

Attention Allocation and Task Representation during Joint Action Planning

Dimitrios Kourtis^{1,2}, Günther Knoblich^{2,3}, Mateusz Woźniak⁴,
and Natalie Sebanz^{2,3}

Abstract

■ We investigated whether people take into account an interaction partner's attentional focus and whether they represent in advance their partner's part of the task when planning to engage in a synchronous joint action. The experiment involved two participants planning and performing joint actions (i.e., synchronously lifting and clinking glasses), unimanual individual actions (i.e., lifting and moving a glass as if clinking with another person), and bimanual individual actions. EEG was recorded from one of the participants. We employed a choice reaction paradigm where a visual cue indicated the type of action to be planned, followed 1.5 sec later by a visual go stimulus, prompting the participants to act. We studied attention allocation processes by examining two lateralized EEG components, namely the anterior directing attention nega-

tivity and the late directing attention positivity. Action planning processes were examined using the late contingent negative variation and the movement-related potential. The results show that early stages of joint action planning involve dividing attention between locations in space relevant for one's own part of the joint action and locations relevant for one's partner's part of the joint action. At later stages of joint action planning, participants represented in advance their partner's upcoming action in addition to their own action, although not at an effector-specific level. Our study provides electrophysiological evidence supporting the operation of attention sharing processes and predictive self/other action representation during the planning phase of a synchronous joint task. ■

INTRODUCTION

Although interpersonal coordination may emerge spontaneously as a function of universal dynamic principles (Schmidt, Morr, Fitzpatrick, & Richardson, 2012; Marsh, Richardson, & Schmidt, 2009), successful interaction often depends on people's ability to intentionally coordinate their actions in space and time to reach a common goal. To lift a heavy object together, to perform a handshake, or to clink glasses, it is helpful and sometimes necessary for co-actors to form an action plan, which may include the representation of their own task as well as the representation of the tasks of others who are involved in the interaction (Butterfill & Sebanz, 2011; Knoblich, Butterfill, & Sebanz, 2011). Implementing a joint action plan is often facilitated by the ability of a person to allocate his or her attention toward the location where a co-actor would perform his or her action (Tipper, 2010; Brennan, Chen, Dickinson, Neider, & Zelinsky, 2007; Tomasello & Carpenter, 2007). This can be beneficial in joint action situations, because it enables interaction partners to link their perceptual experiences and to create "perceptual common ground" (Clark, 1996), which

sometimes allows them to coordinate their actions without the use of verbal or bodily cues. The objective of this study was to obtain electrophysiological evidence to determine whether specific representational and attention allocation processes operate during the planning phase of a joint action (i.e., clinking glasses) to support the specific interpersonal coordination required to achieve a synchronous joint action outcome (Keller, 2008).

Previous research on joint action supports the idea that co-actors represent each other's tasks and actions and suggests that the planning processes for own and others' actions can be highly similar (e.g., Meyer, van der Wel, & Hunnius, 2013; Atmaca, Sebanz, & Knoblich, 2011; Loehr & Palmer, 2011; Sebanz & Knoblich, 2011; Tsai & Brass, 2007; Knoblich & Jordan, 2003; Sebanz, Knoblich, & Prinz, 2003). Such "shared representations" may take place not only at a "higher" cognitive level but also at a "lower" sensorimotor level where another person's action is represented via mechanisms through which observed actions are coded in terms of their perceptual effects (Becchio, Sartori, & Castiello, 2010; Rizzolatti & Sinigaglia, 2010; Hommel, Müssele, Aschersleben, & Prinz, 2001; Jeannerod, 1997; Prinz, 1997). Additional evidence supporting the sensorimotor representation of others' actions during jointly performed tasks has been provided by a growing number of electrophysiological and imaging studies. These have either employed turn taking tasks

¹Ghent University, ²Donders Institute for Brain, Cognition and Behaviour, Nijmegen, Netherlands, ³Central European University, Budapest, Hungary, ⁴Jagiellonian University, Kraków, Poland

with low coordination demands (e.g., Holländer, Jung, & Prinz, 2011; Newman-Norlund, Bosga, Meulenbroek, & Bekkering, 2008; Tsai, Kuo, Hung, & Tzeng, 2008; Sebanz, Knoblich, Prinz, & Wascher, 2006) or have addressed expert performance in the musical domain (Novembre, Ticini, Schütz-Bosbach, & Keller, in press; Loehr, Kourtis, Vesper, Sebanz, & Knoblich, 2013; Goebel & Palmer, 2009). In a recent EEG study, we investigated the planning phase of a spatiotemporally coordinated joint task (i.e., passing an object) and showed that the action onset of the person who initiated the joint task was represented in the motor system of the follower. However, the interpersonal coordination demands in this task were also rather low, because the task consisted of two sequential, but temporally overlapping actions (Kourtis, Sebanz, & Knoblich, 2013). This study addressed processes of attention allocation and action preparation in a prototypical joint action where two people's actions needed to be performed synchronously to achieve a discrete joint action outcome.

Present Study

In this study, we looked at the planning phase of a joint task that required clinking two beer glasses together (see Figure 1C). Our main objective was to determine by means of high-density EEG how planning to participate in a coordinated joint action (i.e., each person planning to simultaneously lift a glass and clink it with the other person's glass) differs from planning the same individual unimanual action (i.e., one person lifting and moving the glass as if clinking it with another person's glass) and how this differs from planning both parts of the action individually using both hands (i.e., one person lifting and clinking both glasses). For this purpose, we employed a precuing paradigm (Rosenbaum, 1980) in which a fully informative visual cue specified the type of action to be prepared, followed by a delay period (foreperiod) of 1.5 sec, after which a visual go signal prompted the participants to perform the cued action.

Attention Allocation

To investigate attention allocation processes, we examined the modulation of two lateralized ERPs, which are elicited during covert shifts of attention toward a cued location and/or a manual response side, namely, the anterior directing attention negativity (ADAN) and the late directing attention positivity (LDAP). The ADAN and the LDAP reflect an enhanced frontal negativity and enhanced posterior positivity, respectively, which develop a contralateral to an attentional shift induced by a cue. These components are considered to represent supramodal control of spatial attention and specification of different spatial parameters of a prepared movement (Gherri, Van Velzen, & Eimer, 2007; Seiss, Gherri, Eardley, & Eimer, 2007; Praamstra, Boutsen, & Humphreys, 2005; Eimer & Van Velzen, 2002; Hopf & Mangun, 2000).

We predicted that, when participants planned an individual unimanual action, they would allocate their attention toward the side where the to-be-lifted object as well as the responding hand were located, which should result in an ADAN as well as in an LDAP. We expected that the ADAN and the LDAP would be absent during bimanual action planning, because participants need to allocate their attention toward both sides at which the two objects were located and toward both hands. Our most important prediction concerned joint action planning. We expected that if the participants allocated their attention toward the side where their glass and their responding hand was located and also toward the side where their partner's glass and responding hand was located, then the ADAN and the LDAP contralateral to the side of their glass would be significantly reduced, if not absent. In other words, we expected that, although in the joint condition participants had to plan an action that was practically identical to the one in the unimanual individual condition, attention allocation in the joint condition would be more similar to the bimanual individual condition.

