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Predictive representation of other people's actions in joint action planning: An EEG study

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It has been postulated that when people engage in joint actions they form internal representations not only of their part of the joint task but of their co-actors' parts of the task as well. However, empirical evidence for this claim is scarce. By means of high-density electroencephalography, this study investigated whether one represents and simulates the action of an interaction partner when planning to perform a joint action. The results showed that joint action planning compared with individual action planning resulted in amplitude modulations of the frontal P3a and parietal P3b event-related potentials, which are associated with stimulus classification, updating of representations, and decision-making. Moreover, there was evidence for anticipatory motor simulation of the partner's action in the amplitude and peak latency of the late, motor part of the Contingent Negative Variation, which was correlated with joint action performance. Our results provide evidence that when people engage in joint tasks, they represent in advance each other's actions in order to facilitate coordination.

People perform many actions jointly in order to reach a common goal, such as carrying a table or playing a music duet. This requires adjustments to individual action planning and control because the actions to be performed by one's co-actor must be taken into account (Becchio, Sartori, Bulgheroni, & Castiello, 2008; Vesper, Soutschek, & Schubo, 2009). Such adjustments take place even in cases where individuals would do better to ignore the actions of another person in order to effectively perform their tasks. It has been consistently found that co-actors performing complementary, but independent, tasks form representations of each other's tasks, which interferes with their performance (Atmaca, Sebanz, & Knoblich, 2011; Sebanz, Knoblich, & Prinz, 2003, 2005). This takes place even in competitive situations, where the best strategy for an individual would be to focus on his/her own actions in order to receive a monetary reward (de Bruijn, Miedl, & Bekkering, 2008; Ruys

& Aarts, 2010). Thus, it seems that the representation of others' actions occurs automatically in several joint action situations.

In this study, we investigated the cognitive and motor processes supporting the planning of joint actions that involve close interpersonal coordination. Our objective was to determine by means of high-density electroencephalography (EEG) how planning a joint action differs from planning an individual action. Previous EEG research on joint action focused on situations where demands on temporal coordination are low, such as in turn-taking contexts where individual actions are performed independently of the co-actor. These studies revealed that increased inhibitory control demands arise in joint tasks involving turn-taking, because people represent their co-actor's action and then need to inhibit the ensuing tendency to act when it is not their turn (de Bruijn et al., 2008; Sebanz, Knoblich, Prinz, & Wascher, 2006; Tsai, Kuo, Hung,

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& Tzeng, 2008; Tsai, Kuo, Jing, Hung, & Tzeng, 2006). However, little is known about how action planning is adjusted to support joint actions that require coordination in time and space, such as when one person is passing an object to another.

We conducted an EEG experiment where groups of participants sometimes performed individual actions and sometimes performed joint actions. In order to separate action planning from action performance processes, we used a pre-cueing paradigm (Rosenbaum, 1980) in which a visual cue specified whether an individual action or a joint action should be performed later on. The cue was followed by a delay period (foreperiod) of 1 s, after which a visual go signal prompted the participant(s) to perform the cued action. The EEG analyses focused on activity during the foreperiod.

Our general hypothesis was that interaction partners will not only represent their own part of the joint task but also generate a representation of their co-actor's part (Sebanz et al., 2005, 2006). On the basis of the evidence that others' actions are represented in a qualitatively similar way as one's own actions (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997; Rizzolatti & Craighero, 2004; Schütz-Bosbach & Prinz, 2007), we predicted amplitude modulations in several event-related potentials (ERPs) that are known to reflect cognitive and motor processes during individual action planning.

The first ERP of interest was a fronto-central positive potential peaking around 200–300 ms after stimulus onset, which is often identified as the first subcomponent of the well-studied P300 component (also P3, P3 complex; Sutton, Braren, Zubin, & John, 1965). Termed P3a, P3f or novelty P3 depending on the nature of the task (and also P2a, see Potts, 2004), it is thought to reflect the initial evaluation and categorization of task-relevant stimuli with regard to the task at hand. Previous EEG studies showed that the P3a was larger after stimuli that required a person to perform (or withhold) an action in the presence of a co-actor performing a complementary task (Sebanz et al., 2006; Tsai et al., 2006), compared to a situation where the same task was performed alone. This suggests that the P3a depends on the social context of a task and not on the physical features of the stimuli. The authors argued that the enlarged P3a can be interpreted as an indication of the activation of a more complex task representation that included the partner's task rule and allowed participants to categorize the task in terms of whether it was their own turn or the other's turn. Accordingly in this study, we predicted that if interaction partners represent both their own and their partner's part of the task during joint action planning, then the P3a should be larger compared to individual action planning.

