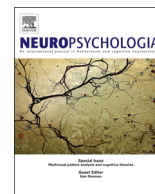




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Neural correlates of non-verbal social interactions: A dual-EEG study

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ABSTRACT

Successful non-verbal social interaction between human beings requires dynamic and efficient encoding of others' gestures. Our study aimed at identifying neural markers of social interaction and goal variations in a non-verbal task. For this, we recorded simultaneously the electroencephalogram from two participants (dual-EEG), an actor and an observer, and their arm/hand kinematics in a real face-to-face paradigm. The observer watched "biological actions" performed by the human actor and "non-biological actions" performed by a robot. All actions occurred within an interactive or non-interactive context depending on whether the observer had to perform a complementary action or not (e.g., the actor presents a saucer and the observer either places the corresponding cup or does nothing). We analysed the EEG signals of both participants (i.e., beta (~ 20 Hz) oscillations as an index of cortical motor activity and motor related potentials (MRPs)). We identified markers of social interactions by synchronising EEG to the onset of the actor's movement. Movement kinematics did not differ in the two context conditions and the MRPs of the actor were similar in the two conditions. For the observer, however, an observation-related MRP was measured in all conditions but was more negative in the interactive context over fronto-central electrodes. Moreover, this feature was specific to biological actions. Concurrently, the suppression of beta oscillations was observed in the actor's EEG and the observer's EEG rapidly after the onset of the actor's movement. Critically, this suppression was stronger in the interactive than in the non-interactive context despite the fact that movement kinematics did not differ in the two context conditions. For the observer, this modulation was observed independently of whether the actor was a human or a robot. Our results suggest that acting in a social context induced analogous modulations of motor and sensorimotor regions in observer and actor. Sharing a common goal during an interaction seems thus to evoke a common representation of the global action that includes both actor and observer movements.

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1. Introduction

Joint actions are defined as actions performed by two or more individuals that coordinate their actions to achieve a common goal; such actions are ubiquitous in everyday life. Individuals need to precisely coordinate their own actions with those of others both spatially and temporally to perform successful joint actions (Sebanz, Bekkering, & Knoblich, 2006). This bidirectional interaction between individuals requires the coupling of perceptive and motor systems to form internal representations that are constantly updated in response to environmental changes (Hari & Kujala, 2009). Therefore, this "interactive loop" appears to be an essential mechanism for adapted social interactions. The discovery of the

mirror neuron system (MNS) provided a novel understanding of the brain networks involved in motor observation. Mirror neurons are motor neurons that fire during the execution of an action and the observation of the same action performed by others. This MNS was initially discovered in monkeys (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992) and has been identified in humans (Buccino et al., 2001; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010; Rizzolatti & Craighero, 2004). The system is active when an individual observes someone performing a movement (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Thus, the MNS seems to be a neuronal mechanism that could create a direct link between the sender and the receiver of an action (Rizzolatti & Arbib, 1998).

Electroencephalography (EEG) studies have tried to identify the role of the MNS in the integration of social cues. Though EEG does not allow for precise localisation, reliable indicators of motor activities are known. Evoked related potentials (ERP) such as the readiness potential (RP) and the late part of the contingent negative variation (CNV) are negative potentials related to motor

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activity (Leuthold, Sommer & Ulrich, 2004). These “movement related potentials” (MRPs) are thought to reflect motor preparation and execution. While the RP is typically observed before self-paced movement and during movement anticipation and observation (Colebatch, 2007), the late part of the CNV is observed when movements are triggered by cued/imperative signals (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). Moreover, studies of brain oscillatory activities identified the rolandic mu rhythm as a further index of motor activity (Gastaut & Bert, 1954; Hari, Salmelin, Mäkelä, Salenius, & Helle, 1997). The mu rhythm is characterised by two frequency components: an alpha component ranging from 8 to 13 Hz and a beta component ranging from 15 to 25 Hz and measured over central electrodes. The alpha-mu component is attributed to sensory-motor areas (S1 M1) (Pfurtscheller, Neuper, & Krausz, 2000), but the beta component is mainly generated by the primary motor cortex M1 and could reflect corticomuscular processes (Caetano, Jousmäki, & Hari, 2007; Hari & Salmelin, 1997). Suppression of the oscillations in these frequency bands is measured when individuals perform a movement (Salmelin & Hari, 1994) and when individuals observe, imagine or anticipate a motor action (Pineda, 2008). Modulations of the mu rhythm (alpha and beta) are considered an index of MNS activation resulting in excitability changes in sensorimotor areas (Pineda, 2008). Therefore, while the MRPs primarily indicate movement preparation or anticipation (Deecke, 1987), the mu rhythm denotes the functional state of the primary motor cortex within the action-perception system (Hari, 2006).

