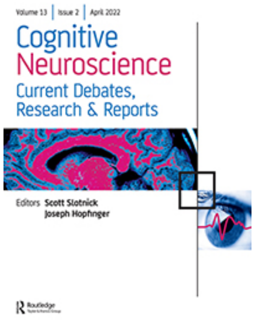

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Sensorimotor representation of observed dyadic actions with varying agent involvement: an EEG mu study

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ABSTRACT

Observation of others' actions activates motor representations in sensorimotor cortex. Although action observation in the real-world often involves multiple agents displaying varying degrees of action involvement, most lab studies on action observation studied individual actions. We recorded EEG-mu suppression over sensorimotor cortex to investigate how the multi-agent nature of observed hand/arm actions is incorporated in sensorimotor action representations. Hereto we manipulated the extent of agent involvement in dyadic interactions presented in videos. In all clips two agents were present, of which agent-1 always performed the same action, while the involvement of agent-2 differed along three levels: (1) passive and uninvolved, (2) passively involved, (3) actively involved. Additionally, a no-action condition was presented. The occurrence of these four conditions was predictable thanks to cues at the start of each trial, which allowed to study possible mu anticipation effects. Dyadic interactions in which agent-2 was actively involved resulted in increased power suppression of the mu rhythm compared to dyadic interactions in which agent-2 was passively involved. The latter did not differ from actions in which agent-2 was present but not involved. No anticipation effects were found. The results suggest that the sensorimotor representation of a dyadic interaction takes into account the simultaneously performed bodily articulations of both agents, but no evidence was found for incorporation of their static articulated postures.

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Action observation; multiple actions; EEG; mirror neuron system; mu rhythm; prediction

Introduction

The actions we observe in the real-world are often carried out by multiple interacting agents. The extent of the contribution of the participating agents will inevitably vary, and some agents may be involved only in a passive manner, but nevertheless form an intrinsic part of the interaction, and could potentially become active partakers. Such interactions often consist of joint actions in which two or more individuals coordinate their actions in space and time to achieve a certain goal (Sebanz et al., 2006). This contrasts sharply with the traditional approach to study action observation using neuroscientific or behavioral techniques in the lab, in which typically individual actions were presented. However, more recently, dyadic and multi-person interactions have received quite some attention (e.g., Petrini et al., 2014; Georgescu et al., 2014; see, Quadflieg et al., 2015; Walbrin & Koldewyn, 2019, for discussions of the relevance of studying multi-agent interactions). Many of these studies though examined certain aspects of social interactions – such as incongruency, fluency, contingency, or meaningfulness – without specifically contrasting multi-agent to individual actions. The multi-agent approach ties in with recent developments in social neuroscience that aim to investigate social cognition under real-world conditions, often called 'second-person neuroscience' (Redcay & Schilbach, 2019; Schilbach et al., 2013).

Recognizing which action is performed by whom, how the actions relate to each other, and what the underpinning (joint or separate) intentions are, involves the recruitment of action representations in the observer's sensorimotor cortex, where presumably an automatic 'simulation' of the observed actions is performed. A principal candidate for carrying out such a motor simulation is the mirror neuron system (MNS; Gallese et al., 1996; Rizzolatti et al., 1996), which includes the ventral premotor cortex (vPMC) and the inferior parietal lobule (IPL), and becomes active when performing and observing similar actions. It operates in concert with other areas of the Action Observation Network (AON; Cross et al., 2009), of which it forms an integral part. The AON encompasses higher-order visual regions encoding biological motion, most notably the superior temporal sulcus (STS; Jellema & Perrett, 2003a; Jellema et al., 2000) and parieto-frontal motor regions. Motor simulation in the MNS has been argued to support an

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immediate grasp of the goal, meaning, or intention of observed actions on the basis of a match with the observer's own motor repertoire and activation of associated representations of behavioral outcomes and visceral states (Rizzolatti & Sinigaglia, 2010). However, such a role is debated (e.g., Heyes, 2010). One objection is that context information is necessary (Kilner et al., 2007), or even sufficient (Csibra, 2008), to infer higher-order goal representations. A commonly used index for MNS activity is suppression of power in the alpha frequency band (8–13 Hz) of EEG recorded over sensorimotor cortex, called the mu rhythm (see, Fox et al., 2016; Hobson & Bishop, 2016, for discussions of the link between the MNS and mu suppression).

Contextual information, including preceding actions that logically lead to the next action within an action chain (Cattaneo et al., 2007), may enable a role for the MNS in action anticipation. Action anticipation is essential for successful social interaction (e.g., Hudson et al., 2012). There is some evidence for an anticipatory role, showing that simulation activity in the MNS may start up to 1s prior to the onset of the observed action, provided the action can be predicted on the basis of contextual cues (Kilner et al., 2007; Maranesi et al., 2014), especially when actions are presented in a real-world context (Krol et al., 2020). Due to its superior temporal resolution, EEG is well suited to detect such anticipation effects.

