Action Co-representation is Tuned to Other Humans

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Abstract

■ The present study attempts to explore the process by which knowledge of another's intentional behavior in a joint-action scenario is represented through the action observation and execution network—also known as the common coding system. Participants (n = 18) were instructed to perform the complementary social Simon task under the implemented belief of interaction with either an unseen human (biological agent) or a computer program, where in fact, all response sequences from either ''partner'' were generated by computer. Results provide behavioral and neurophysiological evidence (P3 and S-LRP) that the believed intentionality of another person's actions is sufficient to facilitate a strong-enough agency-dependent social Simon effect to modulate action planning and anticipation. We suggest that the co-representation of human action may be an evolved biologically tuned default of the human motor system. ■

INTRODUCTION

Humans naturally divide objects in the perceptual world into two distinct categories: animate beings (e.g., people) and inanimate objects. To our perception, the motions performed by a human being are a discrete indicator of animation and biological similarity, and are thus given a separate and distinct identity from all other movement patterns within our brains (Johansson, 1973). Visual identification with a human conspecific's body structure enables us to mimic observed actions and map them to our bodies isomorphically. Kinematically, the movements performed by intentional agents appear to be self-propelled and goal-directed. The mapping of the observed actions of our conspecifics may be advantageous in social interaction and cooperation, as it allows the possibility of consequence prediction and grants valuable insight into another person's probable intentions on the basis of motor knowledge.

Recent studies on mirror neurons illuminate the intimate relationship between perception and action (Blakemore & Frith, 2005), elucidating the direct contribution of motor knowledge to action understanding (Rizzolatti & Craighero, 2004). The neurons in monkey brain area F5, for example, fire both when the monkey is performing an action as well as when it observes the action being performed. Findings in human subjects also demonstrate motor contagion in action perception (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschlager, & Prinz, 2000), indicating a common coding system between motor behavior and the recognition of motor behavior (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997). In addition to implementing motor recognition, the mirror system also holds the capacity to model or represent an action to its typical outcome on completion, based on previous motor experience (Knoblich & Flach, 2001). The common coding system plays a key role as well in joint action (Sebanz, Bekkering, & Knoblich, 2006), whereby the co-representation of another person's actions allows planning of cooperative behavior (Knoblich & Sebanz, 2006).

Still unexplored is the issue of whether the common coding system favors intentional human action over behavior effected by a nonbiological agent in joint-action scenario. If the common coding system can model a subsequent effect in response to how another performs an action, in interaction with a biological agent, intentional stances (Dennett, 1987) would be mapped and simulated for action recognition and prediction. With inherent features of imitability in actions performed by a biological agent (Wilson & Knoblich, 2005), simulation proceeds by activating corresponding motor representations within our motor system (Tsai & Brass, 2007). Co-representation of the joint action can therefore be hypothesized as biologically tuned.

In this study, we employed the joint-action paradigm to explore the nature of co-representation. Participants in a classical Simon task were asked to respond to red and green targets presented either on the right or left side of the screen with a left and a right key (e.g., green target → left key; red target → right key). The Simon effect refers to the finding that participant's performance is always slower when the spatial relationship between stimulus and response is incongruent (de Jong, Liang, & Lauber, 1994). This effect disappears when the same stimulus was performed as a go/no-go task, whereby

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participants were required to respond to only one color attribute (e.g., red target → single key). However, the Simon effect can reappear in the same go/no-go situation when participants are embedded in a social context wherein another individual complementarily co-acts the task (e.g., green target → left-seat participant; red target → right-seat participant) (Sebanz, Knoblich, & Prinz, 2003). Therefore, the nature of co-representation can be explored by manipulating the co-actor in a joint go/no-go task, using either a real third-person or a computer program.

To avoid influences of actor appearance or other social interference, participants performed the task under the prior implemented belief that they were interacting with another. The conditions of the different believed co-actors were manipulated as a within-subject factor. Two LCD monitors connected to the same computer were placed in separate rooms for stimulus display. In the task, a target stimulus in either red or green was presented on the two monitors simultaneously. The participants were instructed to respond to the red targets by pressing a button, and informed that a co-actor outside their electroencephalogram (EEG) chamber would concurrently respond to the green targets with another key (see Figure 1). The key manipulation here was the implemented belief of co-action with different co-actors (see also Methods for details). In one condition, the participants were instructed to believe that they were co-acting with a friend (a biological agent) and, in another, with a computer program (a nonbiological agent). In actual fact, the responses of their ''partner'' in both conditions were random sequences generated by the same computer program. No feedback information from the ''partner'' was presented to the subject in either condition.