Joint action planning may require that all of the actors' specific tasks are represented. In addition, these representations may be linked to a person's motor system in order to predictively simulate all of the involved actions. This can be addressed by examining the amplitude of the parietal P300 or P3b component (often termed "classical P3"), which is traditionally associated with working memory updating or the representation of the task context (Donchin & Coles, 1988; Polich, 2007). More recent accounts on the functional significance of the P3b link this component to decision-making (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Verleger, 2008), assigning it a more integrative role. This integrative role consists in linking perceptual and reactive processes, perhaps by monitoring the decision-making process (Verleger, Jaśkowski, & Wascher, 2005). We predicted that if actors specify in advance both their own and their partner's part of the joint task, the P3b should be larger when planning a joint action, compared to planning an individual action where only their own task has to be specified. The expected enlarged P3b before joint action may indicate the updating of the representation of both partners' specific parts of the task in memory (Polich, 2007) or the monitoring of perception–action links that specify both partners' parts of the task (Verleger, 2008).

In addition, we also expected to find evidence for predictive motor simulation of the partner's action. Previous EEG studies have shown that motor simulation takes place in tasks where participants receive a cue about somebody else's upcoming action (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Kourtis, Sebanz, & Knoblich, 2010) and in tasks where participants take turns in performing actions (Koelewijn, van Schie, Bekkering, Oostenveld, & Jensen, 2008; Tsai et al., 2008; van Schie, Mars, Coles, & Bekkering, 2004). Accordingly, we predicted that participants would simulate in advance their own actions as well as their partner's actions. This could enable them to predict their partner's actions (Ramnani & Miall, 2004) and thereby to optimize joint performance (Knoblich & Jordan, 2003).

To test this hypothesis, we examined the Contingent Negative Variation (CNV), a slow brain potential of negative polarity, which develops during the delay period between an informative stimulus (cue) and an imperative stimulus and peaks at approximately action onset (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV, during its late stages, mainly reflects time-based motor preparation (Leuthold, Sommer, &

Ulrich, 2004; van Rijn, Kononowicz, Meck, Ng, & Penney, 2011).Two specific predictions were derived for the late (motor) CNV. First, if the CNV reflects successful simulation of a partner's actions, its amplitude should correlate with performance measures that reflect the quality of the coordination between two partners. Second, if a partner's actions are accurately simulated, the CNV waveform pattern should correspond to the actual length of the planning period of the partner's actions. More specifically, the CNV should reach its peak amplitude at approximately the time when the partner is starting to move.

METHODS

Participants

Continuous EEG data were simultaneously recorded from eight pairs of right-handed participants. A third actor (confederate) performed only individual actions. The presence of a confederate served the purpose of examining differences in action anticipation depending on the relation between observer and actor. These results have been reported elsewhere (Kourtis et al., 2010).[1] For the purpose of this study, the presence of the confederate ensured that participants performed the task according to the instructions. All participants (nine females and seven males; age = 25.5 ± 6.5 years) had normal or corrected-to-normal vision and had no history of hand or arm injuries or any mental, cognitive, or other neurological disorder. All participants provided their informed consent after full explanation of the study.

Experimental set-up and procedure

The experiment was run in a quiet, normally illuminated room. The participants were seated around a table. The interaction partners were facing each other and a confederate sat at a right angle to them. No data were recorded from the confederate (Figure 1).

A cylindrical candle (height: 13.3 cm, radius: 2.54 cm) was placed on a fixed base at the center of the table. A white wooden disc (radius: 6.35 cm) was attached on the top of the candle. Color-coded stimuli were projected onto the surface of the disk by
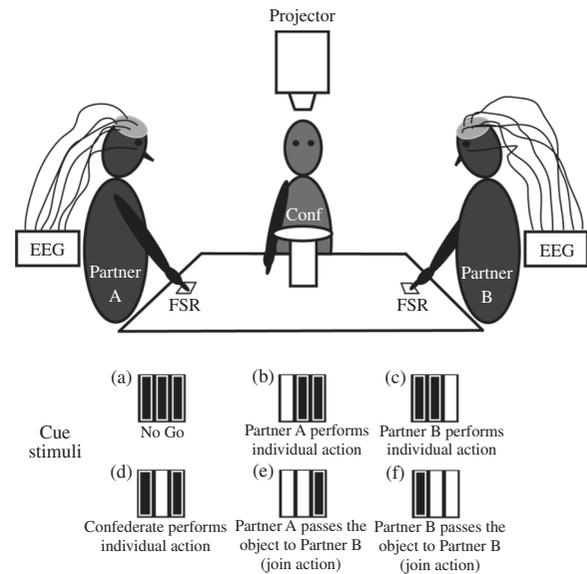
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[1] In Kourtis et al. (2010), we reported data showing that observers show anticipatory motor activation only for upcoming individual actions of an interaction partner but not for upcoming interactions of a "loner" who always performed actions individually.


