

# The neural response is heightened when watching a person approaching compared to walking away: Evidence for dynamic social neuroscience

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## ABSTRACT

The action observation network has been proposed to play a key role in predicting the action intentions (or goals) of others, thereby facilitating social interaction. Key information when interacting with others is whether someone (an agent) is moving towards or away from us, indicating whether we are likely to interact with the person. In addition, to determine the nature of a social interaction, we also need to take into consideration the distance of the agent relative to us as the observer. How this kind of information is processed within the brain is unknown, at least in part because prior studies have not involved live whole-body motion. Consequently, here we recorded mobile EEG in 18 healthy participants, assessing the neural response to the modulation of direction (walking towards or away) and distance (near vs. far distance) during the observation of an agent walking. We evaluated whether cortical alpha and beta oscillations were modulated differently by direction and distance during action observation. We found that alpha was only modulated by distance, with a stronger decrease of power when the agent was further away from the observer, regardless of direction. Critically, by contrast, beta was found to be modulated by both distance and direction, with a stronger decrease of power when the agent was near and facing the participant (walking towards) compared to when they were near but viewed from the back (walking away). Analysis revealed differences in both the timing and distribution of alpha and beta oscillations. We argue that these data suggest a full understanding of action observation requires a new dynamic neuroscience, investigating actual interactions between real people, in real world environments.

## 1. Introduction

In face-to-face daily social interactions, we constantly decipher and predict others' behaviour in order to produce appropriate responses. Research over the past 30 years has identified neural substrates supporting the processing of actions performed by other individuals in a wide sensorimotor brain network, including the occipital-temporal, parietal and premotor cortex, known as the action observation network (Grafton et al., 1996; Cross et al., 2009; Buccino et al., 2001; Caspers et al., 2010; Hari et al., 1998; Rizzolatti and Sinigaglia, 2010; Cattaneo and Rizzolatti, 2009; Hari and Kujala, 2009; Decety and Grèzes, 2006; Gallese et al., 2004). This action observation network represents observed action in the motor system of the observer (Rizzolatti et al., 2001; Sinigaglia, 2013). According to the theory of motor perception (Rizzolatti and Craighero, 2004), our implicit knowledge

about motor principles of movement is obtained by representing observed action in the same areas of the brain as those used for motor execution. However, the overlap in motor brain areas activated during both action observation and real execution concerns not only the kinematics of a given action, but also includes the goal of the action (Rizzolatti and Fogassi, 2014). Indeed, action observation has been proposed to play a key role in predicting others' action intentions or goals, and in the understanding of actions performed by other individuals (Schippers and Keysers, 2011; Hamilton, 2013; Buccino et al., 2001, 2004; Wheaton et al., 2004; Rizzolatti and Fogassi, 2014).

One aspect that we need to evaluate when interacting with others is whether the observed action is directed away from or towards us, allowing for cooperative interaction (for a review see Rizzolatti and Fogassi, 2014). In these terms, the direction of the observed action performed by other people with respect to the perceiver, becomes

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critically relevant. Our interactions, furthermore, are not always mediated by language, and in such circumstances, we need to select the relevant cues to understand the intentions of others in relation to our own goal. According to the sensorimotor communication model (Pezzulo et al., 2013, 2019) during interactions that are not mediated by language, the main source of information is represented by motor signals such as kinematics, sent by other individuals. According to this model, the action direction, the body posture and the kinematics all convey relevant information without the need for previous knowledge or a shared communicative code between individuals (see also Sebanz et al., 2006). The encoding of these motor aspects of an observed action can be activated under a large variety of circumstances in real life, with or without our awareness, and play an essential role in the understanding of others' intentions (Pezzulo et al., 2019; Sebanz et al., 2006). From this perspective the ability to predict other's actions in social interactions is suggested to be supported by the action observation network (di Pellegrino et al., 1992; Rizzolatti et al., 2001) and in particular by the posterior area of the parietal cortex (Bonini et al., 2010; Fogassi et al., 2005). Consistent with this view the role of the posterior parietal cortex in understanding intentions of others has been demonstrated during action observation in primates (Bonini et al., 2010; Fogassi et al., 2005) and in humans (Koul et al., 2018; Patri et al., 2020). These investigations have, however, been mainly carried out using recorded videos or upper limb movements. In real world scenarios, by contrast, we predict and understand others' behaviour by looking at live whole-body motion, which include the simultaneous processing of complex bodily cues, such as direction and whole-body kinematics of the action, embedded in a context. To the best of our knowledge, there are no studies investigating how the direction of an observed live whole-body action might modulate brain activity in a perceiver.

Aside from the direction of the observed action, another feature that might play a relevant role during the observation of others' actions is the position in space of a moving agent with respect to the observer. Indeed, research with monkeys has shown that action observation network activation is modulated by the distance of the observed moving agent, and that 'mirror' neurons are selectively activated when the observed action is performed in the monkey's peripersonal space (Caggiano et al., 2009; Bonini et al., 2014). Generally, peripersonal space designates the immediate space surrounding the body, in which we can directly interact with objects or other agents, whereas extrapersonal personal space designates the space beyond our reach (Holmes and Spence, 2004; Rizzolatti et al., 1997; di Pellegrino and Ládavas, 2015). The processing of the peripersonal space and our ability to act in it is shaped by multiple factors, such as the presence of a tool (Canzoneri et al., 2013), the energetic cost associated with the task (Witt, 2011), and the goal of the intended action (Wamain et al., 2016). To date, studies of peripersonal and extrapersonal spaces in humans have been focused mainly on cognitive processes related to the perception of manipulable objects (Culham et al., 2008; Proverbio, 2012). However, in real-world life, we not only interact with objects, but we also interact with other individuals, performing movements that involve the whole body. Consequently, a key aim of the current study was to examine cortical activation in the context of naturalistic whole-body movements.

The presence of other individuals has been investigated in social psychology studies, according to which invasion of the 'personal space' surrounding the body by other individuals causes private discomfort (Iachini et al., 2014; Bogdanova et al., 2021). By contrast, however, few studies have considered the 'social' aspect of the proximity of other conspecifics to our peripersonal reachable space for the purpose of action interaction (for a recent review see Bogdanova et al., 2021). For example, Fini et al. (2014, 2015) found that the mere presence of another body in the visual scene extended the perceptual judgments of the 'near' space from an egocentric perspective, and Iachini et al. (2014) showed that only the presence of other conspecifics, but not objects, reduced the perception of the extent of the peripersonal space. Similarly, Teneggi et al. (2013) showed that the mere presence of another

individual, but not of an artificial stimulus (i.e., a mannequin) in the extrapersonal space, narrows the boundary of the peripersonal space, suggesting that the boundary of one's peripersonal space representation can be shaped by the presence of others in social interactions. Additionally, Teneggi and colleagues showed that when participants interacted cooperatively (compared to a condition in which they were interacting non-cooperatively), the peripersonal space of the self, merged with the other's peripersonal space, suggesting that the representation of the peripersonal space is not only influenced by the presence of other individuals, but also by the nature of the social interaction.

As far as we are aware, to date no studies have shown how the direction of an observed agent, and the distance of that active agent with respect to the observer, might modulate the cortical activity during action observation. As mentioned above, one reason for this is that action observation neuroimaging studies tend to use videos, rather than live actions, and hence the effect of proximity of the observed agent could not be studied. Thus, the objective of the present study was to investigate whether the direction and distance of a passive observer with respect to a natural agent moving towards and away from the observer would modulate the cortical rhythms commonly associated with action observation (alpha 8–12 Hz and beta 13–25 Hz oscillations). Previous studies of action observation have revealed event-related desynchronization (i.e., suppression of spectral power) over occipital, parietal, and sensorimotor brain areas (Arnstein et al., 2011; Avanzini et al., 2012; Muthukumaraswamy et al., 2004; Babiloni et al., 1999). Consequently, here we predicted that alpha and beta oscillations recorded during live whole-body action observation would be modulated by the direction of the agent with respect to the observer. Additionally, we expected that oscillations in the alpha and beta frequency bands would be modulated by the distance of the agent from the observer, with a stronger suppression when the moving agent is close to the observer compared to when they are far away from the observer. Such modulation would indicate that the action observation network in the brain is particularly sensitive to the proximity of the observed agent.