Electrophysiological data were recorded in the course of the experiment. With use of a joint go/no-go paradigm, the impact of a believed biological agent upon the modulation of action evaluation (go trial), preparation (go trial), and anticipation (no-go trial) was differentiated from that effected by a believed nonbiological agent. Two event-related potential (ERP) components, the P300 (P3) and the stimulus-locked lateralized readiness potential (S-LRP) are of direct relevance. The P3 is generally reported to have a centro-parietal maximum for go trials (go-P3, P3b) and a fronto-central maximum for no-go trials (no-go-P3), with a latency from 300 to 500 msec (Pfefferbaum, Ford, Weller, & Kopell, 1985), assumed to reflect the processing of event evaluation (Kok, 2001). For the evaluation process in the go/no-go task, the go-P3 evoked by target events has, in past literature, been noted to correlate to processes linking reactions to perceived events (Verleger, Jaskowski, & Wascher, 2005). In contrast, the no-go-P3 can reflect action control

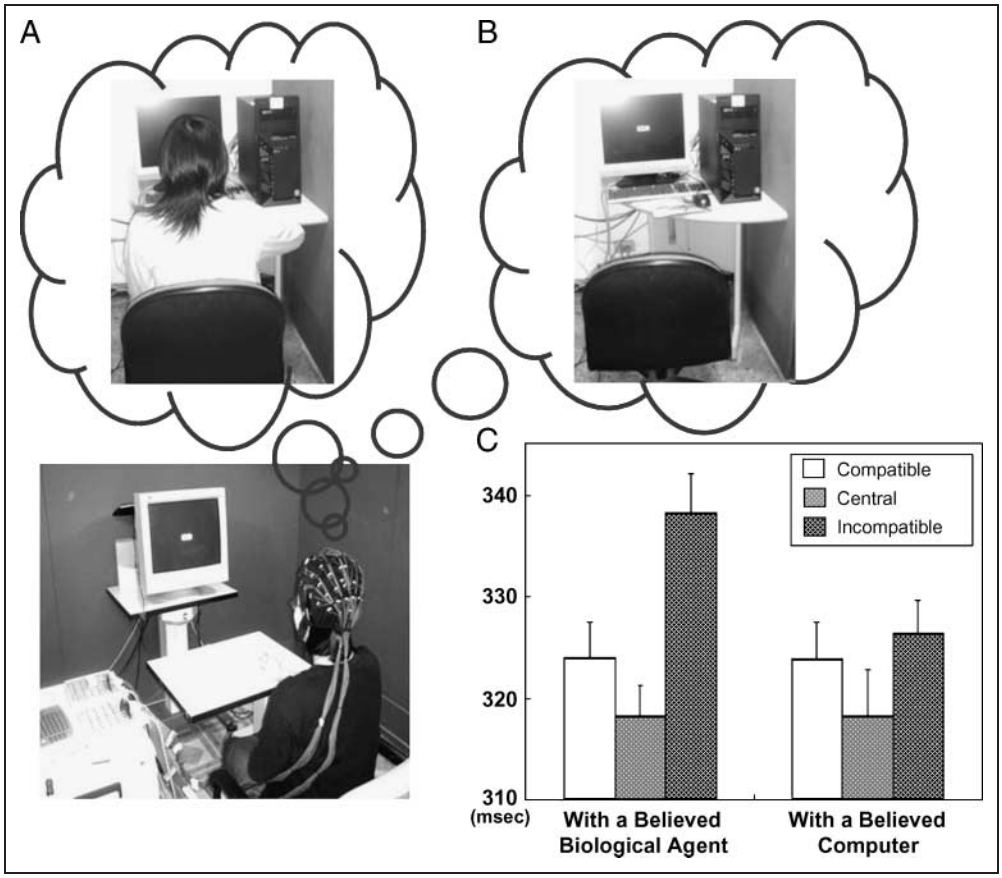

Figure 1. The illustration of experimental setting and behavioral results in two interacting contexts. Participants (sitting inside the EEG chamber) were instructed to perform the go/no-go task under the implemented belief of interacting with different co-actors, (A) biological agent and (B) a computer, placed outside the EEG chamber. In actual fact, the responses of their ''partner'' in both conditions were random sequences generated by the same computer program. Thus, the only difference between these two conditions was the implemented belief that they were interacting with an intentional agent or not. (C) The RT performance (go trials) on compatible, central, and incompatible trials in two co-acting contexts.

(Fallgatter & Strik, 1999) because its cortical generator is similar to that of response monitoring. Recent studies on no-go-P3 have shown that manipulating compatibility between current action and action history would change one's expectations of future events, and thus, increase the no-go-P3 amplitude on incompatible trials (Freitas, Azizian, Leung, & Squires, 2007). In the case of joint action, a subject's go trial involves an evaluation processing that integrates the self and the other's action representations into a single action plan. On the other hand, because the subject's no-go targets are the go targets of his co-actor, action control on incompatible no-go trials should increase, as the participant not only withholds responses to nontarget events but also anticipates the subsequent effects of the other's actions (Sebanz, Knoblich, Prinz, & Wascher, 2006; Tsai, Kuo, Jing, Hung, & Tzeng, 2006).

Another ERP component of note (i.e., S-LRP) is a slow, negative potential that precedes voluntary movements, which is an average waveform of individual trials aligned to stimulus onset (Smulders, Kenemans, & Kok, 1996). S-LRP is sensitive to the manipulation of spatial stimulus–response compatibility, which reflects earlier processing of response preparation (e.g., response selection) and provides information for competitions between the actions activated (Hsieh & Yu, 2003). In the context of joint action, as the ideomotor theory suggests (Prinz, 1997), a response code relative to the noncorresponding hand site would also be activated due to observing or imaging other's actions in the overlapping perception–action networks. The S-LRP results should help to clarify whether the implemented belief influences processing at a later stage such as response selection.