Figure 1. Schematic representation of the experimental set-up and cue stimuli. The cue stimuli were projected on top of the object that was located at the middle of the table. There were six different cue stimuli indicating the type of action to be performed: (a) No action; (b) Partner A lifts the object and then places it back; (c) Partner B lifts the object and then places it back; (d) The Confederate lifts the object and then places it back; (e) Partner A lifts the object and gives it to Partner B, who will then place the object back to its starting location; (f) Partner B lifts the object and gives it to Partner A, who will then place the object back to its starting location.

an LCD projector, encased in a metallic contraption and 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 (∼5 cm from the table edge) in front of each interaction partner in order to record reaction times.

We used a choice-reaction paradigm where a cue stimulus, presented for 200 ms (Figure 1), indicated the type of action to be performed. It was followed by an imperative stimulus (a white "X" on black background; inter-stimulus-interval = 1000 ms), prompting the participants to act (Figure 2). The main target of our EEG analyses was the time interval (foreperiod) between the cue and the imperative stimulus, during which all individuals remained motionless, fixating the cross presented at the top of the object (Figure 2). During this period, different types of action were prepared but not executed.

Symmetrical cue stimuli were used in order to avoid any lateralized brain activity caused by the physical properties of the stimuli (see Figure 1). Three horizontal white frames over black background were placed. From the point of view of each interaction partner (i) a cue with the bottom frame filled with white color indicated individual action, (ii) a cue with the top frame
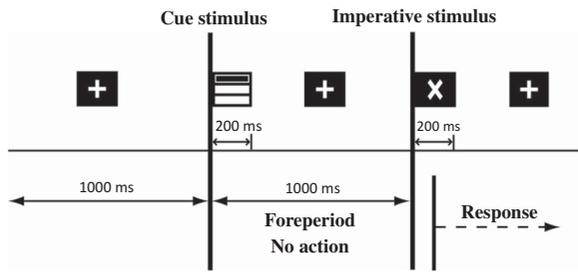
Figure 2. Schematic example of trial. The trial started with the presentation of a fixation cross for 1000 ms. Then a cue stimulus appeared for 200 ms indicating the type of action to be performed (in this example "joint action"). Following another fixation period of 800 ms, the imperative stimulus appeared for 200 ms prompting the participants to act. The period of interest was the time interval (1000 ms) between cue onset and imperative stimulus onset (foreperiod).

filled with white color indicated individual action of the partner, (iii) a cue with the bottom and the middle frames filled with white color indicated giving the object to the partner, (iv) a cue with the top and the middle frames filled with white color indicated receiving the object from the partner, (v) a cue with the middle frame filled with white color indicated individual action of the confederate, and (vi) a cue where none of the frames was filled with white color indicated that no action was required.

In the individual action conditions (i, ii, and v), the cue prompted the person sitting at the side of the filled white frame to plan a reaching action toward the object (without leaning his/her body forward), to lift it vertically to an approximate height of 30 cm, and to return it back to its original position. In the joint action conditions (iii, iv), the cue prompted the person sitting at the side of the filled white frame to plan a reaching action toward the object (without leaning his/her body forward), to lift the object vertically to an approximate height of 30 cm and to pass it to the interaction partner (give condition). The person sitting at the opposite side of the table planned to reach out and to receive the object (without leaning his/her body forward) and to place it back to its original position (receive condition).

The experiment consisted of 10 blocks of 60 trials each, preceded by a practice block of equal length. In half of the blocks, all participants used their right hand and in the other half of the blocks all participants used their left hand. The order of blocks and the order of trials within a block were randomized.

Data acquisition

Action onset was defined as the time interval between the onset of the imperative stimulus 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 (SDs) from the mean action onset within each condition were removed from further analysis.

For each interaction partner, EEG was recorded continuously from 64 Ag/AgCl scalp electrodes relative to an off-line average mastoid reference. The electrodes were placed according to the International 10–20 electrode system using a carefully positioned nylon cap. Vertical eye movements were monitored using one pair of bipolar electrooculography (EOG) electrodes positioned directly under the eyes, while horizontal eye movements were monitored using the nearest to the eyes cap electrodes (FFT9h/FFT10h). EEG and EOG signals were amplified with a band-pass of 0–128 Hz by BioSemi Active-Two Amplifiers and sampled at 512 Hz.

