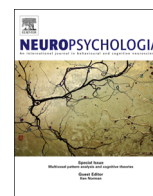




ELSEVIER

Contents lists available at SciVerse ScienceDirect

## Neuropsychologia

journal homepage: [www.elsevier.com/locate/neuropsychologia](http://www.elsevier.com/locate/neuropsychologia)

## History of interaction and task distribution modulate action simulation

Dimitrios Kourtis<sup>a,\*</sup>, Günther Knoblich<sup>b,c</sup>, Natalie Sebanz<sup>c,b</sup><sup>a</sup> Department of Experimental Psychology, Ghent University, Henri Dunantlaan 2, 9000 Ghent, Belgium<sup>b</sup> Department of Cognitive Science, Central European University, Budapest, Hungary<sup>c</sup> Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, Nijmegen, The Netherlands

## ARTICLE INFO

## Article history:

Received 7 December 2012

Received in revised form

19 March 2013

Accepted 1 April 2013

Available online 11 April 2013

## Keywords:

Joint action

EEG

Action simulation

History of interaction

Task distribution

## ABSTRACT

Recent work suggests that social interaction modulates the sensorimotor simulation of an observed action. Recording electroencephalograms during a triadic social interaction, we investigated the effects of two specific aspects of social interaction on action simulation: the recent history of interaction and the distribution of individual parts of a simple joint task between actors. Activation of sensorimotor areas was larger during observation of the individual action of an interaction partner compared to observation of the same action of a person performing only individual actions, unless this person had interacted with the observer in the recent past. In addition, it is likely that the participants simulated the action onset of the individual actions of their interaction partner, but only when their partner was the one who initiated the joint action. These results demonstrate that action simulation can be modulated by present and past interactions between the actor and the observer and by how a joint task is distributed between actors.

© 2013 Elsevier Ltd. All rights reserved.

## 1. Introduction

Action observation is a frequent activity in our everyday life. It allows people to derive numerous aspects of a person's behaviours, goals, and mental states. Many of these aspects are potentially beneficial for ongoing and future interactions. An increasingly popular view in Cognitive Science is that the representation of observed actions is modulated and possibly shaped through people's interactions with others (e.g., Schilbach, Timmermans, Reddy, Costall & Bente *in press*) at multiple levels. The objective of the present study was to investigate two specific aspects of social interaction that may modulate basic representations involved in action observation (1) the recent history of the interaction and (2) the task distribution between the actors involved in the interaction.

The starting point for our investigation was the extensive research on action simulation during action observation which has demonstrated that actions, sensations and emotions perceived in others are represented in a similar manner as the actions, sensations, and emotions in the perceiver (for reviews, Jeannerod, 2001; Keyzers, Kaas, & Gazzola, 2010; Rizzolatti & Sinigaglia, 2010; Sommerville & Decety, 2006). Key neurophysiological support was provided by the discovery of "mirror neurons", located in primates' ventral premotor cortex (PMv) and inferior parietal lobule (IPL), which fire during both action execution and action perception (Di Pellegrino, Fadiga, Fogassi,

Gallese and Rizzolatti, 1992; Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Subsequent studies in humans have repeatedly shown that "mirror-like" activation is not limited to PMv and IPL, but is exhibited in a number of brain areas, including superior temporal sulcus (STS), dorsal premotor cortex (PMd) supplementary motor area (SMA), primary motor cortex (MI), somatosensory cortices (SI and SII) and subcortical structures (for reviews, Keyzers & Gazzola, 2009; Molenberghs, Cunnington, & Mattingley, 2012; Rizzolatti & Sinigaglia, 2010).

With regard to the functional role of the "mirror system" in the action domain, a number of accounts claim that it may serve action recognition (Bonini & Ferrari, 2011), and/or action understanding "from the inside" (Rizzolatti & Sinigaglia, 2010) as well as the prediction of the outcome of others' actions (Kilner, Friston, & Frith, 2007). The latter view is supported by studies showing that the mirror system is activated when the last part of an action cannot be directly observed (Umiltà et al., 2001), and also when participants are asked to predict the effectiveness of an action (Lamm, Fischer, & Decety, 2007) or infer the actors' motor intentions (Iacoboni et al., 2005).

Previous investigations have also shown that the neural representation of an observed action is not a purely automatic process, but it may depend on factors such as the motor expertise/familiarity of the observer with the observed action (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008), and the bodily orientation and gaze of the actor (Kilner, Marchant, & Frith, 2006, 2009). Furthermore, a number of EEG studies have linked the suppression of the 10-Hz mu brain rhythm, which is regarded as a reliable index of sensorimotor activation (Hari, 2006) to the social context of an observed action

\* Corresponding author. Tel.: +32 9 264 64 77.  
E-mail addresses: [dimitrios.kourtis@ugent.be](mailto:dimitrios.kourtis@ugent.be),  
[dimkourtgr@yahoo.com](mailto:dimkourtgr@yahoo.com) (D. Kourtis).

(Oberman, Pineda, & Ramachandran, 2007; Perry, Stein, & Bentin, 2011; Streltsova, Berchio, Gallese, and Umiltà 2010). The results of these studies converge towards the idea that action simulation is enhanced by the social relevance of the observed action and also by the involvement of the observer in a social situation.

We assessed the effects of social interaction on action simulation in a recent EEG study (Kourtis, Sebanz, & Knoblich, 2010), which involved three participants. Two of them performed both individual actions (i.e. lifting an object) and joint actions (i.e. passing the object), while the third participant (“loner”) performed only individual actions. The results showed that a person’s motor system was more active when anticipating to observe an individual action performed by the interaction partner than when anticipating to observe the same action performed by the loner. This finding suggests that interpersonal aspects of the relation between an actor and an observer affect the extent to which predictive action simulation takes place. In particular, the observer’s motor system seems to “favour” simulation of the actions of interaction partners. This also provides a first indication that the history of interaction between an actor and an observer may indeed affect action simulation. A recent finding (Hogeveen & Obhi, 2012) seems to support a similar point. They reported greater activation of the motor system during observation of recorded human actions when the observers had previously engaged in a social interaction. However, unlike our previous study (Kourtis et al., 2010), Hogeveen and Obhi (2012) did not investigate differences in action simulation during a triadic social interaction (participants always observed a hand manipulating an object on a video screen). Rather, they describe a general effect of social interaction on subsequent action observation.

