

Favouritism in the motor system: social interaction modulates action simulation

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The ability to anticipate others' actions is crucial for social interaction. It has been shown that this ability relies on motor areas of the human brain that are not only active during action execution and action observation, but also during anticipation of another person's action. Recording electroencephalograms during a triadic social interaction, we assessed whether activation of motor areas pertaining to the human mirror-neuron system prior to action observation depends on the social relationship between the actor and the observer. Anticipatory motor activation was stronger when participants expected an interaction partner to perform a particular action than when they anticipated that the same action would be performed by a third person they did not interact with. These results demonstrate that social interaction modulates action simulation.

Keywords: action simulation; motor system; social interaction; EEG; favouritism

1. INTRODUCTION

Anticipating what others are going to do next is a principal function of social cognition. Not only cognitive and neurophysiological mechanisms underlying mental state attribution (Amodio & Frith 2006), but also predictive mechanisms in the human motor system may contribute to this function (Wolpert *et al.* 2003; Wilson & Knoblich 2005; Aglioti *et al.* 2008). Research in primates has revealed a 'mirroring' function in groups of neurons in premotor and parietal cortices that fire during execution and observation of goal-directed movements (Gallese *et al.* 1996; Fogassi *et al.* 2005). Evidence for the existence of a topographically similar, human 'mirror-neuron system (MNS)' with analogous functional properties has been provided by neurophysiological and imaging studies (e.g. Calvo-Merino *et al.* 2006; Hari 2006; Southgate *et al.* 2009). In addition, areas with strong reciprocal connections to the MNS, such as the primary motor cortex (MI) and the supplementary motor area (SMA), have been shown to exhibit MNS-like activity (Koski *et al.* 2003; Kilner & Frith 2007).

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In support of anticipatory motor activation, it has been shown that MNS activation occurs prior to an expected action (Kilner *et al.* 2004; Ramnani & Miall 2004) and in the absence of direct action observation (Umiltà *et al.* 2001). Central to the interpretation of these findings is the concept of motor simulation (Jeannerod 2001), which suggests that the overlapping neural activations for observing, anticipating and performing actions can be explained by the assumption that observers simulate others' actions using their own motor system.

The extent to which simulation processes are triggered when others' actions are observed or expected depends on the observer's expertise at performing these actions (Calvo-Merino *et al.* 2006; Aglioti *et al.* 2008). Moreover, it has been demonstrated that MNS activation is modulated by the bodily orientation and gaze direction of the observed actor (Kilner *et al.* 2006, 2009). However, it is unknown whether the social relationship between individuals modulates action simulation. Addressing this question is crucial, because to date studies that have investigated modulations of MNS activity as a function of social context have manipulated physical cues rather than the psychological relationships between the actor and the observer that are constitutive of human social life.

In two electrophysiological (electroencephalogram; EEG) studies, we tested whether anticipatory motor activation is stronger when people anticipate the action of an interaction partner compared with the same action performed by a 'loner'. As a measure of anticipatory motor simulation, we focused on the amplitude of the contingent negative variation (CNV) (Walter *et al.* 1964). The late part of CNV is considered a marker of motor preparation and predominantly reflects SMA and MI activity (for a review, see Leuthold *et al.* 2004). In addition, we investigated brain oscillatory activity (15–25 Hz) within the frequency range of the beta rhythm. The decrease of beta activity prior and during a movement is typically strongest over primary motor areas and constitutes a well-established index of motor activation (Pfurtscheller & Lopes da Silva 1999). Thus, we predicted that participants would show a larger CNV amplitude, as well as a stronger decrease in beta activity, while anticipating an interaction partner's action compared with anticipating the same action performed by a person who always acted alone.

2. MATERIAL AND METHODS

(a) Participants

- *Experiment 1.* EEG was recorded from 16 right-handed participants (10 females and six males; age = 25.3 ± 6.4 years). An interaction partner and a loner were assigned to each EEG participant.
- *Experiment 2.* EEG was recorded from nine pairs of right-handed participants (nine females and nine males; age = 25.5 ± 6.5 years). A loner was assigned to each group. Two participants were removed from the analysis owing to technical problems during data recording.