Given the putative role of the MNS in social cognition, it is surprising that social multiple-agent actions have somewhat been neglected in MNS research. Hence, evidence that the MNS is specifically sensitive to multiple agents and to *inter*actions is still fairly indirect. For instance, the finding that mu suppression increased when participants held four compared to two biological motion stimuli (point light displays) in working memory is suggestive of MNS sensitivity to the number of agents (Gao et al., 2015). Another example is studies that report increases in corticospinal motor excitability during the observation of interactions between two agents as compared to individual actions (e.g., Aihara et al., 2015). Streltsova et al. (2010) used EEG mu suppression to study MNS activation in response to the observation of individual grasping actions and grasping actions as part of a social interaction involving two actors. They did not find enhanced activation in the interaction condition. However, their main goal was to test for the influence of the social context, rather than for social interaction, and in their interaction condition just one actor acted, while the other remained passive throughout. In an fMRI study, Cracco et al. (2019) directly compared single intransitive hand actions with two simultaneously performed different intransient hand actions. They found that the latter produced significantly more activity in premotor and parietal motor areas than the former. In principle, this could suggest that sensorimotor cortex is able to represent 3rd party social encounters. However, the study by Cracco et al. (2019) did not test multiple goal-directed actions constituting a social interaction. An agent's potential to act in an interaction in a particular way often forms an essential piece of information for deciphering the meaning of a social interaction; without which the interaction may be meaningless. For instance, a static supinated hand signals willingness to receive an object, and makes the action of placing an object by another agent meaningful. Such static articulated postures are crucial to social interactions (Jellema & Perrett, 2012), yet it is unknown whether they are incorporated in sensorimotor action representations.

Thus, from previous studies, it remains unclear whether sensorimotor representations of observed social interactions are sensitive to the simultaneously performed actions of multiple agents, as the direct comparison between single vs. multiple simultaneous actions within a social interaction context was not performed. The current study aimed to address this gap in our knowledge by including a direct comparison of single vs. dyadic goal-directed actions in a social interaction, and in addition by testing whether static articulated postures that form an integral part of the social interaction (cf., Begliomini et al., 2017) are represented as well. In the current study, mu power suppression was measured prior to and during the observation of dyadic actions, in which the spatio-temporal dynamics of the action of one of the actors (agent 1) remained as far as possible the same, while the involvement of the other actor (agent 2) progressively increased. The dyadic actions were presented in video clips, in which a simple card game was played according to preinstructed rules, in the following three conditions: (i) Agent-1 acts, agent-2 remains passive and is not involved (place-on-pile condition). (ii) Agent-1 acts, agent-2 partakes in the interaction, but in a passive manner (place-on-hand condition). (iii) Agent-1 acts, agent-2 reacts and is actively involved, constituting a joint action (give-and-receive condition).

We hypothesized that if sensorimotor activation (mu suppression) would reflect just the observed kinematics of the biological action then no differences in mu suppression should be observed between the place-on-pile and place-on-hand conditions, as the visual information and dynamics of these two actions by agent-1 were virtually identical (and agent 2 did not act). However, if the passive involvement of others, and their potential for social interaction (cf., Begliomini et al., 2017), would be incorporated in the representation, then the place-on-hand condition should produce more mu suppression.

For the give-and-receive dyadic action, we predicted further increased mu suppression. Although in both the place-on-hand and give-and-receive actions, agent-1 handed the object over to agent-2, only in the give-and-receive condition the two agents acted simultaneously. If the sensorimotor action representations are sensitive – or possibly even specifically tuned – to the simultaneous actions of multiple agents, then stronger mu suppression should occur in the give-and-receive condition. Overall, we hypothesized that the MNS is tuned to (the potential for) social interaction and that as agent-2 gets gradually more involved in the dyadic interaction, the activation of the MNS will gradually increase. MNS anticipation effects might be visible as increased mu suppression in the three Action conditions (compared to No-Action) during the 1s interval immediately preceding the onset of the action by agent-1, and/or in the Give-and-receive condition (compared to Place-on-hand) during the 1s immediately preceding onset of agent-2's action.

Methods

Participants

Twenty-five healthy adults took part (17 females, 8 males; mean age = 21.8 years, SD = 8.1, range = 18–59). All participants were undergraduate students from the Psychology department of the University of Hull, and received course credits for participating. The study was approved by the ethics committee of the Psychology department of Hull University. Exclusively right-handed participants were requested to take part and handedness was checked with the Edinburgh Handedness Inventory (Oldfield, 1971). All reported normal visual acuity and none reported the presence of any neurological or psychiatric disorders.

Stimuli

The visual stimuli consisted of video-clips depicting hand actions, recorded with a high-definition video camera and edited with Adobe Premiere Pro CS5. They were presented on a 19-inch LCD monitor (resolution 1920 × 1080) using E-prime 2.0 (PST Inc., Sharpsburg, USA).

Playing cards were used as the objects to be manipulated (face cards excluded) because they are well-known, easily manipulated and picked up and received in a specific way (precision grip). All clips lasted for 11s and contained a Rest, Signal, Delay, Action, and Rest phase, in this sequence (except that there was no Action phase in the no-action condition).