In the present study we attempted to directly test the hypothesis that action simulation would depend on the prior interaction history with a particular partner. We employed a similar experimental set-up as in our previous study (Kourtis et al., 2010) with some modifications. There was one participant and two confederates and EEG was only recorded from the participant. During the first part of the experiment, the participant interacted with one of the confederates (the partner) and not with the other (the loner). In the second part of the experiment, the confederates switched roles. Thus, the loner of the first part became the partner in the second part and the partner of the first part became the loner in the second part.

Given the adaptability of the mirror system within the time-course of an experiment (Catmur, Walsh, & Heyes, 2007; Catmur et al., 2008), we investigated whether the pattern of action simulation in the second part of the experiment would mirror the expected pattern of the first part (i.e. greater simulation for the partner’s action) or whether the fact that the new loner had previously interacted with the observer would affect action simulation. Focusing mainly on the modulation of the 10-Hz mu rhythm, which is typically associated with mirror system activity (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011), we predicted that observation of the partner’s action would induce larger mu suppression than the loner’s action in the first part of the experiment. However, if the history of interaction matters, this difference should be smaller, if not absent, in the second part of the experiment, because the new loner had interacted with the observer in the first part of the experiment.

An additional objective was to investigate whether simulation of another’s action depends on the task distribution, which is a critical factor in effective interpersonal coordination (Bosga, Meulenbroek, & Cuijpers, 2010; Konvalinka, Vuust, Roepstorff, & Frith, 2010). “Passing an object” is an asymmetric joint action, where the giver has the task of initiating the action and the receiver needs to adjust the onset of his or her actions to the giver. We have recently shown that when passing an object, it is the receiver who simulates the temporal aspects of the giving action and drives the coordination in give and receive type joint actions (Kourtis, Sebanz, & Knoblich, 2013). Thus, we expected that only the receiver but not the giver

would accurately simulate the action onset of his/her partner’s actions even when knowing that the partner was instructed to perform an individual action.

To test our hypothesis, we assigned each participant only one part of the joint action (i.e. giving or receiving the object) in each part of the experiment. Based on our previous findings, our predictions focused on the late part of Contingent Negative Variation (CNV) (Walter, Cooper, Aldridge, McCallum, & Winter, 1964), a slow brain potential of negative polarity developing between a cue and a go-signal. During its late stages the CNV reflects primarily time-based motor preparation at an effector-unspecific level (Leuthold & Jentzsch, 2009; Leuthold, Sommer, & Ulrich, 2004). We predicted that differences in the CNV between partner and loner would be modulated by the action the partner is required to perform. When the observer is in the mindset of receiving, the difference should be larger than when he or she is in the mindset of giving.

## 2. Methods

### 2.1. Participants

Continuous EEG data were recorded from 24 right-handed participants. All participants (21 female and 3 male; age =  $21.4 \pm 2.2$  yrs) had normal or corrected-to-normal vision. They had no history of hand or arm injuries or diseases or any mental, cognitive, and other neurological disorder. All participants provided their informed consent after full explanation of the study.

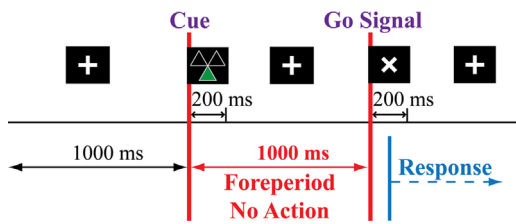
### 2.2. Experimental setup and procedure

The experiment was run in a quiet, normally illuminated, well-ventilated, and electromagnetically shielded room. Two confederates participated in the experiment; one of them was the interaction partner and the other one the loner (i.e. the person performing only individual actions). The roles of the confederates were reversed in the second part of the experiment. The participant and the two confederates were seated around a table, forming an equilateral triangle (Fig. 1).

A cylindrical candle (height: 13.3 cm, radius: 2.54 cm) was placed on a fixed base at the centre of the table. A white wooden disc (radius: 6.35 cm) was attached on the top of the candle. Colour-coded stimuli were projected onto the surface of the disc by an LCD projector (EPSON, EMP-X52). The projector was encased in a metallic contraption, mounted on the ceiling directly above the centre of the table. A (4.5 cm × 4.5 cm) Force Sensing Resistor (FSR) was centrally placed on the table (~7–8 cm from the table edge) in front of each person to record reaction times. We employed a choice-reaction paradigm where a fully informative visual cue, presented for 200 ms, indicated the type of action to be performed. It was followed by an imperative visual stimulus (“go signal”: a white “X” on black background; inter-stimulus-interval = 1000 ms), prompting the participants to act (Fig. 2).



**Fig. 1.** Photo of the experimental setup. The participants were seated around a table forming an equilateral triangle. A candle with a white wooden disc attached on its top was placed onto a fixed base at the centre of the table. A projector, mounted to the ceiling, was displaying stimuli on the surface of the disc. In the instance showed here, the participant (right) is giving the object to her partner (left), while the loner (middle) remains motionless.



**Fig. 2.** Timeline of an experimental trial. Each trial started with the presentation of a focusing cross for 1000 ms. The cross was then replaced by a fully informative visual Cue, presented for 200 ms, which indicated the type of action to be planned (i.e. lifting the object – passing the object – no action). The Cue stimulus was replaced by the focusing cross, presented for 800 ms, which was subsequently replaced by a visual Go signal, presented for 200 ms, which prompted the participants to swiftly perform the indicated action. The participants as well the confederates were motionless during the 100 ms foreperiod and initiated their actions after the display of the Go signal. All stimuli were presented on top of the object.

The cue stimuli were projected onto the disc on top of the candle. They consisted of three white-framed equilateral triangles, overlaid on a black square, the apexes of which met at the centre of the square (see Fig. 2, under the word “Cue”). There were three different types of stimuli: (i) a cue with one triangle filled with green colour indicated individual action planning, (ii) a cue with one triangle filled with green colour and another one with orange colour indicated joint action planning, (iii) a cue where no triangles were filled with colour indicated that no action should be performed in that trial (“no-go” condition).

