NeuroImage 61 (2012) 1249–1254

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Morphometric gray matter differences of the medial frontal cortex influence the social Simon effect

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ARTICLE INFO

Article history:
Accepted 20 March 2012
Available online 29 March 2012

Keywords:
Social interaction
Social Simon effect
Inter-individual differences
Gray matter
Voxel-based morphometry

ABSTRACT

Interacting with others plays a fundamental role in human life. Although several brain regions have recently been associated with complex cognitive control processes, surprisingly little is known about the structural correlates underlying cognitive control processes involved in social interactions. In the present study we used gray matter voxel-based morphometry (VBM) to investigate structural brain correlates of individual performance differences in a social Simon task. Here, two people share a Simon task, which requires each participant to respond to only one of two possible stimuli, rendering the paradigm a go-nogo task, so that a Simon effect – known as the Social Simon Effect (SSE) – is observable across both participants. Using a whole brain approach, we found that inter-individual differences in the SSE are negatively correlated with gray matter (GM) volume of the medial frontal cortex (MFC). The present data indicate that individuals with larger MFC GM volume were those with better conflict resolution in a social Simon task and vice versa. This brain-behavior relationship between cognitive control processes and individual GM volume differences might help to improve our understanding of social interactions in joint task performance.

Introduction

Social interaction plays a fundamental role in human life (Sebanz et al., 2006). Joint action requires a flexible cognitive control system that enables participants to select contextually relevant information (Knoblich and Sebanz, 2006; Liepelt et al., 2009; Sebanz and Knoblich, 2009), to anticipate each other's behavior (Schubotz, 2007) and to organize dynamic coordination of each other's ongoing actions (Liepelt and Prinz, 2011). In laboratory settings, cognitive control processes in single individuals are usually investigated using different kinds of interference tasks that require conflict resolution including the Eriksen flanker (Eriksen and Eriksen, 1974), the Simon (Simon and Rudell, 1967) and the Stroop task (Stroop, 1935). More recently, researchers started to investigate social interactions with a modified version of the Simon task, the so-called Social Simon paradigm. In this paradigm, two people share a task, which is commonly used in the standard Simon task. Here, participants are required to carry out spatially defined responses (e.g., left and right key presses) to non-spatial stimulus attributes (e.g., low pitch vs. high pitch tone) that randomly appear on a loudspeaker placed to the left and right side of the participant. Although stimulus location is completely task irrelevant, responses are faster when they spatially correspond to the stimulus signaling them (e.g., low pitch tone on the left and/or high pitch tone on the right) - a phenomenon that has come to be known as the (standard) Simon effect (Simon and Rudell, 1967). This spatial stimulus–response (S–R) compatibility effect typically disappears when a participant responds with one response to only one of the two stimuli, rendering the task a "go-nogo task" (Hommel, 1996). However, the Simon effect reappears, when two persons share the same go-nogo Simon task so that each of them operates one of the two responses in accordance to their assigned stimulus. This S-R compatibility effect in the joint setting (as mentioned above) is known as the Social Simon Effect (SSE) and is explained by the assumption that both persons co-represent the action or the task of the other person (Sebanz et al., 2003; Tsai and Brass, 2007).

A recent functional imaging study found activations in the medial frontal cortex (MFC) when participants performed the Simon task together with another person (Sebanz et al., 2007). This result is consistent with other neuroimaging findings, emphasizing the involvement of the MFC, the temporoparietal junction (TPJ), the superior temporal sulcus (STS) and temporal poles in social cognition (Adolphs, 2003; Amodio and Frith, 2006; Blakemore, 2008; Frith and Frith, 2007; Saxe, 2006). Whereas the TPJ, the STS and the temporal poles are

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doi:10.1016/j.neuroimage.2012.03.061

generally associated with reasoning about the mental states of self and others, the MFC is assumed to be involved in monitoring and coding one's own and/or other person's action (Frith and Frith, 2007; Obhi and Sebanz, 2011) and intentions (Spengler et al., 2009). Humphreys and Bedford (2011) provided striking evidence supporting this functional dissociation of frontal and tempoparietal areas in social interactions. Whereas patients with tempoparietal lesion showed consistent SSEs, the SSE decreased over time in patients with frontal lesion. Humphreys and Bedford (2011) argued that patients with frontal lesions seemed to have difficulties in marshaling enough processing resources to maintain the coding of one's own and the other person's action over time.