(1) Rest phase (2s). This static phase was identical in all four conditions. The video showed the surface of a table and the right hands and wrists of two female agents sitting opposite each other at the table (Figure 1(a)). The hand of agent-1 (left side of screen) was pronated, the hand of agent-2 (right side) supinated. There was a small tablet PC positioned on the table and a deck of playing cards split into two piles (face side up), one pile positioned on the tablet, the other on the table. The locations of the hand of agent-2 and the pile of cards positioned on the table, were counterbalanced to

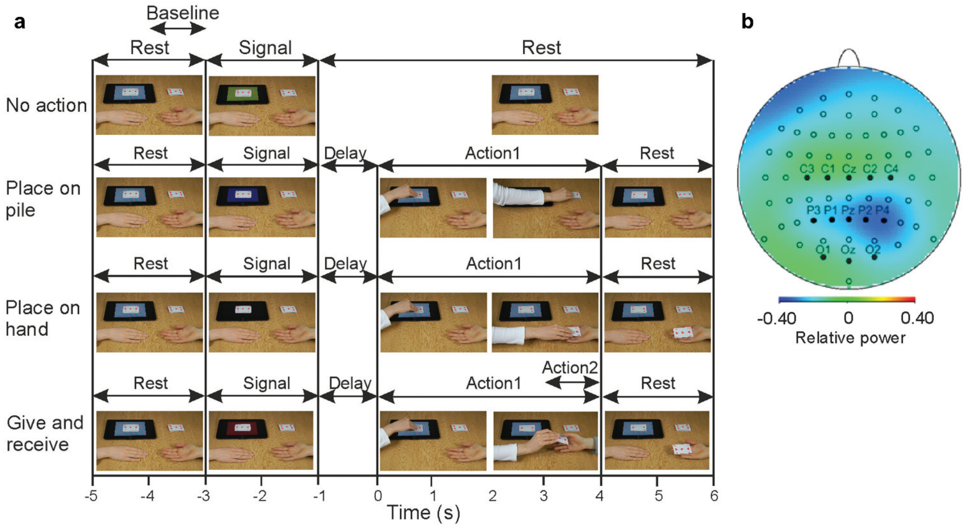

Figure 1. Experimental conditions. (a) The main stimulus events of the four video conditions are displayed. (b) EEG mapping view. The electrodes C3, C1, Cz, C2, C4, P3, P1, Pz, P2, P4, O1, Oz, and O2 of the 10/20 system were preselected for analysis (filled circles). The colors represent changes in power during the Action phase compared to baseline for the pooled action conditions.

control for the difference in motion trajectory; in half of the trials of each condition the hand was in the upper right corner and the cards in the lower right corner, in the other half these positions were switched. Throughout this phase, the tablet PC screen was white.

(2) Signal phase (2s). Throughout this phase the tablet screen displayed a specific color (yellow, blue, red or black) enabling the participant to predict whether, and how, the action will unfold. The pile of cards was positioned on top of the tablet screen to minimize participant's eye movements between the signal and the card to be grasped.
(3) Delay phase (1s). The tablet screen turned again white and remained white till the end of the trial. The Delay phase was interspersed between the offset of the tablet signal and the onset of the action.
(4) Action phase (4s). One of three different action sequences was displayed, or no action was shown. The action sequences always started with an action performed by agent-1, and had been edited to ensure they were visually identical in the first 2s of the action (agent-1 grasping a card) and only differed in the last 2 seconds. None of the observed actions were directed at, or involved, the observer, because then effects of motor preparation causing mu suppression cannot be ruled out (Salmelin et al., 1995).
(5) Rest phase (2s). The last 2 s of the clips consisted of a still frame, depicting the two hands at rest in the same position/orientation as at the start of the clips.

Directly preceding each clip, a gray screen with a central fixation cross was presented for 1s. Directly following each clip, a gray screen was presented for 1, 1.5, or 2s that served as inter-trial-interval.

Procedure

The participants sat at 90 cm distance from the PC monitor to ensure they could observe the full screen without needing to make head or eye movements. The four conditions were divided over two blocks.

Block 1

(1) No-action. The tablet screen turned yellow in the Signal phase, which indicated that no action would follow. The two hands remained still on the table throughout the trial.
(2) Place-on-pile action. In the Signal phase, the tablet screen turned blue. After the 1s delay phase, agent-1 grasped the top card from the deck of cards on the tablet and placed it on the deck of cards positioned on the table, after which the hand moved back to the start position. The hand of agent-2 lay still on the table in supinated position throughout the trial.

Block 2

In this block, the tablet color cue was either black or red. As the cards were also either black (spade and clubs) or red (hearts and diamond), there could be a match (red-red, black-black) or mismatch (red-black, black-red) between cue color and card color.

(3) Place-on-hand action. If there was no match between cue color and card color, then, following the 1s delay, agent-1 picked up the card and placed it on the open hand of agent-2.
(4) Give-and-receive action. If there was a match between cue color and card color, then, following the 1s delay, agent-1 picked up the card and gave it to agent-2, who actively received the card. The hands of both actors then returned to their original positions (the hand of agent-2 with the card displayed on the palm of the hand).