In the individual action condition, the cue instructed the person seated at the side of the green triangle to plan a reaching action towards the object, in order to lift it vertically to an approximate height of 30 cm, and to return it back to its original position. In the joint action, the cue instructed the person seated at the side of the green triangle (“giver”) to plan a reaching action towards the object in order to lift it vertically to an approximate height of 30 cm and to hand it to their interaction partner seated at the side of the orange triangle (“receiver”). The receiver needed to plan to reach out and to receive the object from the giver and to then place it back to its original position. In the no-go condition the cue signalled that none of the participants was going to perform an action.

The experiment was divided into two parts. During each part, the participant performed only one type of joint action. More specifically, for half of the participants (Group A, see Fig. 3) and in the first part of the experiment, there were five different conditions: (1) the participant lifted the object (performing an individual action), while the partner and the loner were passive observers, (2) the partner lifted the object (performing an individual action), while the participant and the loner were passive observers, (3) the loner lifted the object (performing an individual action) while the participant and the partner were passive observers, (4) the participant (Giver) passed the object to his/her partner (Receiver), while the loner was a passive observer, and (5) all participants remained motionless (no-go condition). The crucial comparison was between conditions 2 and 3, where the participant was a passive observer of the individual action of the partner or a passive observer of the individual action of the loner, respectively.

In the second part of the experiment, the confederate who acted as the interaction partner in the first part of the experiment acted as the loner and vice versa. In addition, the roles of the interaction partners in condition 4 were reversed: the participant acted as the Receiver and the confederate/partner acted as the Giver in the performance of the joint action. Consequently, each participant performed different parts of the joint action with different confederates in each of the two parts of the experiment (Fig. 3).

The other half of the participants (Group B) performed the exact same actions. The only difference compared to Group A was that the roles in the joint action condition were reversed. More specifically, the participants were Receivers in the first part of the experiment and Givers in the second part of the experiment (condition 4).

Each experimental part consisted of 6 blocks of 80 trials each, preceded by a practice block of equal length, which resulted in 96 experimental trials per condition in each part. In half of the blocks in each part, all participants used their right hand and in the other half of the blocks they used their left hand. The five experimental conditions occurred with equal probability within each block. The order of blocks and the order of trials within a block were randomized.

### 2.3. Data acquisition

#### 2.3.1. Questionnaires

In order to measure the subjective feeling of closeness that participants experienced towards the confederates, we employed a variation of the Inclusion of the Other in the Self (IOS) scale (Aron, Aron, & Smollan, 1992). The IOS is a single item pictorial measure of self-other inclusion and relationship closeness, with scores ranging from 1 to 7, where higher numbers reflect greater closeness. In our study, the IOS scale was presented on an A4 sheet of paper where two circles were placed at

7 increasing distances to each other. The participants were asked to respond to the following questions “How close did you feel to the person on the left/right”, by selecting the pair of circles that corresponded to their feeling of closeness to the interaction partner and to the loner. This procedure took place after the completion of each experimental part.

#### 2.3.2. Behavioural data

Action onset was defined as the time interval between the onset of the go signal and the release of the FSR. For each participant, all action onsets that were smaller than 100 ms or differed more than two standard deviations (SD) from the mean action onset within each condition were removed from further analysis. There were no statistically significant differences between left hand performance and right hand performance (all  $ps > 0.24$ ). Therefore, the analysis was performed on pooled data from both hands, by means of a  $2 \times 2$  ANOVA with factors Experimental Part (first vs. second) and Relation (partner vs. loner) (see 3).

#### 2.3.3. Electrophysiological data

EEG was recorded continuously using a carefully positioned, equidistant cap (EasyCap, Herrsching, Germany) with 64 Ag/AgCl electrodes relative to an (off-line) average mastoid reference. Vertical eye movements were monitored using one pair of bipolar electro-oculography (EOG) electrodes positioned above and directly under the right eye, while horizontal eye movements were monitored using a pair of bipolar electro-oculography (EOG) electrodes positioned at the outside of each of the eyes. Electrode impedance was kept below 20 kOhm. EEG and EOG signals were amplified with a band-pass of 0–125 Hz by two BrainAmp DC Amplifiers (Brain Products GmbH, Gilching, Germany) and sampled at 500 Hz.

### 2.4. Data processing and analysis

EEG data processing was performed off-line using the Brain Vision Analyzer (V. 1.05, Brain Products GmbH, Gilching, Germany) software. Initially, ocular correction using the Gratton–Coles algorithm (Gratton, Coles, & Donchin, 1983) implemented in Brain Vision Analyzer was used to eliminate or reduce in amplitude artefacts induced by horizontal or vertical eye movements. The corrected EEG data were then segmented off-line into epochs from 300 ms before cue onset to 2200 ms after cue onset. The data were filtered using a low-cut-off filter of 0.05 Hz (24 dB/octave) and a high-cut-off filter of 60 Hz (24 dB/octave) in order to remove slow drifts and excessive noise, respectively. Individual trials containing eye movement artefacts or incorrect responses were removed before averaging.

For analysis of event-related changes in spectral power, epochs were further processed to obtain temporal–spectral–evolution (TSE) waveforms (Salmelin & Hari, 1994). Hence, the individual epochs were first band-pass filtered between 8 and 12 Hz, using Butterworth zero phase-shift filters (24 dB/octave). The filtered epochs were then rectified before averaging to prevent phase cancellation. The resulting average waveforms represent the time-varying magnitude of activity in the selected frequency band.

There were no statistically significant differences between left hand performance and right hand performance (all  $ps > 0.15$ ). Therefore, all analyses were performed on pooled data from both hands. Mu-suppression was defined as the decrease in voltage in the 8–12 Hz frequency band, relative to a 200 ms pre-stimulus baseline period. The statistical analysis of the mu-suppression was conducted by pooling the mean activity from electrodes over left and right primary sensorimotor areas (i.e. electrodes 1, 3, 4, 5, 6, 7, 11, 12, 16, and 17) from 300 until 700 ms after go stimulus onset, which approximately coincided with the first 400 ms of movement (see 3). The resulting values were statistically compared by means of a  $3 \times 2$  ANOVA (Greenhouse–Geisser correction applied) with factors Condition (partner, loner, no-go) and Experimental Part (first, second).