Our study attempts to investigate the influence of motor knowledge regarding different types of believed co-actors (i.e., biological and inanimate agents) upon action planning and control. Thus, to explore this issue, participants were instructed to perform a complementary Simon task with the assumed co-action of a biological agent (i.e., a real third-person) and a nonintentional computer program. If, indeed, the human co-representation system is restricted to our conspecifics, a social Simon effect at behavioral level should only be observed when interacting with a biological agent. The electrophysiological analysis aids the differentiation of the top–down process of belief from the far more elementary processes of action planning and control. We project that for action planning, a compatibility difference on the go-P3 amplitude should be observed in the condition of a believed biological co-actor; and that for the same condition, an increased action control on no-go incompatible trials should also be reflected on the no-go-P3 amplitude due to anticipation based on the common coding system. In addition, the S-LRP should provide information on whether the top–down effect of belief influences the stage of response selection or only occurs during event categorization.

METHODS

Subjects

Twenty-four right-handed National Yang Ming University students (10 men, age from 19 to 24 years) with corrected-to-normal vision volunteered in this experiment. Each participant gave the written consent to the experimental procedure and was paid $14.28 (NT 500) for 2 hr of participation. Six datasets were discarded because they (4 subjects) correctly guessed the purpose of the experiment or because of serious eye blink artifacts.

Experimental Setting and Design

Participants were instructed to perform a go/no-go task with different believed co-actors in two separate conditions. During experiment, participants inside the EEG chamber were informed that they would be cooperating in the task with either a real person (their friend) or a computer, wherein a color target in either red or green situated in one of three locations (left, middle and right) would be presented both upon a monitor before him, and upon another outside his chamber. For the go trials in both conditions, the color targets appeared on the screen until response was given. A single key (the right button of the mouse) was placed on the right side of the table and participants were instructed to respond to the red color target regardless of its location. In Condition 1—co-action with a believed biological co-actor—the participants were informed that a partner would be attending a complementary task on the other computer screen while they responded to the red targets (go trials), and that the green target would vanish from the screen upon their partner's response (no-go trials), which involved a left click response on a mouse. In Condition 2—co-action with a believed nonbiological co-actor—the same task was performed, but the participants were informed that a computer would be attending the complementary task. In actual fact, the computer program administrating the experiment acted as the co-actor in both conditions, ''responding'' in the no-go trials by presenting the green targets on-screen for a short span of time (randomly ranging from 300 to 450 msec) to mimic the reaction time (RT) of a human being. Thus, the only difference between the two conditions was the believed identity of the co-actor.

To reinforce the implemented belief of co-acting with a biological agent, the following procedure was adopted: Pairs of acquainted individuals were explicitly targeted during the participant recruitment process. Upon arriving at the laboratory for the experiment, the paired participants were familiarized with the EEG chamber and other relevant facilities. The interactive functionality of the apparatus and computer set-up was demonstrated to help fabricate the illusion of a cooperative experimental task. A practice version of the experimental task involving actual interaction placed the participants in

adjacent identical rooms for a brief trial prior to the experiment proper. After practice, the experimenter led the inactive participant out of the EEG chamber. To embed the active participant with the belief that they were to be interacting with their partner, the participants were allowed to communicate through an intercom system while not attending the experimental task—both before the task and during the later break. Although co-acting with the believed nonbiological agent, the experimenter informed the active participant that their partner was not available for conversation in this part of experiment. RT and EEG data were collected only for the active participant. The order of the two conditions and the target colors the participants were asked to respond to were counterbalanced across subject-pairs to prevent carryover effect.

Stimuli and Procedure

For visual stimuli, three white circle outlines (1 cm in radius and 0.5 cm between the discs) were horizontally arranged inside a rectangle (9 × 3.5 cm in width and height), appearing at the center of both PC screens. During each trial, one of the three circles would be recolored to either red or green, and thus, flagged to be a target. The fixation and target would extend approximately 1.17° and 3° in height and width.

Each trial started with a cue for 1500 msec for eye blinking. In the following, a fixation was presented for 500 msec, and then, a target was presented either in the right, central, or left disc. For the go trials (target of one's own), there was a period of about 1500 msec for responding before the next trial started. The targets would be presented on the screen until participants pressed the button. They were instructed to respond to their own color targets by pressing the button (only right button be activated), with equal emphasis on speed and accuracy. For the no-go trials (nontarget of one's own), presentation time of the opposite color targets was varied randomly within a certain range (from 300 to 450 msec) to roughly adjust to average human behavioral RTs on go/no-go tasks. For each condition, there were four blocks of 45 go trials and 45 no-go trials (15 go/compatible or the spatially correspondent, and 15 go/incompatible, or noncorrespondent trials).

ERP Recording

Electrophysiological data were recorded from 64 scalp electrodes, and vertical and horizontal electrooculograms (EOGs) were recorded for eye movements. All channels were referenced to the linked mastoids. EEG and EOG were recorded with a sampling rate of 1000 Hz and digitally filtered at a low pass to 30 Hz (12 dB/oct). EEG epochs set at a range of −100 to 600 msec with a 100-msec prestimulus baseline period. Only artifact-free trials were averaged to create ERP. Trials containing eye movement artifact, A/D saturation, or with a baseline drift exceeding 70 μV in any channel were excluded.

