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# Is it really my turn? An event-related fMRI study of task sharing

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Acting together with others is a fundamental human ability. This raises the possibility that we take others' actions into account whenever somebody acts around us. Event-related fMRI was used to identify brain regions responsive to changes in cognitive processing when one and the same go–nogo task is performed alone or together with a co-actor performing a complementary task. Reaction times showed that participants integrated the potential action of their co-actor in their own action planning. Increased activation in ventral premotor cortex was found when participants acted upon stimuli referring to their own action alternative, but only when their partner performed a complementary task. This suggests that knowing about the potential actions of a partner increases the relevance of stimuli referring to oneself. Acting in the presence of a co-actor was also associated with increased orbitofrontal activation, indicating that participants monitored their performance more closely to make sure it really was their turn. These results suggest that our default mode is to interact with others.

## INTRODUCTION

The mind may become less of a mystery when we consider its role in supporting one of the things we are best at: social interaction. While this claim is anything but news to social psychologists (Fiske, 1992; Smith & Semin, 2004), for many years cognitive science and cognitive neuroscience have focused on the study of processes that can presumably be understood by investigating individual minds in isolation. More recently, there has been a surge of interest in studying the

cognitive and neural bases of processes deemed critical for, and specific to, social interaction, including joint attention (Williams, Waiter, Perra, Perrett, & Whiten, 2005), person perception (Frith & Frith, 2006; Liebermann, Gaunt, Gilbert, & Trope, 2002), theory of mind (ToM; Gallagher & Frith, 2002; Saxe, Carey, & Kanwisher, 2004), and empathy (Preston & DeWaal, 20002; Singer & Fehr, 2005). However, how cognitive processes guiding individual action are employed in the service of social interaction has not been investigated much by employing neuroscientific

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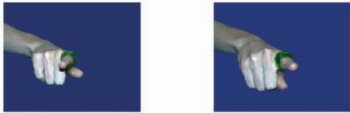



methods. Here, we report an fMRI study aimed at identifying neural correlates of acting in social context.

A range of behavioral, neurophysiological, and brain imaging studies have shown that when we observe someone performing an action, a representation of this action in our own action repertoire is activated (for recent reviews, see Buccino, Binkofski, & Riggio, 2004; Rizzolatti & Craighero, 2004; Viviani, 2002; Wilson & Knoblich, 2005). It has been demonstrated that observing another's action leads to a tendency to perform the observed action (Chartrand & Bargh, 1999), creates interference when one is trying to make an opposite movement (Brass, Bekkering, & Prinz, 2001; Kilner, Paulignan, & Blakemore, 2003), and triggers predictive mechanisms that are also used to predict the outcomes of one's own actions (Knoblich & Flach, 2001; Grosjean, Shiffrar, & Knoblich, in press). Mirror neurons in macaque monkeys' premotor and parietal cortex provide a neural substrate for this close link between action perception and action execution, as they fire both when the monkey performs an action and when the monkey observes someone performing the same action (Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Numerous brain imaging studies demonstrate the existence of a mirror system in humans. Activity in the parietal lobe, the inferior frontal gyrus, and the ventral aspect of the precentral gyrus and sulcus is typically found when participants observe others acting (see Buccino et al.,

2004; Grezes, Armony, Rowe, & Passingham, 2003; Rizzolatti & Craighero, 2004).

Although this research has been extremely important for our understanding of how we perceive and predict others' actions, it leaves open the question of how individuals manage to act together (Knoblich & Jordan, 2002; Pacherie & Dokic, 2006). Many social interactions require that individuals perform different actions side-by-side, take turns, and co-ordinate their actions to reach common goals (Sebanz, Bekkering, & Knoblich, 2006a). It seems likely that these kinds of social interaction shape cognitive processes in ways that cannot be fully captured in studies of action perception. In previous work, we showed that individuals have a tendency to take into account a co-actor's task and the action alternatives available to the other even when this is not required to perform their own task (Sebanz, Knoblich, & Prinz, 2003). As a result of this "task-sharing," individuals represent an action alternative under the other's control in a similar way as an action alternative under their own control (Sebanz, Knoblich, & Prinz, 2003, 2005), and need to engage inhibitory control processes to withhold from acting when it is the other's turn (Sebanz, Knoblich, Prinz, & Wascher, 2006b).

In the present study, we used fMRI to investigate neural correlates of these task-sharing effects. We employed a simple paradigm that can be performed alone (single actor condition) or together with another person who performs a complementary task (co-action condition).

Condition	Person A (Confederate): Left	Person B (Participant): Right
Single Actor	Responds never 	Responds to red Compatible    Incompatible 
Co-action	Responds to green Compatible    Incompatible 	Responds to red Compatible    Incompatible 

**Figure 1.** Illustration of the paradigm. The participant in the scanner (right) performed a go–nogo task, responding to one of the two ring colors (e.g., red). In the single actor condition, the confederate (left) rested her finger on her response key. In the co-acting condition, the confederate responded to the other color (e.g., green). On compatible trials, the finger pointed towards the participant's side in space; on incompatible trials, the finger pointed towards the confederate's side in space.

Participants performed a go–nogo task, responding to the color of a ring on the index finger of a hand (Sebanz et al., 2003). On each trial, participants saw a red or green ring on a hand pointing left or right and pressed a button in response to one of the two colors (see images in Figure 1 for stimuli). Pointing direction was irrelevant for the task. In the co-action condition, each participant responded to one color (one person to red, the other to green). Thus, performing the task in the dyadic setting involved taking turns with another person.

Earlier studies showed that when participants performed the go–nogo task alone and together with a co-actor, their performance differed markedly even though the experiment did not require taking the other's task into account (Sebanz et al., 2003, 2005). Participants acting on their own were able to ignore the pointing direction of the finger and responded equally fast on compatible trials, where the finger pointed towards them, and on incompatible trials, where the finger pointed away from them. In contrast, in the dyad, where participants sat next to a co-actor, they showed slower reaction times (RTs) on incompatible trials, where the finger pointed at the co-actor, compared to compatible trials. This effect indicates that in the co-action condition, participants experienced an action selection conflict on incompatible trials. This can be explained by the assumption that they represented both action alternatives, even though only one of them was under their own control. By this interpretation, the finger pointing at the other person activated a representation of the other's action, which interfered with the planning of one's own action. In contrast, only one action alternative was represented when individuals performed the task alone (Sebanz et al., 2003).

