Pre-SMA Gray-matter Density Predicts Individual Differences in Action Selection in the Face of Conscious and Unconscious Response Conflict

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Abstract

■ The presupplementary motor area (pre-SMA) is considered key in contributing to voluntary action selection during response conflict. Here we test whether individual differences in the ability to select appropriate actions in the face of strong (conscious) and weak (virtually unconscious) distracting alternatives are related to individual variability in pre-SMA anatomy. To this end, we scanned 58 participants, who performed a masked priming task in which conflicting response tendencies were elicited either consciously (through primes that were weakly masked) or virtually unconsciously (strongly masked primes), with structural magnetic resonance imaging. Voxel-based morphometry revealed that individual differences in pre-SMA gray-matter density are related to subjects' ability to voluntary select the correct action in the face of conflict, irrespective of the awareness level of conflict-inducing stimuli. These results link structural anatomy to individual differences in cognitive control ability, and provide support for the role of the pre-SMA in the selection of appropriate actions in situations of response conflict. Furthermore, these results suggest that flexible and voluntary behavior requires efficiently dealing with competing response tendencies, even those that are activated automatically and unconsciously. ■

INTRODUCTION

To optimize our behavior, we must overcome conflicting information in the environment and rapidly select contextually relevant information to achieve our goals. In the lab, this phenomenon has been studied with various "conflict tasks," such as the Stroop, the Simon, or the Eriksen flanker tasks. In these tasks, one response is activated through rapid and direct capture from salient but task-irrelevant stimulus features, and must be subsequently overcome by another, more deliberate response. For example, in the flanker task, participants have to respond as quickly as possible to the direction of a target arrow and ignore flanking distracting arrows. When the target and flankers are incongruent (pointing in opposite directions), responses are generally slowed down compared to congruent trials (target and flankers point in the same direction). Several lines of consistent evidence suggest that human medial frontal cortex (MFC), and the presupplementary motor area (pre-SMA) in particular, is of crucial importance for selecting the appropriate action in such situations of response conflict (Forstmann, van den Wildenberg, & Ridderinkhof, 2008; Mostofsky & Simmonds, 2008; Nachev, Kennard, & Husain, 2008; Rushworth, Buckley, Behrens, Walton, & Bannerman, 2007; Botvinick, Braver, Barch, Carter, & Cohen, 2001).

The aim of the present study was to investigate the link between brain function and brain structure, and to test whether individual differences in the ability to select the appropriate action during response conflict are related to structural differences in the pre-SMA. Furthermore, we were interested in the relation between overcoming response conflict and the level of awareness of conflict. In daily life, people are overwhelmed with visual information from which they have to select the relevant information to guide their behavior. Although a large part of this information probably remains unnoticed (i.e., unconscious), it might still influence our behavior, as evidenced by many subliminal priming (e.g., Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003; Dehaene et al., 1998) and attentional blindness studies (Most, Scholl, Clifford, & Simons, 2005; Mack, 2003). Recent evidence is somewhat contradicting in whether human MFC is important for action selection in the face of unconscious conflict (Ursu, Clark, Aizenstein, Stenger, & Carter, 2009; Sumner et al., 2007; Praamstra & Seiss, 2005; Mayr, 2004; Dehaene et al., 2003). In fact, prefrontal cortex has been assumed to be strongly associated with consciousness (Rees, Kreiman, & Koch, 2002; Dehaene & Naccache, 2001) and even free will (e.g., Haggard, 2008; Lau, Rogers, Haggard, & Passingham, 2004) and tends not to become involved in unconscious operations. However, recently, we and others have shown that even high-level prefrontal cognitive control processes, such as response inhibition (van Gaal, Ridderinkhof, van

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den Wildenberg, & Lamme, 2009; van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008) and task switching (Lau & Passingham, 2007), can be initiated by unconscious (masked) stimuli.

