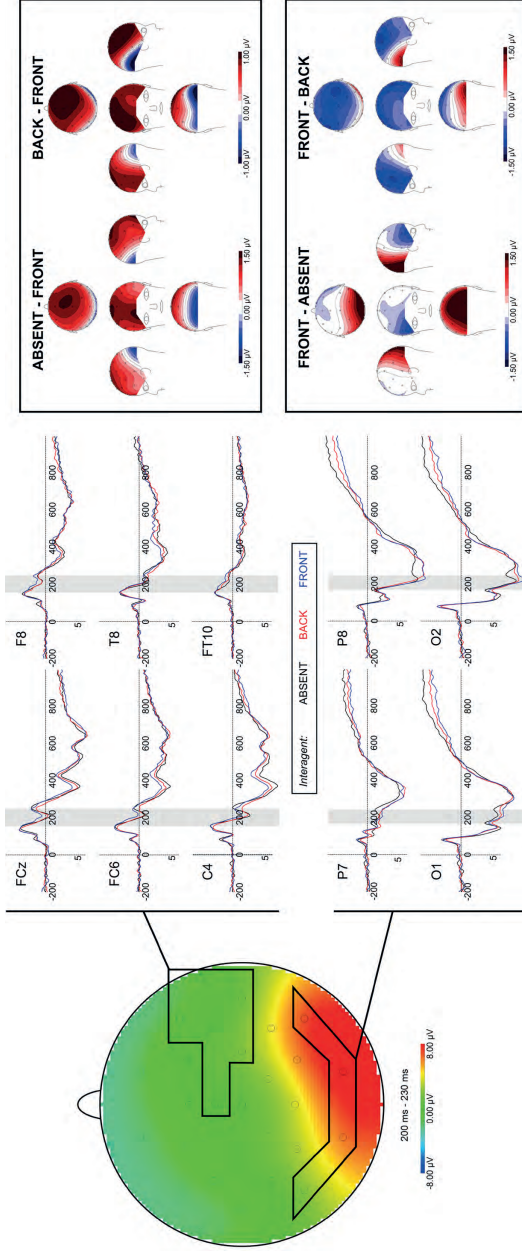


Figure 2. P200 component: topographic map of scalp voltage, group-averaged waves showing statistically significant effects of relational context manipulation, and voltage difference maps for significant pair-wise comparisons