Data processing and analysis

EEG data processing was performed off-line using Brain Electrical Source Analysis (BESA, v. 5.1.8) and Brain Vision Analyzer (BVA, v. 1.05) software. Initially, eye-movement correction was performed in BESA on the continuous EEG data, during which artifacts induced by eye movement were either eliminated or reduced in amplitude. The corrected EEG data were then imported into BVA and segmented off-line in epochs ranging from 300 ms before cue onset to 1700 ms after cue onset. The data were filtered using a low-cut-off filter of 0.1 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 artifacts or incorrect responses were removed before averaging. Averages were constructed for each subject and condition separately. ERP amplitudes were analyzed by pooling the values of neighboring electrodes within regions of interest, identified on the basis of scalp topographies.

RESULTS

Behavioral analysis

The action onsets were M = 382 ms (SD = 82 ms) for acting individually, M = 394 ms (SD = 87 ms) for performing the giving part of the joint action, and M = 776 ms (SD = 120 ms) for performing the receiving part of the joint action. A one-way ANOVA (Greenhouse–Geisser correction applied) with the factor Action Type (individual, give, and receive) showed a significant effect of type of action
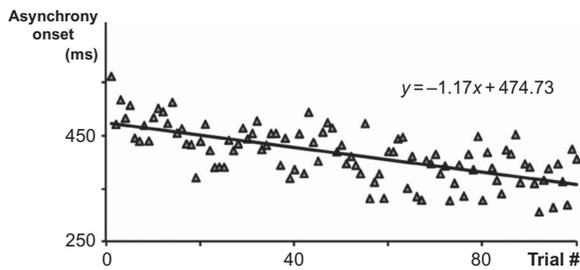
Figure 3. Decrease in asynchrony between the onset of the receive response and the onset of the (earlier) give response on a trial-by-trial basis.

($F(1, 15) = 88.89, p < .001$). Paired t-tests showed that there was no significant difference in action onset for acting individually compared with giving the object to the interaction partner ($t(15) = 1.82, p > .05$). However, participants were significantly slower to initiate the receiving action in the joint condition both compared to initiating individual action ($t(15) = -9.64, p < .001$) and compared to initiating the giving action in the joint condition ($t(15) = -9.34, p < .001$).

Examining action onset times on a trial-by-trial basis (Figure 3) revealed that participants took less and less time to initiate their actions as the experiment progressed. This speed-up was relatively small in the individual condition (-0.25 ms/trial) and in the give condition (-0.23 ms/trial). The speed-up was clearly larger in the receive condition (-1.71 ms/trial). The more extensive speed-up in the receiving condition compared to the giving condition implied a continuous decrease (-1.17 ms/trial) in the asynchrony between the giver's and the receiver's action onsets in joint action trials. Thus, the efficiency of interpersonal coordination was constantly improving throughout the experiment. Compared with a complete lack of improvement in the efficiency of coordination (zero slope), this effect was statistically significant ($t(31) = -5.05, p < .001$).

EEG analysis

Behavioral and EEG results were practically identical for left-hand blocks and right-hand blocks. Therefore, all analyses were performed on pooled data from both hands.

P3a

The first analysis assessed the amplitude of the P3a, which was quantified by pooling the mean activity from 200 to 250 ms after cue onset from electrodes FCz, FC1, FC2, Fz, and Cz (Figure 4a). A one-way ANOVA (Greenhouse–Geisser correction applied) showed a significant effect of type of planned action (individual, give, or receive) on P3a amplitude ($F(1, 15) = 5.37, p < .05$). Post hoc t-tests showed that there was no difference between the two joint conditions where participants planned either to give the object to their partner or to receive it from their partner ($t(15) = .001, p = .99$). However, compared to individual action planning, the P3a was larger in both joint conditions, planning to give ($t(15) = 3.34, p < .01$), planning to receive ($t(15) = 2.60, p < .05$).

P3b

The P3a was followed by the parietal P3b component, peaking at approximately 450 ms after cue onset over mid-parietal areas. An inspection of the EEG waveforms revealed that the P3b should best be divided into two distinct subcomponents. The earlier subcomponent, which we will refer to as lateral-P3b, reached its maximum approximately 320 ms after cue onset over right parietal areas. The later subcomponent, which we will refer to as medial-P3b, peaked approximately 450 ms after cue onset over mid-parietal areas (Figure 4b and c).

The lateral-P3b amplitude was quantified by pooling the mean activity from 270 to 320 ms after cue onset from electrodes P4, P6, PO4h, and PO8. A one-way ANOVA (Greenhouse–Geisser correction applied) showed a significant effect of type of planned action (individual, give, or receive) on lateral-P3b amplitude ($F(1, 15) = 8.76, p < .01$). Post hoc t-tests showed that there was no difference between the two joint conditions ($t(15) = .035, p > .7$). Surprisingly, the lateral-P3b was significantly larger when planning an individual action compared to planning to give ($t(15) = 4.22, p < .001$) and compared to planning to receive ($t(15) = 2.95, p < .01$).