Measuring event-related potentials (ERPs), we showed that task-sharing also affects action control on nogo trials (Sebanz et al., 2006b). On nogo trials, one needs to inhibit one's action because it is not one's turn. An electrophysiological component reflecting response inhibition—the so-called Nogo P3—showed an increased amplitude in the co-action condition compared to the single actor condition (see also Tsai, Kuo, Jing, Hung, & Tzeng, 2006). We believe that participants in the dyad had a stronger tendency to act on nogo trials that needed to be suppressed. Presumably, this tendency arose because they anticipated the other's action (cf. Kilner et al., 2003).

In the present study, participants in the scanner performed the go–nogo task together with a confederate who was sitting next to the scanner and whose actions were visible to the participant (co-action condition). As a control condition, we asked participants to perform the same task while the confederate merely rested her finger on her response key (single actor condition). The stimuli were projected onto a videoscreen in front of the scanner, so that the confederate saw the stimuli on the videoscreen, while participants simultaneously saw the stimuli in a mirror above their head. In the lower half of this mirror, participants also saw their own hand and the confederate's hand next to their own hand.

The main goal of the study was to assess how task sharing affects brain activity. If individuals were to ignore the co-actor, behavioral and brain results in the two conditions should not differ. However, based on previous results, we predicted that participants would form a representation of the action alternative under the co-actor's control, and would include this in their own action planning. Thus, we expected to replicate the finding of a larger compatibility effect (RT difference between compatible and incompatible trials) in the co-action condition compared to the single actor condition.

In terms of brain activity, the main analysis of interest was the comparison of go trials in the two conditions, because the sensory input in these conditions was the same. Both in the single actor and in the co-action setting, participants responded to stimuli while the co-actor did not move. Thus, any differences in brain activity would point towards a modulation of cognitive and neural processes through the context in which actions are performed. We specifically predicted increased activation in medial frontal cortex (MFC) in the co-action condition compared to the single actor condition. This region, in particular its anterior rostral part, has been implicated in a range of tasks that involve thinking about self and other (for a recent review, see Amodio & Frith, 2006). Amodio & Frith (2006) characterized the role of anterior rostral MFC as supporting metacognitive processes whereby intentions and feelings are reflected. It seems likely that this region would be sensitive to changes in task representation that may affect how stimuli relevant to oneself (go stimuli) are processed.

Other regions in MFC might also show increased activity during go trials in the co-action condition. Activity in orbitofrontal cortex has

been linked to the monitoring of action outcomes that are of motivational or emotional value (Kringelbach, 2005; Ramnani & Owen, 2004; Schoenbaum & Setlow, 2001), whereas the dorsal anterior cingulate cortex (ACC) has been implicated in conflict monitoring and cognitive control (Botvinick, Cohen, & Carter, 2004). Several studies have found increased activity in ACC during conflict at the level of response selection (Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Milham et al., 2001; Milham, Banich, & Barad, 2003; Nelson, Reuter-Lorenz, Sylvester, Jonides, & Smith, 2003; Van Veen, Cohen, Botvinick, Stenger, & Carter, 2001). Given that a response selection conflict is expected to occur on incompatible trials in the co-action condition, ACC activity should be increased specifically on these trials.

Of further interest was the comparison of brain activity on nogo trials in the two conditions. During nogo trials in the co-action condition, participants saw the other's finger moving down to press the response button. In the single actor condition, the other's finger rested on the response button. A range of studies has shown that the anticipation (Kilner et al., 2003; Ramnani & Miall, 2004; Van Schie, Mars, Coles, & Bekkering, 2004) and observation of others' actions (e.g., Grezes et al., 2003; Iacoboni et al., 1999) activates brain areas involved in action execution. On the basis of these findings, increased activity in parietal and inferior frontal areas during nogo trials in the co-action condition can be expected. This would suggest that participants covertly simulate the action to be performed by the co-actor.

However, we also expected to find differences in brain activation that reflect the demands posed by taking turns with another person, including keeping oneself from acting when it is the other's turn. Increased response inhibition when individuals had to refrain from acting while another person acted was found in ERP studies (Sebanz et al., 2006b; Tsai et al., 2006). Brain imaging studies using event-related designs have identified the pre-SMA (Humberstone et al., 1997; Mostofsky et al., 2003) and SMA (Durstun, Thomas, Worden, Yang, & Casey, 2002), right inferior frontal cortex (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Konishi, Nakajimal, Uchidal, Sekihara, & Miyashita, 1998), right dorsolateral prefrontal cortex (DLPFC; de Zubicaray, Andrew, Zelaya, Williams, & Dumanoir, 2000; Kawashima et al., 1996; Liddle, Kiehl, & Smith, 2001), and the right inferior parietal lobe (Fassbender et al., 2004;

Garavan, Ross, & Stein, 1999; Garavan, Ross, Murphy, Roche, & Stein, 2002) in behavioral response inhibition. We predicted that at least some of these regions would show increased activity during nogo trials in the co-action condition compared to the single actor condition.

## METHODS

### Subjects

Participants were recruited through the subject pool at the Wellcome Department of Imaging Neuroscience. Twelve right-handed participants (5 male, 7 female, aged 19–60, mean age 28.7) participated in the study. All had normal or corrected-to-normal vision. They gave full written informed consent prior to scanning.

### Stimuli and task

Digital photographs of a human hand pointing to the right or to the left were presented as stimuli. The ring on the index finger of the hand was either red or green. The stimuli were presented centrally, and the ring always appeared in exactly the same location. The stimuli were projected onto an opaque surface in the scanner by an LCD projector. Participants viewed the stimuli through a set of mirrors mounted on the headcoil. In the lower half of the mirror participants looked at, they also saw their own hand and the hand of the co-actor. Participants performed a go–nogo task, responding to one ring color (e.g., red) by pressing a response button. The pointing direction of the finger was task irrelevant. For the data analysis, trials were coded as compatible when the finger pointed towards the button to be pressed and as incompatible when the finger pointed away (see Figure 1).