Action Representation

To investigate processes of action planning, we investigated the modulation of the contingent negative variation (CNV), a slow brain potential of negative polarity, which develops progressively during the time between a cue stimulus and a subsequent imperative stimulus (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV has been associated with the explicit (Macar & Vidal, 2003) and implicit (Praamstra, Kourtis, Kwok, & Oostenveld, 2006) representation of a time interval, and during the late stages of action planning, it predominantly represents time-locked, possibly effector-unspecific activation of premotor areas (Van Rijn, Kononowicz, Meck, Ng, & Peney, 2011; Leuthold & Jentzsch, 2009; Leuthold, Sommer, & Ulrich, 2004). In addition, the CNV has been proven to be a sensitive index of representation of others' actions during the performance of joint tasks (Kourtis et al., 2013; Kourtis, Sebanz, & Knoblich, 2010).

Given that more complex motor tasks enhance the amplitude of the late CNV (Kranzioch, Mathews, Dean, & Sterr, 2010; Cui et al., 2000), our basic prediction was that the amplitude of the CNV would be larger when the participants prepared for bimanual action compared with preparing an individual unimanual action. Our most important prediction concerned the comparison between planning to perform a joint action and planning to perform an individual unimanual action. In either case, the participants needed to plan the same action (i.e., lift the glass and move it to the midline); however, in the joint action condition, the interaction partner also had to plan the performance of his or her own (similar) action. Previous behavioral work suggests that, when planning to engage in joint action, individuals may adapt their motor

plan to meet the needs of a co-actor (Ray & Welsh, 2011), in a similar way as planning an individual bimanual action (Meyer et al., 2013). We predicted that if during joint action planning the participants were planning their own action and simultaneously represented in advance their partner's action, then the amplitude of the late CNV should be larger compared with individual unimanual action planning. In addition, considering that anticipation of action observation typically induces weaker brain activation compared with action planning (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004), we predicted that it is possible that the late CNV amplitude might be smaller during joint action planning compared with individual bimanual action planning.

To investigate action representation during later stages of action preparation, we also examined the modulation of two additional slow brain potentials, which peak approximately at action onset: the movement-related potential (MRP) and the lateralized readiness potential (LRP). The MRP is present both before self-generated and cued actions (Jankelowitz & Colebatch, 2002), and during its late stages, it is characterized by a rapid increase in slope (Siemionow, Yue, Ranganathan, Liu, & Sahgal, 2002; Shibasaki, Barrett, Halliday, & Halliday, 1980; Deecke, Scheid, & Kornhuber, 1969). Our predictions for the MRP were similar to those for the CNV. We expected that the MRP would be larger when planning a unimanual action in the context of a joint action compared with planning the same unimanual action individually. Moreover, the MRP before joint action should be comparable to the MRP before bimanual action.

To specifically investigate the involvement of primary motor areas in action representation, we examined the LRP, which is a slowly increasing negativity over primary motor areas contralateral to an acting hand/arm. It is considered to be an index of motor planning and execution (Leuthold & Jentzsch, 2002; Ulrich, Leuthold, & Sommer, 1998; De Jong, Wierda, Mulder, & Mulder, 1988; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). We expected that the LRP would be present during unimanual action planning, but nearly absent during bimanual action planning, because the lateralized motor activations induced by each responding hand should effectively cancel each other out. Regarding the joint action condition, we predicted that, if in addition to planning the movement of their own hand, the participants simulated in advance the movement of their partner's hand, the LRP contralateral to their responding hand would be significantly enhanced compared with the LRP during individual unimanual action planning.

METHODS

Participants

Continuous EEG data were recorded from 16 participants (14 right-handed and 2 left-handed). All participants

(11 women and 5 men; mean age = 22.7 years, $SD = 1.6$ years) had normal or corrected-to-normal vision. They had no history of hand or arm injuries or diseases nor any mental, cognitive, and other neurological disorder. All participants provided their informed consent after full explanation of the study.

Experimental Setup

The experiment was run in a quiet, dimly illuminated, well-ventilated, and electromagnetically shielded room. A confederate took part in the experiment. No EEG data were recorded from the confederate.

The EEG participant and the confederate were seated at opposite sides of a round table (diameter = 75 cm). A gray rectangular piece of carton paper was taped centrally onto the table. Two coasters were glued on the left and right sides of the carton paper approximately 8 cm away from the midline. A glass of an approximate height of 15 cm was placed on each of the coasters. The distance between the glasses (center to center) was approximately 25 cm. The upper and lower parts of each glass, as well as the coasters, were padded with a thin layer of blue cushion foam to avoid breaking of the glasses and to eliminate the sound of glass clinking. All stimuli were projected onto the middle of the carton paper by an LCD projector (EPSON, EMP-X52). The projector was encased in a metallic contraption, mounted on the ceiling directly above the center of the table. A (4.5 cm × 4.5 cm) force sensing resistor (FSR) was placed on the table (~7 to 8 cm from the table edge) in front of each person's responding hand to record the action onsets (Figure 1).

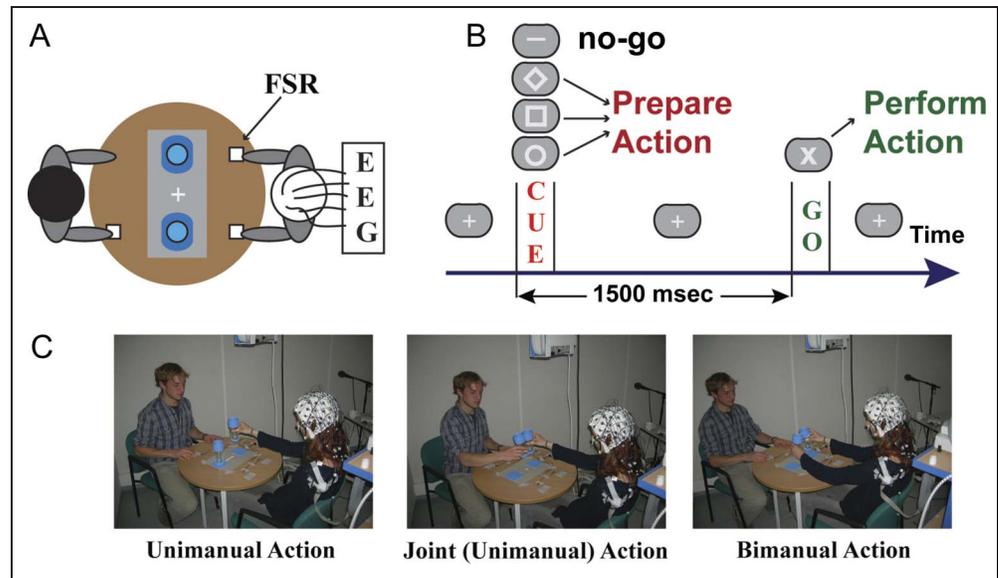
Procedure and Stimuli

The experiment consisted of a cued choice reaction task, divided into 12 blocks of approximately 5 min each. It was preceded by a single practice block of equal duration. In half of the blocks, the EEG participant and the confederate used their left hands to perform unimanual movements, and in the other half of the blocks, they used their right hands. Each block consisted of 60 trials, the structure of which is presented in Figure 1.