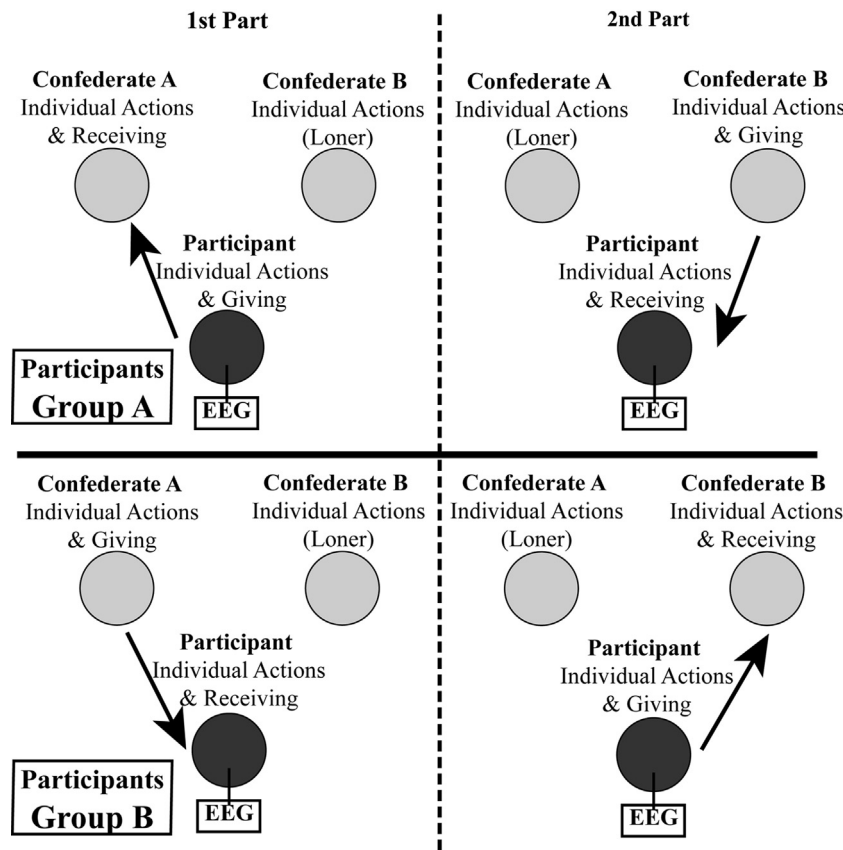
The ERP (i.e. CNV) statistical analysis was conducted by pooling the mean activity (relative to a 200 ms pre-stimulus period) from electrodes 1, 5, 6, 7, 16 and 17, which are located over the left sensorimotor cortex, during the last 200 ms before the onset of the go stimulus (see 3). The resulting values were statistically compared by means of a  $3 \times 2$  ANOVA with factors Condition (giver, loner, no-go) and Experimental Part (first, second).

## 3. Results

There were no statistically significant differences in the behavioural and EEG results between left hand performance and right hand performance ( $ps > 0.15$ ). Therefore, all analyses were performed on pooled data from both hands.

### 3.1. IOS-scale

The analysis of judgments on the IOS scale showed that the participants reported a greater degree of closeness to the interaction



**Fig. 3.** Participants' tasks during the experiment. The experiment was divided into two parts. The participants as well as the confederates were performing individual actions (i.e. lifting the object) throughout the experiment. In addition, half of the participants (Group A) were giving the object to their partner (Confederate A) in the first part of the experiment, whereas Confederate B performed only individual actions (i.e. the "loner"). In the second part of the experiment, the participant was receiving the object from Confederate B (the new partner), whereas Confederate A became the new "loner". The other half of the participants (Group B) were performing the opposite tasks compared to Group A.

partner compared to the loner, irrespective of the partner's task in joint trials (give or receive) for a given part of the experiment ( $ps > 0.49$ ). For this reason, we grouped the ratings given to givers and receivers under the term "partner" and compared them to the ratings given to the loners. The average rating during the first part of the experiment was 4.9 ( $SD=0.9$ ) for the partners and 3.7 ( $SD=0.9$ ) for the loners. During the second part, partners were rated with 4.9 ( $SD=0.9$ ) and loners with 4.0 ( $SD=1.2$ ) on the IOS scale. A  $2 \times 2$  ANOVA (Greenhouse–Geisser correction applied) with factors Experimental Part (first vs. second) and Relation (partner vs. loner), showed that there was a significant main effect of Relation ( $F(1,11)=23.5$ ,  $p < 0.001$ ). The main effect of Experimental Part as well as the interaction did not reach statistical significance. This means that the participants experienced a greater feeling of closeness towards their current interaction partner irrespective of the person they were interacting with and irrespective of their specific task (i.e. giving or receiving the object).

### 3.2. Action onset

The action onsets for the givers were 342 ms ( $SD=77$ ) and 364 ms ( $SD=91$ ) in the first and in the second part, respectively. Action onsets for the receivers were 347 ms (85) and 327 ms (74) in the first and second part. Action onsets for the loners were 352 ms ( $SD=101$ ) and 321 ms ( $SD=74$ ) in the first and second part. Because both confederates were responding equally fast irrespective of their specific task of giving or receiving the object ( $p > 0.5$ ), we grouped givers and receivers under the term "partner" and compared their action onsets to the loners' action onsets. A  $2 \times 2$  ANOVA (Greenhouse–Geisser correction applied) with factors Experimental Part (first vs. second)