### Apparatus

A confederate sat on a high stool next to the scanner (left side from the participant's point of view) throughout the study. A response box with two buttons was placed on the participant's belly so that the participant and the confederate could each press one of the two buttons. The actor oriented her hand in the same way as the confederate so that the two hands were parallel and right next to each other.

## Conditions and design

Participants performed the go–nogo task in four different settings, only two of which are reported in the present article. In the single actor condition, participants could see the co-actor's hand resting on a response button that was next to their own. The co-actor did not perform a task. In the co-action condition, the co-actor responded to the complementary color. For example, when the participant's task was to respond to red, the co-actor responded to green. Participants could see the co-actor's hand pressing the response button. In an additional baseline condition (not reported here), participants performed the task alone and could not see a co-actor. Finally, in an additional dyadic condition (not reported here), the co-actor performed a different task (responding to pointing direction of the stimuli).

Each of the four conditions was repeated twice. Altogether, there were 96 trials per condition. One third of the trials were compatible (from the participant's point of view), one third were incompatible, and one third consisted of null trials, where participants only saw a fixation cross. Null trials were included for jittering purposes and to make sure that participants remained alert during the task. They were not included in the data analyses. The inter-stimulus interval was 2.07 seconds. The two conditions where the co-actor performed a task and the two conditions where the co-actor remained inactive were blocked to avoid having participants switch between different conditions too often. Thus, half of the participants performed both runs of the conditions where the co-actor remained inactive first, and the other half of participants completed both runs of the conditions where the confederate responded to stimuli first. Conditions within these blocks alternated, and the order of conditions was counterbalanced across participants. Altogether, there were 8 runs. Trial order within these runs was randomized. For the present analyses, we used a factorial design with the following three factors: (1) single actor vs. co-action condition; (2) go vs. nogo; and (3) compatible vs. incompatible.

## Image acquisition

A 1.5-T Siemens Sonata MRI scanner was used to acquire gradient-echo, T2\*-weighted echoplanar MRI images with blood-oxygenation level-

dependent (BOLD) contrast. The scanning sequence was a trajectory-based reconstruction sequence with repetition time of 2970 ms. Each volume, positioned to cover the whole brain, comprised 33 axial slices with a slice thickness of 3.75 mm. Data were reconstructed using the trajectory based reconstruction (TBR) SPM toolbox to  $32 \times 32 \times 3$  mm slices. Each run had a duration of 89 scans or 264 seconds. In a run, 116–120 trials were collected. The first five volumes at the start of each run were discarded to allow for T1 equilibration effects.

## fMRI data analysis

A second-order two-level mixed effects model was used to investigate the effects of different trial types across participants using FEAT (fMRI Expert Analysis Tool), part of FSL.

*First level analysis.* The first level analyses consisted of within-run analyses for each condition. So, four (two for single actor condition and two for co-action condition) first level analyses were performed for each subject. The following pre-statistics processing was applied: Motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002), non-brain removal using BET (Smith, 2002), spatial smoothing using a 5 mm FWHM (full-width at half-maximum) Gaussian kernel, global (volumetric) multiplicative mean intensity renormalization, and highpass temporal filtering (Gaussian-weighted LSF straight line fitting, with  $\sigma = 25.0$  s).

Time-series statistical analysis was carried out using FSL's general linear modeling tool, FILM (Woolrich, Ripley, Brady, & Smith, 2001). The model used explanatory variables, which consisted of five binary indicator variables, one corresponding to each trial type. Each such variable has a value of 1 between the onset of a trial and one second after that onset, and 0 at all other points. Regressors for the model were then formed by convolving each explanatory variable with a Gamma function modeling the hemodynamic response. First level contrasts consisted of go–nogo for each condition, compatible–incompatible, and the interaction between go–nogo and compatible–incompatible.

*Second level analysis.* Second level analyses combined subjects and runs using the FSL FLAME (FMRIB's Local Analysis of Mixed

Effects) tool, stage 1 (Beckmann, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004). This analysis used a mixed effects linear model that fits explanatory variables corresponding to the experimental conditions to the parameter estimates acquired from the first level analysis. Mixed effects variance is estimated by a sum of the fixed effects variance (within-run variance, as computed in first level analysis) and random effects variance (the variance estimate of the first level parameter estimates).

FSL FLIRT was used to align subjects to a template image using a 12 parameter affine model using a correlation-ratio-based cost function (Jenkinson & Smith, 2001).  $Z$  (Gaussianized T/F) statistic images were thresholded using clusters determined by  $Z > 1.6$  and a (corrected) cluster significance threshold of  $p < .05$  (Worsley, Evans, Marrett, & Neelin, 1992).

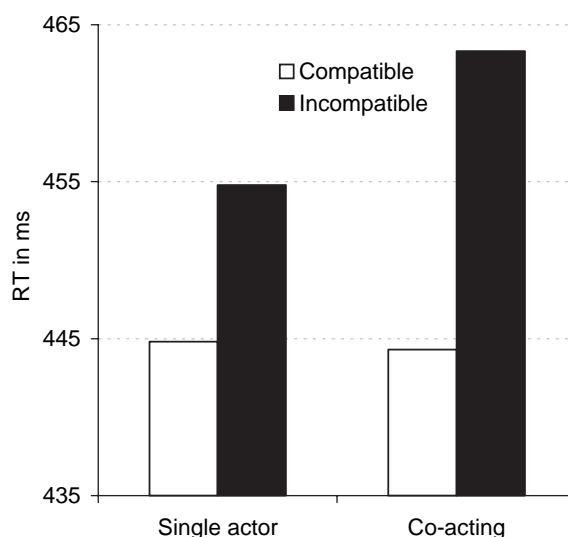
## RESULTS

### Behavioral results

To compare performance in the two conditions, a  $2 \times 2$  within-subjects ANOVA with the factors Compatibility (compatible, incompatible) and Condition (single actor, co-action) was performed on RTs. The main effect of Condition was not significant,  $p > .05$ . There was a significant main effect of Compatibility,  $F(1, 11) = 6.84$ ,  $p < .05$ . RTs were faster on compatible than on incompatible trials (see Figure 2). The interaction between Condition and Compatibility was marginally significant,  $F(1, 11) = 4.57$ ,  $p = .06$ . Separate  $t$ -tests showed a significant difference between compatible and incompatible trials in the co-action condition,  $t(11) = 2.94$ ,  $p < .01$ , but only a trend in the single actor condition  $t(11) = 1.87$ ,  $p = .09$ . These results suggest that a representation of the action alternative not under one's own control was activated more strongly when it was under the co-actor's control than when it was under no one's control.