The EEG participant placed the index fingers of both hands on the FSRs, which were located close to him or her. The confederate was present throughout the whole experiment but performed only unimanual movements, so he placed only the index finger of the responding hand on an FSR; his other hand was placed directly on the table. Participant and confederate were instructed to lift their hands only to perform the required actions and then to immediately return their hands to their original positions.

The cue stimuli were projected on the middle of the gray carton paper at an approximate distance of 80 cm from each participant. Participant and confederate were

Figure 1. Schematic representation of (A) the setup and (B) the time course of a trial. At the beginning of each trial, the participants were seated motionless, keeping their eyes fixated on a display at the middle of the table. The display of a visual cue instructed the participants to plan, but withhold a particular action for 1500 msec. After this interval, a visual go stimulus prompted them to perform the prepared action. In 25% of the trials, the cue stimulus was a no-go signal, indicating that the participants should remain motionless until the display of the next cue stimulus. (C) Photo instances of the end points of all three types of actions.



instructed to fixate their gaze on the middle of the gray carton paper and not to engage in eye contact during the experiment. Each trial started with the display of a white cue stimulus (circle, rectangle, or diamond) presented for 200 msec, which indicated to the participants which action they needed to plan. There were four different types of trials, performed with equal probability (i.e., 25% of the trials):

- (i) Individual Unimanual Action, where the EEG participant had to lift the glass placed at the side of the responding hand and move it inward as if clinking the glass with another person's glass over the center of the table.
- (ii) Joint (Unimanual) Action, where the EEG participant had to perform the same action as in the individual unimanual condition. The difference was that the confederate had to simultaneously perform the same action; consequently, the two glasses were actually clinked over the middle of the table.
- (iii) Individual Bimanual Action, where the EEG participant had to simultaneously lift both glasses and clink them over the middle of the table.
- (iv) In 25% of the trials, the cue signal consisted of a single horizontal line, which signified that the participants should remain motionless throughout the trial (i.e., no-go condition).

The cue stimulus was followed by a delay period of 1500 msec, during which the participants were required to plan their action(s). The delay period was ended by the display of a visual go signal (a white "X") for 200 msec, which prompted the participants to swiftly perform their planned action(s).

Data Acquisition

Behavioral Data

Behavioral data were recorded by the FSRs on which the participants had placed their index fingers.

Electrophysiological Data

EEG was recorded continuously using a carefully positioned, equidistant cap (EasyCap, Herrsching, Germany) with 64 Ag/AgCl electrodes relative to an (offline) average mastoid reference. Vertical and horizontal eye movements were monitored using one pair of bipolar EOG electrodes positioned under the left and right eyes and lateral to the left and right eyes. Electrode impedance was kept below 20 k Ω . 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.

Data Processing and Analysis

Behavioral 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 msec or differed more than two standard deviations (*SD*) from the mean action onset within each condition were removed from further analysis.

Electrophysiological Data

EEG data processing was performed offline using the Brain Vision Analyzer (V. 1.05, Brain Products GmbH, Gilching, Germany) software. The data were filtered

using a low cut-off filter of 0.01 Hz (24 dB/octave) and a high cut-off filter of 40 Hz (24 dB/octave) to remove slow drifts and excessive noise, respectively. For the analysis of stimulus-locked potentials (i.e., CNV, ADAN, and LDAP), the EEG data were segmented offline into epochs from 500 msec before cue onset to 2000 msec after cue onset. For the analysis of the response-locked potentials (i.e., MRP and LRP), the EEG data were segmented offline into epochs from 1950 msec before go signal onset to 50 msec after go signal onset. Individual trials containing eye movement artifacts or incorrect responses were removed before averaging. The CNV and the MRP amplitudes were assessed in the last 100 msec before go stimulus onset and response onset, respectively.

Lateralized activity was calculated separately for each condition using the “double subtraction method” (Coles, 1989). Initially, we computed the voltage difference between homologous electrodes contralateral and ipsilateral to the side of the cued movement. Subsequently, the difference waveforms were averaged to obtain lateralized ERP waveforms. The ADAN and LDAP amplitudes were assessed in the time intervals from 480 to 640 msec and from 680 to 820 msec after cue onset. The LRP amplitude was assessed in the last 200 msec before response onset.

RESULTS

Behavioral Data

Action Onsets

The action onsets of the EEG participants were ($M = 401.5$ msec, $SD = 69.8$ msec) and ($M = 398.5$ msec, $SD = 67.6$ msec) for left and right unimanual individual actions, ($M = 419.9$ msec, $SD = 82.9$ msec) and ($M = 420.5$ msec, $SD = 82.2$ msec) for left and right bimanual actions, and ($M = 405.3$ msec, $SD = 66.0$ msec) and ($M = 411.4$ msec, $SD = 63.0$ msec) for left and right joint (unimanual) actions (Figure 2, top). A 3×2 ANOVA (Greenhouse–Geisser corrected) with factors Action (unimanual, bimanual, joint) and Hand (left, right) showed that there was a significant main effect of Action, $F(2, 30) = 5.42$, $p = .015$. The main effects of Hand and the Action \times Hand interaction were not significant ($ps > .28$). Post hoc t tests showed that there was a significant difference in action onsets only between unimanual individual and bimanual actions, $t(15) = 3.65$, $p = .002$. The differences between the joint action condition and either of the individual action conditions were not significant ($ps > .13$; Figure 2A).

Interpersonal Coordination

The action onsets of the confederate were ($M = 360.1$ msec, $SD = 33.0$ msec) and ($M = 365.2$ msec, $SD = 44.1$ msec) for left and right hand actions, respectively. A 2×2 ANOVA (Greenhouse–Geisser corrected) with factors Actor (EEG participant, confederate) and Hand

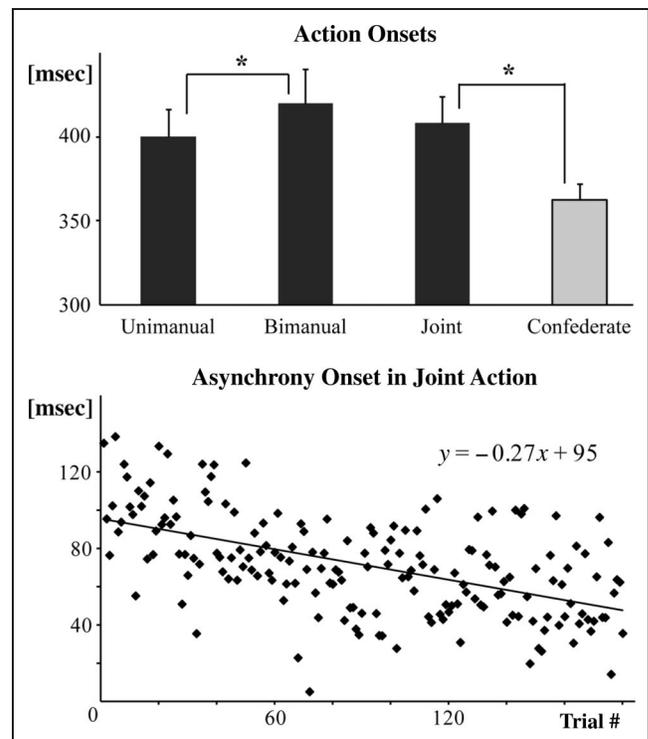


Figure 2. (A) Average action onsets. The error bars represent SEMs. The asterisks indicate significant differences. (B) Interpersonal difference in action onsets in the joint action condition. The difference was becoming progressively smaller in the course of the experiment at a rate of 0.27 msec/trial, indicating an improvement in interpersonal coordination.