Here we used voxel-based morphometry (VBM) to characterize the brain areas important for action selection in the face of strong (conscious) and weak (virtually unconscious) response conflict. To this end, 58 participants performed a masked priming task in which awareness of conflict-inducing stimuli was manipulated (Figure 1A). Participants were required to perform a speeded two-choice response to a target arrow that was preceded by a smaller arrow, the so-called prime. Because the prime fitted within the contour of the target, the target functioned as a (meta-contrast) mask. Under this specific circumstance, participants are generally not aware of the prime when it is presented very briefly, whereas it is clearly visible when presented slightly longer (Kunde, 2003; Breitmeyer, 1984). However, a prime that cannot be perceived is still processed, as evidenced by faster response times and fewer errors when the prime and the target are congruent than when they are incongruent (Kunde, 2003; Vorberg et al., 2003), referred to here as the *correspondence effect*. The magnitude of the correspondence effect is determined by the strength of response activation induced by the prime (stronger activation of the incongruent action leads to greater interference) and the efficiency of the inhibition of this activation (stronger inhibition reduces interference; Ridderinkhof, 2002) and reflects the efficiency of an individual to overcome response conflict.

We hypothesized that if the pre-SMA has a direct role in actively resolving response conflict and deliberately selecting the appropriate action, regional gray-matter density in the pre-SMA should correlate with individual differences in the ability to resolve response conflict. More specifically, we expected to observe a negative correlation between pre-SMA gray-matter density and the correspondence effect across participants because a better developed action selection system (greater pre-SMA gray-matter density) should (on average) lead to more efficient conflict resolution (thus a smaller correspondence effect). Furthermore, because we could calculate correspondence effects for weakly and strongly masked conditions separately, we were able to examine the relation between gray-matter anatomy and individual differences in the ability to overcome strong (conscious) and weak (virtually unconscious) conflict.

METHODS

Participants

Fifty-eight volunteers participated in the experiment for course credits or financial compensation. All procedures were executed in compliance with relevant laws and institutional guidelines and were approved by the local ethical committee. Subjects gave written informed consent before experimentation. Nonoverlapping results from these data have been submitted elsewhere (van Gaal, Lamme, & Ridderinkhof, submitted).

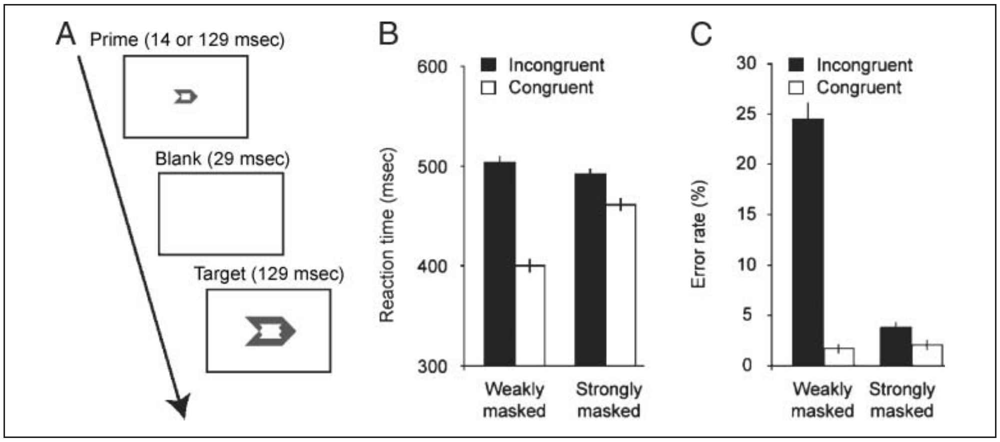

Figure 1. Experimental design and behavioral results. (A) The sequence of events in the masked priming experiment. The prime could either be congruent (pointing in the same direction) or incongruent to the target (pointing in the opposite direction). Prime visibility was manipulated by presenting the prime either briefly (14 msec) or longer (129 msec). Thus, four conditions were created: (1) weakly masked incongruent trials, (2) weakly masked congruent trials, (3) strongly masked incongruent trials, and (4) strongly masked congruent trials. (B) Response times for congruent and incongruent trials for strongly and weakly masked conditions separately (±*SEM*). (C) Error rates for congruent and incongruent trials for strongly and weakly masked conditions separately (±*SEM*).