### fMRI results

Second level analyses showed significant effects for go–nogo contrasts in the co-acting versus single actor condition. There were also significant



**Figure 2.** Reaction time data. The compatibility effect was larger in the co-acting condition.

compatibility/go–nogo interaction effects. There were no significant main effects of compatibility.

*Effects of co-action on go trials.* Using nogo trials as a baseline, we compared brain activity on go trials between the co-action and the single actor condition. The following areas showed increased activity (see Table 1, Figure 3 and Figure 5A): the right rostral superior frontal gyrus (BA 10), the right rostral medial frontal gyrus (BA 10), the left rectal gyrus (BA 11), and the left dorsal anterior cingulate gyrus (BA 32).

*Interaction of compatibility and co-action on go trials.* A two-way interaction showed that the observed differences for go trials between the co-action and the single actor condition were modulated by compatibility. The following areas showed increased activity on compatible go trials in the co-action condition relative to all other trial types (go compatible–nogo compatible > go incompatible–nogo incompatible in co-action condition only; see Table 1, Figure 4 and Figure 5B): the right extrastriate cortex (inferior and middle occipital gyrus, BA 18, and superior occipital gyrus, BA 39), the right medial frontal gyrus (BA 10), the anterior cingulate gyrus in both hemispheres (BA 32), and the right ventral anterior cingulate gyrus (BA 24).

*Effects of co-action on nogo trials.* Using go trials as a baseline, we compared brain activity on nogo trials between the co-action condition and the single actor condition. Parietal areas showed

TABLE 1

Brain activation data. Anatomical regions within significant clusters showing: (1) increased activity on go trials in the co-action condition compared to the single actor condition (baseline: nogo trials); (2) greater activation on compatible go trials in the co-action condition compared to all trial types; and (3) greater activation on nogo trials in the co-action condition compared to the single actor condition (baseline: go trials)

Structure	Brodmann area	# Voxels (2 × 2 × 2 voxels)	Z-score	Talairach co-ordinates		
				x	y	z
<i>(1) Effects of co-action on go-trials</i>						
R superior frontal gyrus	10	83	3.45	21	59	-3
R medial frontal gyrus	10	57	3.58	18	64	6
L rectal gyrus	11	38	3.67	-2	40	-26
L dorsal anterior cingulate gyrus	32	34	3.08	-8	44	8
<i>(2) Interaction of compatibility and co-action on go-trials</i>						
R inferior occipital gyrus	18	71	3.08	41	-89	-3
R middle occipital gyrus	18	38	2.96	32	-94	2
R superior occipital gyrus	39	58	3.00	35	-76	31
R medial frontal gyrus	10	38	3.36	3	49	10
R dorsal anterior cingulate gyrus	32	31	2.93	4	40	-4
L dorsal anterior cingulate gyrus	32	33	3.53	-2	40	0
R ventral anterior cingulate gyrus	24	25	2.90	5	35	1
<i>(3) Effects of co-acting on nogo-trials</i>						
R precuneus	7	254	4.10	7	-61	59
L precuneus	7	138	3.67	-8	-72	52
L superior parietal lobule	7	179	4.24	-14	-69	56
L inferior parietal lobule	40	106	3.11	-39	-43	51
R cingulate gyrus	31	50	2.45	-7	-45	39
R medial frontal gyrus, SMA	6	77	3.19	4	-6	60

Note: Only regions containing more than 25 suprathresholded voxels are reported. All clusters survived a threshold of  $p < .05$  corrected for multiple comparisons (see methods).

increased activity (see Table 1, Figure 6 and Figure 7B). In particular, activation differences were found in the precuneus and the superior parietal lobule in both hemispheres (BA 7), the left inferior parietal lobule (BA 40), and the right dorsal posterior cingulate area 31 (BA 31). Furthermore, this contrast revealed increased activity in the right medial frontal gyrus (BA 6, SMA; see Figure 6 and Figure 7A).