(left, right) showed that the confederate was responding significantly faster than the EEG participant, $F(1, 15) = 6.21$, $p = .025$, possibly because the confederate was familiar with the lab environment and not troubled by movement and blinking constraints that were part of the instructions for the EEG participant. The main effects of Hand and the Action \times Hand interaction were not significant ($ps > .26$). Interestingly, the difference between the two interaction partners was becoming progressively smaller in the course of the experiment at a rate of 0.27 msec/trial, which suggests that participant and confederate learned to achieve more effective interpersonal coordination during the course of the experiment (Figure 2B). The decrease in asynchrony onset was statistically significant, $t(15) = -3.70$, $p = .002$, compared with an absence of change in coordination (i.e., no decrease in asynchrony onset).

Electrophysiological Data

Lateralized ERPs

As expected, when participants prepared an individual unimanual action, there was an anterior lateralized negativity and a posterior lateralized positivity, which correspond to the ADAN and the LDAP, respectively. The ADAN

had an onset of ~ 300 msec, peaked ~ 600 msec after cue onset, and it was significantly different from the baseline, $t(15) = -2.48$, $p = .026$, over frontal areas (electrode pairs [left/right hemisphere] 32/23 and 33/22) in the time interval 480–640 msec after cue onset. The LDAP had an onset of ~ 500 msec, peaked ~ 780 msec after cue onset, and it was significantly different from the baseline, $t(15) = 2.27$, $p = .038$, over occipito-temporal areas (electrode pairs [left/right hemisphere] 45/41 and 58/54) in the time interval 680–820 msec after cue onset (Figure 3A–C).

There was no ADAN or LDAP ($ps > .24$) when participants prepared a bimanual action. Importantly, there was also no ADAN or LDAP ($ps > .41$) when the participants prepared a unimanual action that was part of a joint action (i.e., required a partner's action at the opposite side). The absence of ADAN and LDAP suggests that preparing one's own action in the joint unimanual condition is similar to preparing an action in the individual bimanual condition in terms of attention allocation (Figure 3A–C). The topography of the contrast between the individual and the joint action condition (Figure 3C, E) corresponds largely with the scalp locations where the ADAN and the LDAP are typically recorded during unimanual action planning (e.g., Gherri et al., 2007).

The inspection of the response-locked data showed that there was a clear LRP developing around 400 msec

over primary motor areas (electrode pairs [left/right hemisphere] 6/4, 7/3, 17/11) before the performance of a unimanual action (Figure 3C, D). The amplitude analysis of the R-LRP during the last 200 msec before the recorded action onset showed that it was significantly different from the baseline when the participants were planning to act individually, $t(15) = -3.13$, $p = .007$, but also when they were planning to participate in joint action, $t(15) = -3.23$, $p = .006$. However, the difference between these two conditions was not significant ($p = .43$). This suggests that the participants did not specifically simulate in advance their partners' anticipated hand movement when preparing for joint action. Although there was no R-LRP when the participants planned a bimanual action, there was a slow developing lateralization of positive polarity over primary motor areas. This was probably because of the fact that the participants were using the same hand for unimanual (individual and joint) actions within a block, so in bimanual action planning they would exert more effort to use the hand that remained still in the rest of the trials.

Nonlateralized ERPs

The CNV developed slowly during the planning period and reached its peak approximately at action onset. As predicted, the CNV was larger when participants prepared

Figure 3. Grand-averaged waveforms of stimulus-locked lateralized activity over frontal (A) and occipito-temporal (B) areas. Note that the ADAN and the LRP were only present when the cue indicated the preparation of an individual unimanual action. (C) Flat projection depicting the electrodes on the left hemisphere, which were paired with the equivalent electrodes on the right hemisphere to quantify the ADAN, LDAP, and LRP. (D) Grand-averaged waveforms of response-locked lateralized activity over primary motor areas. (E) Voltage topography maps depicting the difference in lateralized activity between preparing a unimanual action individually compared with preparing the same action together with the partner.