Design

Participants came to the lab for a scanning session and two behavioral sessions. In the behavioral sessions, participants completed a battery of tests including the one described in the present article. All other tests (e.g., working memory task, pattern masking task, visual imagery task) were performed by other researchers and were not related to conflict resolution, as studied here. Participants performed a typical masked priming task, previously used to study response selection in the face of consciously and unconsciously presented distractors (Kunde, 2003). Stimuli were presented using Presentation (Neurobehavioral Systems, Albany, NY) against a white background at the center of a 17-in. VGA monitor (frequency = 70 Hz). Participants viewed the monitor from a distance of approximately 90 cm, so that each centimeter subtended a visual angle of 0.64°. A blue prime arrow (width 0.96°, height 0.64°) was presented for a short duration (14 msec) or a long duration (129 msec), followed by a blank interval (29 msec), and then by a target arrow (129 msec, width 2.20°, height 1.47°) that instructed participants to respond as quickly and accurately as possible to its direction (see Figure 1A). Participants were instructed to ignore the primes that preceded the target. The prime was a smaller version of the target and fitted within the contour of the target. By manipulating prime duration, the prime was either visible (on half of the occasions), or its visibility was sharply reduced (in the other half of the occasions). By this means, four conditions were created: (1) weakly masked incongruent trials, (2) weakly masked congruent trials, (3) strongly masked incongruent trials, and (4) strongly masked congruent trials. Participants performed four blocks, each containing 160 trials (40 per condition, pseudorandomized). Total trial duration was 1400, 1500, 1600, or 1700 msec (equal frequency). Before the main experiment, participants practiced the task briefly (32 trials).

Immediately after the final experimental block, participants performed a two-choice discrimination task on the primes (80 trials; 20 trials of each condition). Stimulus and trial timing was exactly the same as in the masked priming task, except that a pair of choices was presented left and right of fixation after each trial. Participants were asked to determine as accurately as possible whether a left-pointing or right-pointing prime was presented in the preceding trial. Before administrating this task, participants were told that left- and right-pointing primes were presented equally frequently and were instructed to consider this in giving their response. Participants were also told that only accuracy was important in this task, and not the speed of responding. Upon responding, a new trial started.

Behavioral Data Analyses

For the RT analyses (masked priming task), RTs > 100 msec and <1000 msec were included. Mean RTs from correct responses were entered into an ANOVA with within-subjects variables of prime–target correspondence (congruent vs. incongruent) and masking strength (weak vs. strong masking). Subsequently, paired two-tailed t tests were performed for strongly masked and weakly masked trials separately. For the accuracy analyses, the same was done for the square root of response accuracy. Detection performance (percentage correct in the two-choice discrimination task) was tested for significance using a one-sample t test (compared against 50%) evaluated at an alpha level of .05.

VBM Data Acquisition Procedure

In a separate session, magnetic resonance images were acquired using a 3-T scanner (Philips, The Netherlands). We acquired two structural scans from each subject, which were averaged [T1 turbo field echo; 182 sagittal slices; FA = 8°; TE = 4.6 msec; TR = 9.6 sec; slice thickness = 1.2 mm; FOV = 256 * 256 mm; in-plane voxel resolution 1 * 1 mm]. Data were analyzed with VBM (Good et al., 2001) carried out with FSL software (Smith et al., 2004). First, structural images were brain-extracted (Smith, 2002). Next, tissue-type segmentation was carried out using FAST4 (Zhang, Brady, & Smith, 2001). The resulting gray-matter partial volume images were then aligned to MNI152 standard space using the affine registration. The resulting images were averaged to create a study-specific template, to which the native gray-matter images were then nonlinearly re-registered with a method that uses a b-spline representation of the registration warp field (Rueckert et al., 1999). The registered partial volume images were then modulated (to correct for local expansion or contraction) by dividing by the Jacobian of the warp field (Ashburner & Friston, 2000). The modulated segmented images were then smoothed with an isotropic Gaussian kernel with a sigma of 4 mm.

The above-described method creates a measure of gray-matter density for each voxel in the brain, which can be correlated with the RT congruency effect (a measure of the ability of an individual to resolve conflict) across subjects. This can be done for all the voxels in the brain. To this end, in FSL, a voxelwise GLM analysis was performed using permutation-based nonparametric testing (100,000 iterations). The correspondence effect (mean RT incongruent trials − mean RT congruent trials) for the weakly masked, as well as the strongly masked condition, was entered as covariates (2 covariates) to extract the brain areas that explain variance in these behavioral measures.