The four conditions were divided over two blocks to avoid participants becoming confused regarding the meaning of the color cues as otherwise they would have had to remember four different rules at once. In this way, participants can be instructed immediately prior to the start of each block about the implications of the signal color for the subsequent action(s). Two practice trials of the included conditions per block were given to help explain the rules and ensure participants understood them. In the first block, participants observed 20 Place-on-table and 20 No-action clips, presented in random order. In the second block, 20 Place-on -hand and 20 Give-and-receive clips were presented in random order. The block 1/block 2 sequence was then repeated one time; thus in total 160 clips were shown, 40 for each condition (total duration 36 minutes).

We designed the experiment such that participants would remain engaged, as passively observing 160 trials may result in inattentiveness. We did this by introducing variation as far as allowed by the constraints of the experiment, rather than by including a task involving stimuli that need to be detected/reported as that would divert attentional resources away from the action stimuli. (i) In each trial a different card was used (hearts/diamonds/clubs/spade, with a different number). (ii)

Participants were required to perform simple mental operations (i.e., apply a rule) in the initial part of each trial that allowed them to determine which particular action would follow. (iii) Different signal colors were used (blue and yellow in block 1, red and black in block 2). (iv) The simple mental operations at the start of each trial differed between blocks: in block 1 a signal color identified which action would unfold, in block 2, a match/mismatch comparison between the colors of cue and card identified the subsequent action (the blocks were repeated one time). (v) In each block two visually different conditions were presented in random order. To further reduce inattentiveness and fatigue, the blocks were kept fairly short (9 minutes, separated by 5-minute breaks). A test for whether fatigue or inattentiveness nevertheless did occur, and influenced mu suppression, was performed (see Results). The test indicated that there was no difference in mu suppression for later compared to earlier trials during action observation, suggesting that participants kept a steady level of attention throughout the experiment.

In principle, there is the possibility that the different signal colors and different mental operations could themselves induce modulation of alpha power that could be mistaken as being induced by particular action types. To rule this out, we also analyzed mu suppression during the Signal phase. In all four conditions an initial mu suppression was observed following signal onset, which gradually faded out and returned to baseline before the end of the Signal phase. These signal-related mu suppressions did not differ between conditions (see Results). We therefore concluded that the difference in cue colors/rules did not itself affect mu suppression occurring during the subsequent Delay and Action phases.

EEG recording

EEG activity was recorded continuously using the BioSemi ActiveTwo system (BioSemi, Amsterdam, The Netherlands), with 64 Ag-AgCl-tipped electrodes arranged according to the International 10–20 System. During recording, all electrodes were referenced to a common mode sense (CMS), which was located between P1, PO3, and POz. The CMS electrode and the passive driven right leg (DRL) electrode, located between P2, POz, and PO4, formed a feedback loop driving the subject's average potential as close as possible to the analog-to-digital converter reference voltage in the A/D-box (i.e., the amplifier 'zero'). ActiView (BioSemi) was used for EEG data acquisition, where the sampling rate was down-sampled from 8192 Hz to 512 Hz.

EEG analysis

Offline analysis was performed with BrainVisionAnalyzer 2.1.1 (Brain Products GmbH, Gilching, Germany). Temporal spectral evolution (TSE) was used to explore the time course of power in the alpha band; TSE transforms raw data into power in a selected frequency band without inducing changes in the time-domain (Babiloni et al., 2002; Hari et al., 1998; Kourtis et al., 2013; Salmelin et al., 1995). First, data was re-referenced to an average reference and filtered with a Butterworth Zero Phase bandpass filter, selecting the 8–13 Hz frequency band (48 dB/oct), followed by segmentation (11s, duration of clips). Exclusion of segments containing artifacts was done by setting a minimum and maximum allowed voltage amplitude (−50 µV to 50 µV; 5.8% of segments removed). The data were rectified and a baseline correction was applied with as baseline period the 1s epoch starting 4s before action onset (in Rest phase), followed by averaging of the data of all trials per condition. This method resulted in the averaged power in squared microvolt (μV^2) in the alpha band for each condition. The mean power was analyzed for five central electrodes, C3, C1, Cz, C2, and C4, for five parietal electrodes, P3, P1, Pz, P2, and P4, and for three occipital electrodes, O1, Oz and O2 (Figure 1(b)). Although previous research sometimes focused on the central electrodes, posterior electrodes were often found to record significant modulations of mu power in response to action observation (Avanzini et al., 2012; Babiloni et al., 2002; Cracco et al., 2019; Kilner et al., 2006; Southgate et al., 2009; see, Tarhan & Konkle, 2020, for a recent fMRI study). We therefore analyzed responses from both central and parietal electrode clusters, covering the cortical areas involved in sensorimotor representations of hand and arm actions (Babiloni et al., 2002). The occipital electrodes were analyzed to assess to what extent occipital alpha might have contributed to the mu rhythm recorded at the parietal and central electrodes.