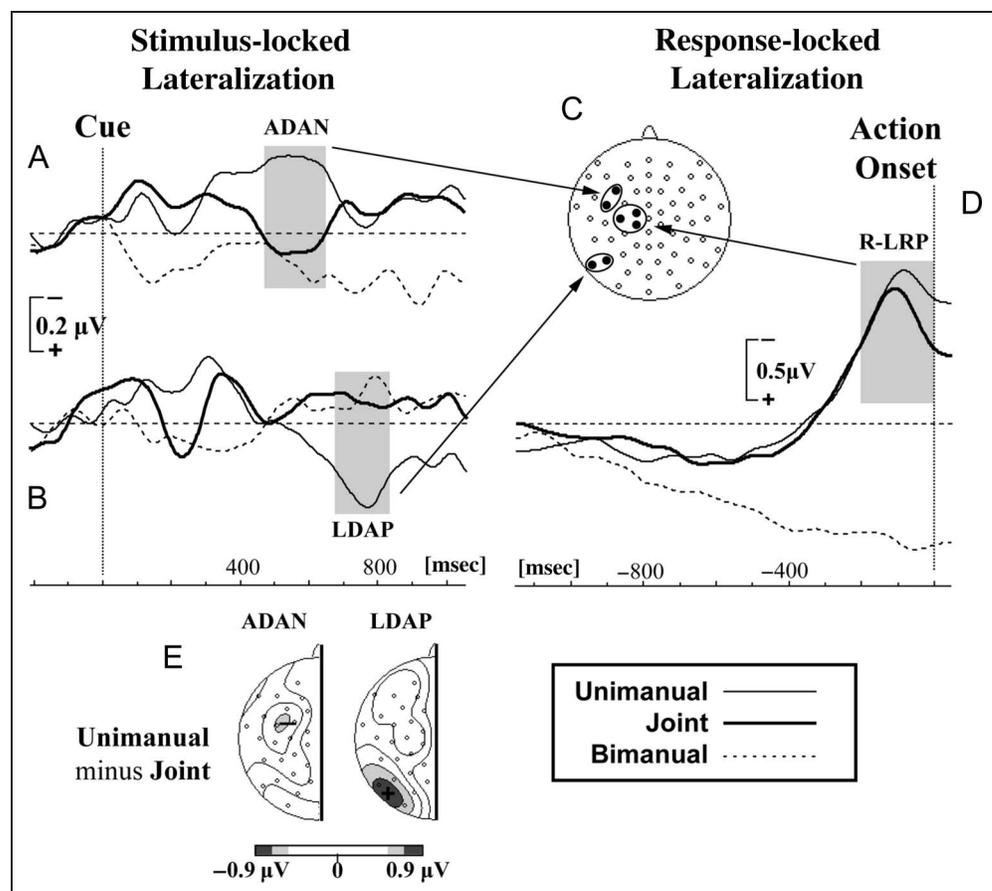
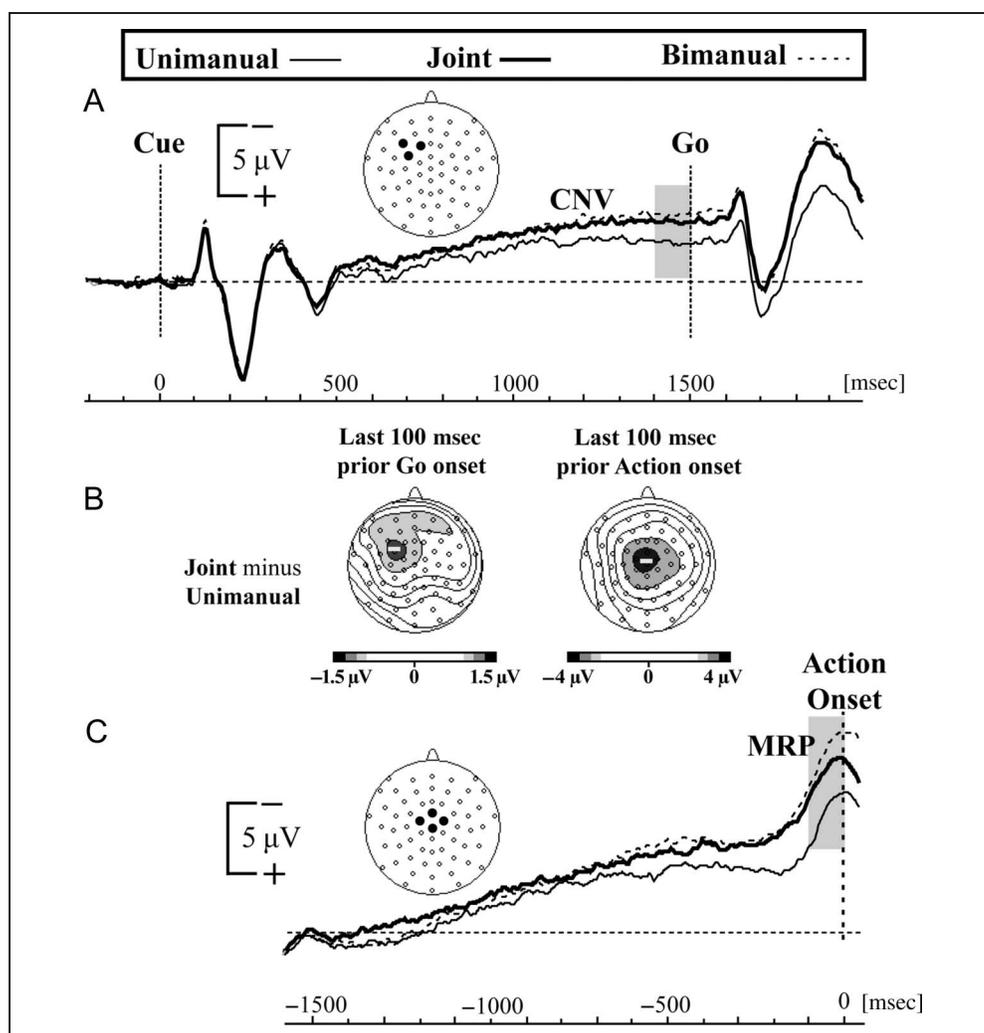


Figure 4. (A) Grand-averaged, stimulus-locked waveforms showing the development of the CNV over left premotor areas and flat projection depicting the electrodes (highlighted as black circles) from which the CNV was derived. (B) Voltage topography maps depicting the contrast in CNV (left) and in MRP (right) during the selected time intervals of analysis between preparing a unimanual action in the joint action condition compared with preparing the same action individually. (C) Grand-averaged, response-locked waveforms showing the development of the MRP over mid-premotor areas and flat projection depicting the electrodes (highlighted as black circles) from which the MRP was quantified.



a unimanual action in the joint action condition compared with planning the same action individually. This suggests that the participants indeed represented certain aspects of their partners' movements before the partner started to act. A close examination of the topography of the contrast between these two conditions (Figure 4B) showed that the difference was larger over left premotor areas before the display of the go signal. The late CNV was quantified by pooling the activity of neighboring electrodes 18, 19, and 33 (Figure 4A) during the last 100 msec before the display of the go stimulus. A 3×2 ANOVA (Greenhouse-Geisser corrected) with factors Action (unimanual, bimanual, joint) and Hand (left, right) showed that there was a significant main effect of Action, $F(2, 30) = 13.09, p < .001$. The main effects of Hand and the Action \times Hand interaction were not significant ($ps > .17$). Post hoc t tests revealed that, when participants planned a unimanual action together with their partners, the late CNV was significantly larger compared with planning the same action individually, $t(15) = 3.57, p = .003$, whereas it was not significantly smaller compared with planning a bimanual action, $t(15) =$

$-1.84, p = .086$. The late CNV was larger when planning a bimanual action compared with planning an individual unimanual action, $t(15) = 4.07, p = .001$.

The modulation of the MRP across conditions was similar to the CNV; however, the topography of the difference between the joint action condition and the individual unimanual condition showed that the difference was larger over mid premotor areas. The MRP was quantified by pooling the activity of neighboring electrodes 1, 2, 3, and 7 (Figure 4C) during the last 100 msec before action onset. A 3×2 ANOVA (Greenhouse-Geisser corrected) with factors Action (unimanual, bimanual, joint) and Hand (left, right) showed that there was a significant main effect of Action, $F(2, 30) = 25.39, p < .001$. The main effects of Hand and the Action \times Hand interaction were not significant ($ps > .28$). Post hoc t tests revealed that, when participants were about to initiate a unimanual action together with their partners, the MRP was significantly larger compared with initiating the same action individually, $t(15) = 5.37, p < .001$, and not significantly smaller compared with initiating a bimanual action, $t(15) = -1.94, p = .072$. The MRP was larger

when planning a bimanual action compared with planning an individual unimanual action, $t(15) = 6.78, p < .001$.

DISCUSSION

We investigated attention allocation and self/other action representation processes during the planning phase of a joint task that had as its goal a discrete event requiring synchronicity of two co-actors' actions. By recording high-density EEG and separating action planning from action execution, we were able to investigate a series of ongoing brain processes that operate during joint action planning in the absence of any bodily or eye movements. Our results demonstrate that when planning to engage in such a joint action, people covertly distribute their attention between the location where they plan to perform their part of the joint action and the location where their partners plan to perform their part of the action. This way of allocating attention resembled attention allocation when planning a bimanual action. Furthermore, participants engaged their own motor system to represent in advance (but not at an effector-specific level) their partners' anticipated action, which may underlie the continuous improvement in interpersonal coordination through the course of the experiment.

