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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).

We expected to measure stronger motor activity in the interactive conditions, as observed in the previous studies. To disentangle the role of this motor modulation, we compared several motor markers. Among the motor markers compared were the movement related potentials (MRP), which would be more indicative of preparatory or simulatory processes, and beta suppression, which could reflect activity of the action-representation system (Hari, 2006). These markers were measured during movement observation and execution in the different contexts. The analysis of these markers could be helpful in identifying which motor processes are modulated by the social context. We expect a modulation of the observer's brain motor activity during the "Interaction" condition, as reported by Kourtis et al. (2010) and Oberman et al. (2007). We also expect modulation of the actor's brain activity even though differences between observer and actor may be seen as a function of role assignment (Dumas et al., 2012).

2. Material and methods

2.1. Participants

Forty healthy participants ((mean age: 21.3, range: 18–27 years), 20 women and 20 men) took part in this experiment. They reported no history of neurological disease or psychological issues. All were right handed (mean scores: 0.82 Edinburgh test (Oldfield, 1971)) and had normal or corrected-to-normal vision. The study was approved by the Ethical Committee CPP Sud-Est II, and all participants gave their written informed consent. They constituted 20 pairs: 6 gender-mixed, 7 male–male and 7 female–female.

2.2. Procedure

The experiment always involved two participants, i.e., one "actor" and one "observer." Participants were seated face to face on each side of a table. The actor was either a human (H) or a robot (R). The experiment contained an interactive ("Interaction") and a non-interactive ("Observation") condition for each of two types of actors: Interacting with a human (InteractionH) or a robot agent (InteractionR) and observing a human (ObservationH) or a robot agent (ObservationR). These four conditions were presented in a block design displayed in Fig. 1.

For all conditions, the actor was instructed to perform object-directed movements toward one of three different objects: a box, a saucer and a candle-holder. The displacing action involved two sub-phases. The first sub-phase consisted of reaching and grasping an object placed to the right of the actor (Reach sub-phase), and the second sub-phase consisted of lifting and moving the object to the middle of the table in front of the observer (Move sub-phase). During the "Observation" conditions, the observer was passively watching the actions. During the "Interaction" conditions, the observer had to perform a complementary action (i.e., placing a lid on the box, a coffee cup on the saucer or a candle on the candle-holder). The 3 different actions were performed randomly 15 times in each condition. In the "Interaction" conditions the observer was instructed to begin his movement only when the actor's hand was back in the starting position. Although this setup was less interactive, this dissociation allowed us to separate the actor's observation from the observer's response. Hence, the movement preparation in the "Interaction" condition could not contaminate the actor's observation. An additional condition, consisting of shaking hands during only the "human–human" interaction (ObservationH and InteractionH) was excluded from analysis because the to-be performed movements were too different (i.e., only one movement toward the observer) from the remaining three grasping-and-displacing actions (i.e., two sub-movements toward the objects placed at the right side of the actor) and because the observer would be able to predict his response from the onset of the actor's movement (and not only when an object would be grasped).

The experiment was divided into 5 blocks. The first and second blocks included the "Observation" conditions (balanced between ObservationH and ObservationR), whereas the third and fourth blocks included the "Interaction" conditions (balanced between InteractionH and InteractionR) (see Fig. 1b). This order was essential to have a "naïve" Observation condition in which the participant ignored the goal of the actor's actions and was unable to associate a response in the Observation conditions. A last block, containing a second "ObservationH" condition (ObservationH₂), was also included. Note that during the first "Observation" blocks participants were given no instruction about the purpose of the actor's movements and the complementary objects were hidden from view. By contrast, during the ObservationH₂ block both participants were aware of the complementary actions, and this block was therefore contaminated by knowledge of the experimental purpose and could induce an unintentional response preparation. Data from this last condition is presented in the Supplementary material.

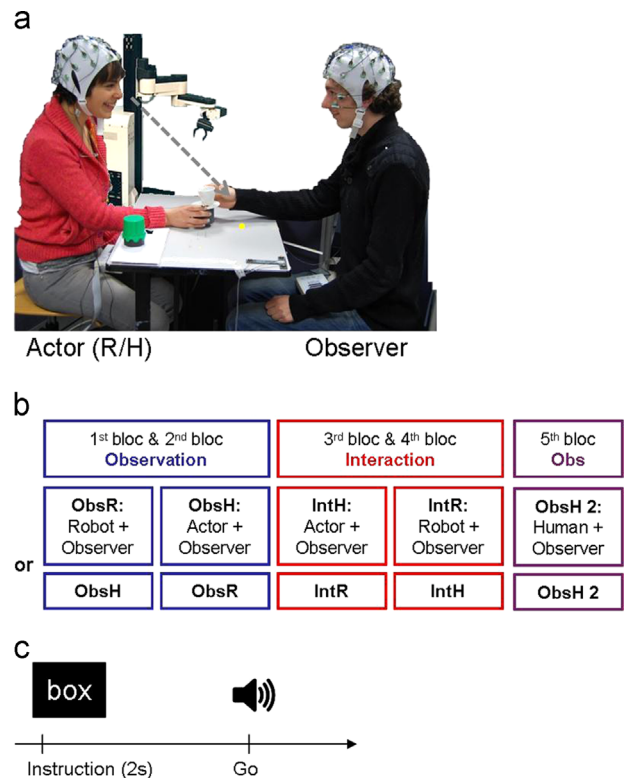


Fig. 1. Experimental setting: (a) experimental setting coupling Dual-EEG and kinematics recording. The "Actor" initiating the movement was either a participant or a robot. The participant that observed or interacted with the Actor was referred to as "Observer". The yellow dot on the table schematically indicates the point to be fixated on by the person on the left. (b) The experiment was composed of 5 blocks presented in two different orders. (c) Trial setting: An instruction appeared on a screen and was visible for 2 s to only the actor. An auditory stimulus served as Go signal for the actor after a random interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

At the beginning and end of each trial, both participants were asked to place their right hand at a starting position on the table, with their right thumb and index finger held in a pinch grip position. To minimise eye movement artefacts, fixation points were placed onto the table at equal distance between each partner's starting position and the middle of the table. The observer was instructed to fixate on the fixation point close to the actor, and vice versa. Both participants were asked to maintain fixation throughout the trial and thus to observe the partner's action in the periphery. Before each trial, written instructions about the object to be grasped were given to the actor on a screen placed behind the observer. An auditory stimulus served as the Go instruction for the actor. In the "Interaction" conditions, the observer was instructed to begin his movement only when the actor's hand was back in the starting position. EEG and kinematics parameters were recorded throughout the experiment.

2.3. Material

The robot used in the experiment was an UMI RT100 robotic arm (Oxim Ltd, Oxon, UK). The robot is a SCARA type robot with 7 degrees of freedom, including the gripper attachment. Maximal velocity was fixed at 165 mm/s resulting in slow and jerky actions. Note that the robot movement was different from the human movement because the robot needed a supplementary sub-phase to grasp the object. First, the robot executed a translation movement behind the object, and then, it performed a movement toward the object to grasp it (Fig. 2b).

2.4. Kinematics acquisition and analysis

An Optotrak 3020 (Northern Digital, Waterloo, Ontario, Canada) was used to record the spatial position of an active marker (infrared light-emitting diode) at a sampling rate of 250 Hz and a spatial resolution of 0.1 mm. The marker was placed on the participant's wrist and characterised the reaching and displacing components (Jeannerod, 1981; Jeannerod & Biguer, 1982).