Stimulus-locked lateralized readiness potential (LRP) was captured from electrode C3 and C4 for calculation. Because subjects used their right hand to respond to the targets, we subtracted ERP at electrode C4 (contralateral to the responding hand site) from that at electrode C3 (ipsilateral to the responding hand site) to conduct LRP-like analysis. After subtraction, the ERP difference waves were averaged and digitally filtered (low-pass cutoff frequency = 12 Hz). In other words, LRP is more negative in situations involving greater potentials contralateral to the responding hand (correspondent to the responding hand site), and is more positive in situations involving greater potential ipsilateral to the responding hand (opposite to the responding hand site), which reflected the competition and the conflict between the two hands.

RESULTS

Behavioral Results

Table 1 (see also Figure 1C) shows the RT data for the compatibility effect when one under the implemented belief of interacting with different co-actors: a biological (human) agent and a computer. A repeated-measure 2 × 3 analysis of variance (ANOVA) with the factors Belief (interacting with a believed biological agent or a computer) and Compatibility (compatible, central, incompatible) was conducted to test the prediction of an agency-dependent compatibility effect. The main effect of Belief [$F(1, 17) = 2.16$, $p = .16$] was not significant. The main effect of Compatibility [$F(2, 34) = 24.78$, $p < .001$] was significant. RT was fastest on central trials (318.2 msec) and was slowest on incompatible trials (332.3 msec).

Table 1. Mean RT (Go Trials) on Compatible, Central, and Incompatible Trials in Two Co-acting Contexts[a]

	Interacting with a Believed Biological Agent			*Interacting with a Believed Computer Program*		
	Compatible	*Central*	*Incompatible*	*Compatible*	*Central*	*Incompatible*
RT (*SD*)	324.3 (14.7)	318.2 (12.6)	338.2 (16.5)	323.8 (15.3)	318.3 (19.2)	326.4 (13.6)
Compatibility		13.9			2.6	
Mean RTs (*SD*)		326.8 (16.9)			322.8 (16.6)	

[a]The compatibility effect = $RT_{\text{incompatible trial}} - RT_{\text{compatible trial}}$.

Importantly, there was a significant Belief × Compatibility interaction [$F(2, 34) = 6.58$, $p < .01$]. A significant simple main effect of Compatibility was found both when interacting with a believed biological agent [$F(2, 68) = 28.13$, $p < .001$] and when interacting with a computer [$F(2, 68) = 4.63$, $p < .05$]. To clarify this, post hoc comparisons showed that a significant Simon-like effect (comparison of compatible vs. incompatible trial) only took place when subjects believed that they were co-acting with a biological agent (14.2 msec, $p < .01$) but not with a computer (2.6 msec, $p > .05$). When under the belief of interaction with another, RTs were significantly slower on incompatible trials. Unexpectedly, there was a general facilitation on central trials across all conditions,[1] which caused a difference in compatibility when interacting with a computer. In both contexts, performance on central trials was significantly faster than on incompatible trials (under belief of interaction with a biological agent: $p < .01$; with a computer: $p < .05$).

In addition, a mixed 2 × 2 × 2 ANOVA, with the between factor instruction order (under Belief of interaction with a biological agent or computer first) and the within factors Belief and Compatibility (compatible and incompatible), was conducted to test the order effect of belief instructions. The main effect of Instruction order [$F(1, 16) = 1.42$, $p = .25$] and the Three-way interaction [$F(1, 16) = 0.31$, $p = .59$] were not significant, neither was the interaction with Belief [$F(1, 16) = 0.30$, $p = .59$] or Compatibility [$F(1, 16) = 0.03$, $p = .87$]. The main effect of Belief [$F(1, 16) = 7.3$, $p < .05$], Compatibility [$F(1, 16) = 45.7$, $p < .001$], and their interaction [$F(1, 16) = 17.4$, $p < .001$] were significant. As shown above, participants demonstrated an agency-specific compatibility effect [interacting with a believed biological agent: $F(1, 32) = 58.0$, $p < .001$; with a believed computer: $F(1, 32) = 1.95$, $p = .18$]. There is no order effect of the belief instruction between two groups (each group, $n = 9$): Participants who were instructed to interact with a believed third-person (biological agent) first (human: 15.2 msec; computer: 2.0 msec) did not show a difference on the compatibility effect compared with participants who were instructed to interact with a believed computer first (human: 13.2 msec; computer: 3.2 msec).