If this is true, one should also find structural correlates in the frontal cortex that influence the size of the SSE considering a strong linkage between brain function and structure (Forstmann et al., 2008a; Huster et al., 2009; van Gaal et al., 2010) and the fast alternation of brain structure in response to rapidly changing environmental demands (Taubert et al., 2010, 2011; Draganski et al., 2004; see Draganski and May, 2008 for a review). Hence, it still remains elusive whether or not individual differences in brain morphology might also account for different behavioral outcomes. Recently, it has been shown that structural brain alterations explain at least some of the individual differences in motor skill learning (Tomassini et al., 2011), as well as in cognitive control processing involved in individual task performance (van Gaal et al., 2010). An open, yet unsolved question is whether or not individual performance differences in joint action show a similar association. It is, however, highly relevant to identify such structural correlates given the huge variance in the size of the SSE across studies and between individuals (e.g., Dolk et al., 2011; Ferraro et al., 2011; Guagnano et al., 2010; Hommel et al., 2009; Liepelt et al., 2011; Ruys and Aarts, 2010; Sebanz et al., 2003; Vlainic et al., 2010).

If the frontal cortex is involved in maintaining the coding of one's own and the other person's action (Humphreys and Bedford, 2011) one should predict that differences in brain morphology in frontal areas are associated with individual performance differences in the social Simon task.

Material and methods

Participants

Twenty-six healthy volunteers (14 female; 20–32 years of age (M = 25,4, SD = 3.5) with no history of neurological or hearing problems participated in the experiment. All participants were right-handed as assessed by the Edinburgh Inventory scale (laterality score: $+100 \pm 23$ (median ± range) over a range of -100 (fully left-handed) and $+100$ (fully right-handed); Olfield, 1971), had normal or corrected-to-normal vision, were naive with regard to the hypothesis of the experiment and were paid for their participation. The ethics committee of the University of Leipzig approved the study and all participants gave their written informed consent to participate in the experiment, which was conducted in accordance with the ethical standards laid down in the 1975 Declaration of Helsinki.

Social Simon task and statistical analysis

Two acoustic signals (A and B), designed by van Steenbergen (2007) were chosen as go and no-go stimuli in an auditory social Simon task and were presented via two loudspeakers separated by a distance of one meter at approximately 60 dB to either the left or right side of both participants. Prior to the instruction phase of the experiment, both participants were seated next to each other in a sound-attenuated dimly lit room and asked to place their respective right index-finger (IF) on a response button (25 cm in front and 25 cm from the midline of a computer monitor) while placing their left hand underneath the table on their left thigh (Fig. 1). Actors, always seated on the right, were asked to respond to their assigned signal (always B) by pressing the right button with their right IF. This was motivated by the fact that we wanted to rule out possible confounds of spatial seating arrangements and handedness. Only actors received a MRI scan before participation. Co-actors, whose performance was not analyzed, were always seated on the left chair and had to press the left button with their right IF to respond to their assigned signal (always A). Participants were not told who the critical participant of interest was neither were they aware if a MRI scan was performed for the other participant or not.