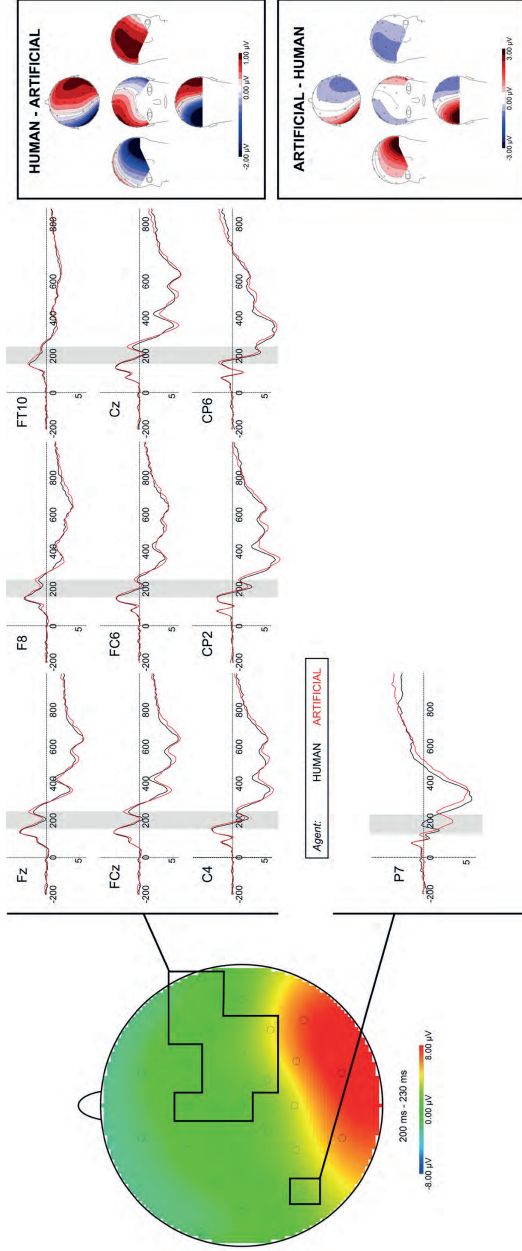


Figure 3. P200 component: topographic map of scalp voltage, group-averaged waves showing statistically significant effect of agent's nature manipulation, and voltage difference maps for significant pair-wise comparisons

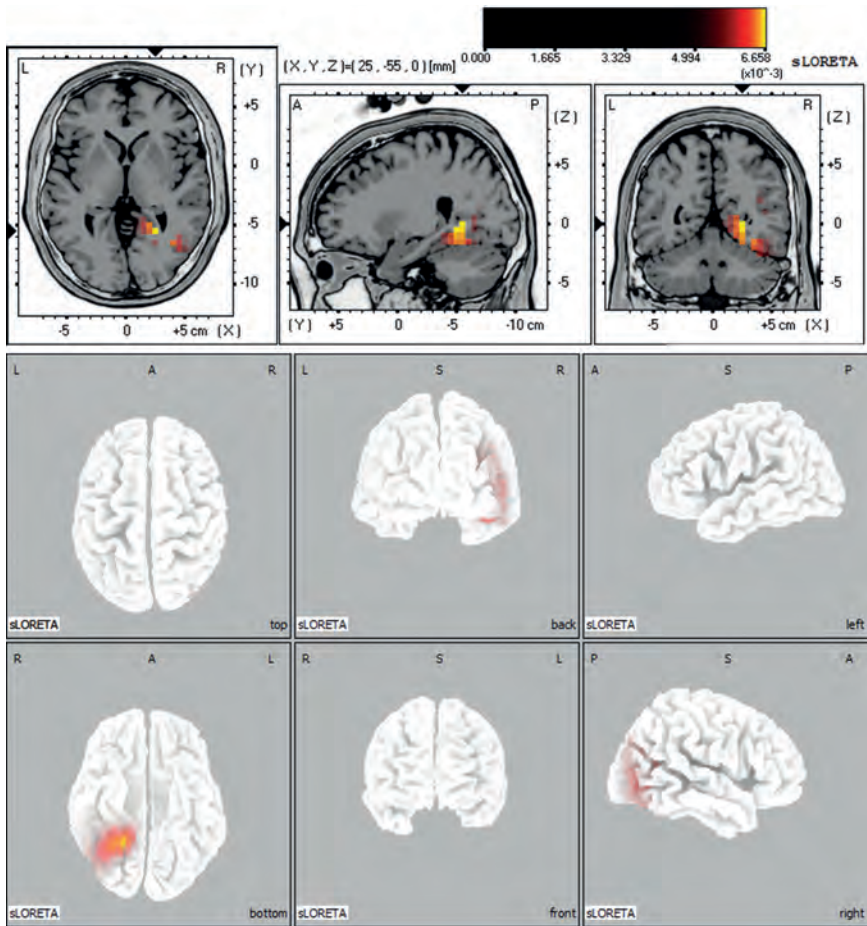


Figure 4. P200 component: eLORETA reconstruction of the main signal sources and 3D modelling