Attention Allocation

Previous EEG research on covert attention orientation and movement preparation has shown that a frontal negativity (i.e., ADAN) and a posterior positivity (i.e., LDAP) develop contralaterally to a cued spatial location and/or response side, shortly after the onset of a directional cue (Gherri et al., 2007; Seiss et al., 2007; Mathews, Ainsley Dean, & Sterr, 2006; Eimer, Forster, Van Velzen, & Prabhu, 2005; Praamstra et al., 2005; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000). In this study, the ADAN and the LDAP were only present when the cue instructed the planning of an individual unimanual action, which indicated that transient attentional shifts occurred toward the responding hand and the location of the object.¹ As expected, the ADAN and the LDAP were absent during the planning of bimanual movements, because the participants attended to both hemispaces. Importantly, the ADAN as well as the LDAP were also absent during joint action planning, although the participants had to plan the same unimanual movement as when acting alone. This strongly suggests that the participants did not selectively attend to the hemispace where their responding hand and the object that they had to grasp were located, but they also covertly attended to the hemispace where their partner's responding hand and object were located.

The ability to align perceptual inputs with interaction partners and to attend jointly to the same location or object in space already manifests itself at a very early age (Tomasello & Carpenter, 2007) and may act as a scaffold-

ing upon which interaction partners can build shared task representations in the service of efficient interpersonal coordination (Brennan et al., 2007; Sebanz, Bekkering, & Knoblich, 2006). Joint attention involves being aware of what one's partner is attending to (Pacherie, 2014), even when the other focuses on a different aspect of an attended object (Böckler, Knoblich, & Sebanz, 2011) or when it is not necessary for the performance of one's own task (Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010). This study demonstrates that, during the planning of a spatiotemporally coordinated joint action, people automatically take into account the locations and/or objects that will require their interaction partner's attention even if these are only relevant to the partner. This study shows that distribution of attention between self-relevant and other relevant locations can be induced by the display of symbolic visual stimuli in the absence of other verbal, bodily, or other types of communicative cues and that it takes place at the early planning stages of a synchronous joint task. Moreover, such distribution of attention takes place even when interaction partners attend to a location that is irrelevant to the performance of their own part of the task.²

Action Representation

The analysis of slow rising MRPs suggests that, during joint action planning, in addition to the partner's attentional focus, the participants represented certain aspects of the partner's anticipated action. The late CNV before go signal onset as well as the MRP before action onset were larger when participants were planning a unimanual action to participate in a joint task compared with planning the same action to act alone.

The late CNV in motor tasks is considered an index of time-based motor planning that possibly takes place at an effector-unspecific level (Van Rijn et al., 2011; Leuthold & Jentzsch, 2009; Leuthold et al., 2004). The CNV has been related to the implicit representation of manual response onset of one's own action (Praamstra et al., 2006) as well as to the representation of a co-actor's action onset during the performance of a joint task (Kourtis et al., 2013). Accordingly in our experiment, the enlarged late CNV amplitude in the joint condition may reflect the planning of one's own action together with the implicit representation of the co-actor's anticipated action at an effector-unspecific level.

The topography of the contrast between the joint action and individual unimanual action condition showed that the difference was larger over left premotor areas, regardless of the responding hand. This finding is consistent with the important role that has been assigned to the left, possibly dorsal premotor cortex in the generation of the CNV (Lu, Arai, Tsai, & Ziemann, 2012; Praamstra et al., 2006). We need to point out of course that EEG records electrical activity at the surface of the head and any claims regarding the brain sources of the ERPs

should be treated with great caution. Keeping this in mind, it is worth mentioning that the left premotor cortex is considered to be part of a larger network that supports the production of object-directed movements (Vingerhoets et al., 2012) and that it is associated with the prediction and organization of effector-independent complex action sequences (Stadler, Schubotz, von Cramon, Springer, & Prinz, 2011; Haaland, Elsinger, Mayer, Durgerian, & Rao, 2004). Thus, it is conceivable that the enlarged CNV during joint action planning may reflect the implicit representation of the partner's upcoming action and the organization of the two individual actions into a complex joint task.

Similar to the CNV, the MRP before unimanual movements was enlarged when the participant planned to participate in joint action compared with planning to act alone. During its late stages, the MRP is typically lateralized over the hemisphere that is contralateral to the unimanual movement, which is regarded as evidence for the involvement of primary motor areas in action planning (Jankelowitz & Colebatch, 2002; Ikeda et al., 1995). However, the topography of the contrast showed that the difference was larger over the scalp midline irrespective of the responding hand. In addition, we recorded no significant difference between the two unimanual conditions in the LRP amplitude, which is a reliable marker of primary motor cortex activation. Taken together, this strongly suggests that primary motor cortex did not (significantly) contribute to the enlargement of the MRP during joint action planning compared with planning an individual unimanual action. Rather, it is more likely that the contrast between the two unimanual conditions could be attributed to an enhanced involvement of the SMA in joint action planning. This hypothesis is consistent with previous intracranial and source localization studies, which have associated the late stages of the MRP with SMA activation (Ikeda et al., 1995; Toro, Matsumoto, Deuschl, Roth, & Hallett, 1993). The SMA has a crucial role in the temporal coordination of movements (Cunnington, Bradshaw, & Iansek, 1996), and it is more strongly activated during bimanual compared with unimanual movements (Toyokura, Muro, Komiya, & Obara, 2002; Ikeda et al., 1995). With regards to our experiment, this implies that the enlarged MRP during joint action planning reflects the demand for coordination of two impending actions (much like in bimanual movements) to successfully perform the joint task. This presupposes the motor representation of both one's own action as well as the partner's action, although most likely not at an effector-specific level.

The motor representation of another person's action may take place within a neural network, similar to the mirror neuron system in monkeys (Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996), in which one's own and others' actions, sensations, or emotions are represented in a qualitatively similar way (Rizzolatti & Sinigaglia, 2010; Keysers & Gazzola, 2009). The enlarged

CNV and MRP amplitudes during joint action planning could be attributed to stronger activation of lateral premotor areas and the SMA, respectively, which are brain areas that exhibit mirror-like properties (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). The activation of these areas before action execution is consistent with the proposed role of the mirror system in predicting the sensory effects of executed and observed actions (Kilner, Friston, & Frith, 2007). On the other hand, the lack of modulation of the LRP by the action context suggests that the participants did not represent in advance the partner's anticipated action in all its details. In our view, this should not be taken as proof for the inability of people to simulate in advance another person's action. Instead, it may be considered as an indication that brain processes serve to plan an (individual or joint) action in the most energy-efficient way (Friston, 2010). The important requirement for success in our joint action task was the synchronous meeting of glasses over the midline. The location where the two glasses had to be clinked remained constant throughout task performance; consequently, the manner in which the participants grasped and moved the glasses to the midline was of little relevance to the successful performance of the task.

It needs to be acknowledged that our experimental design did not include a condition where the two co-actors were required to plan uncoordinated individual actions. This study provides information regarding the brain processes that operate during synchronous joint action planning, but we cannot claim that these processes operate exclusively during action planning and not during the planning of multiple uncoordinated individual actions. However, recent EEG studies suggest that one's sensorimotor system is preferentially tuned to actions of interaction partners compared with actions of outsiders (Kourtis et al., 2010, 2013; Meyer, Hunnius, van Elk, van Ede, & Bekkering, 2011). Thus, it is possible that the (predictive) representation of another person's action depends on whether two persons plan to interact with each other. However, this question requires further investigation.