Using these indexes, Kourtis, Sebanz, and Knoblich (2010), Oberman, Pineda, and Ramachandran (2007) and Kilner, Marchant, and Frith (2006) investigated whether movement observation and anticipation were influenced by social context. They found that social context (e.g., social relevance or observation of social interaction) enhanced motor activity more than did non-social context or actions with less social content. For instance, Kourtis et al. (2010) and Kourtis, Knoblich, and Sebanz (2013) found that anticipatory motor activity (i.e., CNV amplitude and 20 Hz oscillatory activity) was higher during an observation task when participants expected to watch an action executed by a partner rather than by an unknown person. Oberman et al. (2007) found that observing social actions, especially if the social actions involved the participant directly, triggered stronger 10 Hz suppression over central electrodes than did observing non-social actions. However, note that both studies focused on the observer and ignored the actor's perspective.

By contrast, Schippers, Roebroek, Renken, Nanetti, and Keysers (2010) tried to identify the neural basis of reciprocal interaction by using functional magnetic resonance imaging (fMRI). Pairs of participants played a game of charades and were placed by turn in an fMRI scanner while gesturing and guessing. The fMRI images of the two participants were then synchronised to couple the two brains' activity during gestural communication. They found a Granger-causality link between the gesturer's and the guesser's brain activities. The areas traditionally described as part of the MNS, such as the dorsal and ventral premotor cortices, somatosensory cortex, anterior inferior parietal lobule, midtemporal gyrus, and the ventromedial prefrontal cortex were tuned between the two brains. Kokal, Gazzola, and Keysers (2009) further noted that the previously mentioned areas were more activated when participants played in cooperation with a human than when they played with a computer that did not cooperate. Taken together, these results suggest that brain motor areas and particularly the MNS are involved in the encoding of social interactions during both perception and active interaction. However, while instructive, these studies did not study real face-to-face social interaction.

The development of “hyperscanning” techniques now allows the brain activity of two or more participants to be recorded simultaneously. Recently, dual-EEG studies (two synchronised EEG

recordings) investigated inter-brain synchronisation while participants performed various coordinated actions (Dumas, Nadel, Soussignan, Martinerie, & Garnero, 2010; Lindenberger, Li, Gruber, & Müller, 2009; Tognoli, Lagarde, DeGuzman, & Kelso, 2007). In these studies, brain oscillations were recorded when participants performed synchronic movements (of the finger or hand or to play guitar). Tognoli et al. (2007) observed a rhythm in the alpha-mu band (i.e., phi) that was present only when participants performed synchronous movements. Lindenberger et al. (2009) and Dumas et al. (2010) measured interactional synchrony to determine when two areas (inter or intra-brain) were similarly activated. They showed that right centro-parietal regions formed a synchronous inter-brain network in the 10 Hz mu band between the two participants during coordinated actions. According to Dumas et al. (2010), this coupling could represent different aspects of the social interaction, but they could not determine whether the coupling was simply due to synchronic movement or whether it could also represent anticipation of the other participant's action and turn taking.

Notably, most of these studies did not investigate complex joint actions but were interested in only coordinated actions. In a social context, protagonists do not act simultaneously but execute complementary actions in response to actions performed by others (e.g., joint action). Complementary actions differ from simple imitation because they require an understanding of the intention of the co-actor. Accordingly, Astolfi et al. (2010) recorded brain activity of four participants who were playing cards around a table (Astolfi et al., 2010; Babiloni et al., 2007, 2006). They developed a Granger-causality-based method to analyse links between the brain activities of all participants and showed that right prefrontal and parietal activities were correlated between the partners of the game (and not their opponents).

Taking these studies into account, it appears that motor and prefrontal areas seem to be involved in social interactions and display different activations in function of the social context. However, the explanation of this modulation remains poorly known, and three main hypotheses have been introduced. Kourtis et al. (2010) proposed that this modulation could be related to a simulation of the partner's action in joint action situations (Kourtis et al., 2010). Tsai, Sebanz, & Knoblich, (2011) proposed that it could be associated with a modification of the representation of the action, for example by building a common representation of the action in interactive contexts as described by Hari and Kujala (2009). Finally, Meyer, Hunnius, van Elk, van Ede, and Bekkering (2011) suggested that it could be related to an attentional and motivational effect, with the motor system being more recruited during the observation of relevant stimuli (Meyer et al., 2011).

It is still unclear whether the observed modulation was related to the social salience of the human-human interaction or to the modification of the goal of the actions; if so, it is unclear whether “acting” or “observing” during social interactions modulated the participants' brain activity differently (i.e., role assignment, Dumas, Martinerie, Soussignan, & Nadel, 2012).

In the present study, we tested whether (1) the goal and (2) the social relevance of a movement influenced brain activities and motor kinematics in both protagonists of a face-to-face interaction. To do so, we recorded movements and EEG signals of two participants while they were performing or observing object-directed movements. To test whether the goal of an action influenced brain activity, similar actions were performed by an actor in an interactive (e.g., the actor presents a saucer and the observer places the corresponding cup on the saucer) or non-interactive context (e.g., the actor presents a saucer and the observer does nothing). Additionally, to investigate the social relevance (i.e., the specificity of the human-human interactions) these actions were performed by either a human agent (biological action) or a robot agent (non-biological action).

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