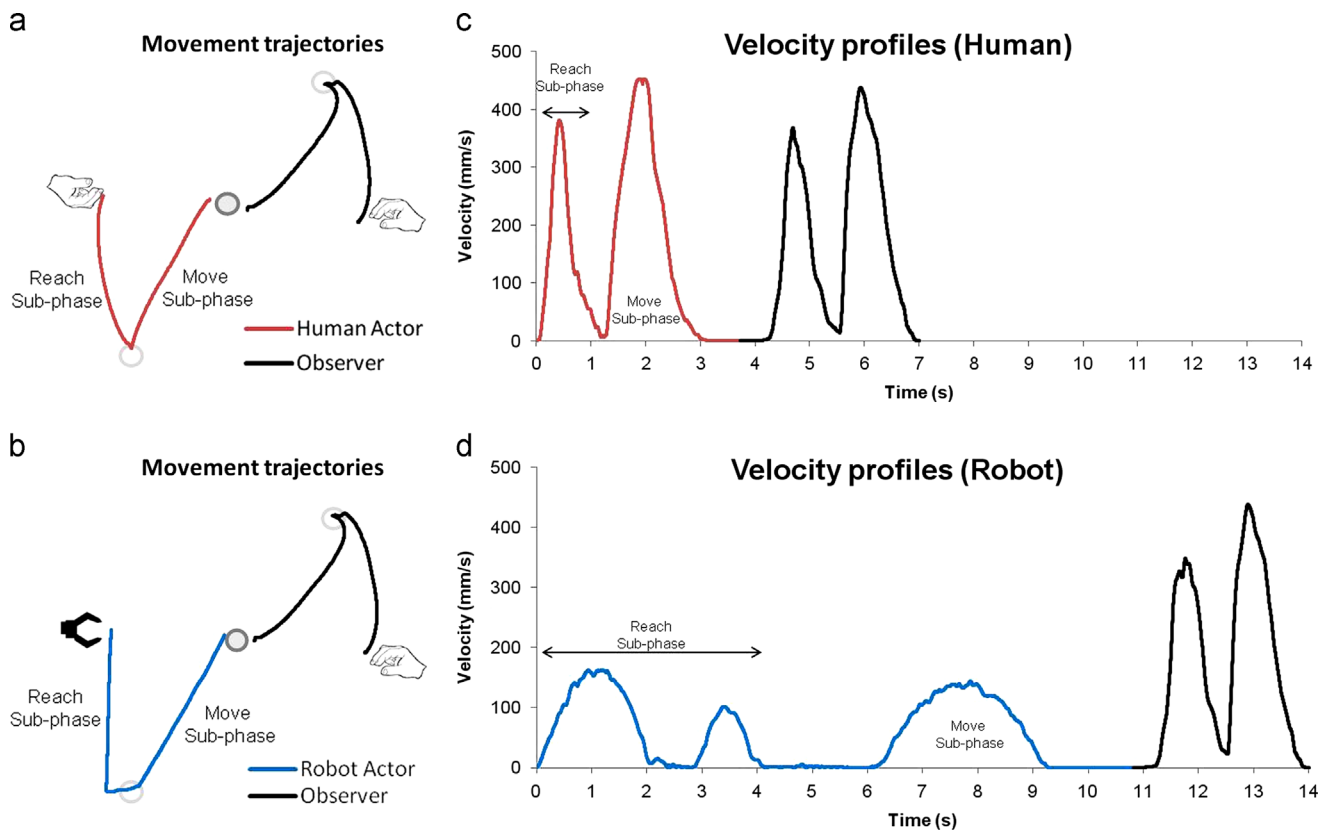


Fig. 2. Movement profiles: (a) and (b) typical trajectories of the actions of the actor (red – (a)) or the robot (blue – (b)) and the observer (black). (c) and (d) Velocity profiles of the movement of the actor (red – (c)), the robot (blue – (d)) and the observer (black). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Raw data were pre-processed using a second-order Butterworth dual-pass filter (cut-off frequency, 10 Hz). Kinematic parameters were assessed for each individual movement using Optodisp software [Optodisp Copyright INSERM-CNRS-UCBL (Marc Thevenet, Yves Paulignan, Claude Prablanc) 2001]. We analysed the amplitude and latency of the wrist velocity peak (mm/s and ms) and movement duration (ms) for the two sub-phases of the movement (reach-to-grasp and displace). Movement onset (reaction time) and termination (offset) were determined to be the first and last value, respectively, in a sequence of at least 11 increasing or decreasing points on the wrist velocity profile. Wrist velocity peak was determined as the maximal value in the velocity profile. Kinematic parameters were determined for each individual trial and were then averaged for each participant and condition. *T*-tests were performed to compare the ObservationH and InteractionH conditions.

For each individual trial, the latency of the onset of the actor's movement was determined to synchronise the participants' EEG with the onset of the actor's movement.

2.5. EEG acquisition and analysis

EEG data were recorded using BrainAmp amplifiers (BrainVision recorder software, BrainProducts GmbH, Munich, Germany). The two participants' EEGs were recorded with a double EEG device using two 32-channel EEG caps with active electrodes (ActiCap BrainProducts) arranged according to the international 10–20 system. Each subject had its own reference (situated at Fpz) and ground (situated at AFz). Impedance was maintained below 20 k Ω . The two EEG devices were synchronised. The signal was sampled at 500 Hz, and a 50 Hz notch filter was used. Moreover, recordings of vertical and horizontal electro-oculograms (EOGs) were made from electrodes above and below the left eye to monitor eye movements and blinks.

EEG data were analysed using BrainProducts Analyser 2 software for ERPs (BrainProducts GmbH, Munich, Germany). FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011), a free toolbox of Matlab 7.0 (MathWorks, Natick, MA), was used for the Time–Frequency analysis. EEG data were first time-locked to the onset of the actor's movement by adding kinematic markers to the EEG signals. These data were then re-referenced for each subject with a mean reference value including all but the EOG electrodes and were low pass filtered at 30 Hz. EEG data were segmented differently for the human and robot actors to include the reach sub-phase of the movement (for details see Section 3.1 below). For the human actor, segments lasted from –1000 ms before to 1500 ms after the onset of actor's

movement; for the robot, segments lasted from –1000 ms to 4000 ms after the onset. Segments with artefacts were removed.

2.6. Specific analyses

2.6.1. ERPs

After segmentation, a baseline correction was applied from –200 ms to 0 ms before the onset of the actor's movement. Averages were calculated within the four conditions (ObservationH/ObservationR/InteractionH/InteractionR). Grand averages for all participants were calculated separately for the observers and the actors.

2.6.2. Time–frequency

After segmentation, a discrete Morlet-wavelet transform was computed for each trial by convolving a Morlet wavelet with the signal using a width of 7 cycles to analyse oscillatory activities over a range of 1–30 Hz in 1 Hz steps. To avoid temporal smearing of motor activity into the baseline, a baseline correction was chosen from –400 to –100 ms before the actor's movement onset.