The medial-P3b was quantified by pooling the mean activity from 450 to 500 ms after cue onset from electrodes Pz, POz, PO3h, and PO4h. A one-way ANOVA (Greenhouse–Geisser correction applied) showed a significant effect of type of planned action (individual, give, or receive) on medial-P3b amplitude ($F(1, 15) = 3.70, p < .05$). Post hoc t-tests showed that there was no difference between the joint conditions, planning to give or planning to receive ($t(15) = .99, p > .3$). The medial-P3b was larger when planning to receive compared to individual action planning ($t(15) = 2.60, p < .05$) and when planning to give compared to individual action planning; however, the latter comparison did not reach statistical significance ($t(15) = 1.81, p = .09$).
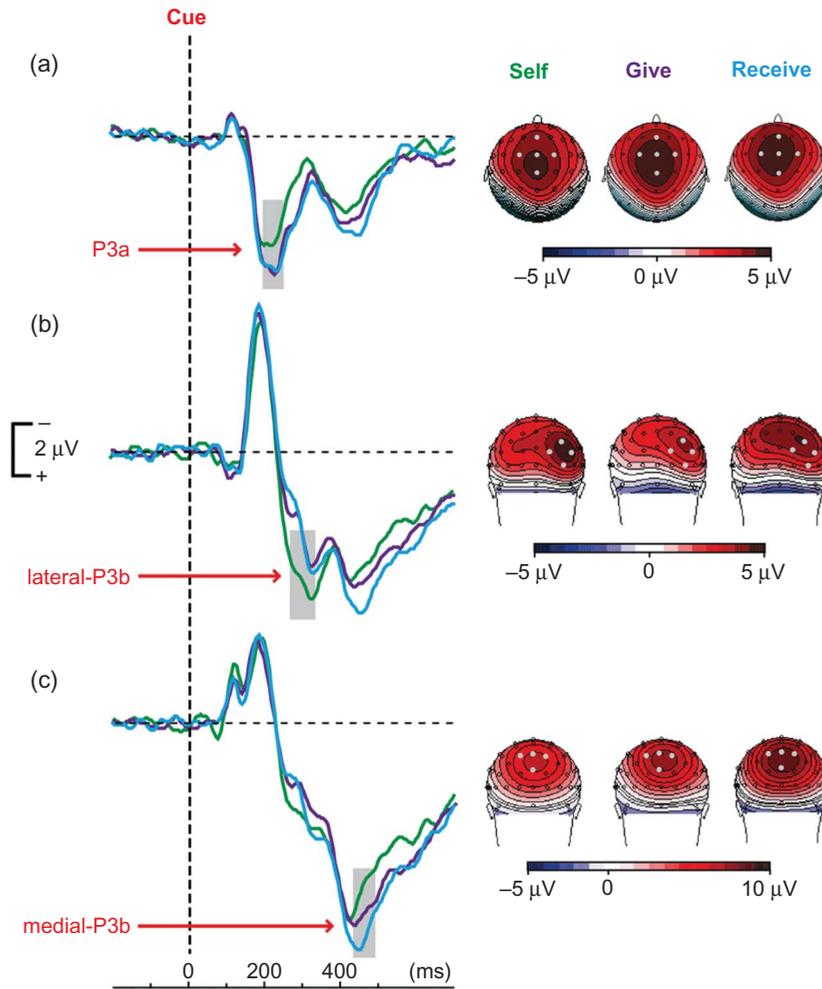
Figure 4. (a) Color-coded, grand average waveforms derived from pooled electrode sites (FCz, FC1, FC2, Fz, and Cz, highlighted as gray circles) and scalp voltage distributions of the P3a component (top view) from 200 to 250 ms after cue onset. (b) Color-coded, grand average waveforms from pooled electrode sites (P4, P6, PO4, and PO8) and scalp voltage distributions of the lateral-P3b component (back view) from 260 to 330 ms after cue onset. (c) Color-coded, grand average waveforms from pooled electrode sites (Pz, POz, PO3, and PO4) and scalp voltage distributions of the medial-P3b component (back view) from 450 to 500 ms after cue onset. The gray bars indicate the latency window for amplitude analysis. The vertical dashed line at time 0 denotes cue onset.