Electrophysiological Results

The P3 component was quantified by measuring mean amplitudes from 320 to 420 msec both for go and no-go trials. It can be determined from the failure of the central trials to perform as a baseline in behavioral analysis that their continued inclusion in the analysis of the ERP findings may result in the obscuring of the comparisons of interest. The current electrophysiological data thus only include compatible and incompatible trials into statistical analysis—a 2 × 2 × 2 × 3 ANOVA with the factors Trial type (go, no-go), Belief (interacting with a believed biological agent or a computer), Compatibility (compatible, incompatible), and Electrode (Fz, Cz, Pz) was conducted. Time windows and the electrodes of interest (i.e., Fz, Cz and Pz) were selected in line with previous studies with typical go/no-go paradigms (Pfefferbaum et al., 1985). The stimulus-locked LRP was quantified by measuring mean amplitudes from 100 to 200 msec for the dip and from 200 to 400 msec for a following negative deflection both for go and no-go trials. The Greenhouse–Geisser adjusted p values were reported when necessary, but original degrees of freedom were given.

P3 Component

Table 2 shows the amplitude of go-P3 (2a) and the no-go-P3 (2b), locked by stimulus onset (see also Figure 2). First, the main effect of Trial type [$F(1, 17) = 2.42$,

Table 2. Electrophysiological Results of the Compatibility (Means and Standard Deviations in μV) at Three Electrode Sites (Fz, Cz, Pz) in Two Co-acting Contexts: (a) Go-P3 and (b) No-go-P3

	With Belief of Interacting with a Biological Agent			*With Belief of Interacting with a Computer*		
	Compatible	*Neutral*	*Incompatible*	*Compatible*	*Neutral*	*Incompatible*
(a) The Mean Amplitude of Go-P3 (320–420 msec after Stimulus Onset)						
Fz	6.879 (4.7)	5.973 (3.0)	6.995 (3.1)	6.530 (3.5)	6.088 (1.7)	7.920 (3.4)
Cz	7.718 (4.9)	7.370 (3.8)	9.239 (5.3)	8.749 (4.4)	7.639 (2.5)	8.832 (4.5)
Pz	8.499 (5.3)	8.092 (4.3)	11.052 (5.7)	10.509 (4.8)	8.736 (1.8)	9.093 (3.6)
(b) The Mean Amplitude of No-go-P3 (320–420 msec after Stimulus Onset)						
Fz	8.763 (4.8)	8.595 (3.5)	12.637 (5.0)	10.753 (4.7)	8.520 (2.3)	9.695 (4.2)
Cz	8.869 (4.8)	8.430 (3.4)	11.442 (4.8)	9.491 (4.4)	8.221 (2.2)	10.024 (4.6)
Pz	7.363 (4.7)	7.242 (3.1)	9.454 (4.2)	8.519 (4.2)	7.307 (2.2)	7.326 (3.6)

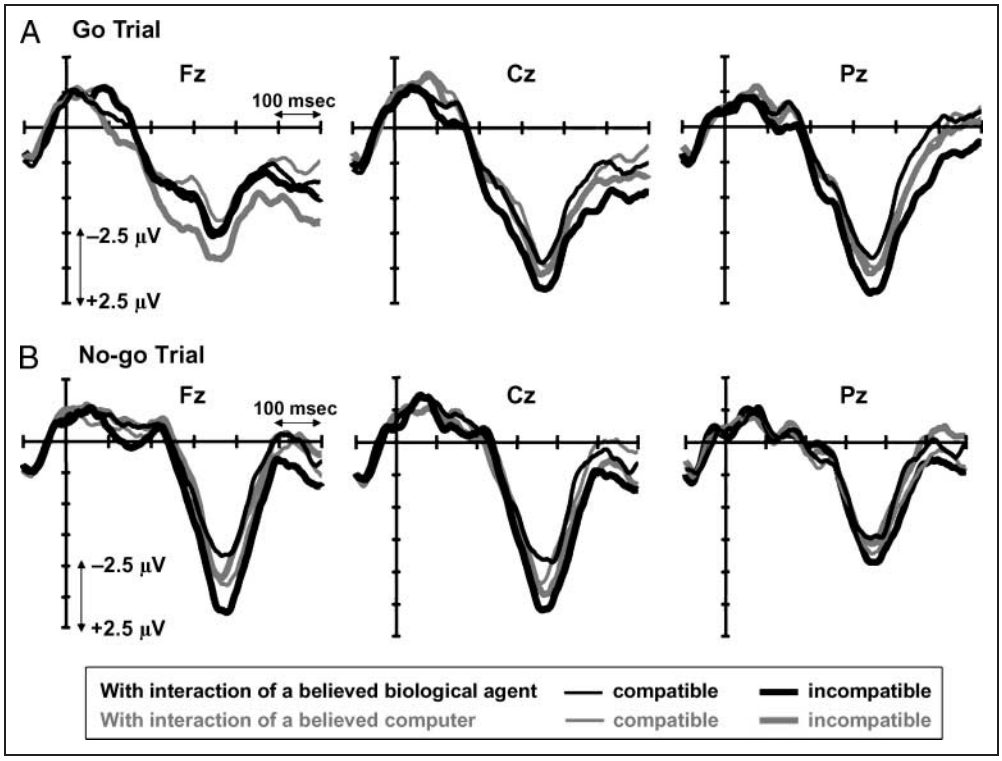

Figure 2. Electrophysiological results of the compatibility (compatible and incompatible trials) at three electrode sites (Fz, Cz, Pz) in two co-acting contexts : (A) go and (B) no-go trial.