Conclusion

This study shows that, when preparing to engage in synchronous joint action, people form an action plan, taking into account their interaction partner's part of the task. At early stages of action planning, individuals covertly distribute their attention between locations in space only relevant to themselves and locations relevant to their partner. Subsequently, they engage their motor system to represent their own action as well as the temporal aspects of the partner's upcoming action. Such effector unspecific representation of the partner's upcoming action was likely related to the particular requirements of our joint task, the successful performance of

which relied heavily on the temporal alignment of the actions of the two interaction partners. Our findings suggest that the representation of a partner's upcoming action may take place concurrently with the planning of one's own action and may be tailored to the specific demands of a joint task.

Reprint requests should be sent to Dimitrios Kourtis, Department of Experimental Psychology, Ghent University, Henri Dunantlaan 2, 9000 Ghent, Belgium, or via e-mail: dimitrios.kourtis@ugent.be.

Notes

1. Note that the participants' movements never crossed the midline. Therefore, the location of the object that they had to grasp and the responding hand were always in the same hemisphere.
2. The location that was relevant to both co-actors was the midline, over which they had to clink the glasses.

REFERENCES

- Arnstein, D., Cui, F., Keyzers, C., Maurits, N. M., & Gazzola, V. (2011). μ -Suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *Journal of Neuroscience*, *31*, 14243–14249.
- Atmaca, S., Sebanz, N., & Knoblich, G. (2011). The joint flanker effect: Sharing tasks with real and imagined co-actors. *Experimental Brain Research*, *211*, 371–385.
- Becchio, C., Sartori, L., & Castiello, U. (2010). Toward you: The social side of actions. *Current Directions in Psychological Science*, *19*, 183–188.
- Böckler, A., Knoblich, G., & Sebanz, N. (2011). Effects of a co-actor's focus of attention on task performance. *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 1404–1415.
- Brennan, S. E., Chen, X., Dickinson, C. A., Neider, M. B., & Zelinsky, G. J. (2007). Coordinating cognition: The costs and benefits of shared gaze during collaborative search. *Cognition*, *106*, 1465–1477.
- Butterfill, S. A., & Sebanz, N. (2011). Joint action: What is shared? *Review of Philosophy and Psychology*, *2*, 137–146.
- Clark, H. H. (1996). *Using language*. Cambridge: Cambridge University Press.
- Coles, M. G. (1989). Modern mind-brain reading: Psychophysiology, physiology and cognition. *Psychophysiology*, *26*, 251–269.
- Cui, R. Q., Egkher, A., Huter, D., Lang, W., Lindinger, G., & Deecke, L. (2000). High resolution spatiotemporal analysis of the contingent negative variation in simple or complex motor tasks and a non-motor task. *Clinical Neurophysiology*, *111*, 1847–1859.
- Cunnington, R., Bradshaw, J. L., & Ianssek, R. (1996). The role of the supplementary motor area in the control of voluntary movement. *Human Movement Science*, *15*, 627–647.
- De Jong, R., Wierda, M., Mulder, G., & Mulder, L. J. (1988). Use of partial stimulus information in response processing. *Journal of Experimental Psychology: Human Perception and Performance*, *14*, 682–692.
- Deecke, L., Scheid, P., & Kornhuber, H. H. (1969). Distribution of the readiness potential, pre-motion positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements. *Experimental Brain Research*, *7*, 158–168.
- Eimer, M., Forster, B., Van Velzen, J., & Prabhu, G. (2005). Covert manual response preparation triggers attentional shifts: ERP evidence for the premotor theory of attention. *Neuropsychologia*, *43*, 957–966.
- Eimer, M., & Van Velzen, J. (2002). Crossmodal links in spatial attention are mediated by supramodal control processes: Evident from event-related potentials. *Psychophysiology*, *39*, 437–449.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*, 662–667.
- Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature Reviews Neuroscience*, *11*, 127–138.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.
- Gherri, E., Van Velzen, J., & Eimer, M. (2007). Dissociating effector and movement direction selection during the preparation of manual reaching movements: Evidence from lateralized ERP components. *Clinical Neurophysiology*, *118*, 2031–2049.
- Goebel, W., & Palmer, C. (2009). Synchronization of timing and motion among performing musicians. *Music Perception: An Interdisciplinary Journal*, *26*, 427–438.
- Gratton, G., Coles, M. G., Sirevaag, E. J., Eriksen, C. W., & Donchin, E. (1988). Pre- and poststimulus activation of response channels: A psychophysiological analysis. *Journal of Experimental Psychology: Human Perception and Performance*, *14*, 331–344.
- Haaland, K. Y., Elsinger, C. L., Mayer, A. R., Durgerian, S., & Rao, S. M. (2004). Motor sequence complexity and performing hand produce differential patterns of hemispheric lateralization. *Journal of Cognitive Neuroscience*, *16*, 621–636.
- Holländer, A., Jung, C., & Prinz, W. (2011). Covert motor activity on NoGo trials in a task sharing paradigm: Evidence from the lateralized readiness potential. *Experimental Brain Research*, *211*, 345–356.
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of even coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, *24*, 878–937.
- Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: An electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, *111*, 1241–1257.
- Ikeda, A., Lüders, H. O., Shibasaki, H., Collura, T. F., Burgess, R. C., Morris, H. H., 3rd, et al. (1995). Movement-related potentials associated with bilateral simultaneous and unilateral movements recorded from human supplementary motor area. *Electroencephalography and Clinical Neurophysiology*, *95*, 323–334.
- Jankelowitz, S. K., & Colebatch, J. G. (2002). Movement-related potentials associated with self-paced, cued and imagined arm movements. *Experimental Brain Research*, *147*, 98–107.
- Jeannerod, M. (1997). *The cognitive neuroscience of action*. Oxford: Wiley-Blackwell.
- Keller, P. E. (2008). Joint action in music performance. In F. Morganti, A. Carassa, & G. Riva (Eds.), *Enacting intersubjectivity: A cognitive and social perspective to the study of interactions* (pp. 205–221). Amsterdam: IOS Press.
- Keyzers, C., & Gazzola, V. (2009). Expanding the mirror: Vicarious activity for actions, emotions and sensations. *Current Opinion in Neurobiology*, *19*, 666–671.
- 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., Vargas, C., Duval, S., Blakemore, S. A., & Sirigu, A. (2004). Motor activation before observation of a predicted movement coding. *Nature Neuroscience*, *7*, 1299–1301.
- Knoblich, G., Butterfill, S., & Sebanz, N. (2011). Psychological research on joint action: Theory and data. In B. Ross (Ed.), *The psychology of learning and motivation* (Vol. 54, pp. 59–101). Burlington, MA: Academic Press.
- Knoblich, G., & Jordan, J. S. (2003). Action coordination in groups and individuals: Learning anticipatory control. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *29*, 1006–1016.
- 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*, 32–42.
- Kranczioch, C., Mathews, S., Dean, P., & Sterr, A. (2010). Task complexity differentially affects executed and imagined motor preparation: Evidence from movement-related potentials. *PLoS One*, *5*, e9284.
- Leuthold, H., & Jentzsch, I. (2002). Distinguishing neural sources of planning of movement preparation and execution: An electrophysiological analysis. *Biological Psychology*, *60*, 173–198.
- Leuthold, H., & Jentzsch, I. (2009). Planning of rapid aiming movements and the contingent negative variation: Are movement direction 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.
- Loehr, J. D., Kourtis, D., Vesper, C., Sebanz, N., & Knoblich, G. (2013). Monitoring individual and joint action outcomes in duet music performance. *Journal of Cognitive Neuroscience*, *25*, 1049–1061.
- Loehr, J. D., & Palmer, C. (2011). Temporal coordination between performing musicians. *Quarterly Journal of Experimental Psychology*, *64*, 2153–2167.
- Lu, M. K., Arai, N., Tsai, C. H., & Ziemann, U. (2012). Movement related cortical potentials of cued versus self-initiated movements: Double dissociated modulation by dorsal premotor cortex versus supplementary motor area rTMS. *Human Brain Mapping*, *33*, 824–839.
- Macar, F., & Vidal, F. (2003). The CNV peak: An index of decision making and temporal memory. *Psychophysiology*, *40*, 950–954.
- 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.
- Mathews, S., Ainsley Dean, P. J., & Sterr, A. (2006). EEG dipole analysis of motor-priming foreperiod reveals separate sources for motor and spatial attention components. *Clinical Neurophysiology*, *117*, 2675–2683.
- Meyer, M., Hunnius, S., van Elk, M., van Ede, F., & Bekkering, H. (2011). Joint action modulates motor system involvement during action observation in 3-year olds. *Experimental Brain Research*, *211*, 581–592.
- Meyer, M., van der Wel, R. P., & Hunnius, S. (2013). Higher-order action planning for individual and joint action manipulations. *Experimental Brain Research*, *225*, 579–588.
- Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current Biology*, *20*, 750–756.
- Newman-Norlund, R. D., Bosga, J., Meulenbroek, R. G., & Bekkering, H. (2008). Anatomical substrates of a cooperative joint-action in a continuous motor task: Virtual lifting and balancing. *Neuroimage*, *41*, 169–177.
- Nobre, A. C., Sebestyen, G. N., & Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event-related potentials. *Neuropsychologia*, *38*, 964–974.
- Novembre, G., Ticini, L. F., Schütz-Bosbach, S., & Keller, P. E. (in press). Motor simulation and the coordination of self and other in real-time joint action. *Social Cognitive and Affective Neuroscience*.
- Pacherie, E. (2014). How does it feel to act together? *Phenomenology and the Cognitive Sciences*, *13*, 25–46.
- Praamstra, P., Boutsen, L., & Humphreys, G. W. (2005). Frontoparietal control of spatial attention and motor intention in human EEG. *Journal of Neurophysiology*, *94*, 764–774.
- Praamstra, P., Kourtis, D., Kwok, H. F., & Oostenveld, R. (2006). Neurophysiology of implicit timing in serial choice reaction-time performance. *Journal of Neuroscience*, *26*, 5448–5555.
- Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, *9*, 129–154.
- Ray, M., & Welsh, T. N. (2011). Response selection during a joint action task. *Journal of Motor Behavior*, *43*, 329–332.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*, 264–274.
- Rosenbaum, D. A. (1980). Human movement initiation: Specification of arm, direction and extent. *Journal of Experimental Psychology: General*, *109*, 444–474.
- Samson, D., Apperly, I. A., Braithwaite, J. J., Andrews, B. J., & Bodley Scott, S. E. (2010). Seeing it their way: Evidence for rapid and involuntary computation of what other people see. *Journal of Experimental Psychology: Human Perception and Performance*, *36*, 1255–1266.
- Schmidt, R. C., Morr, S., Fitzpatrick, P., & Richardson, M. J. (2012). Measuring the dynamics of interactional synchrony. *Journal of Nonverbal Behavior*, *36*, 263–279.
- Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: Bodies and minds moving together. *Trends in Cognitive Sciences*, *10*, 70–76.
- Sebanz, N., & Knoblich, G. (2011). Prediction in joint action: What, when and where. *Topics in Cognitive Science*, *1*, 353–367.
- Sebanz, N., Knoblich, G., & Prinz, W. (2003). Representing others' actions: Just like one's own? *Cognition*, *88*, B11–B21.
- Sebanz, N., Knoblich, G., Prinz, W., & Wascher, E. (2006). Twin peaks: An ERP study of action planning and control in coacting individuals. *Journal of Cognitive Neuroscience*, *18*, 859–870.
- Seiss, E., Gherri, E., Eardley, A. F., & Eimer, M. (2007). Do ERP components triggered during attentional orienting represent supramodal attentional control? *Psychophysiology*, *44*, 987–990.
- Shibasaki, H., Barrett, G., Halliday, E., & Halliday, A. M. (1980). Cortical potentials following voluntary and passive finger movements. *Electroencephalography and Clinical Neurophysiology*, *50*, 201–213.
- Siemionow, V., Yue, G. H., Ranganathan, V. K., Liu, J. Z., & Sahgal, V. (2002). Relationship between motor activity-related potential and voluntary muscle activation. *Experimental Brain Research*, *133*, 303–311.
- Stadler, W., Schubotz, R. I., von Cramon, D. Y., Springer, A., & Prinz, W. (2011). Predicting and memorizing observed action: Differential premotor cortex involvement. *Human Brain Mapping*, *32*, 677–687.
- Tipper, S. P. (2010). From observation to action simulation: The role of attention, eye-gaze, emotion, and body state.