Contingent negative variation

As expected, the CNV developed gradually during the foreperiod in each experimental condition. In order to remove the activity due to stimulus anticipation processes and to keep the motor components of the CNV, we subtracted the CNV in the no-go condition from the CNV in the remaining conditions (Figure 5). The motor CNV reached its maximum amplitude over motor areas and showed a small lateralization toward the left hemisphere. This possibly reflects the dominance of the left hemisphere in motor control (Taylor & Heilmanf, 1980). The amplitude of the motor CNV in the last 200 ms before go stimulus onset (electrodes Cz, C1, FCz, and CPz) was analyzed as a measure of predictive motor simulation. A one-way ANOVA (Greenhouse–Geisser correction applied) showed no indication that the late CNV amplitude differed across the three conditions ($F(1, 15) = 0.26$, $p > .05$). In line with our predictions, the motor CNV in the receive condition peaked at approximately 307 ms (SD = 80 ms) after go signal onset, which clearly corresponds more closely to the time of the partner's (i.e., the "giver's") action onset (M = 394 ms, SD = 87 ms) than to the receiver's own action onset (M = 776 ms, SD = 120 ms).
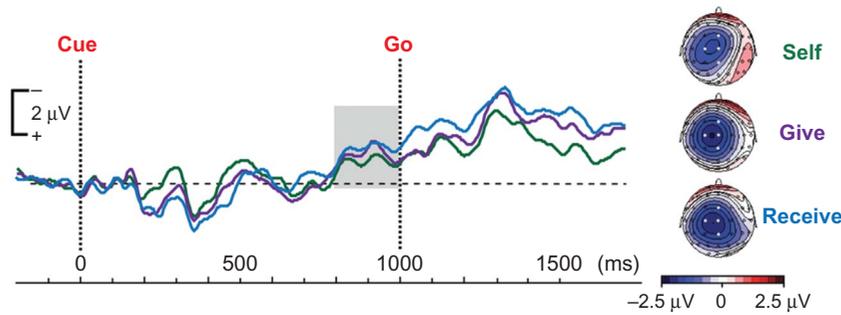
Figure 5. Color-coded, grand average motor CNV waveforms derived from pooled electrode sites (Cz, C1, FCz, and CPz, highlighted as gray circles) and scalp topographies (top view) in the last 200 ms (indicated by the gray square) before go stimulus onset. The gray bars indicate the latency window for amplitude analysis. The vertical dashed lines at times 0 and 1000 denote cue onset and go stimulus onset, respectively.

Correlations

A correlation analysis across participants showed that the medial-P3b and the motor CNV in the receive condition were significantly correlated (Pearson's correlation test, $df = 14$, $r = 0.54$, $p < .05$). In addition, the motor CNV in the receive condition was significantly correlated with the slope of the continuous decrease in asynchrony between the two partners' action onsets (Pearson's correlation test, $df = 14$, $r = 0.58$, $p < .05$). These results indicate that there was a relation between representing the partner's action after the cue and running an anticipatory motor simulation of the partner's action. Furthermore, there was a relation between running a motor simulation of the partner's action and effectively performing the joint task.

DISCUSSION

We found differences between planning joint actions and planning individual actions. It is unlikely that such differences were due to the kinematic differences of the performed actions, considering that the individual action was very similar to the giving action, and also that the planning of the dissimilar parts of the joint task (i.e., "giving" or "receiving" the object) evoked almost identical EEG potentials. Our findings provide electrophysiological evidence that when passing an object, partners represent each other's actions during joint action planning, and that representing each other's action helps them to improve coordination.

P3a

In this study, a cue instructed the participants to plan an individual or a joint task. An early process for planning the correct action is categorizing the upcoming task as an individual or a joint task, thus activating the corresponding task representation. Higher or lower demands associated with this categorization process were likely reflected in the amplitude modulation of the early fronto-central P3a component (Polich, 2007; Verleger, 2008). In line with our predictions, we found that the P3a amplitude was enhanced during joint action planning. This indicates that processing a cue that specified a joint action was more demanding or required more attention (Hagen, Gatherwright, Lopez, & Polich, 2006; Matthews, Martin, Garry, & Summers, 2009) than processing a cue that specified individual action.

P3b

In addition, we expected that specifying the other's task would modulate the amplitude of the parietal P3b in the joint action conditions; however, the information derived from the P3b modulation was richer than expected. The P3b consisted of two subcomponents, which differed in their spatiotemporal characteristics and in the direction of their amplitude modulation depending on the type of the planned action. Specifically, the lateral-P3b was larger before individual action, whereas the medial-P3b was larger before joint action.