2.6.3. EEG statistical analysis

To test for statistical significance, a cluster-based nonparametric permutation test was carried out on ERPs and Time–Frequency data as described in Maris and Oostenveld (2007) and Van Schie et al. (2008). This statistical analysis does not require prior assumption on ERP components and the statistical test takes into account all electrodes and time-windows. This nonparametric test contains two statistical levels: we first performed a running paired *t*-test on all participants, comparing energy at each time-bin (time–frequency bins) for each sensor between two conditions of interest. We then corrected the results for multiple comparisons by performing a second statistical test at the cluster-level. This is performed by thresholding the output of the (two-tailed) *t*-test at $p < 0.025$ and clustering adjacent significant samples in the time–electrode space (respectively time–frequency–electrode space). The statistics used to describe these clusters is T_{sum} , the sum of all *t*-values inside the cluster. A permutation-test is performed by randomly re-assigning the ERP (respectively time–frequency) of each individual between the two conditions because the probability distribution of values in T_{sum} is unknown. This step is repeated a number of times (1000 iterations in our case) sufficient for obtaining an estimate of the distribution of T_{sum} in the null hypothesis. It is then possible to compare the experimental value of T_{sum} to this calculated distribution to decide whether to reject the null hypothesis, with a given alpha

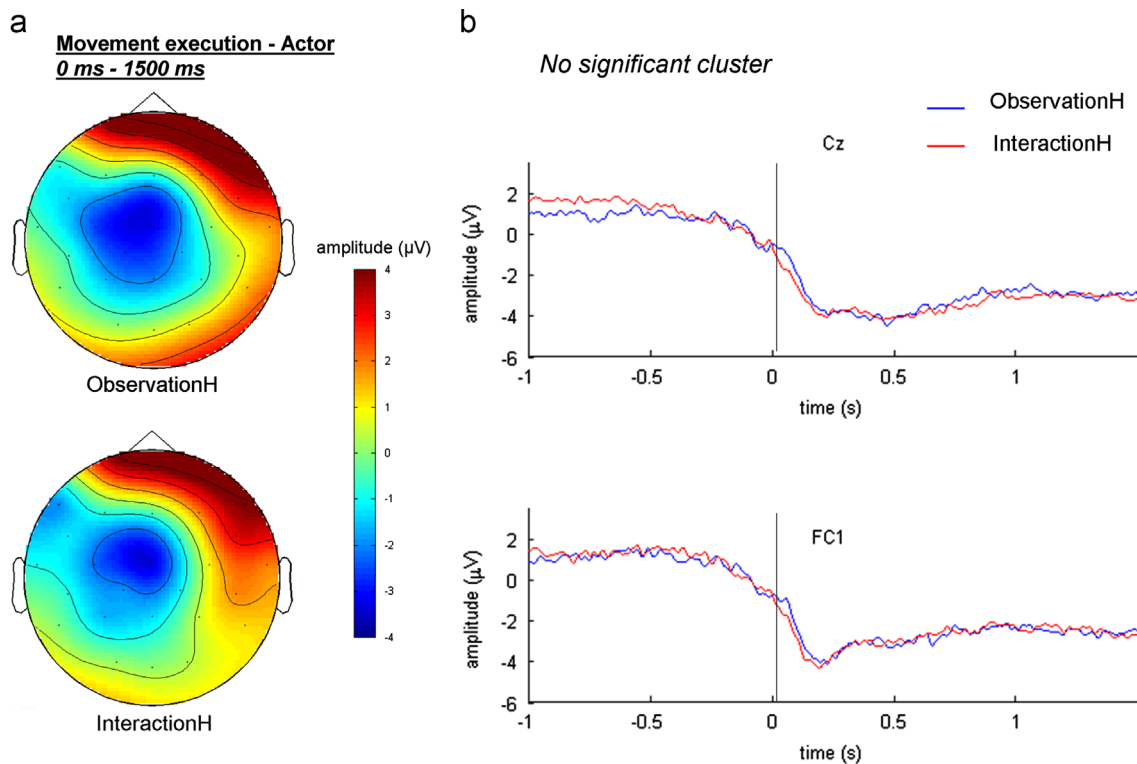


Fig. 3. Actor's ERP synchronised to the onset his/her movement: (a) topography of the movement related potential during the ObservationH and InteractionH conditions. (b) ERPs measured over Cz and FC1 during the ObservationH (blue) and the InteractionH (red) conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

value. For the ERP analysis, we also impose that all considered clusters must be present on at least two adjacent electrodes at each time point. This additional constraint turned out to be too restrictive for the three-dimensional time-frequency analysis (time by frequency by electrodes), and so we took into account all clusters in this case. The clusters identified (electrodes and time windows) are therefore not based on prior hypotheses but are only identified using significant differences.

3. Results

The data from one pair of participants were removed from the analysis because the actor failed to fixate on the correct fixation point during the experiment and was thus unable to see the observer's movement.

3.1. Kinematic results

3.1.1. Actor's movements

Fig. 2 displays the trajectory and velocity profile of the goal-directed action (Reach and Move sub-phases). Maximum velocity, peak amplitude and movement duration were measured for all conditions.

3.1.1.1. Robot. Movements executed by the robot were constant throughout all conditions and experimental blocks. In total, the movement lasted 9.2 s, the Reach sub-phase lasted 4.1 s and the Move sub-phase lasted 2.9 s. There was a 2.2 s break between these two actions. The maximum velocity peak amplitude was 162.2 mm/s.

3.1.1.2. Human. For the actor, the movement duration was on average similar for ObservationH (3.1 ± 0.21 s) and for InteractionH (3 ± 0.19 s [Mean \pm SEM]). The Reach sub-phase of the movement lasted 1.31 ± 0.08 s and 1.28 ± 0.09 s, respectively, and the velocity peak

amplitude was on average 367 ± 21 mm/s and 379 ± 23 mm/s, respectively. None of these parameters differed significantly between the two conditions. For the Move sub-phase of the action, duration was on average 1.61 ± 0.12 s for ObservationH and 1.57 ± 0.1 s for InteractionH; moreover, the velocity peak amplitude was 444 ± 32 mm/s and 415 ± 29 mm/s, respectively. Again, no significant difference was observed between conditions. The results of the ObservationH₂ condition are displayed in the Supplementary material.

Due to the important disparity between human and robot movements, we did not directly compare these conditions in the following analyses. Comparisons between "Observation" and "Interaction" conditions have been processed for the actor and robot observation separately and with different temporal windows. The temporal windows were chosen to include only the reach sub-phase of the movement. Therefore, a segment lasted from -1000 ms before to 1500 ms after the onset of the human actor's movement, and a segment lasted from -1000 ms to 4000 ms after the onset of the robot's movement.