Participants did not know each other before the experiment. They practiced their tasks during a short practice block.

(b) Procedure

For details, see electronic supplementary material, Methods.

- *Experiment 1.* The participant, the interaction partner, and the loner were seated around a table forming an equilateral

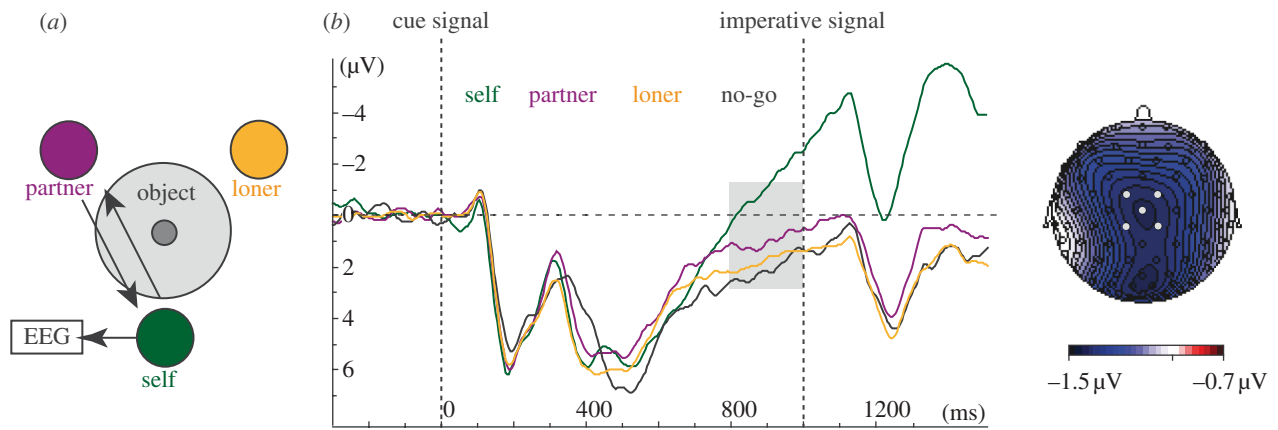


Figure 1. (a) Colour-coded drawing of set-up in Experiment 1. (b) Pooled, colour-coded CNV waveforms (derived from electrodes Cz, FCC1h, FCC2h, CCP1h, CCP2h) and scalp voltage topography (top view) of the difference between partner and loner (average data). The late CNV when anticipating to observe the individual action of the partner (in purple) is significantly higher compared with anticipating to observe the same action performed by the loner (in orange) during the last 200 ms (grey square) before the imperative signal onset. The late CNV before the loner's action did not differ from the CNV in the no-go condition (in black). Presented here as a point of reference, the late CNV was higher when preparing for action execution (in green) than when anticipating to observe another person's action (for similar results, see Kilner *et al.* 2004).