The seemingly paradoxical modulation of the lateral-P3b can be explained when we regard the P3b as an index of preferential processing of group-relevant information. Previous EEG studies have shown that a larger P3 is elicited by the participant's own face (Gunji, Inagaki, Inoue, Takeshima, & Kaga, 2009), own name (Perrin et al., 2005), or other self-relevant stimuli (Gray, Ambady, Lowenthal, & Deldin, 2004; Yu, Tu, Wang, & Qiu, 2010), irrespective of the nature of the stimulus (e.g., faces vs. names, Tacikowski & Nowicka, 2010). Moreover, collective

self-relevant stimuli, such as an Alma mater name, induce a smaller P3 than individual self-relevant stimuli (Zhao et al., 2009). Similarly, in our experiment, the lateral-P3b was smaller in the joint action conditions, which suggests that the cue stimulus was perceived as relevant to the group and not just as relevant to each individual. This in turn implies that the participants did not only plan their part of the joint task in terms of an individual action, but formed a joint action plan instead. This interpretation is consistent with recent theoretical suggestions (Vesper, Butterfill, Knoblich, & Sebanz, 2010) and findings showing that participants form action plans that specify the outcomes of jointly performed actions (Tsai, Sebanz, & Knoblich, 2011).

Furthermore, the lateral-P3b was larger over the right hemisphere. In order to interpret this finding it is important to consider that, although the P3b reflects co-activation of several brain areas, its main generators are located around the temporoparietal junction (TPJ) (Bledowski et al., 2004; Linden, 2005; Polich, 2007; Verleger, 2008). The TPJ is part of the "mentalizing" brain network, which is involved in high-level processes of social cognition (e.g., inferring others' beliefs and intentions), and also in lower-level tasks, such as spatial perspective taking (for a review, see Van Overwalle & Baetens, 2009). The TPJ is associated with integration of multisensory body-related information (Blanke & Arzy, 2005) and is considered to play a major role in various self-referential processes related to self-awareness, perspective taking, and theory of mind (Aichhorn, Perner, Kronbichler, Staffen, & Ladurner, 2006; Blanke, Ortigue, Landis, & Seeck, 2002; Ruby & Decety, 2001; Samson, Apperly, Chiavarino, & Humphreys, 2004; Vogeley & Fink, 2003). The right TPJ in particular is associated with the representation of the mental as well the corporeal self (Daprati, Sirigu, & Nico, 2010; David et al., 2006; Lou et al., 2004) and with third-person perspective taking (Arzy, Thut, Mohr, Michel, & Blanke, 2006; David et al., 2006; Ruby & Decety, 2001, 2004; Saxe & Powell, 2006; Schilbach et al., 2006). It is believed that activation of the right TPJ reflects the operation of a basic computational mechanism that enables the distinction between self and other (Blakemore & Frith, 2003; Decety & Grèzes, 2006; Decety & Sommerville, 2003; Jackson & Decety, 2004). In our study, task representations specifying the actions to be performed jointly may have created the need to distinguish between one's own actions and the partner's actions. Consequently, activation in the right TPJ may have driven the asymmetrical topography of the lateral-P3b.

Following the lateral-P3b, the medial-P3b was larger during joint action planning. According to our hypothesis, this can be taken as an indication that the participants specified both their task and their partner's task. The scalp topography of this subcomponent suggests that it may have originated in the medial posterior parietal cortex (possibly the precuneus), which is assumed to contribute considerably to the generation of the P3b (Holeckova et al., 2008; Mulert et al., 2004). Perrin et al. (2005) reported a significant covariation of the regional cerebral blood flow in the precuneus and the P3 amplitude, which peaked over medial parietal areas (electrode Pz) around 400–500 ms after cue onset, similarly to the medial-P3b in our study. The precuneus has also been considered as a part of the "mentalizing" network and it has been associated with conscious awareness, self-processing, retrieval of episodic memory, and (preparatory) visuo-spatial imagery (Cavanna & Trimble, 2006). It has been hypothesized that the activation of the precuneus is associated with inspection of an internal image in memory (Burgess, Maguire, Spiers, & O'Keefe, 2001), often showing stronger activation during third-person perspective taking compared to first-person perspective taking (Ruby & Decety, 2001; Schilbach et al., 2006; Vogeley et al., 2004). The role of the precuneus seems to be in line with the working-memory updating hypothesis with regard to the functional significance of the P3b (Polich, 2007). Accordingly, the enlarged medial-P3b in the joint action conditions could reflect the inspection/updating of the joint task in memory, which involves the specification of one's own part of the task (involving first-person perspective taking) and also the specification of the partner's part of the task (involving third-person perspective taking).