In the present study we used a natural walking task, which in this case meant that participants observed a human agent walking towards or away from them. As pointed out by Angelini et al. (2018), a general bias of action observation investigations has been to focus on upper limb body effector actions, whereas lower limb movements have been typically less explored. This is perhaps not surprising considering that the direct evidence for the mirror neuron network is largely based on reaching and grasping movements. The focus on upper limb movements may have arisen due to an assessment bias, caused by the inadequacy of methodologies for measuring dynamic executed actions of people moving around compared to observed lower limb actions. However, as discussed above, observation of movements that involve an agent approaching or walking away from the observer are critically relevant for perceiving the impending interaction with others (e.g., Rizzolatti and Fogassi, 2014), akin to the basic survival principle of working out whether a lion is a threat because it is walking towards you, rather than away. As far as we are aware, where previous studies of action observation have involved walking, the paradigms involved participants viewing videos of human (Cochin et al., 1998), or animated pictures (Ulloa and Pineda, 2007; Zarka et al., 2014) of walking, rather than the observation of actual walking made by an agent present in the same room as the observer. As suggested by previous literature (for a review see Cevallos et al., 2015), experiments involving ecological valid stimuli (e.g., observing a human actor instead of animated pictures) might have an important role in revealing action perception mechanisms, not least because brain responses during action observation of videos may be less consistent compared to live actions (Järveläinen et al., 2001; Reader and Holmes, 2016; Prinsen and Alaerts, 2019; Rizzolatti and Fogassi, 2014).

To date, only one recent study examined action observation of live action walking (Kaneko et al., 2021). However, in that study, the actor walked on a treadmill and only one observer point of view (lateral perspective) was investigated. By contrast, in the present study, we

investigated how action observation network activity is modulated by the passive observation of an actor walking towards or away from the observer. In Kaneko et al.'s treadmill study (2021), it was found that action observation of walking modulates both alpha and beta oscillations over sensorimotor areas, but only when participants were requested to observe and simultaneously imagine the movement (kinesthetic motor imagery), compared to passive observation. These modulations were found to be coupled with the observed gait cycle phases. Therefore, in the present study we also investigated whether coupling between the observed gait cycle and cortical oscillations in the alpha and beta frequency bands is dependent on the direction of the action with respect to the observer.

## 2. Methods

### 2.1. Participants

Twenty healthy participants (18 female; age range = 18–44 years; mean age = 21.4 years, SD = 5.6 years) took part in the experiment. Due to the presence of prominent artifacts in EEG recordings, the data of two participants were excluded. The remaining data of eighteen subjects (18 female; age range = 18–44 years; mean age = 21.67 years, SD = 5.9 years) were used in the analysis reported. All the participants had no history of neurological disorder. Before starting the experiment, all the participants gave their written informed consent. Ethical approval was provided by the Research Ethics Panel of the University of Stirling.

### 2.2. Material and procedure

EEG data were continuously recorded using a 32 channels mobile EEG amplifier (ANT-neuro, Enschede, The Netherlands). Participants completed 40 trials for each condition. During the observation of walking conditions, participants stood 1 m away at the head of a carpet, watching the walking actions of a model walking up and down. The observed model was a female (M.M.) and walked in two directions: towards the participant and away, performing six steps on the 6 m carpet in each trial for a total of 80 trials divided in two blocks. The model wore the insoles of the Pedar-x System (novel.de, Munich, Germany), a bluetooth pressure distribution measuring system for monitoring local loads between the foot and the shoe, which allowed the extraction of temporal parameters of gait for this study. Each insole was connected to a controller-box attached to the model's waist with a belt. An Arduino board connected to the TTL port of the EEG amplifier and to the sync-box of the Pedar-x was used to synchronize the recording of the two devices. At the beginning of each recording, a pulse was sent from the Pedar-x to the EEG in order to temporally align the two recordings. The onset/end of each trial was defined using the Pedar-x recording to timestamp the EEG data. The start of the trial was defined by the first step taken by the model on the carpet, recorded by the Pedar-x foot pressure insoles system. At the end of the path, the model took a step off the carpet, which corresponded to the end of the trial. Between each trial, the model turned outside the carpet and waited a few seconds (1–2 s) before starting a new walking path. Trials in which the model walked towards the observer (action observation (AO) of walking Towards condition, 40 trials) were separated offline from trials in which the model walked away, and the observer viewed the back of the model (AO of walking Away condition, 40 trials) in order to compare the two directions in the following analysis. Fig. 1 shows the two experimental conditions.

The conditions of this study were nested and counterbalanced with the conditions of another study, planned to be reported elsewhere, and included the following other conditions: Actual Execution of walking (in which the participant themselves walked up and down the carpet), Motor Imagery of walking (in which the participant imagined walking up and down the carpet) and Mental Counting (in which the participant counted to six paced by a metronome). None of these other conditions can be analysed with regards to the parameters of interest in this study

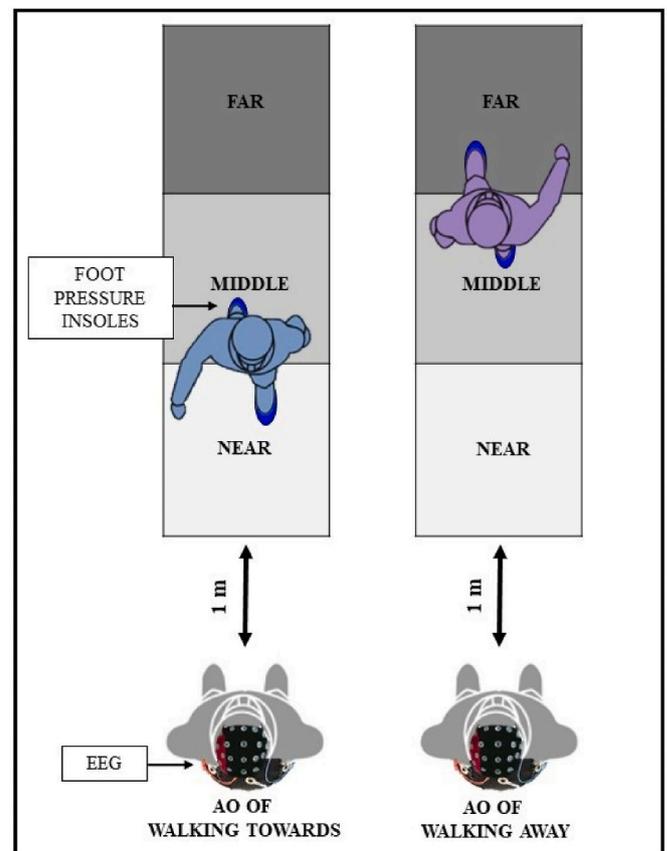


Fig. 1. Representation of the two experimental conditions.

(distance and direction), as they are part of a separate study, and are therefore not included in this manuscript.

### 2.3. EEG acquisition and processing

EEG data was continuously recorded from 32 Ag/AgCl electrodes caps connected to a portable amplifier (ANT-neuro, Enschede, The Netherlands) at a sampling rate of 500 Hz and bandpass filtered at 0.01–250 Hz. Electrodes were positioned according to the International 10–20 system: FP1, FPz, FP2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, M1, T7, C3, Cz, C4, T8, M2, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, POz, O1, Oz, O2, with AFz electrode as ground and CPz electrode as reference. The electrode impedances were reduced below 5 k $\Omega$  before the recording. EEG data analyses were performed using custom scripts written in MATLAB 2019 (The MathWorks) incorporating the EEGLAB toolbox (Delorme and Makeig, 2004). Data from the mastoid channels (M1 and M2) were removed from the analysis, and all remaining EEG data was filtered using a 0.1 Hz–40 Hz bandpass filter. EEG channels with prominent artifacts were automatically selected (kurtosis >5 SDs) and interpolated, and all channels were then re-referenced to the average. The choice of a common average reference was determined by the heavy presence of noise in the mastoid channels (M1 and M2), which were removed. Data were downsampled to 250 Hz and an extended infomax Independent Component Analysis (ICA, Makeig et al., 1995) was performed to identify and remove non-brain signals. Brain-related-ICs were identified using the IClab plugin (Pion-Tonachini et al., 2019). Components exceeding a 90% probability of being eye, muscle, heart, line noise, and channel noise were rejected. Only brain ICs with dipoles located inside the head and a residual variance lower than 15% were kept. An average of (mean  $\pm$  SD)  $7.19 \pm 1.6$  ICs across conditions was retained for the analysis.