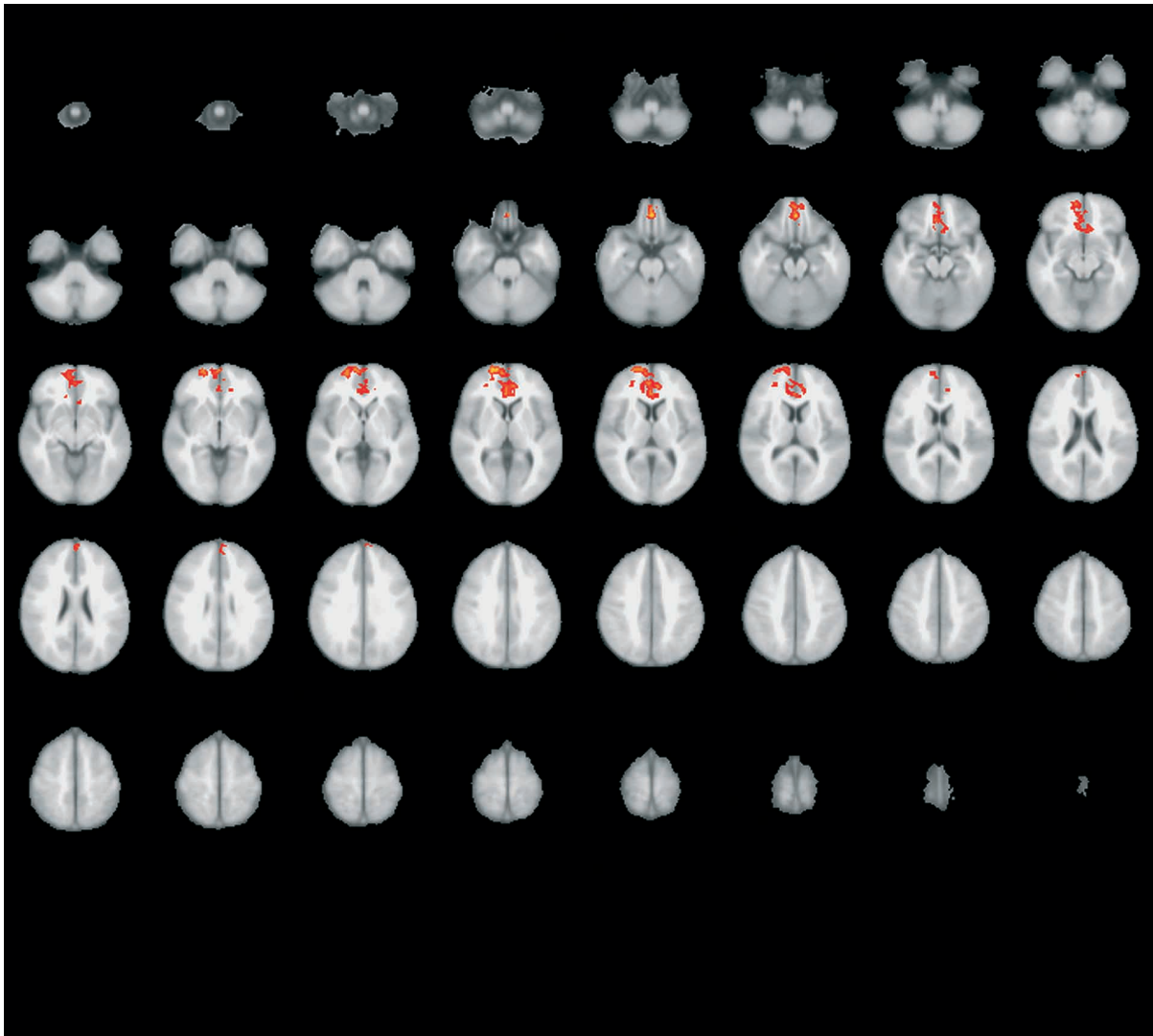
## DISCUSSION

This study provides evidence that individuals take into account a co-actor's task even when co-ordination is not required. The behavioral results replicated earlier findings showing that one and the same task is performed differently in a single actor and a co-action setting. RTs were slowed when the task-irrelevant pointing finger referred to the action alternative at the other's disposal, and were less affected by the pointing finger when the second action alternative was not under anybody's control. This finding is in line with

the assumption that although participants had only one action alternative at their disposal, they formed a representation of both action alternatives (left and right button press) in the co-action condition. Due to the overlap between the spatial feature of the stimuli and the spatial position of the responses, the pointing finger activated the spatially corresponding response (Kornblum, Hasbroucq, & Osman, 1990). This led to a response selection conflict on incompatible trials in the group (Sebanz et al., 2003, 2005). The conflict was less pronounced in the single actor condition, suggesting that the other action alternative is only represented in a similar way as one's own when it is clearly under an agent's control.

It seems likely that the tendency towards a compatibility effect observed in the single actor condition was due to the fact that the confederate's finger on the response button drew participants' attention to her potential actions. In previous studies, participants in the single actor condition were either alone or the confederate was present but did not rest a finger on the