3.2. N250 component

The morphological analysis of the N250 deflection showed that its absolute peak value was influenced by the magnitude of the preceding positive deflection, which showed a mainly posterior distribution. Thus, in this specific case, we decided to compute the ANOVA model on peak-to-peak values (P200-to-N250), in order to overcome potential limitations of applying a classic peak value analysis approach to this particular electrophysiological deflection, to prevent the otherwise notable differences in the amplitude of the negative deflection from being masked by the remarkable variability in P200 amplitude, and to test for experimentally-induced modulation of the actual amplitude of this component. The ANOVA model showed a significant main effect of electrode position ($F[27, 513] = 4.932$; $p < 0.001$; $\eta^2 = 0.206$), of agent-related manipulation ($F[1, 19] = 6.309$; $p = 0.021$; $\eta^2 = 0.249$), and of their interaction ($F[27, 513] = 4.443$; $p = 0.001$; $\eta^2 = 0.190$). The relative difference was particularly pronounced over frontal-central midline areas and over the back of the scalp, and was globally greater in response to scenes including artificial gesturing arms than to scenes including human potential agents ($M_{human} = -4.339$ vs $M_{artificial} = -4.927$). With regard to the interaction effect, pair-wise comparisons showed significantly ampler responses to scenes depicting artificial gesturing arms than to scenes depicting human arms at almost all left electrode sites (see *Figure 5*; all $p < 0.05$).

Source localization applied to the N250 ERP component (time window= 235-265 ms) showed that the main signal sources were in the right middle temporal gyrus and angular gyrus (BA22, MNI: X= 40, Y= -60, Z= 15; BA39, MNI: X= 35, Y= -65, Z= 25; *Mean value* = $8.89E^{-3}$ A/m²; see *Figure 6*). Non-parametric mapping comparisons of estimated intra-cerebral current density modulations associated to scenes depicting human *vs.* artificial gesturing arms highlighted greater activity in response to the presence of artificial agents in correspondence to the right insula, the right superior, transverse and middle temporal gyri, the right inferior parietal lobule, the right angular gyrus and the right supramarginal gyrus (all $p < 0.05$).

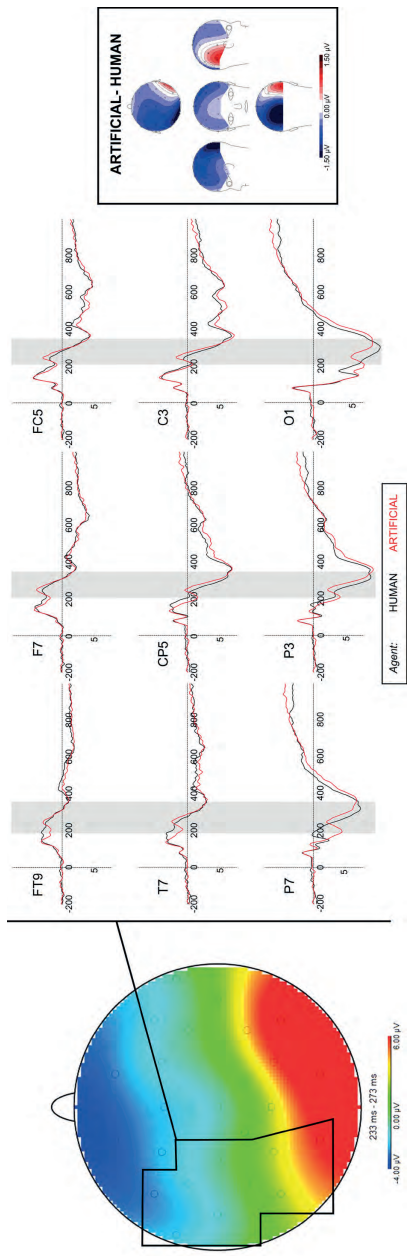


Figure 5. N250 component: topographic map of scalp voltage, group-averaged wave showing statistically significant effects of agents' nature manipulation, and voltage difference maps for significant pair-wise comparisons