2.4. Event related spectral perturbation (ERSP) analysis

EEG data were segmented in 4.5s epochs from -500 ms before and 4000 ms after the start of the trial (time 0). Single channel spectrograms were time warped to the median latency of the end of the trial across participants for each condition, which corresponded to 3056 ms for the AO of walking towards condition and 3258 ms for the AO of walking away condition. As the design included naturalistic observation of walking, and the participants observed a model which was continuously walking the path in both directions, we did not have a pre-stimulus baseline as the model was always present in the visual scene. Therefore, event related spectral perturbation (ERSP) was extracted using a Fast Fourier Transform (FFT), computed as the mean difference between single trial log spectrograms for each channel and each participant across conditions and the mean power of the overall trial (from 0 to

4000 ms). Middle line single channel time frequency spectrograms (Cz, Pz, POz, Oz; Fig. 2) were visually inspected to identify relevant changes in the spectral power. In a data-driven manner, plots suggested two main spectral changes from baseline (event related desynchronization and event related synchronization) occurring in a range from 8 to 25 Hz. We defined the two frequency bands of interest namely alpha (8–12 Hz) and beta (13–25 Hz).

2.5. Statistical analyses

Alpha and beta oscillations were analysed by pooling the activity of neighbouring electrodes in relevant regions of interest (ROI) over sensorimotor (FC1, FC2, C3, C4, CZ, CP1, CP2) and parietal-occipital (P3, P4, PZ, O1, O2, OZ, POZ) areas. Both AO conditions were examined in two separate statistical analyses, described below.

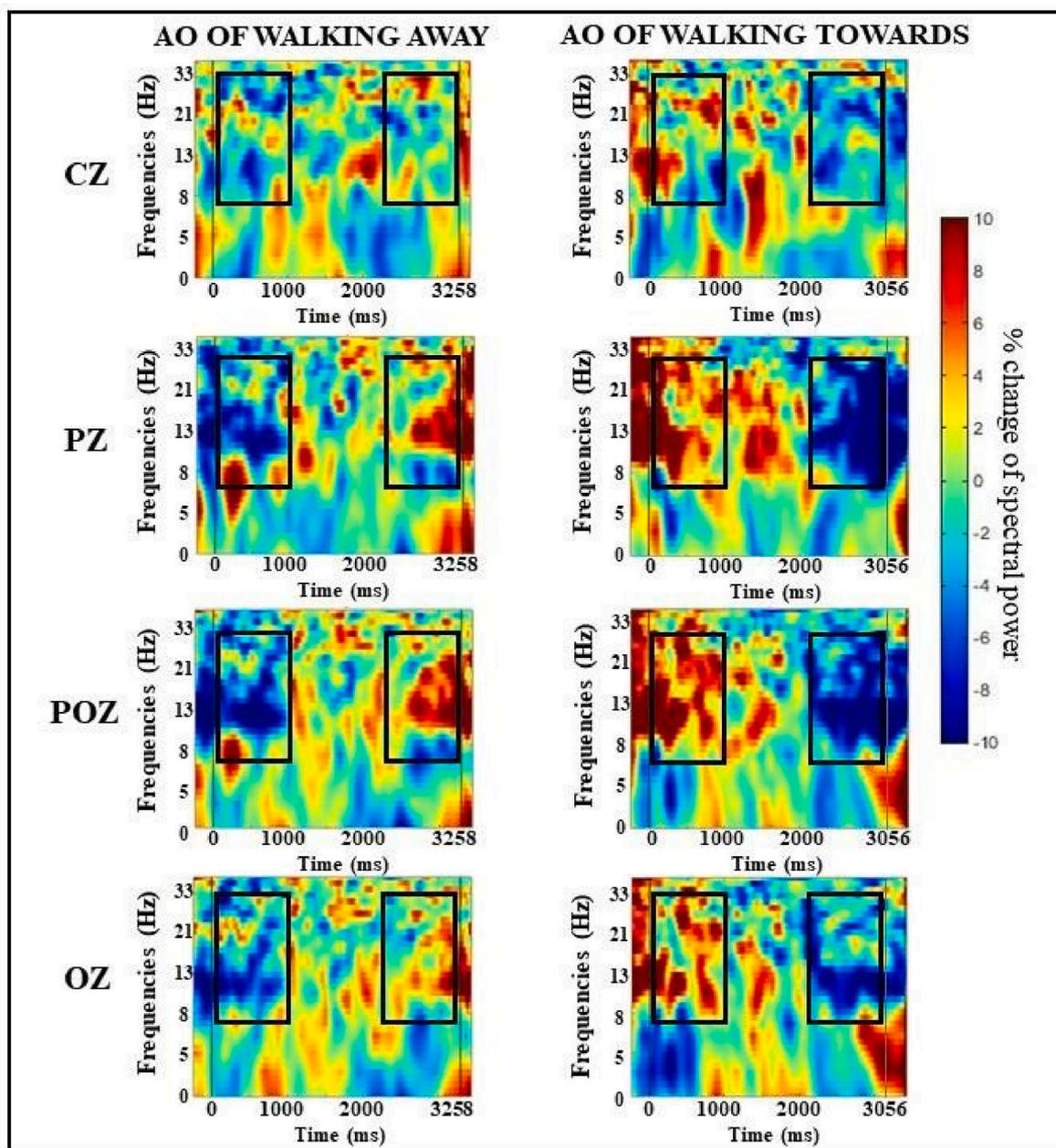


Fig. 2. Time-frequency spectrograms of midline channels (in order Cz, Pz, POz, Oz) across conditions. The onset of the trial is at 0 ms. Time warped median latencies are indicated by the grey lines (3258 ms for the AO of walking Away condition and 3056 ms for the AO of walking Towards condition).

- (a) Effect of direction and distance. In order to investigate the effect of both the direction of the action with respect to the observer and the distance of the model from the observer on cortical activation in the alpha and beta frequency bands during AO, the overall length of each time-warped epoch was divided in 3 distances: the near, the middle and the far distances. The distance of the model with respect to the observer was operationalised a posteriori, dividing the length of the overall trial in 3 time windows which matched the position of the model with respect to the observer. Significant changes in the spectral power were assessed with  $2 \times 3 \times 2$  Repeated Measures ANOVAs with Condition (AO of walking Away, AO of walking Towards), Distance (near, middle, far) and ROIs (central, parietal-occipital) as within subject factors, separately for each frequency band.
- (b) Cortical modulation depending on gait phases. In order to investigate whether cortical activation during AO is modulated by the gait phases, the model's heel strike latencies were extracted from the Pedar-x step analysis output and were used to analyse the EEG data of the participants (observers). To explore whether alpha and beta modulations were related to the direction of the observed gait cycle, a gait cycle performed by the model (i.e., 3 consecutive heel strikes) was selected during the first time window of AO conditions (i.e., at the beginning of the trial). EEG data were segmented into epochs relative to the observed first heel strike (time 0) and single trial spectrograms were time warped to the median of the second and the third consecutive heel strike. Each gait cycle was then divided in percentage following the standard division of Perry and Davis (1992): stance phase (0–60%) and swing phase (60–100%). These phases were subdivided into: loading response (0–10%), mid-stance (10–30%), terminal stance (30–50%) and pre-swing (50–60%) for the stance phase; and initial swing (60–73%), mid-swing (73–87%) and terminal swing (87–100%) for the swing phase. ERSP was computed for each gait phase as the difference between each log spectrogram and the mean of the baseline (mean activity of the overall gait cycle) for each channel and participant within each condition. We assessed through two separate  $2 \times 7 \times 2$  Repeated Measures ANOVAs with Condition (AO of walking Away and AO of walking Towards), Gait Phase (loading response, mid-stance, terminal stance, pre-swing, initial swing, mid-swing, terminal swing) and ROIs (central, parietal-occipital) as within subject factors, separately for each frequency band.