For analysis purposes, the time course was divided in three consecutive time-epochs: epoch-1, consisting of the Delay phase (1s duration); epoch-2, consisting of the initial part of the Action phase (3s duration), during which exclusively agent-1 acted in each of the three action conditions, and epoch-3, consisting of the final 1s of the Action phase, during which in the Give-and-receive condition both agents acted (the analysis epochs are indicated at the top of Figure 2). Post-hoc comparisons were planned in advance (i) for Place-on-pile *vs.* No-Action conditions, to assess the influence of the anticipation and observation of an action (epochs 1 and 2), (ii) for the Place-on-hand *vs*. Place-on-pile conditions, to assess the influence of the social vs. nonsocial goal of an action (epoch 2), and (iii) for the Give-and-receive vs. Place-on-hand conditions, to assess the influence of interaction with the 2nd agent (epoch 3). Additionally, the latter two conditions were compared during the 1s interval immediately preceding onset of the action of agent-2 (i.e., the 3rd second of Action epoch 1), to explore anticipation of agent-2's action. Such an anticipation effect should be absent in the Place-on-hand, but present in the Give-and-receive, condition, where it would add to the mu suppression induced by agent-1's action (which action is very similar in both conditions).

Results

Central electrode cluster

A 4 × 3 repeated measures ANOVA was performed on the averaged power recorded from the central electrode cluster, with within-subject factors Condition (No-action, Place-on-pile, Place-on-hand, Give-and-receive) and

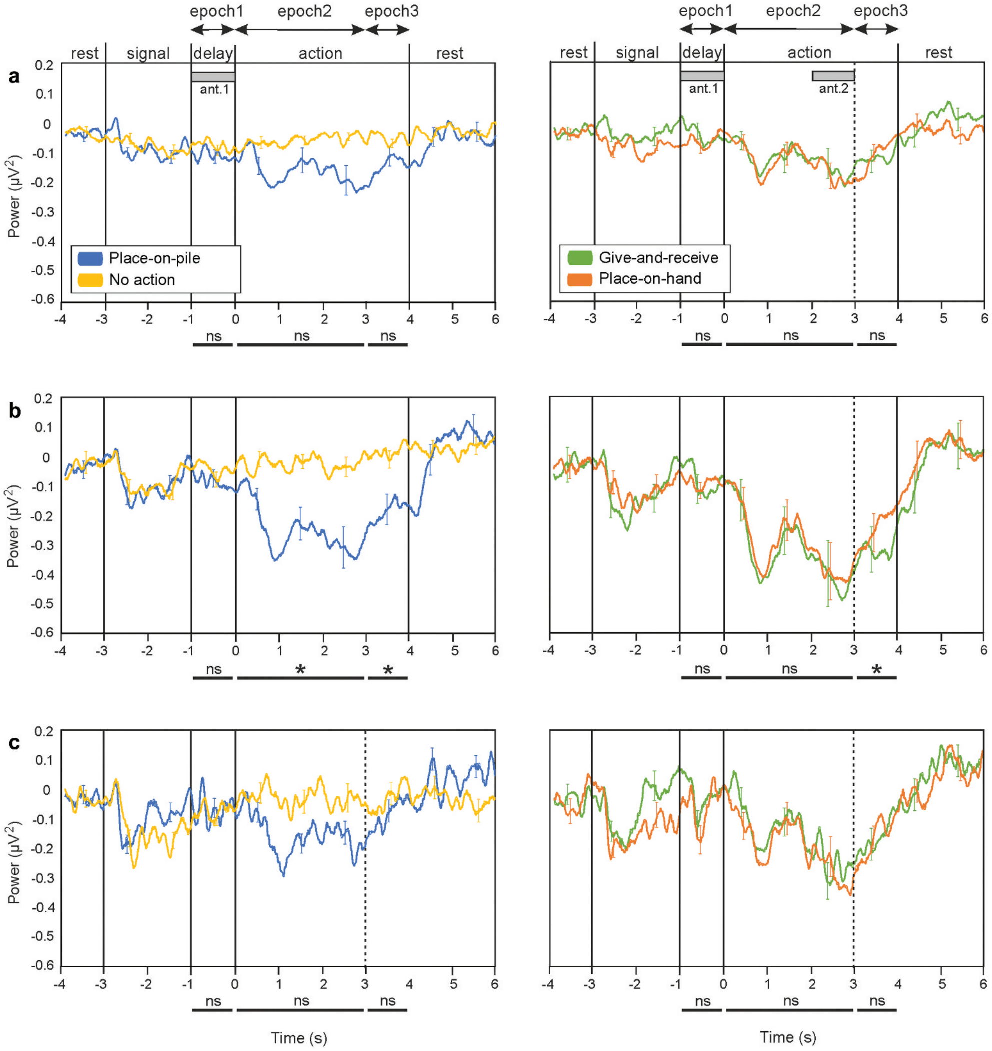

Figure 2. Time course of power suppressions in the 8–13 Hz frequency band during the presentation of the video clips in the four conditions for (a) the pooled central electrodes, (b) the pooled parietal electrodes, and (c) the pooled occipital electrodes. The place-on-pile and no-action conditions are shown in the panels on the left, the give-and-receive and place-on-hand conditions on the right. The three analysis epochs are indicated at the top. The vertical dotted line in the right-side panels indicates the onset of the action by agent-2 in the give-and-receive condition. The two anticipation periods preceding the onsets of the actions of agents 1 and 2, are indicated by gray horizontal bars (ant.1 and ant.2), respectively. Error bars reflect the averaged ± 1 SE per second. Significant differences between the conditions for each of the three analysis epochs are indicated (ns, non significant; *, $P < .05$).