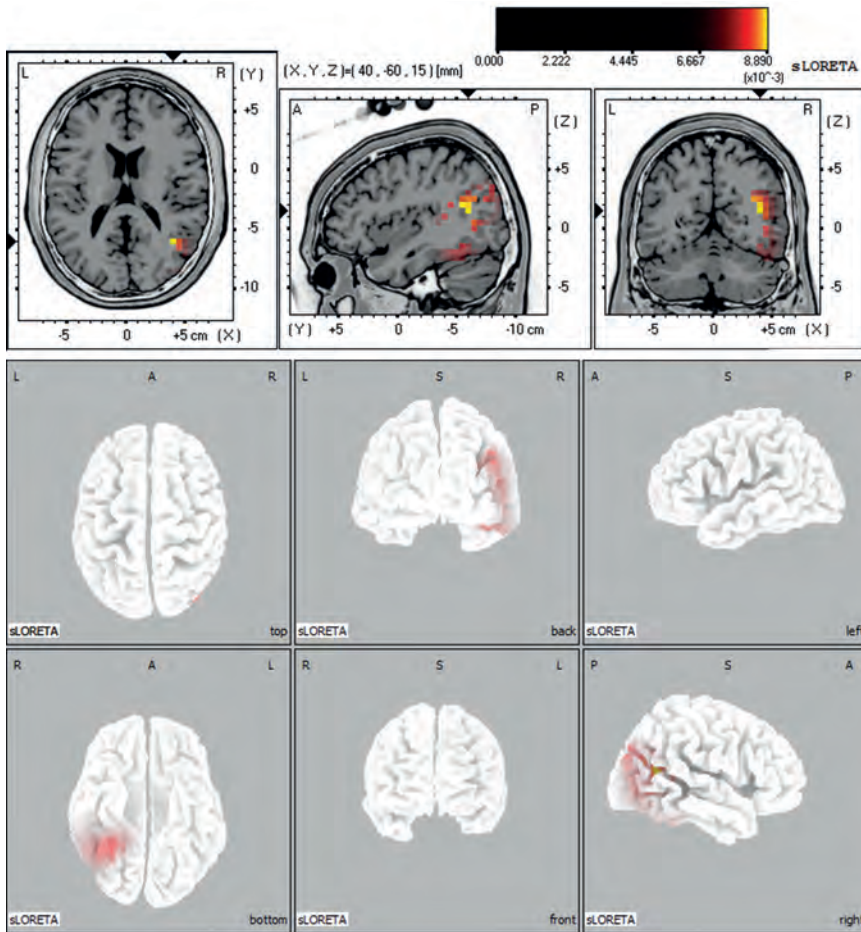


Figure 6. N250 component: eLORETA reconstruction of the main signal sources and 3D modelling

4. DISCUSSION

The present study aimed at exploring electrophysiological correlates of information-processing for the detection and perception of potential intentional agents in a realistic environment and in a simple interaction situation. The manipulation of three crucial sources of information for social perception –

i.e. the human vs artificial nature of the primary agent, the intention that guided its action (instrumental vs relational), and relational context cues conveyed by the position of the interagent (out of the scene vs giving his/her back to the primary agent vs facing the primary agent) – lead to the modulation of specific relevant middle-latency ERP components, namely a positive deflection peaking around 210 ms after stimuli presentation and a negative deflection peaking around 260 ms after the onset. To further investigate such components and their neural underpinning, we also estimated their cortical generators and tested possible differences in terms of intra-cerebral current density distribution between experimental conditions.

4.1. P200 component: retrieval of information for the recognition of action schemata

The amplitude of the first relevant positive deflection – labelled as P200 – gradually increased moving from frontal to posterior electrode sites and reached its maximum over right parietal-occipital sites. eLORETA source localization pointed out the right parahippocampal gyrus (BA30) as the main source of surface signal. P200 was modulated by both context-related and agent-related manipulations. In particular, scenes where the interagent was able to see the gesture and, thus, could co-regulate with the other agent elicited ampler deflections than the other scenes over parietal-occipital areas, and lower deflections over right inferior frontal-temporal areas. Similarly, scenes including a human gesturing arms elicited ampler deflections than those including artificial gesturing arms over right frontal-central areas, while the contrary was true over left inferior parietal areas.