Statistical analyses were performed using SPSS statistical package. For all analyses, the Greenhouse – Geisser correction was applied whenever the sphericity assumption was violated and post-hoc paired sample t-tests were adjusted using Bonferroni correction to investigate significant main effects and interactions.

### 3. Results

As can be seen in Fig. 2, which illustrates the time frequency spectrograms of Cz, Pz, POz, Oz channels, the two AO conditions showed a distinct pattern of power decrease and increase. The main differences appear to be confined to the extremities of the epoch (areas highlighted in the black rectangles in Fig. 2) in which the model was near or far from the observer, indicating an effect related to the proximity of the moving agent. Furthermore, the two patterns appear to be reversed depending on the direction of the observed action (highlighted in the black rectangles in the plots in Fig. 2).

#### 3.1. Effect of direction and distance

##### 3.1.1. Alpha

The ANOVA revealed a main effect of Distance [ $F(1, 17) = 4.859, p = .016, \eta_p^2 = 0.222$ ] with an overall stronger decrease of alpha power

when the observer was near to the model compared to when the model was in the middle of the walk ( $t(17) = 2.855, p = .033$ ) and a marginally significant difference when the model was near compared to far ( $t(17) = 2.855, p = .066$ ). There was no significant difference in alpha modulation between the middle and far distance ( $p = .872$ ).

A main effect of ROIs [ $F(1, 17) = 6.139, p = .049, \eta_p^2 = 0.209$ ] showed an overall stronger decrease of alpha power over parietal-occipital areas compared to central brain areas.

A significant interaction between ROIs and Distance [ $F(1, 17) = 4.383, p = .020, \eta_p^2 = 0.205$ , see Fig. 3, panel (a)] showed a significantly stronger decrease of alpha power over parietal-occipital compared to central areas when the model was near to the observer ( $t(17) = 3.382, p = .012$ ), but showed no significant differences for the middle and far distances ( $p = .596$ ).

##### 3.1.2. Beta

The ANOVA revealed a main effect of Distance [ $F(1, 17) = 9.293, p = .001, \eta_p^2 = 0.353$ ] with an overall stronger decrease of beta power when the model was near to the observer compared to when the model was in the middle ( $t(17) = 3.415, p = .009$ ) and far from the observer ( $t(17) = 4.056, p = .003$ ). There was no significant difference in beta modulation between the middle and the far distance ( $p = .279$ ) (see Fig. 3, panel (b)).

A significant interaction between Condition and Distance [ $F(1, 17) = 5.103, p = .016, \eta_p^2 = 0.231$ , see Fig. 4] showed that a stronger decrease of beta power occurred when the model was near and walking towards the observer (i.e., the model facing the observer) compared to when the model was near and walking away from the observer (i.e., the model showing her back to the observer), ( $t(17) = 2.713, p = .035$ ). Post-hoc paired sample t-tests did not reveal any statistically significant difference between beta modulation across the two directions when the model was in the middle ( $p = .264$ ) compared to when far ( $p = .060$ ).

A significant interaction between Condition and ROIs [ $F(1, 17) = 8.424, p = .001, \eta_p^2 = 0.331$ ] showed a significant stronger decrease of beta power over parietal-occipital areas when the model was walking towards the participants compared to the condition in which the model was walking away ( $t(17) = 2.189, p = .043$ ). In the condition of AO of walking Away, there was a stronger decrease in beta power over central areas compared to parietal-occipital areas ( $t(17) = 2.816, p = .012$ ).

A significant interaction between ROIs and Distance [ $F(1, 17) = 10.083, p = .001, \eta_p^2 = 0.372$ , see Fig. 3, panel (b)] showed a significant stronger decrease of beta power over parietal-occipital areas compared to central when the model was near to the observer ( $t(17) = 3.539, p = .009$ ) and a stronger decrease over central areas compared to parietal-occipital areas when the model was far from the observer ( $t(17) = 3.539, p = .015$ ). There was no significant difference in beta modulation over central and parietal-occipital areas when the model was in the middle distance ( $p = .806$ ).

#### 3.2. Cortical modulation depending on the direction of gait phase/cycle

##### 3.2.1. Alpha

Fig. 5 shows alpha modulation during the gait cycle across the two different conditions. As we can see from the graph, alpha modulation presents an inverse pattern depending on the direction of the observer with respect to the direction of the gait cycle of the model. Furthermore, the graph indicates that alpha modulation is stronger in the condition in which the model was walking towards the observer. The ANOVA did not reveal any significant main effect of Condition ( $p = .730$ ) or Gait Phase ( $p = .209$ ) or ROIs ( $p = .716$ ). A significant two-way interaction between Condition and Gait Phase [ $F(1, 17) = 3.206, p < .05, \eta_p^2 = 0.159$ ] indicated that, averaged across central and parietal occipital ROIs, differences in alpha modulation occurred during the first gait cycle of both AO conditions. Paired-sample post-hoc t-tests showed a significantly stronger decrease of alpha power in AO of walking Towards compared to AO of walking Away during the mid-stance, just before the second heel

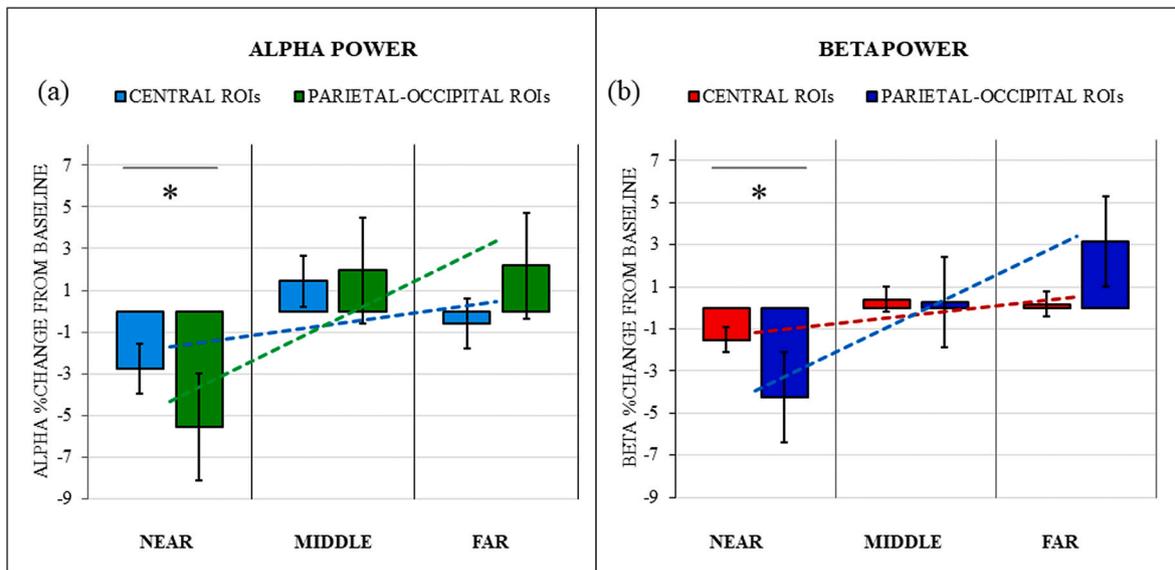


Fig. 3. Significant two-way interactions between ROIs and Distance as indicated by the ANOVA. (a) Alpha percentage change from the baseline across ROIs and Distance (with relative standard error bars and dashed linear trendline). (b) Beta percentage change from the baseline across ROIs and Distance (with relative standard error bars and dashed linear trendline).