However, other studies suggest that the precuneus is involved in the processing of intentions (Abraham, Werning, Rakoczy, von Cramon, & Schubotz, 2008; Ciaramidaro et al., 2007). This hypothesis ascribes a more tactical role to the precuneus and is closer to the view that the P3b is indirectly related to decision-making (Nieuwenhuis et al., 2005; Verleger, 2008). Moreover, a number of neuroimaging studies have introduced the idea that the precuneus could be the human homolog of the monkey's parietal reach region, which is activated when a monkey plans to perform a reaching movement (Connolly, Andersen, & Goodale, 2003; Naranjo et al., 2007). Hence, the medial-P3b may not simply reflect updating of the representation of both partners' specific parts of the task. Rather it may reflect monitoring of whether all the necessary steps have been taken in order to simulate both partners' specific parts of a joint (reaching) task. This

interpretation is further supported by the significant correlation of the medial-P3b and the motor CNV in the "receive" condition, which suggests that taking the partner's perspective and representing his or her intention (reflected by the medial-P3b) may be a crucial precondition for anticipatory action simulation (reflected by the motor CNV),

Contingent negative variation. In agreement with our prediction that the CNV waveform pattern should correspond to the actual length of the planning period of the partner's actions, the (motor) CNV of a "receiver" peaked approximately at the time of the partner's response. This suggests that in the receiving condition participants were not only preparing their own actions but also sampling the average speed their partner took to initiate the giving action. This, in turn, allowed them to predict the time their partner would take to initiate the giving action on a given trial.

Support for this interpretation in terms of motor simulation is provided by source localization studies suggesting that the cortical generators of the late/motor CNV are mainly the supplementary motor area (SMA), the dorsal premotor cortex (Pmd), and possibly the primary motor cortex (MI) (Jentzsch & Leuthold, 2002; Leuthold & Jentzsch, 2001, 2009; Nagai et al., 2004; Praamstra, Kourtis, Kwok, & Oostenveld, 2006). The SMA is one of the brain areas where neurons with mirror properties were first recorded in humans (Mukamel, Ekstrom, Kaplan, Iacoboni & Fried, 2010). The term "mirror" refers to the property of neurons (or brain areas) to show similar activation during action perception and action execution. Initially discovered in monkeys' ventral premotor cortex (PMv) and inferior parietal lobule (IPL) (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996), the "mirror mechanism" has been found in a number of human brain areas including not only PMv and IPL but also PMd, MI, superior temporal sulcus (STS), somatosensory cortices (SI and SII), and subcortical structures (for reviews, Keysers & Gazzola, 2009; Rizzolatti & Sinigaglia, 2010). It is believed that this "mirror mechanism" serves as a basis for motor simulation of another person's actions. Motor simulation does not only occur during observation of an action but also occur when observers anticipate that someone will perform an action (Kilner, Friston, & Frith, 2007). Thus, it is conceivable that the peaking of the receiver's motor CNV at the giver's response onset is indeed a reflection of predictive motor simulation of the giver's action.

It should also be considered that there was a significant correlation between the receiver's motor CNV amplitude and the improvement in coordination. The behavioral analysis clearly showed that the speed-up in receiving led to the improvement in coordination as receiving was getting faster at a greater rate than giving. This finding can be well explained by the assumption that motor simulation allowed the receiver to predict the timing of the giver's action and to improve coordination by decreasing the asynchrony in action onset between initiating the giving and receiving action.

Limitations

A limitation of this study concerns the correlational relation between some of the results. The correlation analysis showed a systematic relation between the receiver's medial-P3b and the motor CNV and also between the receiver's motor CNV and the improvement in coordination; however, such correlations do not establish causal relationships. For example, we cannot argue with certainty whether greater or more detailed motor simulation would lead to further improvement in coordination and we cannot exclude the possibility that other parameters contributed to this effect.

In addition, it has to be acknowledged that due to the novelty of our paradigm and experimental set-up, as well as the limited spatial resolution of the EEG, a certain degree of speculation was used with regard to the interpretation of our findings. Definitive answers with regard to the involvement of the proposed brain areas in the generation and modulation of the recorded ERPs in our task can only be provided by equivalent imaging studies.

SUMMARY AND CONCLUSION

Intuitively, performing joint actions seem to require that agents take each other's actions into account. Although there is considerable evidence that co-actors represent each other's tasks in situations involving turn-taking, little is known about how individual action planning is modulated in the service of interpersonal coordination. The results of this study suggest that planning of joint actions that require tight temporal coordination modulates specific brain processes that operate during planning of (externally triggered) individual actions. Initially, an informative cue is categorized according to task representations stored in memory and then evaluated according to the relevance of the subsequent action. At the same time, it becomes important to differentiate between one's own

and the partner's actions. Following that, an updating of an internal representation of the specific roles of each interaction partner may take place via visuospatial imagery. This may involve third-person perspective taking and the representation of motor intentions. Finally, the partner's expected action is simulated at the motor level, which probably facilitates effective performance of the joint action. To our knowledge, this study is the first to provide electrophysiological evidence of the notion that joint action planning involves cognitive and motor representations of the action partner's task, which can improve coordinated task performance.

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