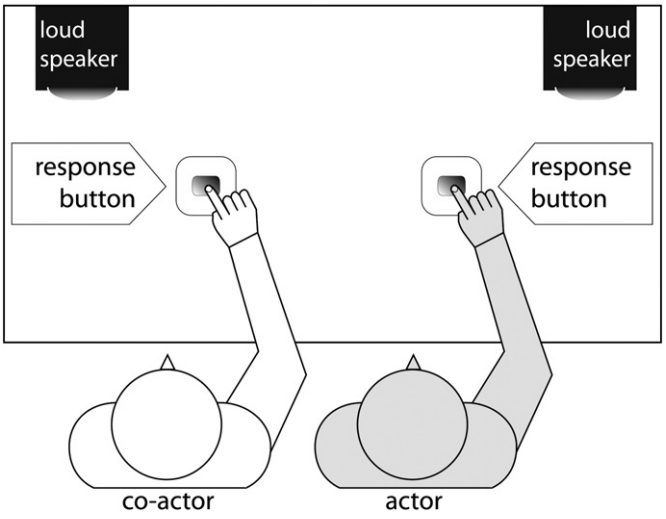

Fig. 1. Experimental setting. Gray shaded subject indicating the actor, whose performance was analyzed in the present experiment. For a detailed description of the social Simon task see text.

To familiarize participants with the task, the experiment started with an instruction phase (~5 min) including the presentation of the two signals, their assignment to each participant and a training of 20 trials in total. After the instruction phase was completed, the experimental phase started. There were three blocks of 64 trials for each participant and co-actor (32 with spatial stimulus–response compatibility and 32 with no spatial stimulus–response compatibility), separated by short breaks of 2 min in order to maintain vigilance throughout the experimental procedure. Each trial began with the presentation of a warning sound for 300 ms. After 1 s, the critical sound – either signal A or B – was presented for 300 ms to the right or the left side of both actor and co-actor. Participants were instructed to respond as quickly and as accurately as possible to their individual target signal (either signal A (co-actor) or B (actor)). After a response was given or 1700 ms had passed, a 1 s Inter-Stimulus-Interval (ISI) followed. The whole experiment took approximately 40 min.

In accordance with previous studies (Liepelt et al., 2011; Röder et al., 2007), we excluded all trials in which responses were incorrect (2.6%) and faster than 150 ms or slower than 1000 ms (2.0%) for the statistical analysis of reaction times. Since our primary research goal was to investigate if morphometric gray matter differences influence the SSE, we had to exclude two participants from further analyses since they showed a negative SSE, which may be related to unknown external factors. Responses were coded as compatible (stimulus ipsilateral to the correct response side) and incompatible (stimulus contralateral to the correct response side). Correct reaction times (RTs) were analysed using a paired *T*-test.

Image acquisition

Prior to the social Simon task, structural MR imaging (MRI) data were acquired on a 3 Tesla Magnetom Tim Trio scanner (Siemens,

Erlangen, Germany) using either a 12 (n = 15) or a 32-channel head coil (n = 11) with an identical scanning protocol. T1-weighted images were acquired using a MPRAGE (magnetization-prepared rapid acquisition gradient echo) sequence (TR = 1300 ms; TE = 3.46 ms; flip angle = 10°, FOV = 256 mm × 240 mm; 176 sagittal slices; voxel size = 1 × 1 × 1.5 mm). The acquisition for the anatomical MRI scan took 13 min.

MRI data processing and analysis

Pre-processing of T1-weighted images was performed in SPM5 (Wellcome Trust Centre for Neuroimaging, UCL, London, UK; http://www.fil.ion.ucl.ac.uk/spm) using the VBM Toolbox 5.1 (http://dbm.neuro.uni-jena.de/vbm.html) running under a Matlab environment (Mathworks, Sherborn, MA, USA, Version 7.7). We applied standard routines and default parameters under VBM 5.1. T1-weighted images were bias field corrected, tissue classified, and registered using linear (12-parameter affine) and non-linear transformations (Ashburner and Friston, 2005). Subsequently, gray matter (GM) segments were modulated (with linear components) in order to preserve the total GM signal. Finally, the modulated GM volumes were smoothed with a Gaussian kernel of 8 mm full width at half maximum (FWHM).

According to the scope of our study we tested for individual differences in GM volume using (A) the individual SSE-size (expressed as mean RT [ms] of incompatible trials minus mean RT of compatible trials) and (B) mean RT for compatible and incompatible trials, respectively. We used a whole-brain correlation analysis with gender (female, male), age, global intracranial volume (including gray, white matter and cerebrospinal fluid [mm3]) and head coil (12 or 32-channel) as covariates for each participant.