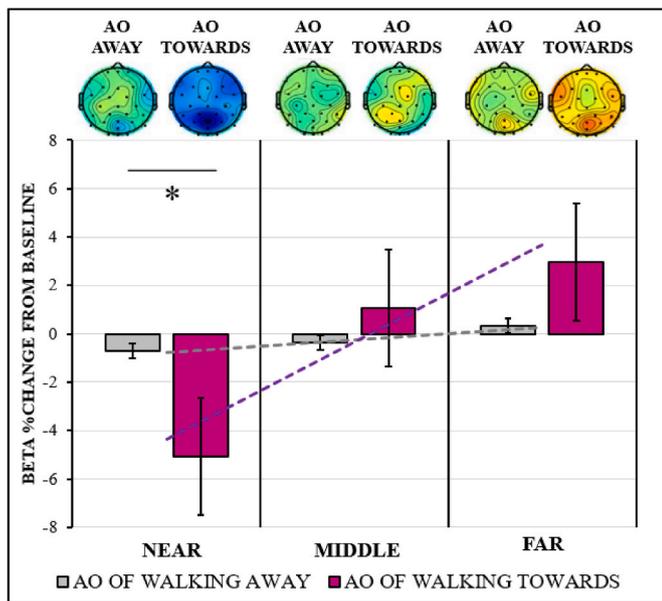


Fig. 4. Significant two-way interaction between Condition and Distance as indicated by the ANOVA. Specifically, the graph shows beta percentage change from the baseline averaged across central and parietal-occipital ROIs, across Conditions and Distance (with relative standard error and dashed linear trendline). Scalp topographies of beta activity for each condition (AO of walking Away; AO of walking Towards) across distances (near, middle, far) are shown on top of the relative bars. As can be seen from the trendlines, there was a weak modulation of beta power when the model was moving away from the observers. On the contrary, there was a strong modulation when the model moved towards the observers, approaching them.

contact ( $t(17) = 2.823, p = .035$ ). During the pre-swing and initial swing (just after the second heel contact) a significantly stronger decrease of alpha power occurred in AO of walking Away compared to AO of walking Towards (pre-swing:  $t(17) = 2.679, p = .042$ ; initial swing:  $t(17) = 2.504, p = .028$ ). The ANOVA did not reveal any other significant interaction between factors ( $p > .05$ ).

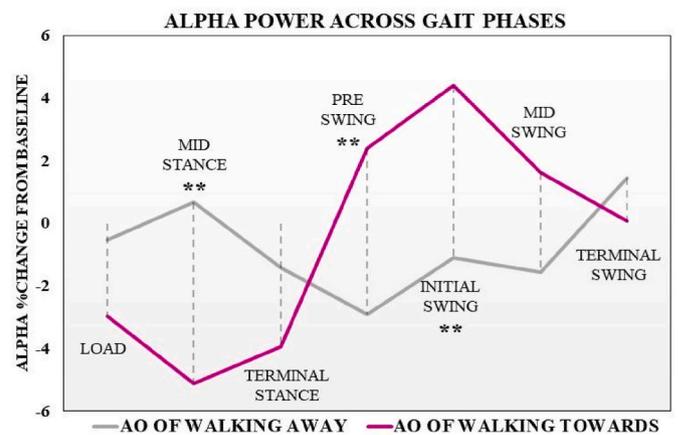


Fig. 5. Alpha percentage change from the baseline averaged across central and parietal-occipital ROIs, across AO conditions and gait phase. Dashed lines represent the alignment between time points of the different gait phases across two conditions, respectively defined: load (0–10%), mid-stance (10–30%), terminal stance (30–50%), pre-swing (50–60%), initial swing (60–73%), mid-swing (73–87%) and terminal swing (87–100%).

### 3.2.2. Beta

The ANOVA did not reveal significant main effects of Condition ( $p = .562$ ), Gait Phase ( $p = .818$ ) or ROIs ( $p = .304$ ). Additionally, the ANOVA did not reveal any significant interactions between factors ( $p > .05$ ).

## 4. Discussion

This study establishes that during the observation of a live agent walking away or towards the observer, the action observation network is sensitive to both the direction of the action and the distance of the observer relative to the moving agent. By examining the time course and distribution of the cortical activation associated with action observation, we revealed distinct patterns of modulation in the alpha and the beta frequency bands depending on the distance and the direction of the observed action. This dissociation between the two frequencies suggests that alpha is tuned to spatial and visual information, such as a person's

proximity, whereas beta is tuned to those situations in which we are approached by other people when moving in the real world environment.

The analysis revealed that alpha recorded during action observation was modulated only by the distance of the model from the observer, demonstrated by a stronger decrease of power over parietal-occipital brain areas when the model was nearest to the observer compared to further away, regardless of direction. This pattern is analogous to observations in previous primate research, which has shown that mirror neurons of the brain area F5 responded selectively to object-directed actions performed in the peripersonal space of the monkey (Caggiano et al., 2009; Bonini et al., 2014). Similarly, human EEG studies, investigating peripersonal and extrapersonal space, reveal alpha suppression of power over parietal areas when participants estimate the reachability of manipulable objects placed within compared to outside their peripersonal space (without making overt action) (Wamain et al., 2016). Furthermore, suppression of occipital alpha and beta power has been associated with the processing of the saliency of objects placed in the visual scene (Vanni et al., 1997), the anticipation of forthcoming stimuli (Bauer et al., 2014; Cravo et al., 2013) and increased general excitability (Schubring and Schupp, 2019). These data are also supported by brain imaging studies which showed that the parietal-occipital brain areas are involved in the encoding of objects placed within the reachable space of the hand (Gallivan et al., 2009). Taken together these findings suggest that brain activation is moderated by the location of an object in the space relative to the subject, as well as being enhanced when the object is within peripersonal space and the subject can directly interact with the object (Wamain et al., 2016). Building on these earlier data, the present research findings demonstrate that the proximity of a moving agent approaching the peripersonal space of an observer moderates neural activity within the action observation network.

One important outcome of the current study is further clarification of the circumstances under which the action observation network operates. In the present study design, the movement of the model did not imply the use of any object or any explicit goal-directed behaviour towards the subject, thus our results suggest that even in the absence of an object or an explicit intention of an interaction, alpha and beta oscillations over parietal-occipital areas are selectively modulated by the proximity of others. As previously shown by a large body of evidence, the parietal-occipital cortex is part of the action observation network involved in the representation of space for action (Colby and Goldberg, 1999; Husain and Nachev, 2007), in motor planning (Andersen et al., 1997; Andersen and Cui, 2009; Buneo and Andersen, 2006; Busan et al., 2009), in the action observation of object and non-object directed actions (Iacoboni et al., 2004; Evangelidou et al., 2009; Buccino et al., 2001) and in processing social information during action observation (Tunik et al., 2007; Pobric and Hamilton, 2006). The present data furthermore suggest that when the model is far away, an increase of power occurs both in the alpha and in the beta bands, suggesting a reverse oscillatory pattern compared to when the model is near to the observer. We speculate that this distinctive pattern of activity suggests the involvement of attentional processes, visible in the relative increase of alpha spectral power when the agent is farther away from the perceiver, when attentional demands are more likely to be reduced (Foxye and Snyder, 2011; Talsma et al., 2010). These results are consistent with the accounts that suggest alpha power is inversely related to effortful attentional processing, such that increased power reflects a reduction in cognitive load (Foxye et al., 1998; Vanni et al., 1997; Van Diepen et al., 2019). At least in part, however, the apparent increase in alpha power visible during the moment in which the model is farther away from the perceiver might also reflect the fact that the baseline was computed over the entire epoch. As can be seen in Fig. 3, alpha power values relative to the baseline are negative when the model is near the observer and positive when the model is farther away from the observer. Regardless, our results support the view that alpha oscillations over parietal-occipital areas reflect a mechanism which underlies the processing of relevant

visual and spatial information of the observed action, such as the distance of another agent from the observer.