First, we tested our a priori hypothesis that structural variance in the pre-SMA region is related to individual differences in overcoming response conflict. To this end, we restricted our search space to the right and left superior frontal gyrus (SFG) separately. In functional imaging studies related to action selection during conflict, peak voxels generally lie in the (anterior) part of the SFG (for a meta-analysis, see Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). The SFG was taken from the Harvard–Oxford Cortical

Structural Atlas that accompanies FSL (using a 95% probability threshold). In an omnibus ANOVA (*F* test), we tested whether voxels in the SFG explained a significant amount of variance across both RT congruency measures. Statistical significance was determined using a voxel height threshold of $p < .05$, corrected for multiple comparisons (False Discovery Rate; Genovese, Lazar, & Nichols, 2002).

Note that from the thresholded statistical maps derived from the *F* test, one does not yet know the direction of the observed effect (positive/negative correlation) and whether the effect is driven by the weakly masked condition, the strongly masked condition, or both. To test this, the region surviving the *F* test (pre-SMA) was used as a mask to extract gray-matter values for each participant. These values were then correlated (Spearman) with the correspondence effect for both conditions across subjects to unravel the directionality and nature of the effect. Next, more exploratory analyses were performed across the whole brain (see Results).

RESULTS

Behavioral Results

As expected, participants were significantly faster on congruent conditions than on incongruent conditions [$F(1, 57) = 513.91, p < .001$]. This difference was significant in the weakly masked [$t(57) = 21.63, p < .001$] as well as strongly masked conditions [$t(57) = 16.16, p < .001$; see Figure 1B], but was significantly larger for the weakly masked condition than for the strongly masked condition [$F(1, 57) = 297.04, p < .001$]. Additionally, participants made more response errors on incongruent trials than on congruent trials [$F(1, 57) = 194.47, p < .001$]. Again, this difference was reliable in the weakly masked [$t(57) = 14.18, p < .001$] as well as strongly masked [$t(57) = 6.14, p < .001$] conditions (see Figure 1C); but again, the magnitude of the correspondence effect reflected in error rates was significantly larger for the weakly masked conditions than the strongly masked conditions [$F(1, 57) = 200.68, p < .001$].

Prime Visibility

The two-choice discrimination task administered after the masked priming experiment revealed an overall percentage correct for weakly masked primes of 92.4% (*SD* = 12.1) versus 59.4% (*SD* = 9.1) for strongly masked primes. Participants were significantly better at detecting weakly masked primes than strongly masked primes [$t(57) = 17.6, p < .001$]. Although prime visibility was low in the strongly masked condition, it was significantly above chance level [$t(57) = 7.88, p < .001$].

Pre-SMA and Action Selection during Conflict

First, correlations with brain anatomy and the correspondence effects for both weakly and strongly masked con-