For statistical analyses, we excluded all voxels with a GM value below 0.2 (with a maximum value of 1) to avoid possible partial volume effects near the border between GM and white matter (WM). Cluster size was corrected according to the local smoothness values using non-stationary cluster-extent correction (Hayasaka et al., 2004). We report effects for clusters of voxel exceeding a voxel-level threshold of $p<0.001$ (uncorrected) and a cluster size threshold of $p<0.05$, family-wise error (FWE) corrected for multiple comparisons in the context of Gaussian random field theory (Friston et al., 1996).

Results

Social Simon task

A paired *T*-test revealed that responses were faster with stimulus–response compatibility (mean RT = 305.0 ms ± 11.9 ms (SD)) than with stimulus–response incompatibility (mean RT = 329.0 ms ± 13.0 ms; $t(1,23) = 9.315$, $p<0.001$; see Fig. 2A), leading to an overall SSE of 24 ms (± 12.6 ms, see Fig. 2B).

Voxel-based morphometry

In order to test whether individual differences in GM volume across participants influence social Simon task performance, we performed a whole brain correlation analysis. We found that GM volume in the left MFC (peak coordinates: x = −3, y = 40, z = 26; Z = 3.75) negatively correlated with inter-individual differences in the SSE ($p<0.05$ corrected; see Fig. 3, and Table 1), indicating that participants with the largest GM volume in left MFC showed a small SSE [ms] and vice versa.

Further, we correlated GM volume with the mean RT for compatible and incompatible trials. This analysis showed a significant negative correlation in bilateral medial frontal gyrus (MFG) for compatible trials (peak coordinates left: x = −29, y = 48, z = 17; Z = 3.78; peak coordinates right: x = 37, y = 51, z = 9; Z = 4.00; $p<0.05$ corrected; see Fig. 4 and Table 1) and incompatible trials (peak coordinates left: x = −28, y = 49, z = 17; Z = 3.99; peak coordinates right: x = 37, y = 51, z = 9; Z = 3.92; $p<0.01$; see Fig. 4 and Table 1). Additionally, we also found a negative correlation of the mean RT for incompatible trials in the left dorsal premotor cortex (dPMC; peak coordinates left: x = −27, y = −2, z = 53; Z = 4.25; $p<0.05$; see Fig. 4 and Table 1).

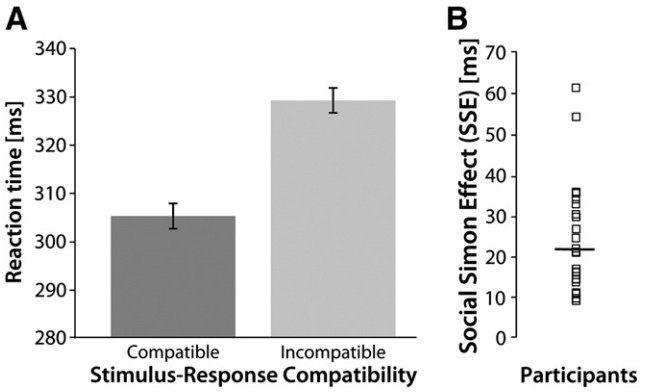

Fig. 2. (A) Mean reaction time as a function of spatial stimulus–response compatibility. Error bars represent standard errors of the mean differences. (B) Individual distribution of social Simon task performance in ms (squares). The Black bar illustrates mean participants performance.

Discussion

In the present study we investigated whether structural variations in cortical GM volume are related to individual performance differences in a social Simon task. Whole brain correlation analyses of GM volume revealed a negative correlation between the size of SSE and the GM volume of the left MFC, indicating that individuals with larger MFC GM volume were those with a smaller SSE and vice versa. Based