Crucially, the present results demonstrated that, differently from alpha, oscillations in the beta frequency band are modulated not only by distance, but also by the direction of the observed action. The analysis revealed a stronger decrease of beta spectral power over parietal-occipital brain areas when the model was facing the participant (AO of walking towards) compared to when observed walking from the back (AO of walking away). Furthermore, beta power suppression was more prominent during approach when the model was near and walking towards the participant. Beta oscillations have previously been shown to be an index of the activity of the action observation network in humans (Cochin et al., 1998; Hari et al., 1998). The direction of the action (but not distance) was previously considered in an EEG study of action observation of video recorded meaningless hand gestures by Kilner and colleagues, which showed that beta was modulated by the direction of the model in respect to the observer (Kilner et al., 2009). Indeed, Kilner et al. (2009) found a stronger beta power suppression over sensorimotor areas only when the model was facing the participant, compared to in a condition in which the model was facing away. This finding has been interpreted as a modulation in visuospatial attention driven by the social relevance of the observed action. Kilner et al. (2006) described a similar pattern in the alpha frequency band over parietal areas, which was modulated by the side of the screen in which the movement occurred, suggesting that alpha oscillations might reflect visual and spatial relevant information of the observed movements. However, our results partially differ from Kilner et al. (2009) with regards to the modulation of beta frequency band, as we found that beta power suppression was stronger over parietal and occipital areas (compared to central brain areas) and this modulation was sensitive to the walking direction. Conversely, Kilner et al. (2009) found beta suppression over sensorimotor areas when the model was facing the participant. The divergence between the present results and the findings of Kilner et al. (2009) might be due to the difference in task, which in the present study involve the live action of walking toward a person, whereas in Kilner et al. (2009) participants observed a video of a standing person performing arm movements. Thus, in the present study the relevance of a real-world dynamic action directed towards the participants might have driven the different brain activations. More broadly, this finding highlights that, in order to understand cortical processes during action observation, it is necessary to investigate whole-body dynamic movements, as they are in real life.

The current finding is important because it demonstrates that the two cortical rhythms have partially distinct roles during action observation. In a further dissociation, we found that only oscillations in the alpha frequency band were modulated by the gait phases of the observed model. It has been shown that cortical activity in the alpha and in the beta frequency bands over the sensorimotor cortex is locked to gait phases (Gwin et al., 2011; Seeber et al., 2014; Wagner et al., 2012). A similar modulation has been reported during the simultaneous observation and imagination of treadmill walking (Kaneko et al., 2021; to our knowledge the only other study that integrated brain signals of the observer with the live movements of the observed). Indeed, in their recent study Kaneko et al. (2021) reported beta power suppression at the stance and mid-swing phases, and alpha and beta power increases at the terminal stance, when participants were required to imagine walking and observe a model walking on a treadmill from the lateral perspective. The data reported in the present study suggest that only oscillations in the alpha, but not in the beta frequency band, are modulated by the gait phases during action observation, and that this modulation depends on the direction of the action performed by the model. These results are consistent with evidence showing that beta power suppression, typically observed during movement execution, is not associated with the effector (Salmelin et al., 1995), movement type (Wheaton et al., 2009; Stančák and Pfurtscheller, 1997) or to movement complexity (Leocani et al., 2001), suggesting that rather than reflect a pure motor process, beta

power suppression might index cognitive aspects of motor control (Kilavik et al., 2013). Conversely, in the present study alpha oscillations were modulated by gait phase. This result is in line with the findings of Kaneko et al. (2021), showing that alpha and beta power modulation are coupled with gait phases, but only when action observation was performed concurrently with the kinaesthetic imagery of walking (the imagination of the ‘feeling’ of walking without actually doing it) and not during action observation alone or during resting state. In the present study, participants were instructed only to observe, but not simultaneously imagine, the movement. Therefore, as the task only involves action observation, and not the imagination of walking, which might enhance the motor activation, we found that only alpha oscillations were modulated by gait parameters, most likely reflecting the processing of visual and temporal gait related information (see Liang et al., 2018).

#### 4.1. Implications and conclusion of the present study

Due to the novelty of employing both a dynamic (mobile) brain imaging method and a novel experimental design, this study was able to significantly advance our understanding of the cognitive and neural processes supporting observation of real-world action. The live presence of the moving agent meant that we could examine the neural correlates of the dynamic features of action observation, where the moving agent was closer or further away from the observer. We showed that alpha and beta suppressions were stronger when actions were performed near to the observer - close to the participant’s peripersonal space - compared to actions performed far away from the observer. It is also notable that earlier studies in non-human primates have shown that the action observation network is activated when the observed action is performed in the peripersonal compared to extrapersonal space (Caggiano et al., 2009; Bonini et al., 2014), providing support for the claim that the distance of another person modulates the activation of brain areas included in the action observation network.

Furthermore, our data showed that in real world action observation of a person approaching or walking away, the direction of the observed action is tracked by changes in parietal brain area beta oscillations, as we found a stronger beta suppression of power over parietal-occipital brain areas when the model is facing the participant. Previously, action observation investigations used only videos, not live actions, and furthermore showed only part of the body when displaying movements usually of the upper limb. Here, by contrast, we used a live action involving the actual presence (and therefore whole body) of the moving agent, typical of real life social interactions. The fact that we found that in live action observation the action observation network responds to both direction and proximity, highlights the need to examine this kind of real life interaction to fully characterise action observation. The present findings suggest that in daily life action observation, the observer is monitoring and assessing multiple sources of information from the observed action, including the orientation of the agent moving towards the observer and the distance between the observer and the approaching agent.

Finally, our study suggests that alpha and beta oscillations are dissociable, playing distinct roles during action observation. Previous studies have not typically separated the two bands, describing the two rhythms together as the index of a general mechanism involved in the regulation of inhibition/activation of cortical visual, somatosensory, and sensorimotor brain areas (Pfurtscheller & Lopes da Silva, 1999). However, recent evidence points towards different functional and topographical distribution for alpha and beta activity (Stolk et al., 2019). Indeed, alpha rhythm has been proposed to signal the allocation of attention toward relevant task-related information (Foxe and Snyder, 2011; Brinkman et al., 2014; Babiloni et al., 2006), while beta oscillations are thought to be related to motor activation (Ronnqvist et al., 2013). Our results provide additional support for these accounts (e.g., see Kilner et al., 2009) and demonstrate that whereas alpha oscillations signal the brain response to salient visual aspects of an observed action

(i.e. the presence of an agent near to our peripersonal space), beta oscillations reflect processing that filters and discriminates between relevant and possibly social motor information of action performed by others (i.e., the direction of the interaction).

Overall, the changing pattern of brain oscillations revealed in the current study provides neural evidence for the significance of interactions between people, and highlights that in order to understand social interactions we need to investigate dynamic real-world behaviour. To do this, it is necessary to employ methodological approaches suited to a new dynamic social neuroscience, such as mobile neuro-imaging techniques, bringing experimentation into the real world.

#### Author contributions

M.M., D.K., M.G.E., D.I.D. and M.I. conception and design of the study; M.M. performed the experiment; M.M. analysed data; M.M., D.K., M.G.E., D.I.D. and M.I. interpreted results and all authors contributed to the manuscript.

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#### Declaration of competing interest

The authors declare no conflict of interest or relationship, financial or otherwise.

#### Data availability

Data will be made available on request.

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#### References

- Andersen, R.A., Snyder, L.H., Bradley, D.C., Xing, J., 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu. Rev. Neurosci.* 20 (1), 303–330.
- Andersen, R.A., Cui, H., 2009. Intention, action planning, and decision making in parietal-frontal circuits. *Neuron* 63 (5), 568–583.
- Angelini, M., Fabbri-Destro, M., Lopomo, N.F., Gobbo, M., Rizzolatti, G., Avanzini, P., 2018. Perspective-dependent reactivity of sensorimotor mu rhythm in alpha and beta ranges during action observation: an EEG study. *Sci. Rep.* 8 (1), 1–11.
- Arnstein, D., Cui, F., Keysers, C., Maurits, N.M., Gazzola, V., 2011.  $\mu$ -suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *J. Neurosci.* 31 (40), 14243–14249.
- Avanzini, P., Fabbri-Destro, M., Dalla Volta, R., Daprati, E., Rizzolatti, G., Cantalupo, G., 2012. The dynamics of sensorimotor cortical oscillations during the observation of hand movements: an EEG study. *PLoS One* 7 (5), e37534.
- Babiloni, C., Carducci, F., Cincotti, F., Rossini, P.M., Neuper, C., Pfurtscheller, G., Babiloni, F., 1999. Human movement-related potentials vs desynchronization of EEG alpha rhythm: a high-resolution EEG study. *Neuroimage* 10 (6), 658–665.
- Babiloni, C., Vecchio, F., Bultrini, A., Luca Romani, G., Rossini, P.M., 2006. Pre- and poststimulus alpha rhythms are related to conscious visual perception: a high-resolution EEG study. *Cerebr. Cortex* 16 (12), 1690–1700.
- Bauer, M., Stenner, M.P., Friston, K.J., Dolan, R.J., 2014. Attentional modulation of alpha/beta and gamma oscillations reflect functionally distinct processes. *J. Neurosci.* 34 (48), 16117–16125.
- Bogdanova, O.V., Bogdanov, V.B., Dureux, A., Farne, A., Hadj-Bouziane, F., 2021. The Peripersonal Space in a Social World. *Cortex*.
- Bonini, L., Rozzi, S., Serventi, F.U., Simone, L., Ferrari, P.F., Fogassi, L., 2010. Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cerebr. Cortex* 20 (6), 1372–1385.