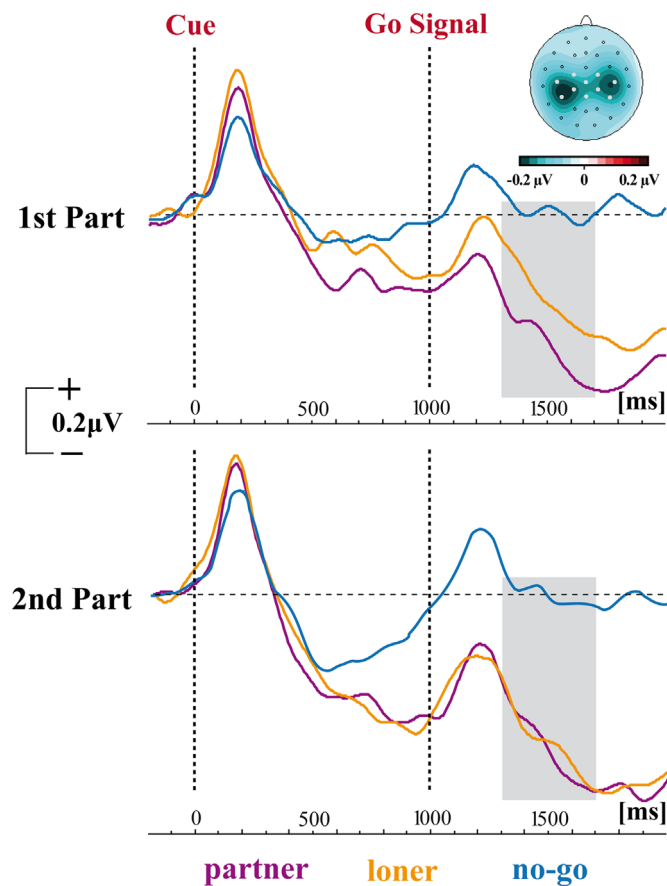
and Relation (partner vs. loner) showed that there was a significant main effect of Experimental Part ( $F(1,23)=6.5$ ,  $p=.018$ ), due to shorter action onsets in the second part of the experiment. The main effect of Relation and the interaction did not reach statistical significance. This shows that partners and loners initiated their action equally fast and all of them initiated their actions faster in the second part of the experiment.

### 3.3. Electrophysiological data

#### 3.3.1. Temporal spectral evolution—10 Hz mu rhythm

The amplitude analysis of cortical oscillations between 8 and 12 Hz revealed that the suppression of mu oscillations, induced by observation of the partner's individual actions, did not depend on the partner's task in joint trials for a given part of the experiment ( $ps > 0.58$ ). For this reason, we grouped the data obtained during observation of individual action of giving and receiving partners. These data were compared to the data obtained in a condition where the loner performed the same individual actions as the partner and the no-go condition where no action was performed.

In the first part of the experiment, the amplitude suppression of the mu rhythm was larger during observation of a partner's individual action than during observation of the same action performed by a loner (Fig. 4). However, in the second part of the experiment, the actions of the partner and the loner induced equal amounts of mu suppression. Both patterns were already present when participants anticipated the upcoming action by a partner or a loner. In addition, a small suppression in mu amplitude was present during the foreperiod in the no-go condition throughout the experiment, but it was completely absent after the onset of the go signal (Fig. 4).



**Fig. 4.** 10 Hz mu rhythm suppression. Colour-coded grand average mu rhythm waveforms in the first and the second part of the experiment, recorded from electrodes overlying left and right sensorimotor cortices (i.e. highlighted electrodes 1, 3, 4, 5, 6, 7, 11, 12, 16 and 17). The grey rectangles indicate the latency window for amplitude analysis. The topographical maps depict the difference in voltage between the “partner” and the “loner” conditions from 300 to 700 ms after go signal onset in the first part of the experiment. The vertical dashed line at times 0 and 1000 denotes cue and go signal onset, respectively.

We quantified the mu suppression by pooling the mean activity from electrodes over left and right primary sensorimotor areas (i.e. electrodes 1, 3, 4, 5, 6, 7, 11, 12, 16, and 17, Fig. 4) from 300 until 700 ms after go signal onset, which approximately coincided with the first 400 ms of movement. A  $3 \times 2$  ANOVA (Greenhouse–Geisser correction applied) with factors Condition (partner, loner, no-go) and Experimental Part (first, second) revealed a significant main effect of Condition ( $F(2,46)=14.5, p<0.001$ ) and a significant main effect of Experimental Part ( $F(1,23)=8.6, p=0.008$ ) confirming that the mu suppression was larger in the second part of the experiment. In addition, there was a significant interaction between the two factors ( $F(2,46)=3.7, p=0.035$ ), because the partner’s action induced larger mu suppression than the loner’s action ( $t(23)=-2.8, p=0.011$ ) in the first part of the experiment, whereas no such difference was present in the second part of the experiment ( $t(23)=-0.2, p=0.823$ ). Furthermore, the mu suppression induced by the partner’s as well as the loner’s action was larger than the mu suppression induced in the no-go condition in both experimental parts ( $ps < 0.015$ ).

### 3.3.2. ERP analysis

A CNV-like slowly rising negativity, developing during the one second long preparation interval between the onset of the cue and the onset of the go-signal was evident in all conditions. The CNV amplitude was of similar amplitude when the participant

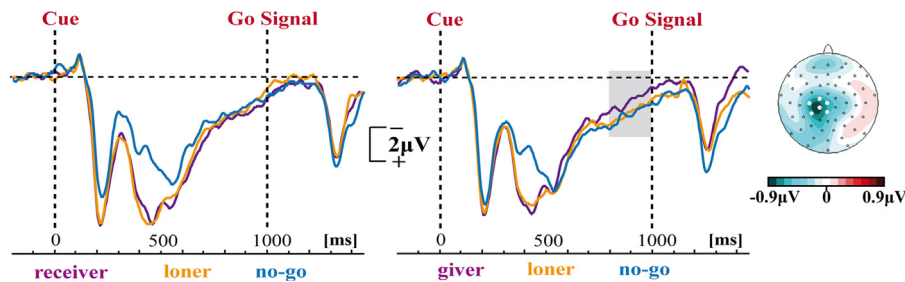
anticipated a partner’s individual action and a loner’s individual action when the partner was the receiver of the object in the joint task (Fig. 5, left). However, when the participant anticipated a giver’s individual action the CNV amplitude was larger in the partner condition than in the loner condition. The voltage topography of this difference during the last 200 ms before go signal onset (Fig. 5, right) showed that it was larger over mid- and left sensorimotor cortices, irrespective of the responding hand, possibly reflecting the documented dominance of the left hemisphere in motor control for right-handed persons (Taylor & Heilman, 1980).