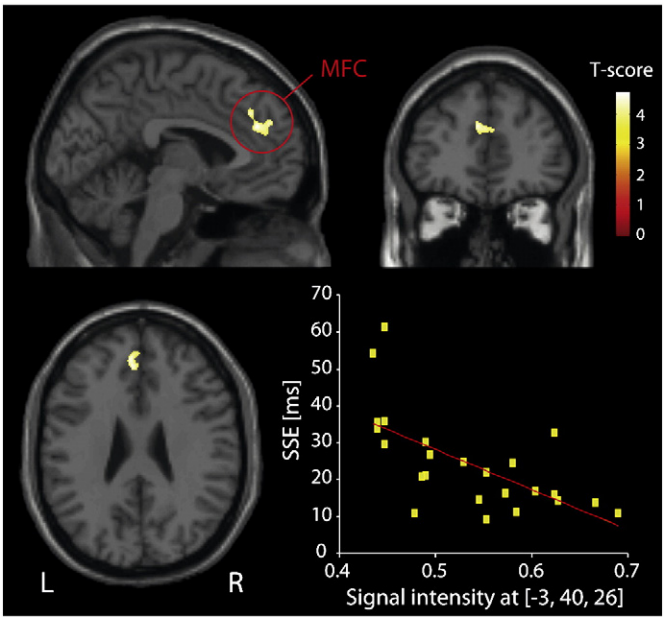

Fig. 3. Whole brain linear correlation analysis between GM volume differences and the individual size of the SSE [ms]. We found a significant negative correlation in MFC (MNI coordinate: x −3, y = 40, z = 26) indicating that participants with a small SSE showed the largest GM volume in left MFC and vice versa. Results are displayed in coronal, sagittal and axial sections shown at $p<0.001$ with an extend threshold of $p<0.05$, FWE correction on cluster level. The colour bar indicates the respective T-score. Please note that there was a significant correlation in left MFC only (peak voxel from parametric correlation analysis in left MFC, r = −0.641; p = 0.001). For details see text. L: left; R: right.

Table 1
Correlations between gray matter volume and performance in the social Simon task showing: (1) a negative correlation between gray matter volume differences and the size of SSE; (2) a negative correlation between gray matter volume differences and compatible trials; (3) a negative correlation between gray matter volume differences and incompatible trials.

Structure	MNI co-ordinates							
	BA	H	Z value	cluster size	*p* value*	x	y	z
(1) Negative correlation with size of the SSE								
Medial frontal cortex	32	L	3.75	1129	0.029	−3	40	26
(2) Negative correlation with compatible trials								
Middle frontal gyrus	9/10	L	4.76	946	0.008	−29	48	17
Middle frontal gyrus	9/10	R	4.00	770	0.023	37	51	9
(3) Negative correlation with incompatible trials								
Middle frontal gyrus	9/10	L	3.99	968	0.007	−28	49	17
Middle frontal gyrus	9/10	R	3.92	931	0.009	37	51	9
Dorsal premotor cortex	6	L	4.25	797	0.019	−27	−2	53

* Cluster-level p values after $p<0.001$ (uncorrected) and non-stationary cluster-extent correction with $p<0.05$; BA, Brodmann area; H, hemisphere.

on this finding, it is reasonable to assume that a larger GM volume in MFC seems to support the detection and evaluation of response selection conflict in joint action. In a further analysis, we found that individual variations in bilateral MFG negatively correlated with participant's response time of different trial-types (compatible and incompatible). Thus, individuals with greater GM volume in MFG were faster in selecting the appropriate action in both compatible and incompatible trials in the social Simon task as compared to those with smaller GM volume. Only in incompatible trials, GM volume differences in dPMC also correlated negatively with individual performance differences. Taken together, these results support previous findings, which suggest a crucial role of the MFC in conflict resolution (Botvinick et al., 2001; Botvinick et al., 2004; Kerns, 2006; Ridderinkhof et al., 2004, 2010 for a review) and more importantly, in joint action control (Humphreys & Bedford, 2011). These brain-behavior relationships suggest an interplay of monitoring the contextual relevant information (MFC), selecting the appropriate action (MFG) and responding sufficiently to the changing environmental requirements (dPMC), to be crucially involved in joint action control.