- Bonini, L., Maranesi, M., Livi, A., Fogassi, L., Rizzolatti, G., 2014. Space-dependent representation of objects and other's action in monkey ventral premotor grasping neurons. *J. Neurosci.* 34 (11), 4108–4119.
- Brinkman, L., Stolk, A., Dijkerman, H.C., de Lange, F.P., Toni, I., 2014. Distinct roles for alpha-and beta-band oscillations during mental simulation of goal-directed actions. *J. Neurosci.* 34 (44), 14783–14792.
- Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., et al., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* 13 (2), 400–404.
- Buccino, G., Binkofski, F., Riggio, L., 2004. The mirror neuron system and action recognition. *Brain Lang.* 89 (2), 370–376.
- Buneo, C.A., Andersen, R.A., 2006. The posterior parietal cortex: sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia* 44 (13), 2594–2606.
- Busan, P., Monti, F., Semenic, M., Pizzolatto, G., Battaglini, P.P., 2009. Parieto-occipital cortex and planning of reaching movements: a transcranial magnetic stimulation study. *Behav. Brain Res.* 201 (1), 112–119.
- Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., Casile, A., 2009. Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *Science* 324 (5925), 403–406.
- Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., Serino, A., 2013. Tool-use reshapes the boundaries of body and peripersonal space representations. *Exp. Brain Res.* 228 (1), 25–42.
- Caspers, S., Zilles, K., Laird, A.R., Eickhoff, S.B., 2010. ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage* 50 (3), 1148–1167.
- Cattaneo, L., Rizzolatti, G., 2009. The mirror neuron system. *Arch. Neurol.* 66 (5), 557–560.
- Cevallos, C., Zarka, D., Hoellinger, T., Leroy, A., Dan, B., Chéron, G., 2015. Oscillations in the human brain during walking execution, imagination and observation. *Neuropsychologia* 79, 223–232.
- Cochin, S., Barthelemy, C., Lejeune, B., Roux, S., Martineau, J., 1998. Perception of motion and qEEG activity in human adults. *Electroencephalogr. Clin. Neurophysiol.* 107 (4), 287–295.
- Colby, C.L., Goldberg, M.E., 1999. Space and attention in parietal cortex. *Annu. Rev. Neurosci.* 22 (1), 319–349.
- Cravo, A.M., Rohenkohl, G., Wyart, V., Nobre, A.C., 2013. Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex. *J. Neurosci.* 33 (9), 4002–4010.
- Cross, E.S., Kraemer, D.J., Hamilton, A.F.D.C., Kelley, W.M., Grafton, S.T., 2009. Sensitivity of the action observation network to physical and observational learning. *Cerebr. Cortex* 19 (2), 315–326.
- Culham, J.C., Galloway, J., Cavina-Pratesi, C., Quinlan, D.J., 2008. fMRI investigations of reaching and ego space in human superior parieto-occipital cortex. *Embodiment, ego-space and action* 247–274.
- Decety, J., Grèzes, J., 2006. The power of simulation: imagining one's own and other's behavior. *Brain Res.* 1079 (1), 4–14.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134 (1), 9–21.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G., 1992. Understanding motor events: a neurophysiological study. *Exp. Brain Res.* 91 (1), 176–180.
- di Pellegrino, G., Ladavas, E., 2015. Peripersonal space in the brain. *Neuropsychologia* 66, 126–133.
- Evangelidou, M.N., Raos, V., Galletti, C., Savaki, H.E., 2009. Functional imaging of the parietal cortex during action execution and observation. *Cerebr. Cortex* 19 (3), 624–639.
- Fini, C., Costantini, M., Committeri, G., 2014. Sharing space: the presence of other bodies extends the space judged as near. *PLoS One* 9 (12), e114719.
- Fini, C., Brass, M., Committeri, G., 2015. Social scaling of extrapersonal space: target objects are judged as closer when the reference frame is a human agent with available movement potentialities. *Cognition* 134, 50–56.
- Foxe, J.J., Simpson, G.V., Ahlfors, S.P., 1998. Parieto-occipital-10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport: An International Journal for the Rapid Communication of Research in Neuroscience* 9 (17), 3929–3933.
- Foxe, J.J., Snyder, A.C., 2011. The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Front. Psychol.* 2, 154.
- Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., Rizzolatti, G., 2005. Parietal lobe: from action organization to intention understanding. *Science* 308 (5722), 662–667.
- Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. *Trends Cognit. Sci.* 8 (9), 396–403.
- Galloway, J.P., Cavina-Pratesi, C., Culham, J.C., 2009. Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *J. Neurosci.* 29 (14), 4381–4391.
- Grafton, S.T., Arbib, M.A., Fadiga, L., Rizzolatti, G., 1996. Localization of grasp representations in humans by positron emission tomography. *Exp. Brain Res.* 112 (1), 103–111.
- Gwin, J.T., Gramann, K., Makeig, S., Ferris, D.P., 2011. Electroocortical activity is coupled to gait cycle phase during treadmill walking. *Neuroimage* 54 (2), 1289–1296.
- Hamilton, A.F., 2013. The mirror neuron system contributes to social responding. *Cortex* 49 (10), 2957–2959.
- Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., Rizzolatti, G., 1998. Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc. Natl. Acad. Sci. USA* 95 (25), 15061–15065.
- Hari, R., Kujala, M.V., 2009. Brain basis of human social interaction: from concepts to brain imaging. *Physiol. Rev.* 89 (2), 453–479.
- Holmes, N.P., Spence, C., 2004. The body schema and multisensory representation (s) of peripersonal space. *Cognit. Process.* 5 (2), 94–105.
- Husain, M., Nachev, P., 2007. Space and the parietal cortex. *Trends Cognit. Sci.* 11 (1), 30–36.
- Iachini, T., Coello, Y., Frassinetti, F., Ruggiero, G., 2014. Body space in social interactions: a comparison of reaching and comfort distance in immersive virtual reality. *PLoS One* 9 (11), e111511.
- Iacoboni, M., Lieberman, M.D., Knowlton, B.J., Molnar-Szakacs, I., Moritz, M., Throop, C.J., Fiske, A.P., 2004. Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *Neuroimage* 21 (3), 1167–1173.
- Järveläinen, J., Schürmann, M., Avikainen, S., Hari, R., 2001. Stronger reactivity of the human primary motor cortex during observation of live rather than video motor acts. *Neuroreport* 12 (16), 3493–3495.
- Kaneko, N., Yokoyama, H., Masugi, Y., Watanabe, K., Nakazawa, K., 2021. Phase dependent modulation of cortical activity during action observation and motor imagery of walking: an EEG study. *Neuroimage* 225, 117486.
- Kilavik, B.E., Zaepffel, M., Brovelli, A., MacKay, W.A., Riehle, A., 2013. The ups and downs of beta oscillations in sensorimotor cortex. *Exp. Neurol.* 245, 15–26.
- Kilner, J.M., Marchant, J.L., Frith, C.D., 2006. Modulation of the mirror system by social relevance. *Soc. Cognit. Affect Neurosci.* 1 (2), 143–148.
- Kilner, J.M., Marchant, J.L., Frith, C.D., 2009. Relationship between activity in human primary motor cortex during action observation and the mirror neuron system. *PLoS One* 4 (3), e4925.
- Koul, A., Cavallo, A., Cauda, F., Costa, T., Diano, M., Pontil, M., Becchio, C., 2018. Action observation areas represent intentions from subtle kinematic features. *Cerebr. Cortex* 28 (7), 2647–2654.
- Leocani, L., Toro, C., Zhuang, P., Gerloff, C., Hallett, M., 2001. Event-related desynchronization in reaction time paradigms: a comparison with event-related potentials and corticospinal excitability. *Clin. Neurophysiol.* 112 (5), 923–930.
- Liang, M., Starrett, M.J., Ekstrom, A.D., 2018. Dissociation of frontal-midline delta-theta and posterior alpha oscillations: a mobile EEG study. *Psychophysiology* 55 (9), e13090.
- Makeig, S., Bell, A., Jung, T.P., Sejnowski, T.J., et al., 1995. Independent Component Analysis of Electroencephalographic Data. *Adv. Neural Inf. Process. Syst.* 8.
- Muthukumaraswamy, S.D., Johnson, B.W., McNair, N.A., 2004. Mu rhythm modulation during observation of an object-directed grasp. *Cognit. Brain Res.* 19 (2), 195–201.
- Patri, J.F., Cavallo, A., Pullar, K., Soriano, M., Valente, M., Koul, A., Avenantu, A., Panzeri, S., Becchio, C., 2020. Transient disruption of the inferior parietal lobule impairs the ability to attribute intention to action. *Curr. Biol.* 30 (23), 4594–4605.
- Perry, J., Davids, J.R., 1992. Gait analysis: normal and pathological function. *J. Pediatr. Orthop.* 12 (6), 815.
- Pezzulo, G., Donnarumma, F., Dindo, H., 2013. Human sensorimotor communication: a theory of signaling in online social interactions. *PLoS One* 8 (11), e79876.
- Pezzulo, G., Donnarumma, F., Dindo, H., D'Ausilio, A., Konvalinka, I., Castelfranchi, C., 2019. The body talks: sensorimotor communication and its brain and kinematic signatures. *Phys. Life Rev.* 28, 1–21.
- Pfurtscheller, G., Lopes da Silva, F.H., 1999. Functional Meaning of Event-Related Desynchronization (ERD) End Synchronization (ERS).
- Pion-Tonachini, L., Kreutz-Delgado, K., Makeig, S., 2019. ICLABEL: an automated electroencephalographic independent component classifier, dataset, and website. *Neuroimage* 198, 181–197.
- Pobric, G., Hamilton, A.F.D.C., 2006. Action understanding requires the left inferior frontal cortex. *Curr. Biol.* 16 (5), 524–529.
- Prinsen, J., Alaerts, K., 2019. Eye contact enhances interpersonal motor resonance: comparing video stimuli to a live two-person action context. *Soc. Cognit. Affect Neurosci.* 14 (9), 967–976.
- Proverbio, A.M., 2012. Tool perception suppresses 10–12 Hz  $\mu$  rhythm of EEG over the somatosensory area. *Biol. Psychol.* 91 (1), 1–7.
- Reader, A.T., Holmes, N.P., 2016. Examining ecological validity in social interaction: problems of visual fidelity, gaze, and social potential. *Culture and brain* 4 (2), 134–146.
- Rizzolatti, G., Fadiga, L., Fogassi, L., Gallese, V., 1997. The space around us. *Science* 277 (5323), 190–191.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2 (9), 661–670.
- Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192.
- Rizzolatti, G., Sinigaglia, C., 2010. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat. Rev. Neurosci.* 11 (4), 264–274.
- Rizzolatti, G., Fogassi, L., 2014. The mirror mechanism: recent findings and perspectives. *Phil. Trans. Biol. Sci.* 369 (1644), 20130420.
- Ronnqvist, K.C., McAllister, C.J., Woodhall, G.L., Stanford, I.M., Hall, S.D., 2013. A multimodal perspective on the composition of cortical oscillations. *Front. Hum. Neurosci.* 7, 132.
- Salmelin, R., Hämeäläinen, M., Kajola, M., Hari, R., 1995. Functional segregation of movement-related rhythmic activity in the human brain. *Neuroimage* 2 (4), 237–243.
- Schippers, M.B., Keysers, C., 2011. Mapping the flow of information within the putative mirror neuron system during gesture observation. *Neuroimage* 57 (1), 37–44.
- Schubring, D., Schupp, H.T., 2019. Affective picture processing: alpha-and lower beta-band desynchronization reflects emotional arousal. *Psychophysiology* 56 (8), e13386.