- The Quarterly Journal of Experimental Psychology*, *63*, 2081–2105.
- Tomasello, M., & Carpenter, M. (2007). Shared intentionality. *Developmental Science*, *10*, 121–125.
- Toro, C., Matsumoto, J., Deuschl, G., Roth, B. J., & Hallett, M. (1993). Source analysis of scalp-recorded movement-related electrical potentials. *Electroencephalography and Clinical Neurophysiology*, *86*, 167–175.
- Toyokura, M., Muro, I., Komiya, T., & Obara, M. (2002). Activation of pre-supplementary motor area (SMA) and SMA proper during unimanual and bimanual complex sequences: An analysis using functional magnetic resonance imaging. *Journal of Neuroimaging*, *12*, 172–178.
- Tsai, C. C., & Brass, M. (2007). Does the human motor system simulate Pinocchio's actions? Coacting with a human hand versus a wooden hand in dyadic interaction. *Psychological Science*, *18*, 1058–1062.
- Tsai, C. C., Kuo, W. J., Hung, D. L., & Tzeng, O. J. (2008). Action co-representation is tuned to other humans. *Journal of Cognitive Neuroscience*, *20*, 2015–2024.
- Ulrich, R., Leuthold, H., & Sommer, W. (1998). Motor programming of response force and movement direction. *Psychophysiology*, *35*, 721–728.
- 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*, 91.
- Vingerhoets, G., Acke, F., Alderweireldt, A. S., Nys, J., Vandermaele, P., & Achten, E. (2012). Cerebral lateralization of praxis in right- and left-handedness: Same pattern, different strength. *Human Brain Mapping*, *33*, 763–777.
- Walter, W. G., Cooper, R., Aldridge, V. J., 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.