More importantly, the present results extend previous functional imaging studies in two fundamental ways: first, by associating morphometric differences with individual variations in joint task performance, and second, by suggesting that structural correlates within frontal regions (e.g., MFG/dPMC) might be related to resolving response selection conflict in joint action (Botvinick et al., 2001; Carter et al., 1998; Kerns, 2006; Kerns et al., 2004; MacDonald et al., 2000; Ridderinkhof, et al., 2004).

While the exact nature of cellular mechanisms underlying inter-individual differences in gray matter morphology are still poorly understood (Draganski and May, 2008; May and Gaser, 2006) several studies successfully demonstrated a tight link between human brain structure alterations as a consequence of long-term skill learning (Draganski, et al., 2004, 2006; Driemeyer et al., 2008; Taubert et al., 2010, 2011) and variations in cognitive processes based on structural differences in the human brain (Forstmann et al., 2008a; van Gaal et al., 2010; Huster et al., 2009).

In the present study, we can only speculate about the underlying sources of inter-individual GM volume differences. For example, it might be reasonable to assume that differences in dendritic and/or axonal structure, genetic predispositions, musical expertise or other skill acquisition are potential candidate mechanisms that might result in inter-individual morphometric alterations (DeBello, 2008; May and Gaser, 2006; Pezawas et al., 2004; Trachtenberg et al., 2002; Xu et al., 2009). Other studies have shown that anatomical variability of the MFC with respect to the presence/absence of the (left) paracingulate sulcus (PCS) might be associated with individual differences in cognitive abilities (Fornito et al., 2004, 2006; Huster et al., 2007, 2009; Paus et al., 1996). Accordingly, the presence of the PCS was found to be associated with better performance across verbal and non-verbal executive tasks (Fornito et al., 2004) as well as decreased Stroop interference (Huster et al., 2009), compared to the absence of the PCS. Therefore, sulcal variability in the MFC might be another potential source of inter-individual differences in joint task performance.

Apart from the limited knowledge about the exact nature that mediates morphometric brain variations, our results might have important implications for the understanding of inter-individual variations in a wide range of higher cognitive functions (see Kanai and Rees, 2011 for a review). In fact, previous research investigating the SSE showed a huge variability across studies and between individuals in terms of the effect size ranging between 5 and 41 ms (Dolk et al., 2011; Ferraro et al., 2011; Guagnano et al., 2010; Hommel et al., 2009; Liepelt et al., 2011; Ruys and Aarts, 2010; Sebanz et al., 2003; Vlainic et al., 2010). Based on our findings, it might be tempting to speculate that one potential determinant for the source of this variance on a behavioral level is related to structural brain differences within individual participants. In the past, such inter-individual differences were mostly neglected by averaging performance values on a group level. However, especially these differences could be attributed to the variability in predisposed brain structure and/or function.

Interestingly, cognitive control processes in the human brain were recently associated with similar brain regions within the MFC for single participants performing various kind of interference tasks (Botvinick et al., 1999; Forstmann et al., 2008a, 2008b; Kerns, 2006; Nee et al., 2007; Ridderinkhof et al., 2004; van den Wildenberg et

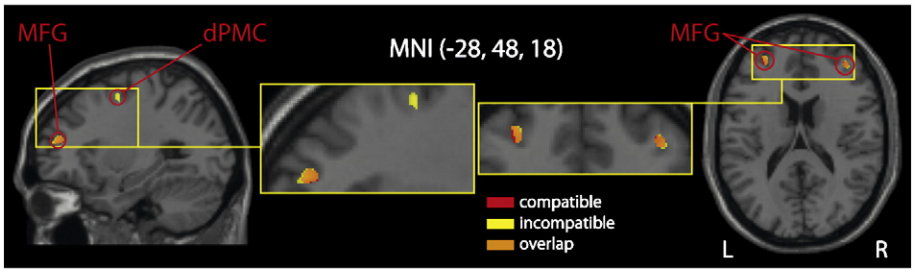

Fig. 4. Overlay of results obtained from two additional correlation analyses (whole brain) comparing GM volume differences and the individual RT for compatible and incompatible trials in the auditory social Simon task. For compatible trials, we found a significant negative correlation in bilateral MFG (left MFG: x = −29, y = 48, z = 17; Z = 3.78; right MFG: x = 37, y = 51, z = 9; see also Table 1). On the other hand, for incompatible trials, we found a negative correlation in bilateral MFG (left MFG: x = −28, y = 49, z = 17; right MFG: x = 37, y = 51, z = 9) as well as in left dPMC (x = −27, y = −2, z = 53).Red cluster illustrate compatible, yellow cluster incompatible trails. Orange cluster represent the special overlay of both correlation analyses. The overlay is displayed at the following coordinates: x = −28, y = 48, z = 18. For details see text. L: left; R: right.