The pre-movement CNV amplitude was quantified by pooling the voltage amplitudes during the last 200 ms before the onset of the go stimulus from electrodes 1, 5, 6, 7, 16 and 17 (Fig. 5). A  $3 \times 2$  ANOVA (Greenhouse–Geisser correction applied) with factors Condition (giver, loner, no-go) and Experimental Part (first, second) revealed a main effect of Condition ( $F(1,11)=4.9, p=0.039$ ). The main effect of Experimental Part and the interaction were not statistically significant ( $ps > 0.4$ ). Post-hoc *t*-tests revealed that the CNV was larger when the participant was anticipating to observe the giver’s individual action compared to anticipating the loner’s identical action ( $t(11)=-4.1, p=0.002$ ) or the no-go condition ( $t(11)=-2.3, p=0.045$ ). There was no difference between the loner condition and the no-go condition ( $t(11)=-0.6, p=0.583$ ).

## 4. Discussion

The present work builds on the idea that social interaction modulates the activation of the motor system in anticipation of an action and also during action observation (Hogeveen & Obhi, 2012; Kourtis et al., 2010). Consistent with our previous study (Kourtis et al., 2010), the present findings show that sensorimotor areas are more active when anticipating and observing the individual actions of an interaction partner, compared to anticipating and observing actions performed by a person that the observer never interacts with (i.e. the loner). Notably, the partner and the loner performed the same action (lifting an object) equally fast and at the same location. Therefore, this “favouritism” of the sensorimotor system towards the interaction partner is unlikely to be caused by differences in sensory input (cf. Becchio et al., 2012). Instead, the most likely explanation is that the occasional performance of joint actions enforced the development of a social relation between the interaction partners, which exerted a top-down influence on the sensorimotor simulation of the partner’s individual actions. This may be interpreted as a difference in task representation that reflects an individual’s propensity to view the partner’s individual action as a potential component of a joint action (Tsai, Sebanz, & Knoblich, 2011; Vesper, Butterfill, Knoblich, & Sebanz, 2010).

Our findings are consistent with the “associative learning hypothesis” of action understanding (Heyes, 2010), which states that the mirror system is forged through sensorimotor experience, a large part of which is obtained through interaction with others. Previous studies have shown that mirror system activation can be abolished (Heyes, Bird, Johnson, & Haggard, 2005), enhanced (Press, Gillmeister, & Heyes, 2007) or temporarily reversed (Catmur et al., 2007, 2008) by sensorimotor training. Expanding these results, we showed that sensorimotor activation depends on past and present interactions with others and also on the distribution of a joint task. Our study does not provide arguments in favour or against the assumed role of the mirror system in action understanding (Rizzolatti & Sinigaglia, 2010), which in fact is not incompatible with the associative learning hypothesis (Press, Heyes, & Kilner, 2011). However, in accordance with the recently formulated “interactive account of social cognition” (Schilbach et al., in press), it highlights the important role of present and past human interaction in social cognition.



**Fig. 5.** CNV waveforms. Colour-coded grand average ERP waveforms, recorded from electrodes overlying mid- and left sensorimotor cortices (i.e. highlighted electrodes 1, 5, 6, 7, 16, and 17), when the interaction partner was assigned the receiving part of the joint action (left) or the giving part of the joint action (right). The grey rectangle indicates the latency window for amplitude analysis. The topographical map depicts the difference in voltage between the “giver” and the “loner” conditions during the last 200 ms before go signal onset. The vertical dashed line at times 0 and 1000 denotes cue and go signal onset, respectively.

#### 4.1. History of interaction

In the first part of the experiment, the suppression of the mu rhythm was larger in relation to the partner's individual action compared to the mu suppression in relation to the loner's identical individual action. This difference was numerically evident during action anticipation, but became statistically significant after response onset over primary sensorimotor areas (Fig. 4). The movement-related suppression of the mu rhythm is considered a reliable index of sensorimotor activation (Arroyo et al., 1993; Hari, 2006) and it is believed to reflect the transformation process from “perceiving” into “doing” (Pineda, 2005). This integrative role of the mu rhythm, along with its topographical cortical distribution has led to the idea that the mu suppression is associated with activation of the mirror system (Arnstein et al., 2011; Bernier, Dawson, Webb, & Murias, 2007; Lepage & Théoret, 2006; Muthukumaraswamy, Johnson, & McNair, 2004; Pineda, 2005).

Our results provide further evidence that the mirror system favours the observed actions of persons that the observer occasionally interacts with. Moreover, the joint task distribution does not seem to be of particular importance, since the action of giver and receiver induced equal mu suppression. This also speaks against the possibility that the mu suppression reflected the observer's involuntary preparation to receive the object, as specified by her or his individual contribution to the joint task because half of the participants were givers in the joint task and thus never received the object from their partners.

Unlike during the first part of the experiment, the mu suppression during the second part was equally large in relation to the new partner's and the new loner's action. This is unlikely to be caused by fatigue or disengagement from the task because the mu suppression was larger than in the first part of the experiment. Instead, it implies that the loner maintained his or her previous status of an interaction partner in the participant's mind. Thus, the present study demonstrates for the first time that action simulation may not only be modulated by the current actor–observer relationship, but also by their (recent) history of their interaction.

#### 4.2. Task distribution

The assignment of specific roles in the joint task (i.e. giver and receiver) had a clear effect on the amplitude of the late CNV potential, which developed during the preparation period. The late CNV was larger when the participant anticipated observing a partner's individual action rather than a loner's individual action. Notably, this difference was only present when the partner was the one giving the object in the joint task.