Parahippocampal activations are classically associated to memory processes (Cabeza, Dolcos, Graham & Nyberg, 2002; Spatt, 2002). Nonetheless, the parahippocampal gyri – together with the amygdalae – are thought to be involved in emotional evaluation and learning processes (see, for example, Wood, Romero, Knutson & Grafman, 2005) and the right parahippocampal gyrus has been found to be active during observation of meaningful actions (Decety et al., 1997). This last result, in particular, may be explained by the crucial role of information retrieval in the recognition of meaningful actions since the latter plausibly grounds on a kind of matching-mechanism with stored action-models. Thus, we suggest that the positive deflection we found to be primarily generated by parahippocampal cortex might have been modulated by the retrieval of relevant information for coding and processing the interaction situation with prototypical potential agents. Though such first suggestion surely need to be further tested and explored by more focused

studies, it is worth noting that even results of SnPM contrast analyses seem to point in that direction. Parahippocampal areas were indeed significantly more activated by scenes where the interagent was facing towards the gestures than by those where it was facing backward and, as a consequence, could not actually interact.

In addition, it is worth noting that, while the differences in the experimental paradigm account for differences in spatial features and functional interpretation between the reported P200 component and the well-known oddball P2 component, our findings are consistent with the limited ERP literature on detection of agents. In particular, Wang and colleagues (2010) investigated the time course of persons detection and complex understanding of scenes that involved mind-reading by presenting subjects with cartoons depicting scenes without people, scenes with people, and scenes with people that needed mind-reading to be understood. Relevant to this discussion, the authors found a positive component that occurred at about 200 ms, was maximal over posterior areas, and selectively marked cartoons depicting people (regardless of their complexity and of the need of mind-reading) compared to cartoons without people. The authors concluded that we are able to distinguish persons from scene backgrounds at early processing stages, consistently with the hypothesis concerning the role of precursors for mentalizing skills, which include the ability to distinguish between animate and inanimate entities.

In agreement with Saxe (2006), who underlined that the first step towards reasoning about other peoples' actions is detecting the presence of intentional actors and that they usually come in the form of human bodies, we suggest that the P200 component we observed marks the retrieval of information for the recognition of action/interaction schemata on the basis of the outcome of previous body-part detection mechanisms (see Crivelli & Balconi, 2015).

4.2. N250 component: integration of visual cues and processing of intentional biological movement patterns

After the P200 deflection, we observed an additional negative component – labelled as N250 – that proved to be sensitive to our experimental manipulations. Peak-to-peak analysis highlighted that it was actually ampler over frontal-central midline and posterior sites, and it was globally ampler in response to scenes including artificial potential agents than to scenes including human ones. Furthermore, we observed a wide lateralization effect as a function of agent's nature: almost all left electrode sites recorded significantly

amplifier peak-to-peak differences in response to scenes depicting artificial gesturing arms than to scenes depicting human arms. eLORETA solution of the inverse problem located the main sources of N250 signal in the right middle temporal gyrus and angular gyrus. Furthermore, statistical non-parametric mapping pointed out significantly greater intra-cerebral signal in response to the presence of artificial agents than to the presence of human agents in correspondence to the right insula, the right superior, transverse and middle temporal gyri, the right inferior parietal lobule, the right angular gyrus and the right supramarginal gyrus.

As noted above, the electrophysiological literature on our topic is really scarce, and then a focus on estimated neural generators of the negative deflection may help in interpreting its functional correlates. The middle and the superior temporal gyri surround the Superior Temporal Sulcus (STS), which, in conjunctions with the orbitofrontal cortex and the limbic system, is thought to form a network that is involved in social understanding (Allison et al., 2000; Adolphs, 2009). Instead, the angular gyrus, the supramarginal gyrus and the caudal part of the superior temporal gyrus are usually considered to be part of the Temporo-Parietal Junction (TPJ), roughly defined as the cortical region surrounding the caudal part of the Sylvian fissure, where the parietal and temporal lobes meet