Time (epoch1: Delay, epoch2: initial Action, epoch3: final Action; Figure 2(a)). In this and subsequent analyses, Greenhouse-Geisser corrections were applied whenever Mauchly's test of sphericity was significant. The main effect of Condition was non-significant ($F(3,72) = 2.24$, $p = .09$, $\eta_p^2 = .09$). The main effect of Time was significant ($F(2,48) = 4.05$, $p = .02$, $\eta_p^2 = .14$).

The Condition by Time interaction was significant ($F(3.6,86.0) = 4.52$, $p = .003$, $\eta_p^2 = .16$), which was further explored in three one-way ANOVAs, one for each three time epochs. In the Delay phase, there were no significant differences between the four conditions ($F(3,72) = 1.43$, $p = .24$, $\eta_p^2 = .06$). The effect of Condition was significant in the initial Action phase (epoch2, $F(2.3,55.0) = 3.52$, $p = .03$, $\eta_p^2 = .13$) and final Action phase (epoch3, $F(3,72) = 2.85$, $p = .04$, $\eta_p^2 = .11$). However, none of the three planned post-hoc comparisons (initial action epoch2: Place-on-pile *vs*. No-Action, Place-on-hand *vs*. Place-on-pile, final action epoch3: Give-and-receive vs. Place-on-hand) were significant (Bonferroni corrected alpha value of 0.0167). The Give-and-receive and Place-on-hand conditions did not differ significantly during the 1s anticipation period immediately preceding onset of the action of agent-2 ($t(24) = .17$, $p = .87$, $d_z = .14$).

Parietal electrode cluster

The 4 (Condition) x 3 (Time) ANOVA performed for the parietal electrode cluster revealed significant main effects of Condition ($F(1.6,38.7) = 6.02$, $p = .008$, $\eta_p^2 = .20$) and Time ($F(1.3,30.3) = 11.91$, $p = .001$, $\eta_p^2 = .33$). The Condition by Time interaction was also significant ($F(2.6,63.4) = 6.99$, $p = .001$, $\eta_p^2 = .23$; Figure 2(b)), which was further explored in one-way ANOVAs for each of the three time epochs. For the Delay phase (epoch1), the effect of Condition was non-significant ($F(3,72) = .39$, $p = .76$, $\eta_p^2 = .02$). For the Action phase (epochs 2 and 3), Condition was significant (epoch2: $F(1.5,36.7) = 7.43$, $p = .004$, $\eta_p^2 = .24$; epoch3: $F(1.5,36.7) = 7.49$, $p = .004$, $\eta_p^2 = .24$). During the initial Action epoch2, the posthoc comparisons of Place-on-pile *vs*. No-Action was significant ($t(24) = -3.62$, $p = .001$, $d_z = -.72$), though the other two comparisons were non-significant (Place-on-hand *vs*. Place-on-pile, $t(24) = -.61$, $p = .55$, $d_z = -.12$; Give-and-receive vs. Place-on-hand, $t(24) = -1.13$, $p = .27$, $d_z = -.23$; Bonferroni corrected alpha of 0.0167). However, during the final Action phase (epoch3, 1s), which was the interval during which the second agent moved her hand to receive the card, the Give-and-receive condition (M = −.29, SD = .42) induced significantly more mu suppression than the Place-on-hand condition (M = −.22, SD = .35; $t(24) = -2.68$, $p = .010$, $d_z = -.51$). The Place-on-hand and Place-on-pile conditions did not differ from each other ($t(24) = .88$, $p = .39$, $d_z = -.18$), while in the Place-on-pile condition, there was again more mu suppression than in the No-action condition (M = .04, SD = .15; $t(24) = -3.11$, $p = .005$, $d_z = -.62$; alpha = 0.0167). The Give-and-receive and Place-on-hand conditions did not differ significantly during the 1s anticipation period immediately preceding onset of agent-2's action ($t(24) = -1.35$, $p = .19$, $d_z = .17$).

Occipital electrode cluster

The 4 (Condition) x 3 (Time) ANOVA performed for the occipital electrode cluster indicated that the main effect of Condition was non-significant ($F(1.8,44.0) = 1.59$, $p = .22$, $\eta_p^2 = .06$). The effect of Time was significant ($F(1.5,37.9) = 10.43$, $p = .001$, $\eta_p^2 = .30$), and the Time by Condition interaction was significant ($F(3.4,82.8) = 5.06$, $p = .002$, $\eta_p^2 = .17$). The latter was again further explored in one-way ANOVAs for each time-epoch. The four conditions did not differ in the Delay phase (epoch1, $F(3,72) = .55$, $p = .65$, $\eta_p^2 = .02$), nor in the final Action epoch3, $F(2.1,50.8) = 2.96$, $p = .06$, $\eta_p^2 = .11$). For the initial Action epoch2, the effect of Condition was significant ($F(1.7,39.6) = 3.72$, $p = .04$, $\eta_p^2 = .13$). However, the planned t-tests did not show significant differences (Bonferroni adjusted alpha 0.0167).