$p = .15$], Belief [$F(1, 17) = 0.2, p = .66$], and Electrode [$F(2, 34) = 1.65, p = .22$] were not significant. The main effect of Compatibility [$F(1, 17) = 16.51, p < .001$] was significant. The most important of all, the four-way interaction, was significant [$F(2, 34) = 10.0, p < .001$]. The two-way interactions, Trial type × Electrode [$F(2, 34) = 44.2, p < .001$] and Belief × Compatibility [$F(1, 17) = 28.4, p < .001$] were also significant.

Secondly, for the analysis of interaction Trial type × Electrode, it showed different scalp distribution for go [$F(2, 68) = 22.33, p < .001$] and no-go [$F(2, 68) = 15.79, p < .001$] trial types. It showed a centro-posterior maximum (Fz = 6.731 μV; Cz = 8.258 μV; Pz = 9.330 μV) on go trials and a fronto-central maximum on no-go trials (Fz = 9.827 μV; Cz = 9.413 μV; Pz = 7.869 μV), which was in line with the well-established finding with go/no-go paradigm (Falkenstein, Hoormann, & Hohnsbein, 1999; Fallgatter & Strik, 1999). Thus, we selected Pz and Fz as the representative electrode for go and no-go trial type in the following report.

Third, for the analysis of the Belief × Compatibility interaction, it demonstrated an agency-specific compatibility effect: There was a significant compatibility effect when interacting with a believed biological agent [$F(1, 34) = 44.6, p < .001$], no such compatibility effect was found when interacting with a believed computer [$F(1, 34) = 1.4, p = .24$]. The belief manipulation caused differences both on compatible [$F(1, 34) = 5.6, p < .05$] and incompatible trials [$F(1, 34) = 9.8, p < .01$]. Further analysis of the interaction Belief × Compatibility in different trial types was also concerned. For go trial type, the significant interaction Belief × Compatibility was found at representative electrode Pz [$F(1, 102) = 16.7, p < .001$]: The compatibility effect was biologically tuned to the interaction with a believed human another [$F(1, 204) = 15.68, p < .001$], but not to the interaction with a believed computer [$F(1, 204) = 0.02, p = .90$]. On the other hand, the significant interaction Belief × Compatibility on no-go trial was found at representative electrode Fz [$F(1, 102) = 25.96, p < .001$]: A significant compatibility effect was found when interacting with a believed human agent [$F(1, 102) = 36.0, p < .001$]. No such compatibility effect was found when interacting with a believed computer [$F(1, 102) = 2.7, p = .12$].

Stimulus-locked LRP

Figure 3 presents the LRP locked by stimulus onset time when co-acted with different believed partners for go (Figure 3A) and no-go (Figure 3B), compatible and incompatible trials (see also Table 3). A repeated-measure 2 × 2 ANOVA with the factors Belief and Compatibility was conducted to test separately for a positive dip first (100–200 msec) and a following delayed negative deflection (200–400 msec) due to a conflict between spatial and response dimensions. First, for the positive dip on go response, the main effect of Belief [$F(1, 17) = 6.2, p < .05$], Compatibility [$F(1, 17) = 17.1, p < .001$], and their interaction [$F(1, 17) = 4.5, p < .05$] were all significant. Further analysis showed that on incompatible trials, there was an agency difference [$F(1, 34) = 10.6, p < .01$], whereas no such difference was found on

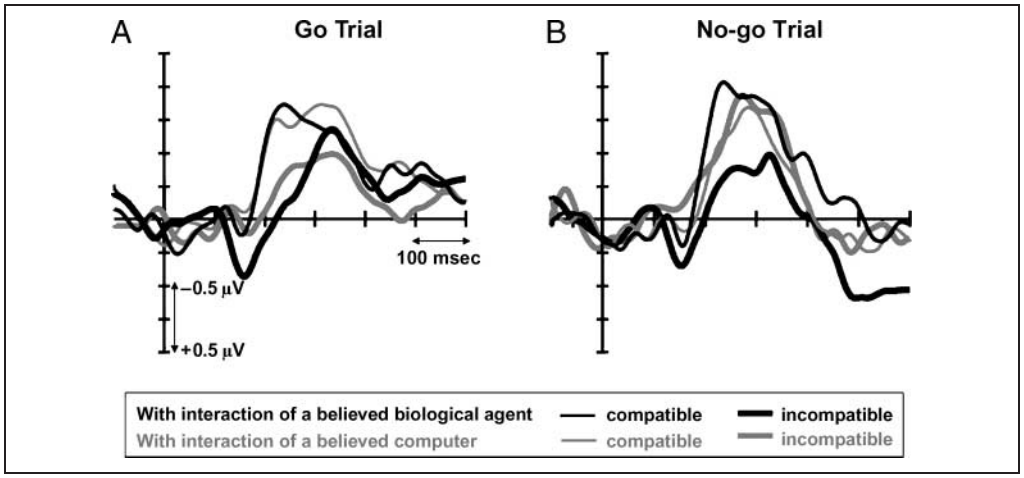

Figure 3. LRP results of the compatibility difference in two co-acting contexts: (A) go and (B) no-go trial.