The late CNV is considered to reflect predominantly time-locked, effector-unspecific activation of (pre)motor areas in anticipation of a relevant event (Leuthold & Jentzsch, 2009; Leuthold et al., 2004; Van Rijn, Kononowicz, Meck, Ng, & Penney, 2011). In addition and

depending on the task, frontal, temporal and parietal areas often contribute to the late CNV (Praagstra, Kourtis, Kwok, & Oostenveld, 2006; Verleger, Wauschkuhn, van der Lubbe, Jaśkowski, & Trillenberg, 2000). The centro-parietal distribution of the difference waveforms between the giver and the loner (Fig. 5) suggests that the participants may have employed their sensorimotor system to represent in advance the action onset of their partner. However, this was only the case when the observed actor initiated the joint task (performed the giving part in joint trials). Consistent with the findings of our previous study (Kourtis et al., 2010), this suggests that social interaction may indeed constrain anticipatory action simulation, and this effect depends on the specific roles of the actor and observer in the interaction.

However, an alternative interpretation of this effect needs to be considered. Given the fact that the CNV amplitude modulation was only present in participants who had the role of the Receiver in the joint task, it is possible that when the participants anticipated observing the partner's action, they were involuntarily preparing a complementary receiving action. Recent studies speak against this interpretation as they have shown that even in cases when a complementary action is primed by the action context, observers first simulate the action of another person, and prepare a complementary response only after the actor directs her movement at them (Sartori, Cavallo, Bucchioni, & Castiello, 2011, 2012). Thus, although the possibility that the participants were covertly preparing a receiving action cannot be ruled out with certainty, it is more likely that they were simulating the onset of their partners' anticipated action.

#### 4.3. Judgements of closeness

The analysis of the IOS questionnaire showed that the participants judged the interaction partners to be closer to them compared to the persons that did not interact with them. Consistent with the view that social connection can emerge from interpersonal coordination (Marsh, Richardson, & Schmidt, 2009), our study shows that the performance of a coordinated joint task can induce a subjective feeling of closeness towards the interaction partner. However, this feeling does not seem to depend on the history of interaction or the role of the partner (giving or receiving) in the joint task. Judgements of closeness did not correlate with the modulation of the CNV amplitude or the mu suppression, both of which depended on task distribution and history of interaction. Thus, the present results indicated that judgements of closeness may arise (at least partly) independently of sensorimotor simulation of another person's action (Frith & Frith, 2008).

## 5. Conclusion

The present study shows that social interaction, in the form of coordinated joint action, can exert a top-down influence on the

sensorimotor simulation of another person's action and can also induce feelings of closeness, even if at that time the observer does not intend to interact with the actor. This is the case not only when the observer and the actor occasionally engage in interaction with each other, but also when they have interacted in the recent past. In addition, it highlights the importance of joint task distribution, suggesting that the observer simulates in advance the movement onset of the actor, only if the actor is the person who initiates the joint task. The present study provides valuable insights into the factors that affect action simulation and it may potentially have implications for several lines of social cognition research, such as emotion processing and in-group vs. out-group relations. Our findings suggest that people should not only be studied detached from their environment, but present and past interactions with others should also be taken into account.

## Acknowledgements

This research was funded by a EURYI grant awarded to Natalie Sebanz by the European Science Foundation and by NWO through the ESF EuroUnderstanding programme.