Interestingly, the right angular gyrus was specifically found to be active during the observation of static images depicting both cooperative and affective interactions involving two persons in a study on the neural bases of social intention understanding (Canessa et al., 2012). Instead, TPJ – especially the right one – is thought to be a crucial node of the mentalizing network (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). Even if the exact functional role of TPJ is still under debate (Decety & Lamm, 2007), its contribution to perspective-taking – both in space and from a psychological point of view – is widely accepted, and consistent evidences suggest that the right TPJ is involved in the identification and processing of action intentionality at both the perceptual and higher-cognitive levels (Van Overwalle, 2009). On the basis of empirical evidences and anatomical organization, it has been suggested that structures encompassing TPJ and the posterior part of STS may act as an interface between neural networks supporting action understanding (mirror system) and mentalizing, and that the interaction between those networks might be crucial for high-level attribution of mental states (Van Overwalle, 2009; Van Overwalle & Baetens, 2009; Canessa et al., 2012). Furthermore, the posterior part of the right STS and superior temporal areas have been associated also to the perception of biological movement, the automatic detection of intentionality and to the perception of intentional actions (Saxe, Xiao, Kovacs, Perrett & Kanwisher, 2004; Schultz et al., 2005; Grossman,

2006; Gao, Scholl & McCarthy, 2012). Finally, inferior and posterior parietal areas and the insula are also classically associated to the processing of agency, online control of action and bodily awareness (David, 2010). And again – as shown also by clinical studies (e.g. Spence et al., 1997) – parietal and cingulate regions seems to be involved in processing the authorship of behaviour and in pathological and functional attribution of agency to other entities.

Given those evidences, we suggest that the negative deflection we found to be primarily sensitive to the agent's nature manipulation and to be generated by right temporal and angular gyri might mark a pre-reflective detection of intentional agents by the integration of visual motion cues and the recognition of biological movement patterns. Such a simple form of social understanding may be based on low-level perceptual information, according to which potential agents are perceived as intentional in the sense that they tend to something or someone. That early processing stage would involve right temporal-parietal structures and would act as the starting point for successive and more elaborated operations, which are crucial for a complete understanding of others' cognitive and affective mental states (Van Overwalle & Baetens, 2009). Within this framework, greater activations observed in response to artificial potential agents can plausibly mirror differences in computational and cognitive demand. In other words, the artificial arms we created were human-like enough to activate biological movement recognition and intentionality detection processes, but also sufficiently artificial to be deemed as ambiguous and to request a greater allocation of resources to be recognized as part of an active intentional agent. It is worth noting that we digitally edited real-captured actions executed by human actors in order to manipulate the nature of potential agents. As a consequence, motion dynamics and global shape of our artificial arms were similar to those of actual human arms. This choice has surely been an advantage over other experimental designs that compared human and robotic actions or actors or that presented over-simplified or highly degraded stimuli such as point-light displays (see Crivelli & Balconi, 2009), indeed we can rule out alternative explanation of our results related to stimuli kinematic specificities or related to extreme shape differences.

5. CONCLUSION

To sum up, initial ERPs/eLORETA evidences showed that agent-related perceptual information and context-related information may be processed within the first 300 ms from the appearance of the stimulus at different inter-

dependent processing stages, while gesture-related information seemed not to modulate electrophysiological responses during early processing stages.

Going down to specifics, the lack of observed ERPs modulation due to differences in meaning and valence of executed gestures, though unexpected, is rather in line with the limited amount of evidences concerning the time course of electrophysiological processes associated to gestures recognition. For example, Nakamura and colleagues (2004) explored the chronometry of gestures processing by means of magnetoencephalography and suggested that the actual interpretation of the meaning of a gesture might occur between 240 and 380 ms from the appearance of the stimulus. Thus, it is plausible that our gesture-related experimental conditions, given their fine distinction and the fact that we presented gestures within a complex realistic context and within an actual interaction scene, would elicit processing differences at later stages.

Middle-latency posterior ERPs deflections – which likely mirrored high-level perceptual and retrieval processes for the detection and model-matching of intentional action schemata – marked instead the presence of human agents in the scene. Interestingly – and contrary to our initial framing hypothesis on the simple modulatory role of interaction context cues – the presence and position (forward-facing or backward-facing) of an interagent in the scene modulated selectively but independently the same ERP component, with maybe a potential association to information retrieval even for the recognition of interaction opportunities during the observation of realistic communication exchanges. Differently, the presence of artificial agents elicited greater activation of higher right temporo-parietal areas during a later time window, probably due to the greater demand on resources for their recognition as potential intentional agent.

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