compatible trials [$F(1, 34) = 0.07$, $p = .79$]. The difference of compatibility was caused by a positive dip on incompatible trials when under the belief of interaction with a biological agent [$F(1, 34) = 17.4$, $p < .001$]. Interacting with a believed computer did not cause a significant compatibility difference [$F(1, 34) = 0.59$, $p = .44$]. Secondly, for the negative deflection on go response, there was a significant difference between compatible and incompatible trial [$F(1, 17) = 9.41$, $p < .01$]. The main effect of Belief [$F(1, 17) = 0.0$, $p = 1.0$] and the Belief × Compatibility interaction were not significant [$F(1, 17) = 0.02$, $p = .88$]. No agency-dependent effect was found in this analysis. Thirdly, for the positive-going dip on no-go response, the main effect of belief was significant [$F(1, 17) = 7.56, p < .05$]. The main effect of compatibility [$F(1, 17) = 2.5, p = .14$] and the interaction Belief × Compatibility [$F(1, 17) = 3.2$, $p = .09$] were not significant. There was a more positive-going dip when interacting with a believed biological agent (0.48 μV) than with an unseen computer (−0.26 μV). Finally, for the negative deflection on no-go response, the main effect of Belief [$F(1, 17) = 5.32, p < .05$], Compatibility [$F(1, 17) = 9.74, p < .01$], and their interaction [$F(1, 17) = 7.58, p < .05$] were all significant. The interaction was driven by a significant compatibility effect when participants believed they performing with an agent [$F(1, 34) = 17.27, p < .001$], which was not significant when participants believed they were performing with the computer [$F(1, 34) = 0.54$, $p = .46$].

DISCUSSION

Building upon the findings of our previous study, we have demonstrated here that the ''social Simon effect'' (the difference between incompatible and compatible trials) is biologically tuned and that it is predicated solely upon the belief of cooperation with a biological agent, emerging thus even in the absence of any visual–auditory feedback indicating that said agent is actually human. Our current findings indicate an agency-dependent compatibility difference on (1) behavioral RTs and ERP amplitudes at (2) go-P3 and (3) no-go-P3 when co-acting upon a joint Simon task with a believed biological agent, suggesting that the perceived intentionality of another's actions modulate action planning and action anticipation. In addition, this effect extends its influence downward to the processing stage of response selection. (4) The S-LRP also demonstrates an agency-dependent compatibility difference in an initial positive dip at the nonresponding site during the incompatible go trials and a subsequent difference at a negative deflection on the no-go trials during

Table 3. LRP Results of the Compatibility Effect (Compatible vs. Incompatible Trial) (Means and Standard Deviations in μV) in Two Co-acting Contexts: (a) Go and (b) No-go Responses

	Positive Dip (100–200 msec)				*Negative Deflection (200–400 msec)*			
	With a Believed Biological Agent		*With a Believed Computer*		*With a Believed Biological Agent*		*With a Believed Computer*	
	COM	*IMC*	*COM*	*IMC*	*COM*	*IMC*	*COM*	*IMC*
(a) Go	−0.091 (1.0)	1.324 (1.36)	−0.194 (0.89)	0.067 (0.75)	−1.426 (1.76)	−0.274 (2.11)	−1.353 (2.04)	−0.335 (1.99)
(b) No-go	0.076 (0.68)	0.885 (1.17)	−0.220 (1.12)	−0.295 (0.93)	−2.150 (1.65)	−0.573 (1.44)	−0.831 (1.84)	−0.553 (1.78)

the implementation of believed interaction with conspecifics. We will discuss each of these findings in detail below.

Agency-dependent Effect

RT data provide evidence that the social Simon effect is predicated solely upon believed interaction with a biological agent, which allows it to occur even in the absence of visual–auditory feedback from a human co-actor. This finding strongly suggests the existence of a biologically tuned co-representation system. The robustness of this effect cannot be accounted for with time-differential attentional demands or any inhomogeneity between two conditions, as the order of condition presentation was counterbalanced. Rather, it is the believed animation of the co-actor that allows the participant to formulate an appropriate action plan. In the previous study, a direct matching mechanism was demonstrated to implement this agency-dependent compatibility effect by comparing perceived co-actor behavior with executed actions (Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004; Kilner, Paulignan, & Blakemore, 2003). What a perceived action elicits of the common coding system is the projected result of an action simulation on the basis of motor experience. In the context of joint action, it is possible to represent perceived motor behavior effected by another person within our own motor repertoire and incorporate such in the planning of subsequent actions (Tsai & Brass, 2007). The lack of a compatibility effect when co-acting with a computer suggests that believed interaction with a mechanical device fails to activate the same mechanism that codes human motor behavior; direct matching cannot therefore occur.

Action Planning

P3 (classical P3 or P3b) is widely recognized to index decision processing, popularly interpreted as a point in time at which an individual's moment-to-moment representation of the environment context produces and updates a schedule of planned behavior. When under the belief of interacting with an intentional agent, the co-representation system is triggered to map the subsequent action of the co-actor in the context of an action plan integrating both the self and the other's projected motor behavior (Sebanz, Knoblich, & Prinz, 2005).