## References

- Arnstein, D., Cui, F., Keysers, C., Maurits, N. M., & Gazzola, V. (2011). M-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *Journal of Neuroscience*, *31*, 14243–14249.
- Aron, A., Aron, E. N., & Smollan, D. (1992). Inclusion of other in the Self Scale and the structure of interpersonal closeness. *Journal of Personality and Social Psychology*, *63*, 596–612.
- Arroyo, S., Lesser, R. P., Gordon, B., Uematsu, S., Jackson, D., & Webber, R. (1993). Functional significance of the mu rhythm of human cortex: An electrophysiologic study with subdural electrodes. *Electroencephalography and Clinical Neurophysiology*, *87*, 76–87.
- Becchio, C., Cavallo, A., Begliomini, C., Sartori, L., Feltrin, G., & Castiello, U. (2012). Social grasping: From mirroring to mentalizing. *NeuroImage*, *61*, 240–248.
- Bernier, R., Dawson, G., Webb, S., & Murias, M. (2007). EEG mu rhythm and imitation impairments in individuals with autism spectrum disorder. *Brain and Cognition*, *64*, 228–237.
- Bonini, L., & Ferrari, P. F. (2011). Evolution of mirror systems: a simple mechanism for complex cognitive functions. *Annals of the New York Academy of Sciences*, *1225*, 166–175.
- Bosga, J., Meulenbroek, R. G., & Cuijpers, R. H. (2010). Intra- and interpersonal movement coordination in jointly moving a rocking board. *Motor Control*, *14*, 440–459.
- Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, *15*, 1243–1249.
- Catmur, C., Walsh, V., & Heyes, C. (2007). Sensorimotor learning configures the human mirror system. *Current Biology*, *17*, 1527–1531.
- Catmur, C., Gillmeister, H., Bird, G., Liepelt, R., Brass, M., & Heyes, C. (2008). Through the looking glass: counter-mirror activation following incompatible sensorimotor learning. *European Journal of Neuroscience*, *28*, 1208–1215.
- Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research*, *91*, 176–180.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, S., & Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science*, *308*, 662–667.
- Frith, C. D., & Frith, U. (2008). Implicit and explicit processes in social cognition. *Neuron*, *60*, 503–510.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in premotor cortex. *Brain*, *119*, 593–609.
- Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, *55*, 468–484.
- Hari, R. (2006). Action-perception connection and the cortical mu rhythm. *Progress in Brain Research*, *159*, 253–260.
- Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience and Behavioral Reviews*, *34*, 575–583.
- Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Brain Research Cognitive Brain Research*, *22*, 233–240.
- Hogeveen, J., & Obhi, S. S. (2012). Social interaction enhances motor resonance for observed human actions. *Journal of Neuroscience*, *32*, 5984–5989.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, *3*, e79.
- Jeanerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage*, *14*, S103–109.
- Keysers, C., & Gazzola, V. (2009). Expanding the mirror: Vicarious activity for actions, emotions, and sensations. *Current Opinion in Neurobiology*, *19*, 666–671.
- Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, *11*, 417–428.
- Kilner, J. M., Marchant, J. L., & Frith, C. D. (2006). Modulation of the mirror system by social relevance. *Social Cognitive and Affective Neuroscience*, *1*, 143–148.
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processing*, *8*, 159–166.
- 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*, e4925.
- Konvalinka, I., Vuust, P., Roepstorff, A., & Frith, C. D. (2010). Follow you, follow me: Continuous mutual prediction and adaptation in joint tapping. *Quarterly Journal of Experimental Psychology*, *63*, 2220–2230.
- Kourtis, D., Sebanz, N., & Knoblich, G. (2010). Favouritism in the motor system: Social interaction modulates action simulation. *Biology Letters*, *6*, 758–761.
- Kourtis, D., Sebanz, N., & Knoblich, G. (2013). Predictive representation of other people's actions in joint action planning: An EEG study. *Social Neuroscience*, *8*, 31–42.
- Lamm, C., Fischer, M. H., & Decety, J. (2007). Predicting the actions of others taps into one's own somatosensory representations—A functional MRI study. *Neuropsychologia*, *45*, 2480–2491.
- Lepage, J. F., & Théoret, H. (2006). EEG evidence for the presence of an action observation-execution matching system in children. *European Journal of Neuroscience*, *23*, 2505–2510.
- Leuthold, H., & Jentzsch, I. (2009). Planning of rapid aiming movements and the contingent negative variation: are movement duration and extent specified independently? *Psychophysiology*, *46*, 539–550.
- Leuthold, H., Sommer, W., & Ulrich, R. (2004). Preparing for action: Inferences from CNV and LRP. *Journal of Psychophysiology*, *18*, 77–88.
- Marsh, K. L., Richardson, M. J., & Schmidt, R. C. (2009). Social connection through joint action and interpersonal coordination. *Topics in Cognitive Science*, *1*, 320–339.
- Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: a meta-analysis of 125 fMRI studies. *Neuroscience and Biobehavioral Reviews*, *36*, 341–349.
- Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of a goal-directed grasp. *Brain Research Cognitive Brain Research*, *19*, 195–201.
- Oberman, L. M., Pineda, J. A., & Ramachandran, V. S. (2007). The human mirror neuron system: A link between action observation and social skills. *Social Cognitive and Affective Neuroscience*, *2*, 62–66.
- Orgs, G., Dombrowski, J. H., Heil, M., & Jansen-Osmann, P. (2008). Expertise in dance modulates alpha/beta desynchronization during action observation. *European Journal of Neuroscience*, *27*, 3380–3384.
- Perry, A., Stein, L., & Bentin, S. (2011). Motor and attentional mechanisms involved in social interaction—Evidence from mu and alpha EEG suppression. *NeuroImage*, *58*, 895–904.
- Pineda, J. A. (2005). The functional significance of mu rhythm: Translating “seeing” and “hearing” into “doing”. *Brain Research Brain Research Reviews*, *50*, 57–68.
- Praamstra, P., Kourtis, D., Kwok, H. F., & Oostenveld, R. (2006). Neurophysiology of implicit timing in serial choice reaction-time performance. *Journal of Neuroscience*, *26*, 5448–5455.
- Press, C., Gillmeister, H., & Heyes, C. (2007). Sensorimotor experience enhances automatic imitation of robotic action. *Proceedings of the Royal Society of London, Biological Sciences*, *274*, 2509–2514.
- Press, C., Heyes, C., & Kilner, J. M. (2011). Learning to understand others' actions. *Biology Letters*, *7*, 457–460.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*, 264–274.
- Salmelin, R., & Hari, R. (1994). Spatiotemporal characteristics of sensorimotor neuro-magnetic rhythms related to thumb movement. *Neuroscience*, *60*, 537–550.
- Sartori, L., Cavallo, A., Buccioni, G., & Castiello, U. (2011). Corticospinal excitability is specifically modulated by the social dimension of observed actions. *Experimental Brain Research*, *211*, 557–568.
- Sartori, L., Cavallo, A., Buccioni, G., & Castiello, U. (2012). From simulation to reciprocity: The case of complimentary actions. *Social Neuroscience*, *7*, 146–158.
- Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., & Voegeley, K. Toward a second-person neuroscience. *Behavioral and Brain Sciences*, in press.
- Sommerville, J. A., & Decety, J. (2006). Weaving the fabric of social interaction: Articulating developmental psychology and cognitive neuroscience in the domain of motor cognition. *Psychonomic Bulletin & Review*, *13*, 179–200.
- Streltsova, A., Berchio, C., Gallese, V., & Umiltà, M. A. (2010). Time course and specificity of sensory-motor alpha modulation during the observation of hand motor acts and gestures: A high density EEG study. *Experimental Brain Research*, *205*, 363–373.
- Taylor, H. G., & Heilman, K. M. (1980). Left-hemisphere motor dominance in right-handers. *Cortex*, *16*, 587–603.
- Tsai, J. C., Sebanz, N., & Knoblich, G. (2011). The GROOP effect: Groups mimic group action. *Cognition*, *118*, 135–140.

- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron*, *31*, 155–165.
- Van Rijn, H., Kononowicz, T. W., Meck, W. H., Ng, K. K., & Penney, T. B. (2011). Contingent Negative Variation and its relation to time estimation: A theoretical evaluation. *Frontiers in Integrative Neuroscience*, *5*.
- Verleger, R., Wauschkuhn, B., van der Lubbe, R., Jaskowski, P., & Trillenber, P. (2000). Posterior and anterior contribution of hand-movement preparation to late CNV. *Journal of Psychophysiology*, *14*, 69–86.
- Vesper, C., Butterfill, S., Knoblich, G., & Sebanz, N. (2010). A minimal architecture for joint action. *Neural Networks*, *23*, 998–1003.
- Walter, W. G., Cooper, R., Aldridge, V. G., McCallum, W. C., & Winter, A. L. (1964). Contingent Negative Variation: An electric sign of sensorimotor association and expectancy in the human brain. *Nature*, *203*, 380–384.