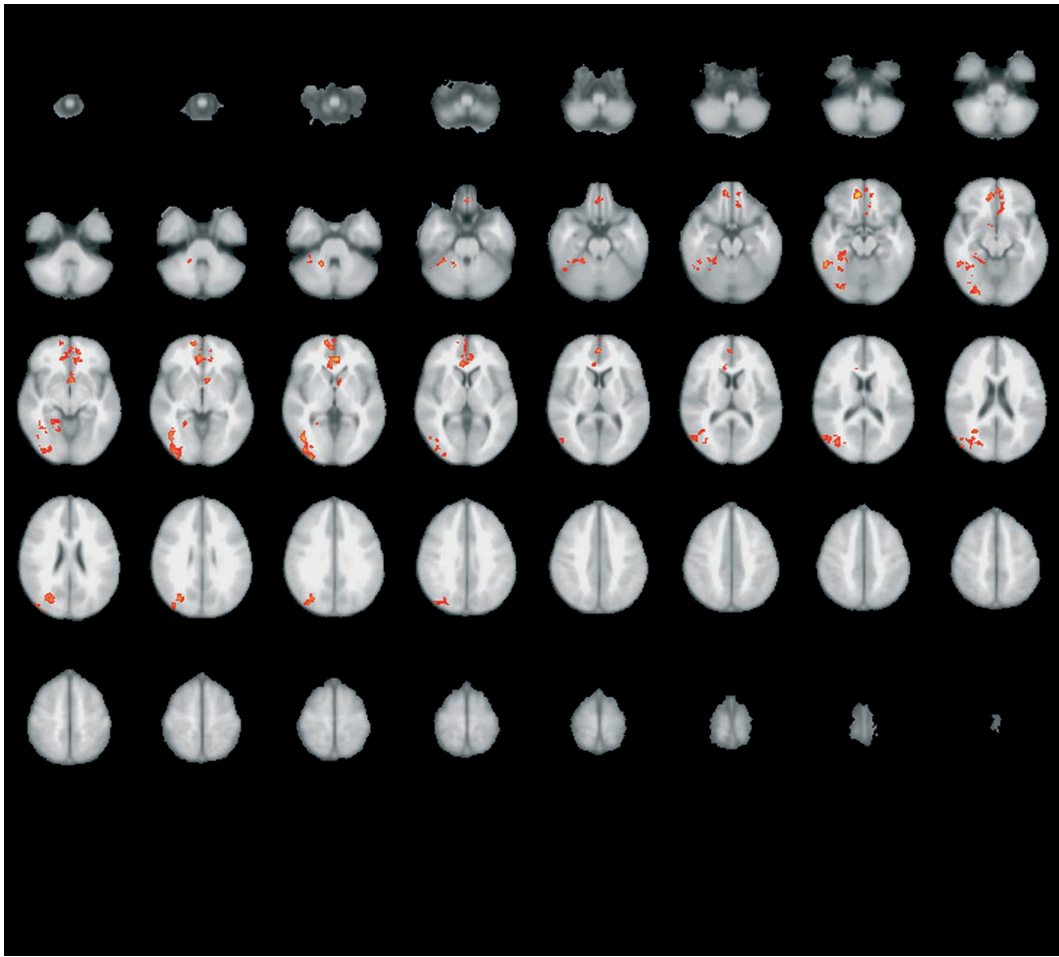


**Figure 3.** Brain areas showing increased activity on go trials in the co-action condition compared to the single actor condition. Images are radiological.

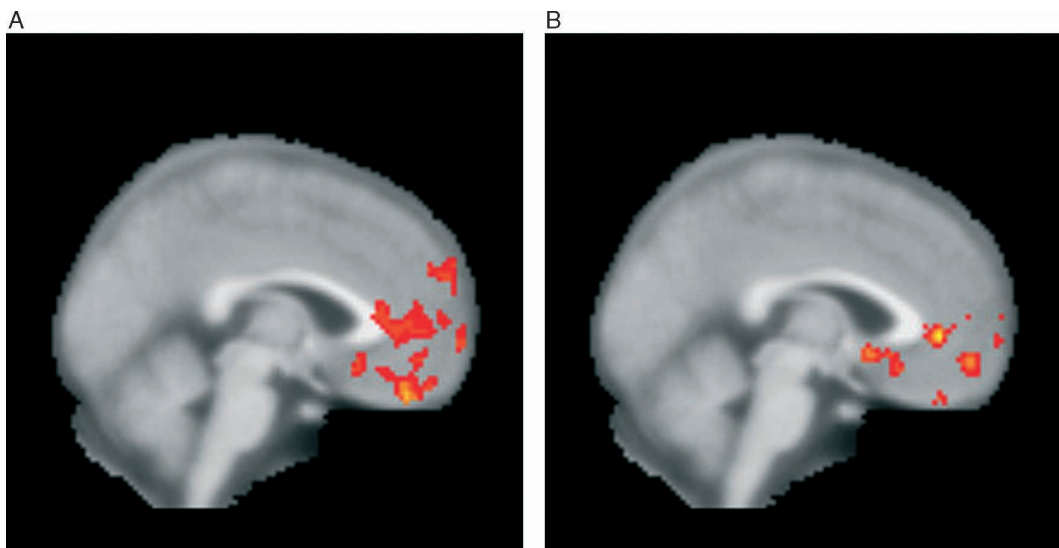
response button (Sebanz et al., 2003). Under these conditions, no reliable difference between compatible and incompatible trials was observed. However, studies on compatibility effects in go–nogo tasks have shown that a compatibility effect can be obtained when a second response is not executed, but kept in a state of readiness (Hommel, 1996). Presumably, in the present experiment, the other action alternative was not completely ignored because the co-actor created an impression of “readiness” by resting her finger on the response key. This might also explain why the interaction between Condition and Compatibility was only marginally significant.

### Self-referential processing

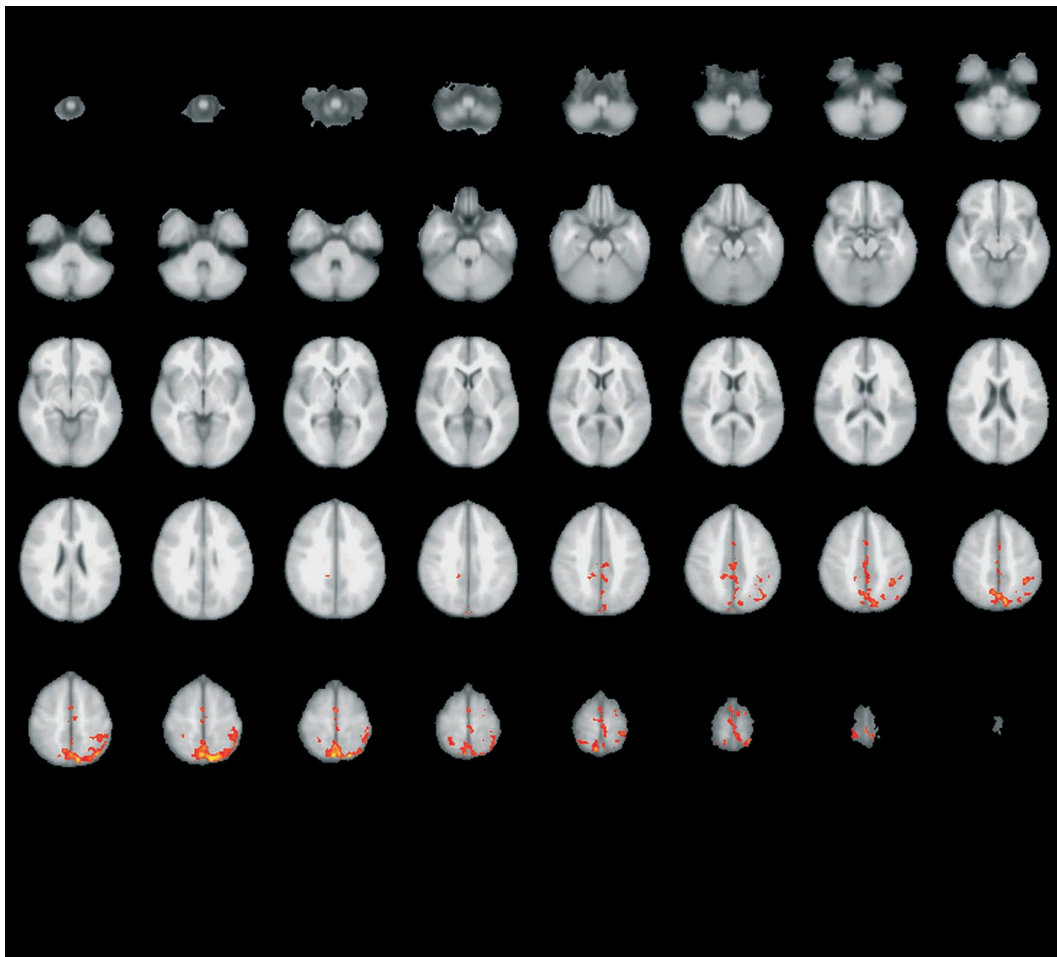
Analysis of the fMRI data showed activation differences in ventral MFC (BA 10) when performance of one and the same task in the two different settings was compared. Interestingly, a region in ventral MFC seemed to be sensitive to stimulus compatibility in the co-action setting (Talairach co-ordinates 3 49 10). Although BA 10 has been shown to be engaged in a range of different tasks (Gilbert et al., 2006; Ramnani & Owen, 2004), this activation corresponds well with activations found in studies on self-evaluation and self-referential processing (Gusnard, Akbudak, Shulman, & Raichle, 2001; Johnson