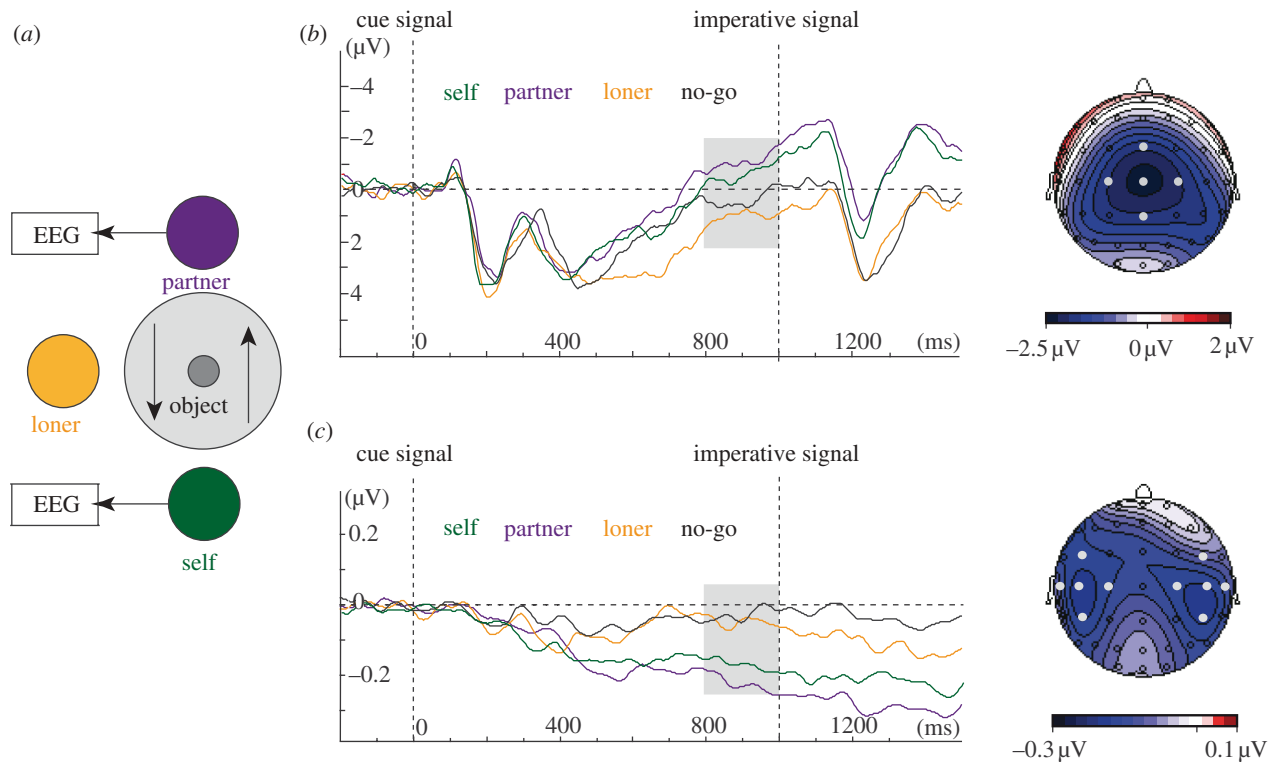


Figure 2. (a) Colour-coded drawing of set-up in Experiment 2. (b) Pooled, colour-coded CNV (derived from electrodes Cz, C1, C2, FCz, CPz). (c) Beta activity waveforms (derived from electrodes C1, C3, C5, FC3, CP3; C2, C4, C6, FC4, CP4) and scalp voltage topographies (top view) of the difference between the partner and the loner (average data).

triangle. They performed a choice-reaction task, where visual cues indicated the type of action to be performed, followed 1000 ms later by an imperative visual stimulus prompting them to act. All three people had a clear view of each other and their respective movements. Their task was lifting an object placed in the middle of the table and either returning it to its original position (individual action) or passing it to another person/receiving it from another person (joint action). During joint action, participants equally often passed the object and received it from the partner. All three people performed individual actions. Half of the blocks were performed with the left hand and the other half with the right hand. The participant engaged with the 'partner' in joint action, whereas the 'loner' always acted alone and

never interacted with the others. The loner performed individual actions three times as often as each of the partners to ensure that all individuals were active equally often. In one-eighth of the trials, the cue instructed all three individuals not to act (no-go condition). EEG was recorded from one of the partners (figure 1a). The critical period for our analysis was the time interval between the cue and the imperative stimulus, during which all participants remained motionless, fixating a cross presented on top of the object.

— *Experiment 2.* We employed the same experimental paradigm, with the important difference that partners were facing each other, while the loner was sitting at the side (figure 2a). The loner performed individual actions as often as each of the partners, to establish a higher frequency of interaction

between the partners. Moreover, EEG was recorded from both partners.

3. RESULTS

We examined motor activation when anticipating to observe an individual action (object lifted and placed back) performed by one's partner compared with anticipating the same action performed by the loner.