3.1.2. Observer's movements

In the "Interaction" conditions, the observer's movement started approximately 4.1 ± 0.3 s after the onset of the human actor's movement (InteractionH) and 11.1 ± 0.2 s after those of the robot (InteractionR). Total movement duration was on average shorter in the InteractionH (2.63 ± 0.10 s) than in the InteractionR conditions (2.93 ± 0.09 s [Mean \pm SE]; $p < 0.01$). Similarly, shorter durations were observed in the InteractionH (1.28 ± 0.05 s) than in the InteractionR conditions (1.43 ± 0.05 s; $p < 0.01$) for the Reach sub-phase of the movement. Velocity peak amplitude was larger in the InteractionH (375 ± 21 mm/s) than in the InteractionR conditions (343 ± 17 mm/s; $p < 0.04$). Shorter durations were observed in the InteractionH (1.36 ± 0.05 s) than the InteractionR conditions

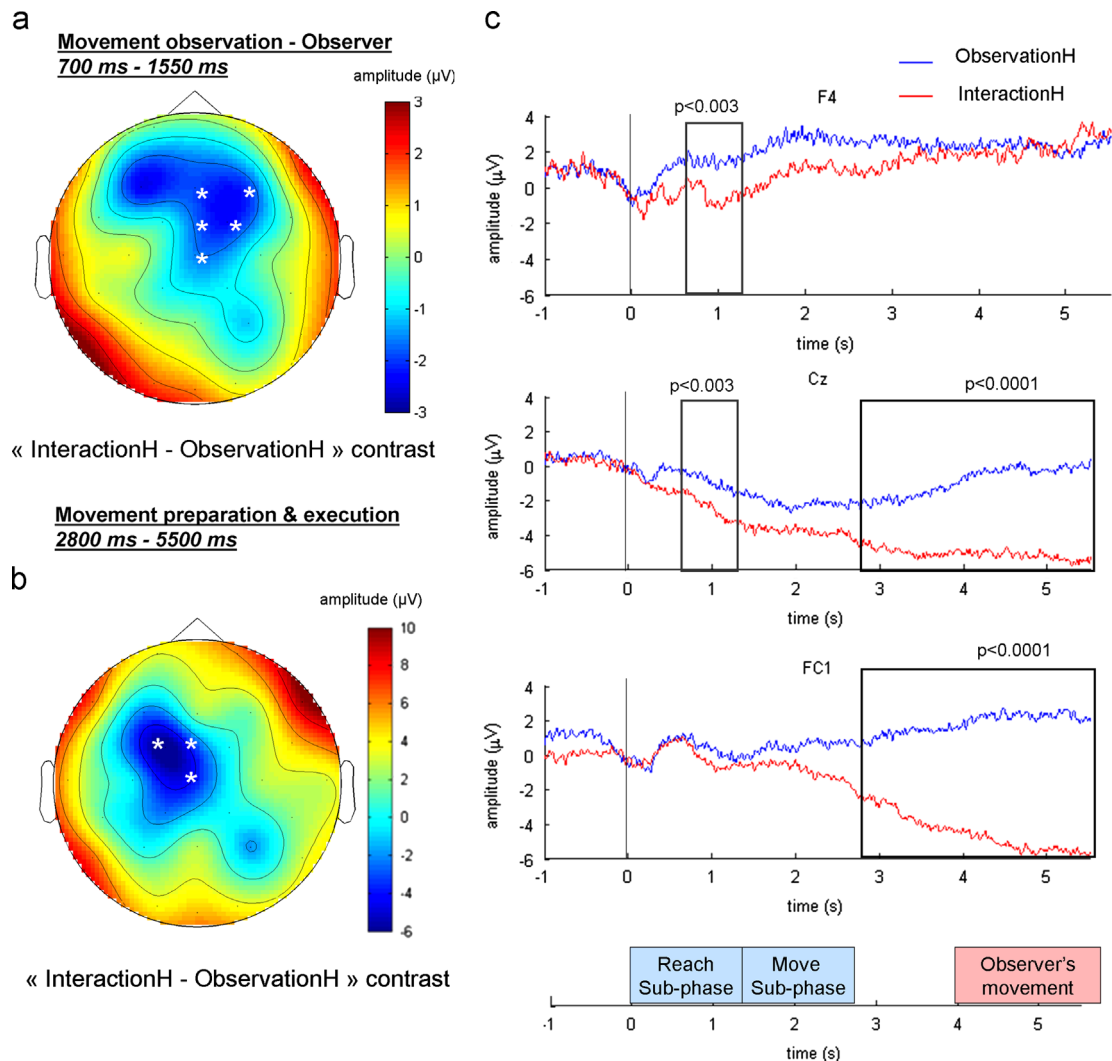


Fig. 4. Observer's ERP synchronised to the onset of the human actor's movement. The segmentation performed included both the actor's and the observer's movements. The observer executed a movement only in the InteractionH condition: (a) topography of the contrast "InteractionH–ObservationH" during the observation of the human actor (700–1550 ms). (b) Topography of the contrast "InteractionH–ObservationH" reflecting the preparation and the execution of the movement (InteractionH condition only; 2800–5500 ms). (c) ERPs measured over F4, Cz and FC1 during the ObservationH (blue) and the InteractionH (red) conditions. Rectangles represent the significant differences between the conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(1.50 ± 0.04 s; $p < 0.01$) for the Move sub-phase, but velocity peak amplitude did not significantly differ between conditions (451 ± 16 mm/s and 439 ± 16 mm/s, respectively). In conclusion, complementary actions performed by the observer when interacting with the robot were generally slower than those performed when interacting with the human.

3.2. Electrophysiological results

All results of the ObservationH₂ condition are displayed in the Supplementary material.

3.2.1. ERP analysis

3.2.1.1. Performing the initial reach action (actor's data). Fig. 3 shows that MRPs were observed in both experimental conditions for the actor, who performed the same action in the ObservationH and InteractionH conditions. The MRPs were measured over left central electrodes (Cz, C3, FC1 and CP1) (Fig. 3a) and were comparable between the conditions. The statistical analysis did not identify any cluster with significant differences between the conditions.

3.2.1.2. Observing the human actor and performing the complementary action (observer's data). To differentiate activity induced by observing the actor's movement in different contexts from activity related to the preparation and execution of the observer's own movement (InteractionH), we analysed the observer's EEG during the whole trial duration time-locked to the onset of actor's movement (Fig. 4). The statistical analysis identified two main clusters displaying significant differences between the two conditions. The first cluster displayed in Fig. 4a was identified during the actor's reach sub-phase from 700 ms to 1400 ms after the actor's movement onset and involved Cz, FCz, FC2, Fz and F4 ($p < 0.003$). The second cluster (Fig. 4b) ranged from 2900 ms to the end of the segment and was located over Cz, FCz and FC1 ($p < 0.0001$). Note that the observer's movement began on average at time 4.1 s.

The observation of the ERPs over FC1 (Fig. 4c) indicated that the second cluster may represent motor preparation and execution. Indeed, a negative MRP was measured over this electrode in only the InteractionH condition approximately, 2000 ms after the onset of the actor's movement. Moreover, the topography of the cluster identified was comparable to the one measured for the actor (see Fig. 3).