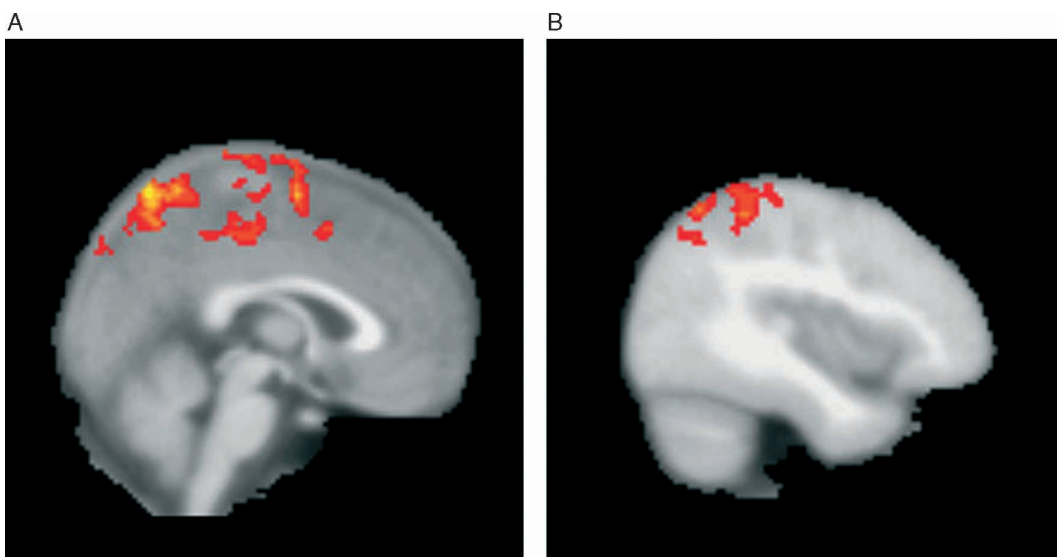
**Figure 4.** Brain areas showing increased activity in the compatibility/condition interaction. Images are radiological.



**Figure 5.** Sagittal slices showing the medial prefrontal activation observed (A) in the go–nogo contrast and (B) in the interaction.



**Figure 6.** Brain areas showing increased activity on nogo trials in the co-action condition compared to the single actor condition. Images are radiological.



**Figure 7.** Sagittal slices showing activations observed on nogo trials in the co-action condition compared to the single actor condition in (A) SMA and (B) parietal cortex.

et al., 2002; Kelley et al., 2002; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Mitchell, Macrae, & Banaji, 2006; Schmitz, Kawahara-Baccus, & Johnson, 2004; Zysset, Huber, Ferstl, & von Cramon, 2002). Vogeley et al. (2004) found activity in this region of ventral MFC when participants judged a visual scene from their own perspective as opposed to another's perspective ( $-2.586$ ). Williams et al. (2005) reported increased activity in this region when participants experienced joint attention, directing their gaze to an object at the same time as another individual (20475). Notably, these two studies also found activations in similar regions of ACC as the present study (Vogeley et al., 2346; Williams et al.,  $-4329$ ).

Thus, it seems likely that the activation differences in ventral MFC and ACC observed in the present study reflect changes in stimulus processing that are due to performing the task together with another co-actor. When acting in the presence of a co-actor, a stimulus pointing at oneself (compatible stimulus) elicits more self-reflective processing than when the same stimulus is perceived while acting on one's own. Where might this increased self-reflection stem from? We suggest that stimuli referring to oneself receive a different meaning in the context of co-action because the other is taken into account as a potential actor. At the very least, this would entail knowledge that the other is seeing a stimulus referring to oneself, similar to a joint attention situation, where one knows the other to be attending to the same object or event as oneself. In the single actor condition, participants could not be sure whether the other attended to the stimuli, because the other was never required to act. In contrast, in the co-action condition participants knew that the other was attending to the same stimuli at the same time because she responded when it was her turn. An interesting difference to the study by Williams et al. (2005) is that in the co-action condition, participants could not see the other's gaze, but merely knew that the other was attending to the same stimuli at the same time. In future studies, it would be interesting to address the question of whether knowing that someone attends to the same entity and following another's gaze activates the same neural structures.