- *Experiment 1.* As predicted, the late CNV was more pronounced when participants anticipated the partner to act individually compared with when they expected that the same action would be performed by the loner (figure 1*b*). A 3×2 ANOVA with the factors anticipated action (none, loner, partner) and hand (left versus right) showed a significant main effect of action ($F_{2,30} = 5.90$, $p < 0.01$). The late CNV was more pronounced for the partner compared with the loner ($t_{15} = 2.28$, $p < 0.05$). The late CNV for the loner was not significantly different from the no-go condition ($t_{15} = 1.16$, $p = 0.27$). There was no effect of responding hand nor a significant interaction. These results indicate that simulation of another person's action, as reflected in activation of motor cortices, is more pronounced when the other is perceived as an interaction partner.
- *Experiment 2.* To further validate the observed effect of social interaction on action simulation, Experiment 2 tested whether a more salient contrast between the partner and the loner would increase the observed differences in the late CNV. Confirming our prediction, the results showed a larger difference in the late CNV between anticipating the partner's individual action and the loner's individual action (figure 2*b*). The 3×2 ANOVA revealed a significant main effect of the anticipated action ($F_{2,30} = 5.83$, $p < 0.01$). There was no effect of responding hand nor a significant interaction. As in Experiment 1, the late CNV was more pronounced for the partner than for the loner ($t_{15} = 3.21$, $p < 0.01$). Again, the loner was not significantly different from the no-go condition ($t_{15} = 1.46$, $p = 0.17$).

The analysis of beta oscillations as an index of motor activation further corroborates these findings. Whereas no significant modulations of beta activity were observed in Experiment 1, beta activity in Experiment 2 revealed a similar pattern as the late CNV. The decrease in beta activity was stronger when participants anticipated the partner's individual action compared with the loner's action (figure 2*c*). A $3 \times 2 \times 2$ ANOVA with the factors anticipated action (no-go, loner, partner), hand and hemisphere verified the statistical significance of this result, $F_{2,30} = 6.36$, $p < 0.01$, for the main effect of action; none of the other effects or interactions were significant. There was a significant difference between the partner and the loner ($t_{15} = 2.69$, $p < 0.05$), but no significant difference between the loner and the no-go condition ($t_{15} = 0.77$, $p = 0.45$).

4. DISCUSSION

The present results indicate that motor activation during action anticipation depends on the social relationship between the actor and the observer, formed during the performance of a joint action task. Simulation of another person's action, as reflected in the activation of motor cortices, gets stronger the more the other is perceived as an interaction partner. This finding extends previous work showing that the activation of brain areas of the human MNS is influenced by factors such as the motor expertise of the observer (Calvo-Merino *et al.* 2006), as well as body and gaze cues that may affect the 'social relevance' of the actor (Kilner *et al.* 2006, 2009). Our results cannot be attributed to predictive eye movements, since no action was taking place during the foreperiod and participants fixated the object. To our knowledge, the present findings provide the first demonstration that, besides physical cues, the social relationship between an actor and an observer constrains action simulation.

One may argue that observers did not simulate the impending individual action of their partner, but instead prepared to act themselves, erroneously preparing for joint action. According to this view, the higher frequency of interaction in Experiment 2 could have led to the stronger motor preparation observed in this experiment. Results from a control experiment where the frequency of interaction was manipulated argue against this explanation (see electronic supplementary material, Control Experiment). In this experiment, the late CNV was not affected by the frequency with which participants performed joint actions with two partners.

Our results are consistent with prior evidence that demonstrates considerable flexibility of the MNS. In particular, incompatible visuomotor training has been shown to lead to reversed patterns of mirror responses in the brain (Catmur *et al.* 2007). The present findings extend this research by demonstrating that modulations of MNS activity can occur without prior training, reflecting top-down modulations governed by social interaction. Whereas the motor system does not seem to be activated by the impending actions of those whom we do not interact with, it favours the actions of our interaction partners. While it is already known that social relations modulate empathic brain responses (Singer *et al.* 2006), the present study provides the first evidence, to our knowledge, that social relations modulate action simulation.

All participants gave informed consent and the study conforms to the terms of the Declaration of Helsinki.

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