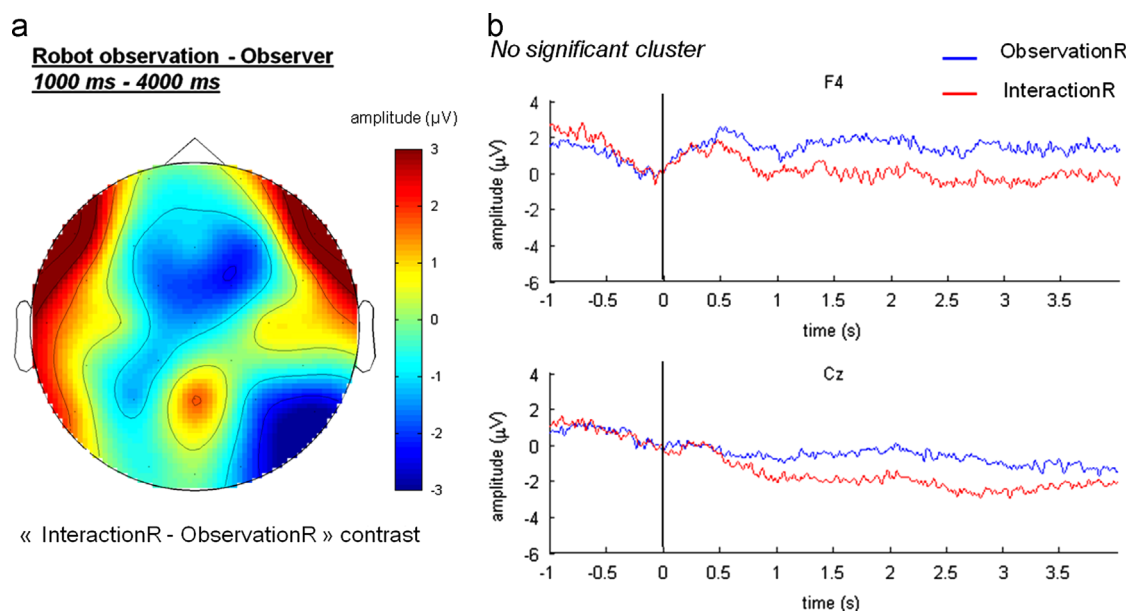


Fig. 5. Observer's ERP synchronised to the onset of the robot's movement: (a) topography of the contrast "InteractionR–ObservationR" during the observation of the robot (1000–4000 ms) and (b) ERPs measured over F4 and Cz during the ObservationR (blue) and the InteractionR (red) conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

However, during the actor's Reach sub-phase (from 700 ms to 1400 ms after actor's movement onset) the first cluster topography of the contrast InteractionH–ObservationH was different and displayed a stronger negativity in the InteractionH than in the ObservationH condition over right frontal and central electrodes. Activity measured over Cz displays both differences (i.e., early and late cluster) while the electrode F4 displays only the early cluster. Therefore, the different topographies of these effects may be indicative of two different neuronal processes.

3.2.1.3. Observing the robot actor (observer's data). Fig. 5 shows the ERPs measured for the observer during robot movements. The activity measured over fronto-central electrodes seems comparable to the ones measured during the observation of the human actor for both conditions. In this case also, the activity seems more negative in the InteractionR condition compared to the ObservationR condition. However, the statistical analysis did not identify any cluster with significant difference between the two experimental conditions.

3.2.2. Time–frequency analysis

The statistical analysis was performed including all frequency bands from 1 to 30 Hz and between 0 and 1300 ms. To analyse motor related events, we focused our examinations on only alpha/mu and beta oscillations.

A strong fronto-posterior alpha rhythm was present and made it difficult to distinguish between mu and alpha activities. Due to this strong attentional bias, only the analysis of the beta oscillations is presented in the next section.

3.2.2.1. Performing the initial reach action (actor's data). Performing an action induced a suppression of beta oscillations (17–21 Hz) around movement onset principally over central electrodes (C3 and C4) (Fig. 6a) for both conditions. This suppression remained until the end of the segment (Fig. 6b). Suppression over fronto-central electrodes (F3 and FC1) was also observed in the InteractionH condition. The statistical analysis revealed two clusters that displayed significant differences. The first cluster ranged from 200 ms to 1250 ms over C4 and CP6 electrodes, and the second cluster was measured over F3 and FC1 from 450 ms to

1200 ms (Fig. 6c). A stronger suppression was observed for the InteractionH than ObservationH condition for both clusters.

3.2.2.2. Observing the human actor (observer's data). Shortly after the onset of the actor's movement, the analysis of beta rhythm (17–21 Hz) revealed a clear suppression of 17–21 Hz oscillations in both conditions principally over central electrodes for movement observation (see Fig. 7). A cluster of several electrodes (mainly CP1 but also Cz, C3, FC2 and C4) showed significant differences between the two conditions. The 17–21 Hz oscillations over these electrodes displayed a significantly stronger suppression in the InteractionH than in the ObservationH condition from 350 ms to 1300 ms after the onset of the actor's movement (Fig. 7b).

Note that all these effects were observed more than 3 s before the onset of the observer's movement and are thus unlikely to result from movement preparation.

3.2.2.3. Observing the robot actor (observer's data). Observing the robot also elicited 17–21 Hz suppression in the two conditions shortly after movement onset (Fig. 8). In this case also, the suppression was stronger in the InteractionR condition than in the ObservationR condition. The difference between ObservationR and InteractionR was significant between 1300 ms and 3800 ms over CP1, C3, CP2 and C4 electrodes (Fig. 8b).

4. Discussion

Our study focused on how complementary actions and social relevance (i.e., specificity of human–human interaction vs. robot–human interaction) influence motor system activity during the observation and execution of actions. Additionally, we wanted to disentangle the function of this motor modulation and examine the differences and similarities between the two participants' brain activities. For this purpose, different indicators of neural motor activity (beta (17–21 Hz) oscillations and MRPs) in both participants of the interaction were analysed during the first phase of an actor's displacing action. Synchronising EEG signals to the actor's movements rather than to an external go signal allowed us