- Sebanz, N., Bekkering, H., Knoblich, G., 2006. Joint action: bodies and minds moving together. *Trends Cognit. Sci.* 10 (2), 70–76.
- Seeber, M., Scherer, R., Wagner, J., Solis-Escalante, T., Müller-Putz, G.R., 2014. EEG beta suppression and low gamma modulation are different elements of human upright walking. *Front. Hum. Neurosci.* 8, 485.
- Sinigaglia, C., 2013. What type of action understanding is subserved by mirror neurons? *Neurosci. Lett.* 540, 59–61.
- Stancák Jr., Andrej, Pfurtscheller, Gert, 1997. Effects of handedness on movement-related changes of central beta rhythms. *J. Clin. Neurophysiol.* 14 (5), 419–428.
- Stolk, A., Brinkman, L., Vansteensel, M.J., Aarnoutse, E., Leijten, F.S., Dijkerman, C.H., et al., 2019. Electrocorticographic dissociation of alpha and beta rhythmic activity in the human sensorimotor system. *Elife* 8, e48065.
- Talsma, D., Senkowski, D., Soto-Faraco, S., Woldorff, M.G., 2010. The multifaceted interplay between attention and multisensory integration. *Trends Cognit. Sci.* 14 (9), 400–410.
- Teneggi, C., Canzoneri, E., di Pellegrino, G., Serino, A., 2013. Social modulation of peripersonal space boundaries. *Curr. Biol.* 23 (5), 406–411.
- Tunik, E., Rice, N.J., Hamilton, A., Grafton, S.T., 2007. Beyond grasping: representation of action in human anterior intraparietal sulcus. *Neuroimage* 36, T77–T86.
- Ulloa, E.R., Pineda, J.A., 2007. Recognition of point-light biological motion: mu rhythms and mirror neuron activity. *Behav. Brain Res.* 183 (2), 188–194.
- Van Diepen, R.M., Foxe, J.J., Mazaheri, A., 2019. The functional role of alpha-band activity in attentional processing: the current zeitgeist and future outlook. *Current opinion in psychology* 29, 229–238.
- Vanni, S., Revonsuo, A., Hari, R., 1997. Modulation of the parieto-occipital alpha rhythm during object detection. *J. Neurosci.* 17 (18), 7141–7147.
- Wagner, J., Solis-Escalante, T., Grieshofer, P., Neuper, C., Müller-Putz, G., Scherer, R., 2012. Level of participation in robotic-assisted treadmill walking modulates midline sensorimotor EEG rhythms in able-bodied subjects. *Neuroimage* 63 (3), 1203–1211.
- Wamain, Y., Gabrielli, F., Coello, Y., 2016. EEG  $\mu$  rhythm in virtual reality reveals that motor coding of visual objects in peripersonal space is task dependent. *Cortex* 74, 20–30.
- Wheaton, K.J., Thompson, J.C., Syngeniotis, A., Abbott, D.F., Puce, A., 2004. Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *Neuroimage* 22 (1), 277–288.
- Wheaton, L., Fridman, E., Bohlhalter, S., Vorbach, S., Hallett, M., 2009. Left parietal activation related to planning, executing and suppressing praxis hand movements. *Clin. Neurophysiol.* 120 (5), 980–986.
- Witt, J.K., 2011. Action's effect on perception. *Curr. Dir. Psychol. Sci.* 20 (3), 201–206.
- Zarka, D., Cevallos, C., Petieau, M., Hoellinger, T., Dan, B., Cheron, G., 2014. Neural rhythmic symphony of human walking observation: upside-down and uncoordinated condition on cortical theta, alpha, beta and gamma oscillations. *Front. Syst. Neurosci.* 8, 169.