Although the data from previous studies utilizing a classical Simon task observed increased P3 amplitude on compatible trials (Ragot, 1984), the current study finds a reverse pattern, with larger readings on incompatible trials. Decreased P3 amplitude has, in the past, been associated with heavier loading in task demand, and so we speculate that our data might be accounted for in the processing of additional social meaning within the task setting; possibly, a positional ''belonging'' on the basis of the placement of the self relative to that of the believed partner.

Action Anticipation

In accordance with previous findings (Sebanz, Knoblich, et al., 2006; Tsai et al., 2006), an increased no-go-P3 amplitude on incompatible trials was observed in the biological agent condition, indicating an augmented level of action control so to suppress, we believe, the imitation of motor behavior mapped from the believed human other; ergo, we hypothesize that suppression occurs as a result of a schedule of anticipated actions drawn from the experiential motor repertoire, representing the overall cooperative process. The larger no-go-P3 amplitudes on incompatible human trials correspond to a reconciliation between action anticipation and response inhibition.

Action Preparation

The representation of an upcoming event also influences S-LRP, an index of a higher-order, nonmotoric process of response selection, reflecting competition between the action codes of the two hands. Current results at S-LRP show that co-action with a biological agent evokes a greater positive deviation at onset for go-incompatible responses due to conflict between the equivalent-purpose coding attributed to self response and to the response of an analogous other. In the context of the above, motor-related potentials bearing significant positive deviation reflect the activation of response codes at the nonresponding hand site.

Modulation at S-LRP during the no-go trials—including the negative deflection following stimulus onset—was protracted versus the results of the go trial. It is interesting to note that the local pattern of agency-dependent effects between trial types was distinct across the stimulus-locked timeframe of S-LRP. This phenomenon may be accounted for in the absence of action execution and feedback on no-go trials (van Schie, Mars, Coles, & Bekkering, 2004); the motor behavior of the believed other is represented as if effected by the self, but with greater temporal indistinctiveness with regard to action onset. Concurrent with our previous findings (Tsai et al., 2006), the results at S-LRP support the idea that the representation of an upcoming event can downward-extend its influence to action preparation.

Conclusion

In this study, we explored the characteristics of the biologically tuned common coding system with an in-depth examination of the agency-dependent compatibility effect in joint action. Where such studies have in the past (Tai et al., 2004; Kilner et al., 2003) primarily monitored action execution concurrently mirrored between

a participant and a biological other, the present study has demonstrated that a similar activation pattern can emerge even in the absence of any concurrent action. Also, although previous studies have indicated that the process of indirect motor interaction selectively activates such regions of the brain as the superior temporal sulcus (Allison, Puce, & McCarthy, 2000), current findings suggest that the visual–motor coupling response—which is modulated with compatibility—may be a consequence of the premotor mirror system or may, indeed, be part of the ''simulation'' mechanism used in action observation and execution, extending into the parietal cortex (Rizzolatti & Craighero, 2004). Assuming that the motor representations of both the self and any other human within an interactive context require the engagement of similar representational mechanisms (Grezes & Decety, 2001), the lack of compatibility with inanimate co-actors may result in failure to submit their motor behavior to mapping from our experiential motor repertoire, as reflected in brain activity (Rizzolatti, Fogassi, & Gallese, 2001).

Recent experimental findings with monkeys have, as in humans, revealed a mirror system tuned to biological others (Tai et al., 2004; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Knoblich and Jordan (2002) have pointed out, however, that the presence of such a system is, being inherently egocentric and noninclusive of others (in the context of an action plan) in function, insufficient to account for cooperative behavior (Knoblich & Jordan, 2002). To this end, research with the neural correlates of on-line mentalization has uncovered a system of activation extending beyond the mirror neurons—into the anterior paracingulate cortex—during immersive social interaction with an unseen biological other, not present in analogous interaction with a computer (Ramnani & Miall, 2004; Gallagher, Jack, Roepstorff, & Frith, 2002).

It is interesting to note that in departing from a highly similar research paradigm using participants previously unacquainted with each other, the social Simon effect we have presently observed between close friends is significantly stronger than in most past demonstrations of the phenomenon. Although we have opted not to explore this issue in depth, we speculate that the participants' tendency to better co-represent an acquaintance implicates the action of an empathetic system; indeed, the human mirror system has, in some relevant literature, been associated with empathetic ability (Iacoboni & Dapretto, 2006). Further imaging studies are necessary to better illuminate the neural basis of these processes and to establish the groundwork in the debate between the ''Simulation Theory'' and ''Theory–Theory.''

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Note

1. Although the central trials in previous social Simon studies with seen human partners (Sebanz, Knoblich, et al., 2006; Tsai et al., 2006) supplied an ideal baseline against which to judge compatible and incompatible experimental data, in the present experiment, they unexpectedly suffered a general facilitation effect across all conditions. Sebanz et al. (2003, Experiment 2) observed a similar phenomenon in a version of the experimental paradigm wherein participants received no visual or auditory feedback from their partner. A possible ad-hoc explanation poses that the absence of a positional association between stimulus and subject response removes the center key from the representation of sidedness within the action plan, and thus, prevents any conflict that might result. Given that this priming effect was unspecific to either condition, the present study's observation of an agency-dependent effect suffers no confound.

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