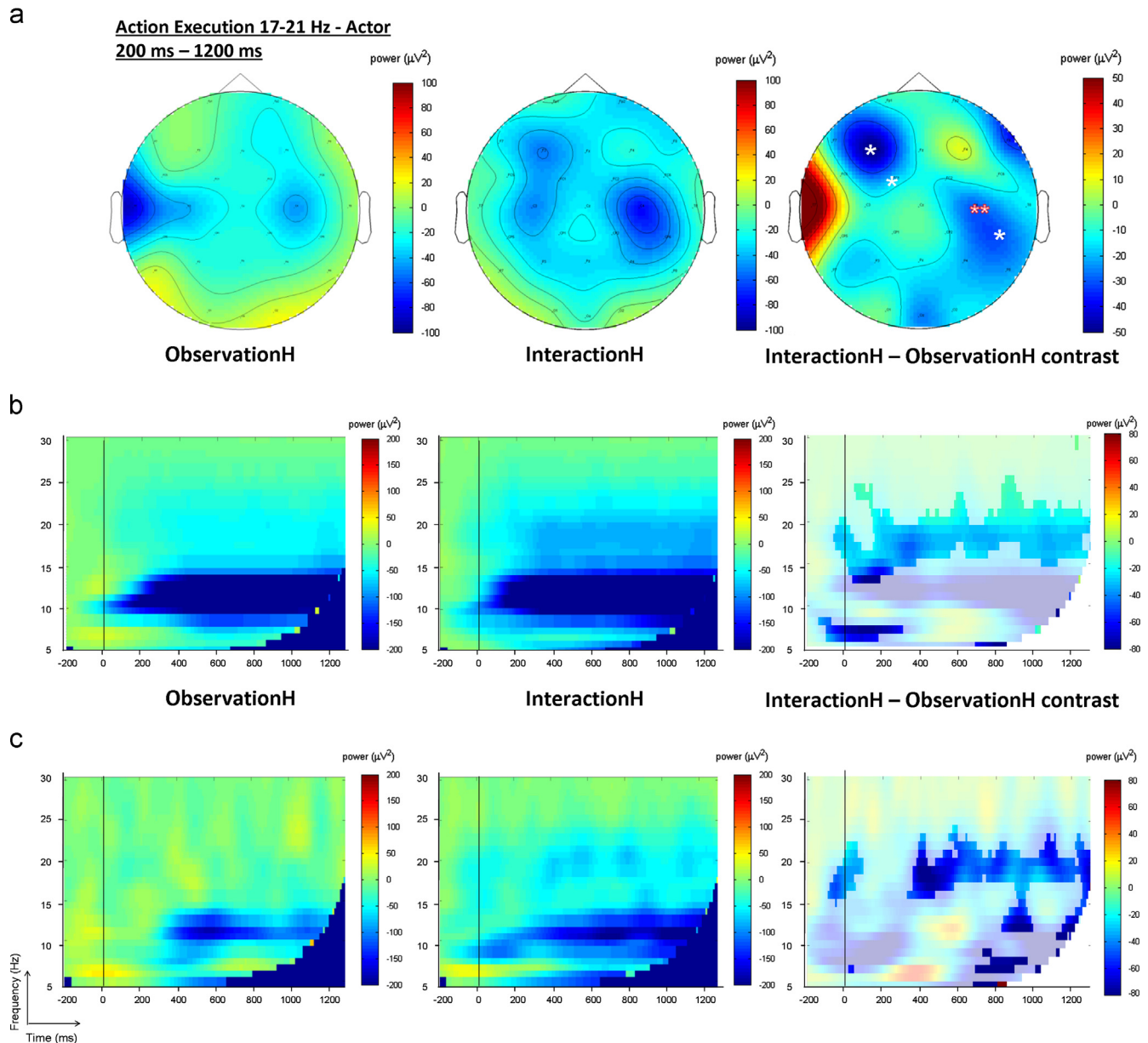


Fig. 6. Actor's time–frequency plots: (a) topography of the beta suppression during the ObservationH, InteractionH conditions and contrast ObservationH–InteractionH. $*p < 0.05$. (b) and (c) Wavelet measured over (b) C4 and (c) F3 during the ObservationH, InteractionH conditions and contrast ObservationH–InteractionH. Rectangles represent the significant differences between the conditions.

to show that the motor activity of both participants varied with the type of interaction (“Observation” and “Interaction”), with social relevance (human vs. robot) and with the role of the participants (actor or observer). A modulation of motor activity in both actor and observer as a function of the interactive context was measured.

4.1. Influence of the goal of an action on brain activity

Execution and observation related motor activities were observed during our experiment in the “Observation” and “Interaction” conditions. Both a negative going MRP and suppression of beta oscillations were observed in the actor over central electrodes shortly before and during motor onset. Similarly, suppression of beta oscillations and observation related MRPs were observed in the observer during movement observation. While the MRP has been associated with motor cortical excitability (Deecke, 1987), the

beta suppression reflects sensory-motor and action-perception processes (Hari, 2006).

Interestingly, though the actors' motor output (kinematic parameters) was essentially the same in the “Observation” and “Interaction” conditions, our results showed that beta activity differed in the two conditions. When the actor expected a complementary action (InteractionH condition) or had knowledge of the complementary action (ObservationH₂), 17–21 Hz suppression was stronger over the C4 electrode and over left fronto-central electrodes (FC1 and F3). Given that repetitive observation of a movement typically results in weaker mu-suppression (Perry & Bentin, 2009), it is unlikely that these effects result from the order of conditions. Observation-related beta suppression (17–21 Hz) was also seen in the observer, and it appeared as soon as the actor initiated his/her movement. Similarly, this suppression was stronger in the “Interaction” condition compared to the “Observation” condition independently of whether the actor was

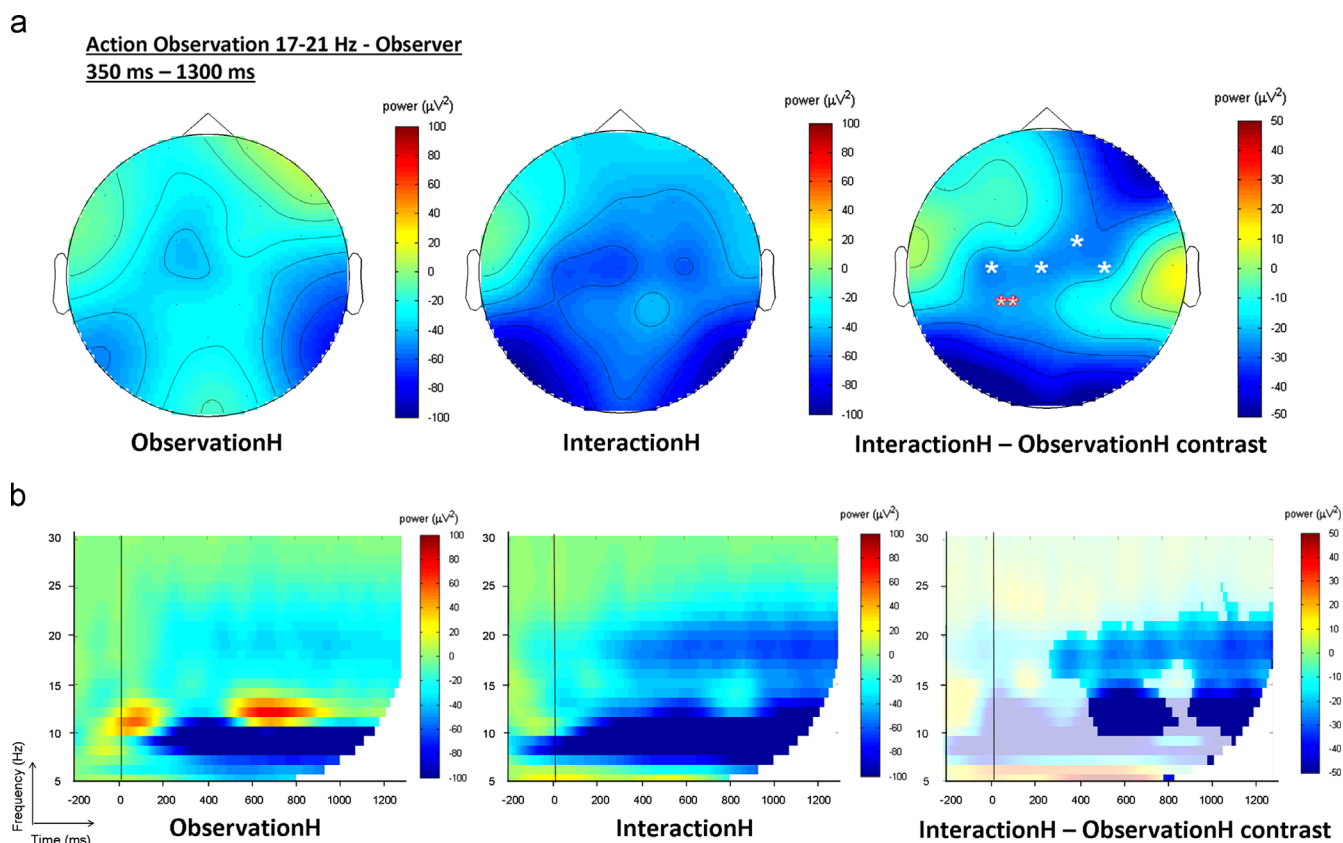


Fig. 7. Observer's time–frequency plots during the human actor observation: (a) topography of the beta suppression during the ObservationH, InteractionH conditions and contrast ObservationH–InteractionH. * $p < 0.05$. (b) Wavelet measured over CP1 during the ObservationH, InteractionH conditions and contrast ObservationH–InteractionH. Rectangles represent the significant differences between the conditions.

a human or a robot. Given that the actor motor behaviour did not differ between the “Interaction” and “Observation” conditions, motor commands and pure motor encoding cannot account for the context sensitivity of this modulation. These results are consistent with several recent studies that investigated movement-related neural activity (Kilner et al., 2006; Kourtis et al., 2010; Oberman et al., 2007; Streltsova, Berchio, Gallese, & Umiltà, 2010). For instance, Kourtis and colleagues described modulations of MRP and beta oscillations during action simulation (Kourtis et al., 2010). Kilner et al. (2006), Oberman et al. (2007) and Streltsova et al. (2010) observed stronger mu suppression during observation of actions in a social than in a non-social context. More specifically, Kilner et al. (2006) described mu suppression for observed movement from an actor forward-facing the subject but not from an actor that was away from the subject. These authors argued that the human mirror system could be sensitive to the social relevance of an observed action through posterior superior temporal sulcus (pSTS) input. Additionally, some authors found that complementary actions modulated brain motor activity. For example, Newman-Norlund and collaborators found that the human MNS is more activated by complementary than by imitative actions (2007). In the same vein, Sartori, Cavallo, Bucchioni, and Castiello (2011) observed that motor excitability was increased when observing an action that required a complementary action (although no movement was actually performed). In our study, we reported modulation of neural motor parameters for both actor and observer and thus extend these previous findings from observation to the execution of actions in interactive contexts.