Recording of power suppressions at the occipital electrodes allowed to assess whether the mu rhythm recorded over sensorimotor cortex may have an occipital source (Kajikawa & Schroeder, 2015). Occipital alpha, in contrast to parietal alpha, is specifically responsive to visual attention (Foxe & Snyder, 2011). This gives rise to two predictions with respect to the Signal and Action phases, which we used to test our claim that the parietal mu suppression reflected sensorimotor activity, rather than visual attention activity. (i) During the Action phase, alpha power suppression (pooled over the three action conditions) should be larger over parietal than over occipital sites. Mean power suppression at the parietal cluster (M = −.25, SD = .34) was significantly larger than at the occipital cluster (M = −.13, SD = .19; $t(24) = -2.36$, $p = .03$, $d_z = -.47$). (ii) During the Signal phase, alpha power suppression should be larger over occipital sites than over parietal sites. The reasoning here is that the Signal phase (the tablet adopts a color) would induce visual attention but not sensorimotor activity. However, a problem is that alpha suppression in response to the signal can be 'contaminated' by anticipatory alpha (mu) suppression in response to the upcoming action. Therefore, just the No-action condition was analyzed in a one-way ANOVA (central vs parietal vs occipital cluster). In this condition, the Signal phase is present (tablet is yellow) but the participant knows that no action will follow (and thus no contamination can occur). Alpha suppression in the three electrode clusters for the no-action condition was analyzed with a one-way ANOVA, which revealed a significant effect of cluster ($F(2, 48) = 3.57$, $p = .04$, $\eta_p^2 = .13$). Alpha suppression was not significantly different between the central cluster (M = −.04, SD = .10) and the parietal cluster (M = −.05, SD = .16; $t(24) = .42$, $p = .68$, $d_z = .09$), while suppression in the occipital cluster (M = −.10, SD = .12) was larger compared to the parietal cluster ($t(24) = 3.01$, $p = .006$, $d_z = .62$).

The Signal phase was further analyzed to explore potential (differential) contributions to the power modulations caused by the visual processing of the different color cues. None of the clusters yielded significant differences between the four conditions (Central, $F(3,72) = 2.14$, $p = .12$, $\eta_p^2 = .08$; Parietal, $F(3,72) = 1.11$, $p = .30$, $\eta_p^2 = .04$; Occipital, $F(3,72) = 2.42$, $p = .07$, $\eta_p^2 = .09$).

A check for a possible decrease in participants' attentiveness due to fatigue increment over the course of the video presentations, which would be reflected by a decrease in mu suppression, was performed by comparing the averaged mu suppression in the place-on-pile and place-on-hand conditions during the initial reaching-out action by agent-1 (i.e., the 1st second of the action phase). This initial action is identical in both conditions. Since the latter condition was presented after the former, a possible fatigue effect should be more prominent in the latter condition. Mu suppression in this time-epoch in the two conditions did not differ significantly (Place-on-pile, M = −.17, SD = .20; Place-on-hand, M = −.20, SD = .29; $t(24) = -.57$, $p = .58$, $d_z = -.12$), suggesting that progressive fatigue and inattentiveness did not play a role.

Discussion

In all three electrode clusters, power was reduced during the observation of actions compared to the no-action condition. However, power suppressions were largest in the parietal cluster, and only in this cluster did the action conditions differ from each other. Dyadic interactions in which both agents were actively involved (give-and-receive condition) resulted in increased power suppression compared to interactions in which agent-2 was passively involved (place-on-hand condition), which did not differ from actions in which agent-2 was present but not involved (place-on-pile condition). This means that, broadly speaking, progressive increases in involvement of agent-2 resulted in progressively greater mu suppression. The difference between the place-on-hand and give-and-receive conditions occurred exclusively during the last second of the 4s action phase, during which agent-2 actively received the card and the two agents thus moved their arms and hands simultaneously.

Multiple observed actions

Increased cortical sensorimotor activity in response to the observation of two actions compared to one action seems the most parsimonious explanation for the finding of increased mu suppression during the last second of the action phase. Even though, obviously, the sensorimotor system controls the execution of just one's own actions, the current study shows that it is able to represent the observed actions of multiple agents that are simultaneously performed. If one takes the view that the motor responses to action observation amount to a 'simulation' of the observed action (Gallese & Goldman, 1998) leading to an understanding of the agent's goals/intentions in an 'experiential manner, from the inside' (Rizzolatti & Sinigaglia, 2010), then this means that the observer's motor system can 'resonate' and 'identify' with multiple agents simultaneously. Sensitivity of the motor system to multiple, simultaneously presented, actions has been suggested before (Cracco et al., 2019). In their fMRI study, Cracco et al. (2019) showed that the observation of videos depicting two isolated intransitive actions (gestures performed simultaneously by two right hands) caused more activation in MNS areas than single intransitive hand actions. However, isolated, simultaneously performed, intransitive actions do not resemble a social interaction. The current research investigated meaningful goal-directed dyadic actions rather than isolated intransitive gestures, and provides further support for the claim that the motor system, and especially its parietal part, is able to represent – and simulate – goal-directed actions from two agents simultaneously. The two actions were different (i.e., giving and receiving) and were carried out by the right hands/arms of two agents, and could thus not have been executed simultaneously by the observer.