Activation in similar regions of ventral MFC was also found when individuals thought about similar others (Mitchell et al., 2006), and when they adopted the perspective of an opponent during online games (Gallagher, Jack, Roepstorff,

& Frith, 2002; McCabe, Houser, Ryan, Smith, & Trouard, 2001). Given these findings, it seems possible that in the co-action condition, participants adopted the other's perspective in the sense that they inferred the meaning of the stimulus with respect to the other's task (compatible stimuli were incompatible for the other). However, we consider it more likely that the observed activations reflect changes in self-relevance of the stimuli associated with representing the other as a potential actor. Interestingly, a study on the inhibition of observed finger movements (Brass, Derfuss, & von Cramon, 2005) identified activation in the same region of MFC as the present study (1509). It could be that participants in our study inhibited an automatic action tendency elicited by the pointing stimulus because they wanted to make sure it really was their turn and not the other's. This would also explain why RTs in the co-action condition showed interference on incompatible trials, whereas no facilitation on compatible trials was observed.

The finding of increased activity in the visual association cortex on compatible trials in the co-action condition is consistent with this interpretation. This activation is somewhat surprising given that the visual input was the same in the co-action and the single actor condition. However, top-down effects of emotional valence on activity in extrastriate cortex have been shown (Avikainen, Liuhanen, Schuermann, & Hari, 2003). Thus, the observed activation differences in visual association cortex could reflect top-down modulation based on the perceived relevance of the stimuli in social context.

Somewhat surprisingly, we did not find any clear evidence for the assumption that acting together increases demands on cognitive control, in particular on incompatible trials. The increased ACC activation in the co-action condition does not correspond to the ACC activations typically observed in conflict monitoring studies (Barch et al., 2001; Botvinick et al., 2004; Carter et al., 1998) as it is more anterior and more inferior (see also Amodio & Frith, 2006). Rather, it seems likely that the observed ACC activation reflects cross-talk with ventral MFC, as BA 10 and cingulate cortex have reciprocal connections (Andersen, Asanuma, & Cowan, 1985; Arikuni, Sako, & Murata, 1994; Bachevalier, Meunier, Lu, & Ungerleider, 1997; Morecraft & Van Hoesen, 1993).

The activation in the orbitofrontal area (BA 11) observed in the go-nogo contrast for the co-action compared to the single actor condition, but not

observed in the interaction, may also be considered part of this network. Orbitofrontal cortex has direct reciprocal connections with the cingulate cortex (Öngür & Price, 2000; Van Hoesen, Morecraft, & Vogt, 1993), and the interplay between these areas is considered to support decision making, performance, and outcome monitoring (Kringelbach, 2005). Orbitofrontal cortex seems to be recruited primarily when the motivational or emotional value of incoming information plays a role (Kringelbach, 2005; Ramnani & Owen, 2004; Schoenbaum & Setlow, 2001). Thus, we consider it likely that participants monitored their task performance more closely in the co-action condition because responding when it is not one's turn means taking something away from the other. The orbitofrontal activity may reflect a monitoring process setting in immediately after action execution whereby participants checked if it really was their turn. Given that participants responded on go trials regardless of stimulus compatibility, it makes sense that the orbitofrontal activation was found for compatible and incompatible trials.

### Action observation and response inhibition

The analysis of nogo trials showed increased activity in the inferior and superior parietal lobe as well as in the supplementary motor area (BA 6) in the co-action condition. All of these areas have been found to be activated in at least some studies on action observation, so that the increased activation during nogo trials in the co-action condition could reflect activation of action representations triggered by observing the other's action (e.g., Buccino et al., 2001; Grezes et al., 2003; Hamilton & Grafton, 2006; Johnson-Frey et al., 2003). Using a similar go–nogo paradigm where people believed they were taking turns with another actor, Ramnani and Miall (2004) found activation in ventral premotor cortex during nogo trials where participants anticipated the other's action. It seems possible that we did not find ventral premotor cortex activation during nogo trials because participants observed the other's action rather than imagining it (cf. Grezes & Decety, 2001; Hamilton & Grafton, 2006). An additional difference to the study by Ramnani and Miall is that we did not ask participants to monitor the other's actions.

Although some studies have implicated the superior parietal lobe and the SMA in action

observation (e.g., Buccino et al., 2001; Cross, Hamilton, & Grafton, 2006), it should be noted that these areas have also been shown to be involved in the inhibition of motor responses during simple go–nogo tasks that do not include any additional cognitive or attentional components (Durstun et al., 2002; Humberstone et al., 1997; Mostofsky et al., 2003). Hence, it seems likely that the increased activity on nogo trials during co-action in these areas, in particular in the SMA, presents a neural correlate of the increased inhibition demonstrated in previous ERP studies (Sebanz et al., 2006b; Tsai et al., 2006).

To summarize, the results of this study showed that one and the same task is performed differently depending on the social context. Even though co-ordination was not required, participants integrated the potential action of a co-actor in their own action planning. Responses to stimuli referring to an action alternative under the other's control were slowed, whereas responses to the same stimuli were less affected when the co-actor was not in charge of an action alternative. Increased activation in ventral PMC, ACC and visual association cortex was found when participants acted upon stimuli referring to their own action alternative compared to stimuli pointing away, but only when their partner performed a complementary task. This suggests that knowing about the potential actions of a partner increases the relevance of stimuli referring to oneself. We also found increased activity in orbitofrontal cortex when participants acted in the presence of a co-actor, suggesting that they monitored their performance more closely to make sure that when they responded, it really was their turn. Increased activation in the SMA on nogo trials where the other acted, compared to nogo trials where nobody acted, could be an indication for increased demands on response inhibition during co-action.

The present study was a first attempt to investigate the neural bases of social interactions that involve the physical presence of two co-actors. It complements previous neuroimaging studies that have investigated effects of the implied presence of others (Gallagher et al., 2002; Ramnani & Miall, 2004), as well as studies that have focused on higher-level processes like decision making in social interaction (Decety, Jackson, Sommerville, Chaminade, & Meltzoff, 2004; McCabe et al., 2001; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). Although the go–nogo task used in the present

study was extremely simple, we believe that the paradigm captures some essential features of joint action: the physical presence of two agents, the complementary nature of two tasks, and the need to take turns. We hope that future studies will extend our knowledge by investigating cooperative situations that involve the spatial and temporal co-ordination of actions (Knoblich & Jordan, 2003; Sebanz et al., 2006a). The observed tendency to integrate another's task in one's own action planning could be an important precursor to more complex forms of co-ordination.

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