However, different effects have been measured between actor and observer concerning the motor potentials (MRPs). The actor's MRPs did not differ between the type of interaction (“Observation

(H and H₂)” and “Interaction”). A negative observation-motor related potential was also evident for the observer in both conditions over central electrodes (Cz). This MRP was observed independently of whether the actor was a human or a robot. In the case of a human actor, a cluster of frontal and central electrodes displayed a more negative activity during the actor's movement (700–1500 ms) when a complementary action was required (Fig. 4a). The topography of the effect differed from pure motor system activity (Fig. 4b) and is therefore not related to the motor preparation of the complementary action.

4.2. Specificity of social relevance?

The condition in which the observers interacted with the robot allows us to compare and analyse the effect of social interaction in itself (vs. robot interaction).

First, the analysis of the indexes of motor activity revealed an unexpected activation of motor areas during the observation of the non-biological agent, and this was discernible by the modulation of beta-activity and the observation related potential over central electrodes. Such an effect has already been described in previous studies (Cross et al., 2011; Gazzola, Rizzolatti, Wicker, & Keysers, 2007), but these results remain controversial (Perani et al., 2001; Press, Gillmeister, & Heyes, 2006; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004).

Second, the comparison between the ObservationR and the InteractionR conditions revealed different modulations of the MRPs and the beta suppression.

Concerning the ERPs analyses and contrary to the human actor conditions, no significant difference was measured when observing or interacting with the robot (ObservationR and InteractionR). The absence of such differences indicates that this negative

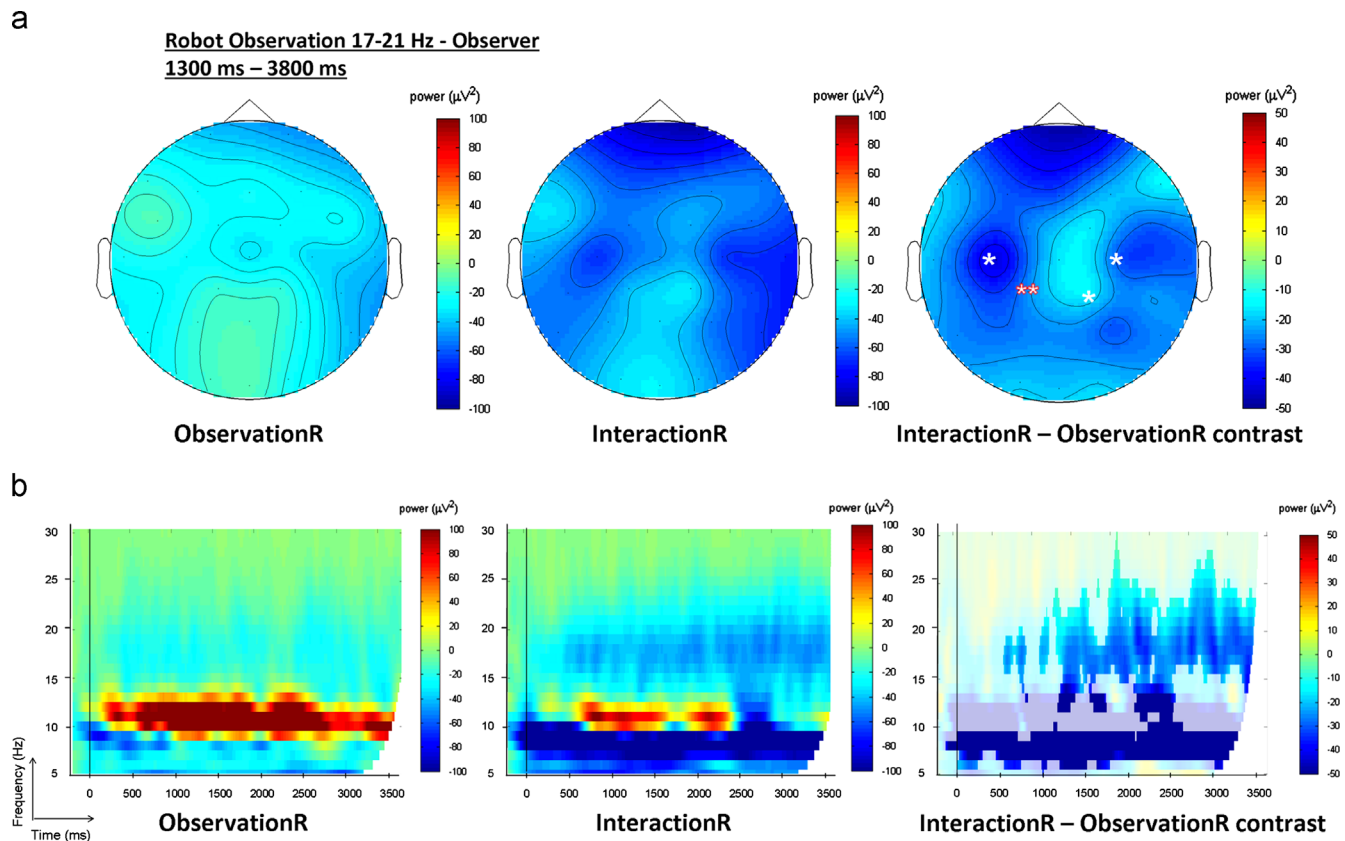


Fig. 8. Observer's time–frequency plots during the robot observation: (a) topography of the beta suppression during the ObservationR, InteractionR conditions and contrast ObservationR–InteractionR. * $p < 0.05$. (b) Wavelet measured over CP1 during the ObservationR, InteractionR conditions and contrast ObservationR–InteractionR. Rectangles represent the significant differences between the conditions.

potential, involving right fronto-central areas, may represent a mechanism specific to social interactions. However, the robot condition differed from the human condition in the present study in both agentivity of the actor and kinematics because the robot produced extremely slow and jerky movements. Therefore, it is possible that our setup fails to capture such potential effect.

Concerning the beta modulation and similar to the human–human interaction condition, suppression of the beta oscillation was stronger in the InteractionR condition than in the ObservationR condition. This result is in contradiction with [Kokal et al.'s study \(2009\)](#), which did not observe an interactive effect for robots. However, the present study required the observer to interact with the robot, which performed the same actions as the human actor. Therefore, it is possible that although the interaction does not involve a real person, the necessity to encode the robot action and execute a correct response is the same independently of the nature of the actor. The modulations of MNS activity during complementary action ([Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007](#); [Sartori et al., 2011](#)) would then occur when interacting with non-human agents ([Müller et al., 2011](#)).