Passive involvement in interaction

The current data does not provide evidence for the notion that representations of dyadic interactions in the MNS incorporate – or are modulated by – the passive involvement of agents. In the place-on-hand condition, agent-2 was clearly involved in the dyadic action, holding her hand in supinated position, signaling readiness to receive an object. In the place-on-pile condition, agent-2 was present but in no way involved. However, the two latter conditions produced similar mu suppression.

The underlying question is whether the sensorimotor representation of an interaction takes into account all relevant bodily aspects of the interaction, including static postures that are integral to the interaction. In a similar vein, are anticipated actions – i.e., actions that are not yet executed, but are expected to be executed – included in such a representation? Indirect support for their inclusion comes from studies showing that the mere sight of a manipulable object (e.g., a tool) can induce mu suppression (e.g., Kumar et al., 2013; Proverbio, 2012; De Vega et al., 2019), presumably on the basis of the specific object affordances (Gibson, 1977). In these studies, the object is observed from a 1st person perspective and the observer presumably 'simulates' the action afforded by the object. However, if the observer looks at an agent who is looking at a manipulable object (i.e., a 3rd person perspective), then a similar simulation might happen in a vicarious manner, again resulting in mu suppression (cf., Kumar et al., 2013). Therefore, it seems plausible that the agent's passive *involvement*, holding the potential for a specific meaningful articulation, is included in the sensorimotor representation of the interaction. Nevertheless, in our study mu suppression, used as an index for sensorimotor activation, was not sensitive to passive involvement (comparison between place-on-pile and place-on-hand conditions). It is possible that mu suppression recordings are not sensitive enough to detect such subtleties, or that the study was not sufficiently powered. Alternatively, the passive *involvement* of agents may be represented elsewhere, possibly in the STS (Superior Temporal Sulcus). In the STS, static bodily postures and consequent, or implied, articulations are known to be represented (e.g., Jellema & Perrett, 2003a, 2003b).

Social vs. nonsocial goals

The results also did not provide evidence for a specific sensitivity of MNS representations for social (place-on-hand) as compared to nonsocial (place-on-pile) goals of actions (cf., Tarhan & Konkle, 2020). It has been argued that the goal of the observed action is a determining feature of the MNS response (Gallese et al., 1996). Possibly the social and nonsocial characteristics of these actions were not pronounced enough to allow discrimination.

Anticipation of upcoming actions

The recorded mu suppression did not reflect anticipation of the upcoming actions of agent-1 and agent-2. Predictability of the onset and type of upcoming actions is a precondition for any MNS-related anticipation effects (Kourtis et al., 2013; Krol et al., 2020; Maranesi et al., 2014; Southgate et al., 2009). In our paradigm, the color cues enabled to predict actions with 100% certainty whether or not an action would follow, and if so which one. However, the onset of mu suppression followed the onset of the observed actions and no mu suppression occurred in the 1s Delay period, nor in the 1s immediately preceding onset of action 2. This contrast starkly to the finding of anticipation effects in a similar paradigm tested in a real-world context (Krol et al., 2020). Possibly, a certain level of engagement with the stimulus is required, which is achieved more easily in real-world presentations.

Visual attention effects

Although occipital alpha is in particular thought to reflect visual attention (e.g., Foxe & Snyder, 2011), sensorimotor alpha may to some extent also reflect attentional and low-level visual processing (Hobson & Bishop, 2016). It is therefore relevant to ascertain that the mu suppressions recorded at the parietal cluster had not been generated at occipital sites and reached the parietal sites through passive volume conduction (Kajikawa & Schroeder, 2015). Two experimental findings suggested this was not the case.

First, the finding that at the occipital electrodes none of the action conditions differed from each other during action observation (while they did differ at parietal sites), with power suppression being significantly smaller than at the parietal electrodes, suggests this is not the case. In other studies from our lab, that used a similar paradigm (Krol et al., 2020), a similarly weakened mu suppression was found at the occipital electrodes during action observation. Second, during the Signal phase (yellow color) of the no-action condition, where the participant knows that no action will follow (and thus no contamination by action anticipation occurs), alpha power suppression was significantly larger over occipital sites than over central and parietal sites. As the Signal phase is assumed to induce visual attention but not sensorimotor activity, this suggests that the source of visual-attentional processing is occipital rather than central/parietal. Taken together, this argues against a visual attention source for the parietal mu suppressions.

Limitations

The current experiment did not investigate the question of whether the *interactive* nature of the observed dyadic actions played a role, over and above the two actions *per se*. Sensitivity of the MNS for specifically the interactive nature of actions has been proposed (Csibra, 2008; Streltsova et al., 2010). Future studies could include a condition in which two agents simultaneously perform actions independently from each other (no coordination between them), which may help to delineate the role of the MNS in representing *interactions*. The current data suggest that agent involvement *per se*, or the potential for active involvement, are not incorporated in the sensorimotor action representation of the dyadic interaction. However, this lack of evidence may be inherent to the current paradigm or to insufficient power and more studies are required.

In conclusion, the current data suggests that sensorimotor representations of observed dyadic actions are sensitive to the extent of bodily articulations performed simultaneously by multiple agents. The findings contribute to our understanding of the neural processes underpinning perception of realistic interactions between multiple agents who vary in their degree of involvement.

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