al., 2010; van Veen and Carter, 2002 for a review; van Veen et al., 2001). According to these studies, the present findings may suggest that the MFC is crucially involved in enabling individuals to behave contextually appropriate (performing the task alone or together with another person) and to achieve desired goal states.

However, since the peak coordinate of our correlation analysis is located directly at the boarder between dorso-medial and posterior MFC, we can only speculate whether the brain-behavior relationship between cognitive control processes and individual GM volume differences found in the present study might reflect general cognitive processes of action/ conflict monitoring irrespective of the social/ non-social nature of the task (posterior region of the rostral MFC; cf., Ridderinkhof et al., 2004) and/or processes of social cognition such as mentalizing (anterior region of the rostral MFC; cf., Amodio and Frith, 2006). Although the theoretical interpretation of the mechanisms underlying the SSE are still a matter of debate, there is increasing evidence that the source of the SSE is not necessarily due to the co-representation of another person's task (e.g., one's own and the other's specific S-R mappings) that elicits response conflict for non-corresponding S-R mappings in joint action (Dolk et al., 2011). Instead, recent findings suggest that conflict may be induced by determining whose turn it is in a given trial (Liepelt et al., 2011, 2012; Wenke et al., 2011), supporting rather more general processes of action/ conflict monitoring (posterior region of the rostral MFC; cf., Ridderinkhof et al., 2004). Nevertheless, since the setting of our social Simon task involves or creates an interactive context, it might require and highlight the importance of a functional interplay between both, action/ conflict monitoring as well as mentalizing. This reasoning might explain why the peak coordinate of the present study is located directly at the boarder of both, the dorso-medial and posterior MFC. Thus, an interesting line of future research would require the comparison of various interference task like the Stroop (Stroop, 1935) or Flanker task (Eriksen and Eriksen, 1974) in different settings (e.g., individual and joint performance) to specify the (functional and structural) role of the MFC in inter- and intra-individual action control.

Apart from the yet, well documented involvement of the MFC in single and joint action control (e.g., Kerns, 2006; Radke et al., 2011; Sebanz et al., 2007), other brain areas such as the temporoparietal junction (TPJ), the superior temporal sulcus (STS) and temporal poles were additionally emphasized to be associated with social cognition (Adolphs, 2003; Amodio and Frith, 2006; Blakemore, 2008; Frith and Frith, 2007; Saxe, 2006). However, we did not find structural correlates for inter-individual performance differences in the above mentioned brain areas. This result is in line with the findings of Humphreys and Bedford (2011), highlighting the importance of the MFC for joint action control in the social Simon task and emphasizing the dissociation of cognitive control processes from other aspects of social cognition (e.g., perspective taking; self-other distinction). In the study by Humphreys and Bedford (2011), patients with tempoparietal lesion demonstrated consistent SSEs, whereas the SSE decreased over time in patients with frontal lesion, which suggests that patients with frontal lesion seem to have difficulties in maintaining the coding of one's own and the other person's action over time (Humphreys and Bedford, 2011). Based on these reasoning one might speculate that irrespective of whether performing a Simon task individually or together with another person seems to require the coding of one's own action as left/right or me/ not me (Dolk et al., 2011; Hommel, 1996; Hommel et al., 2009; Liepelt et al., 2011). This appears to be a crucial issue that needs to be addressed in future studies to gain a better understanding of the specific role of MFC in social and non-social action control.

Acknowledgement

We would like to thank Juergen Dukart for useful discussions during the process of data analysis.

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