The behavioural results of the observer's actions tend to support this assumption. Indeed, the velocity of movement was reduced when the observer interacted with the slower robot compared to interacting with a human actor. This adaptation of motor behaviour could account for a coupling between the human and the robot strong enough to induce a motor adaptation. However, it is possible that the slow robotic movements induced a simulation in the observer of the movement to-be-executed as part of his own motor system.

These results suggest that the observed modulations of beta oscillations are not specific to social salience and acting with the

robot; a non-biological agent can modulate brain motor regions similarly to a human actor. However, a specific indicator of social salience could be indexed by the frontal activity observed in the ERPs.

4.3. Role of this motor modulation

The present study showed that motor system activation as identified through beta oscillations and MRP was sensitive to the context of the action (“Interaction” vs. “Observation”) both for actor and observer. For both protagonists, beta suppression was generally stronger in the “Interaction” than in the “Observation” condition. This modulation did not seem specific to social interaction itself but rather to the joint action knowledge. Indeed, this effect held for the observer independently of whether the actor was a human or a robot. Moreover, the modulation was also observed for the actor in the ObservationH₂ condition, when the actor had acquired knowledge about the interaction. The increased activity of motor areas in the “Interaction” context can have several origins that could be identified by analysing several markers of motor activity. Although both beta oscillations and MRP reflect motor activity, these indexes are indicative of different processes: the MRP is more related to motor cortical excitability and sensory feedback to primary motor cortex, and beta suppression reflects sensory-motor and action-perception processes.

4.3.1. Simulation of the other action

It has been postulated that participants simulate their partner's actions during joint action in addition to their own actions ([Kourtis et al., 2010](#); [Novembre, Ticini, Schütz-Bosbach, & Keller, 2013](#); [Vesper, van der Wel, Knoblich, & Sebanz, 2013](#)). For instance,

Kourtis et al. (2010) showed that the mental simulation could be modulated as a function of the social relation of individuals. Such simulation could help to achieve coordination (Novembre et al., 2013; Vesper et al., 2013). This simulation hypothesis is consistent with our data on beta oscillations, which reflect activity in somatosensory areas (Gastaut & Bert, 1954; Hari et al., 1997). Moreover because no effect was observed on the MRPs for the actor, this effect is not related to direct motor excitability. Additionally, given that the modulation of beta oscillations were comparable between the actor and the observer, we show here that simulation is reciprocal between the two partners of the interaction. However, the modulation of beta remains in the ObservationH₂ condition for the actor and partially for the observer and was also present during the observation of the robot. This result is consistent with Kourtis et al. (2013). Though it could represent a long-lasting effect of the partner's movement simulation, this modulation may not only be related to the simulation of the partner's action but could also represent a modification of the action representation into a "joint" representation.

4.3.2. Common representation of the global action

The modulation of the beta suppression could also represent the setting up of a common representation of the global action. We could assume that the programming of the actor's initial action (i.e., grasp and displace the saucer) is modified by the context to process the two complementary actions within the frame of a common "goal" (i.e., displace the saucer toward your partner who will place the cup on it). From the start of the movement, the participants might develop an internal model of what ought to be the observer's adapted response. The participants' beta activity could therefore reflect anticipation of the observer's response in terms of sensory consequences. Previous study indeed showed that mirror areas may be involved in the discrimination or understanding of intentions (Iacoboni et al., 2005) or, more generally, in building an anticipated representation of others' motor behaviour (Rizzolatti & Sinigaglia, 2010). Motor studies suggested that sub-phases of an action (in our case each participant's action) are defined with respect to the global goal of the action and are programmed conjointly (Fargier, Ménoiret, Boulenger, Nazir, & Paulignan, 2012; Johnson-Frey, McCarty, & Keen, 2004; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Rand & Stelmach, 2000; Weiss et al., 2000). Therefore, in line with the suggestion of Hari and Kujala (2009), the goal of the action would integrate the action of the two protagonists (e.g., to place the cup on the saucer). Such a common representation of the action would be formed and maintained throughout diverse interactions. This may explain the results measured for the robot and the ObservationH₂ condition. This hypothesis is consistent with recent studies (Kirschner & Tomasello, 2009; Tsai et al., 2011). For example, Tsai et al. (2011) showed in a joint Simon task that participants formed a "we-representation" of the action, diverging from an individual perspective (simulation of the participant's own action and the partner's action distinctively) to a common motor representation (representation of the global action).

4.3.3. Attentional and motivational effect

The two hypotheses outlined above do not explain the ERPs results for the observer, namely that the right fronto-central electrodes displayed a significant increase in activity only when the observer was going to interact with the human actor. This increased activity in frontal areas could reflect expectancy (anticipation), motivational or attentional factors (Meyer et al., 2011; Perry, Stein, & Bentin, 2011) relevant for the interaction. It has been shown that when participants are engaged in joint actions the partner's actions become more relevant (Frith & Frith, 2010; Schilbach et al., 2011) and need to be understood to produce an

adequate response. This increased attention could be triggered by frontal areas that have been involved in the processing of social cues during theory of mind, emotional or social representation tasks (Blakemore et al., 2003; Frith, 2007; Gallagher & Frith, 2004; Gallagher et al., 2000; Ramnani & Miall, 2003; Saxe, 2006). For example, the medial prefrontal cortex has been involved in the observation of social interactions (Gallagher & Frith, 2004; Iacoboni et al., 2004), the prediction of other's action (Ramnani & Miall, 2003), mentalisation and Theory of Mind processes (Blakemore et al., 2003; Gallagher et al., 2000), person and self-perception and second order representation of mental states (for a review see Frith, 2007). Saxe proposed a role for the medial prefrontal cortex in all situations including "triadic human representation", i.e., joint action situations (Saxe, 2006). Therefore, the implication of frontal areas could be associated to an increased expectancy and motivation to interact during the InteractionH conditions.

4.4. Effect of the role assignment in the interaction

Finally, our results provide evidence of both common and different processes between the actor and the observer that take place during the "Interaction" condition. Indeed, the common modulation of beta oscillations between the observer and the actor is indicative of a common process for both participants that could be related to a shared action representation. However, we also measured a certain asymmetry between the two participants' brain activities relative to their role assignment, and these differences were principally observed over frontal areas. These results are consistent with several hyperscanning studies (Babiloni et al., 2007; Dumas et al., 2012) that have explicitly investigated the interbrain relationship between a leader and a follower. Though these studies did not analyse the partners' brain activities independently, they have reported both symmetric couplings and an asymmetric relationship between the leaders and the followers. These twofold effects during social interactions (symmetric and asymmetric) may help to dissociate between common and individual actions, or they could be indicative of the different implications of the participants in the interaction.

4.5. Conclusion

In this experiment, EEG recordings of two interacting individuals allowed us to uncover modulations of activity in motor regions by the social context and the action's goals. Although modulations of the motor system occurred in both protagonists of the joint action, these modulations were dependent on the context ("Interaction" vs. "Observation") and role assignment (actor vs. observer). The recruitment of a fronto-parietal network during interactive contexts might therefore enable the construction of an "interactive loop" to build a common representation of action in both protagonists of an interaction.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at: <http://dx.doi.org/10.1016/j.neuropsychologia.2013.10.001>.

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