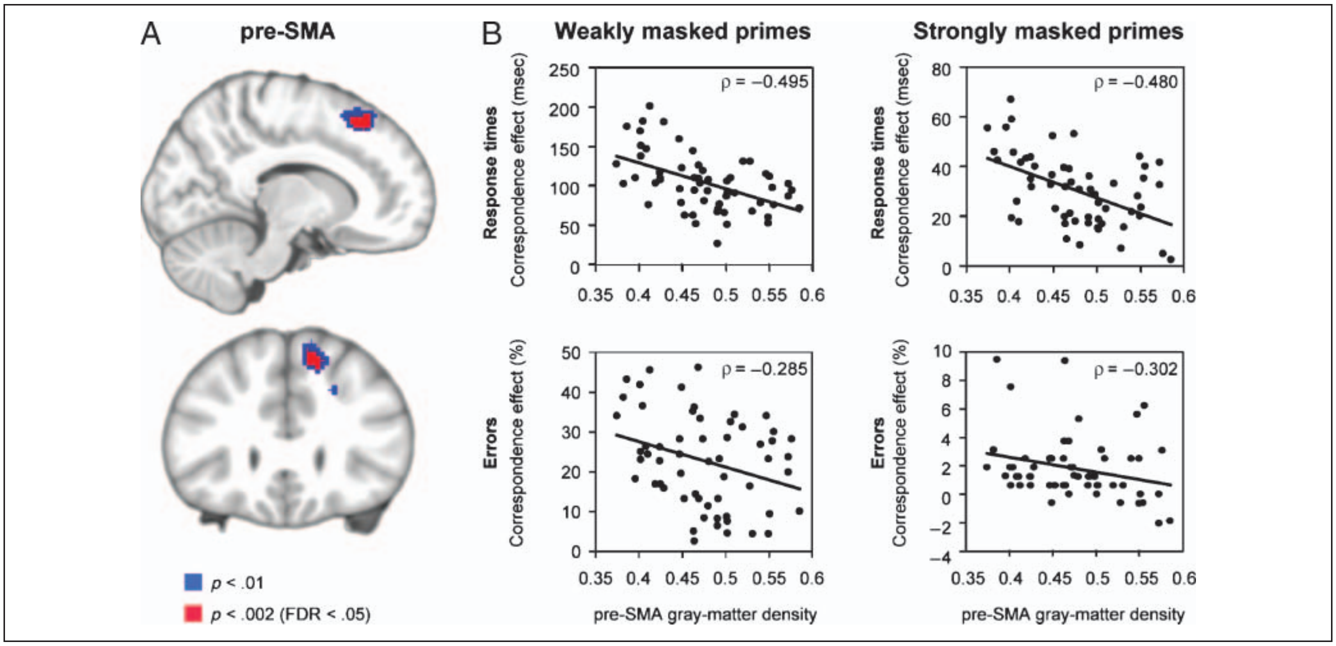

Figure 2. Pre-SMA and action selection in the face of conflict. (A) Pre-SMA gray-matter density (13, 27, 51) correlated with the ability to select contextually relevant information in the face of response conflict irrespective of the awareness of conflict ($p < .05$, FDR corrected, in red). Also voxels at a more liberal threshold ($p < .01$, in blue) are shown to observe the extension of the significant pre-SMA cluster. MNI coordinates reflect the center of gravity. (B) Scatterplots for the correlation between pre-SMA gray-matter density values and the correspondence effect derived from the weakly masked (left) and strongly masked (right) conditions. RT correspondence effects (top); error correspondence effects (bottom).

ditions were examined together (omnibus ANOVA; see Methods). The *F* test revealed a significant gray-matter cluster in the right pre-SMA (Figure 2A; $p < .05$, FDR corrected across a small volume of interest). Next, we used this region as a mask to extract individual pre-SMA gray-matter values and correlated these values with the correspondence effect for both conditions across subjects. Consistent with our predictions, pre-SMA gray-matter density correlated negatively with the correspondence effect derived from the weakly masked conditions across individuals ($\rho = -0.495, p < .001$; see Figure 2B, upper left panel). Interestingly, gray-matter density in the pre-SMA correlated just as strongly with the correspondence effect derived from the strongly masked conditions ($\rho = -0.480$, $p < .001$; upper right panel).

To further explore this finding, pre-SMA gray-matter density values were correlated with a second measure, namely, the difference in the number of response errors on incongruent and congruent trials. Note that this measure was not entered as a covariate in the initial VBM analysis and, therefore, was not used to select the pre-SMA region. Pre-SMA gray-matter density correlated negatively with error rates observed in the weakly ($\rho = -0.285, p = .030$; see Figure 2B, lower left panel) as well as the strongly masked conditions ($\rho = -0.302, p = .021$; lower right panel). We would like to note that, although the error rates were not used in the initial ROI selection procedure, these two measures were correlated ($\rho = 0.595$ for the weakly masked conditions, and $\rho = 0.313$ for the strongly masked conditions; both *p*s < .05) and, therefore, are not completely independent.

Further, we were interested in whether pre-SMA structure was specifically related to individual differences in the ability to resolve conflict. To this end, we correlated the gray-matter values in the pre-SMA region with some other behavioral measures that could be derived from the present experiment. To this end, we correlated it with overall mean RT in the masked priming task and discrimination performance in the two-choice discrimination task. Pre-SMA gray-matter density did not correlate with mean RT ($\rho = 0.119, p = .375$) or discrimination performance for weakly masked ($\rho = -0.092, p = .494$) or strongly masked primes ($\rho = 0.115, p = .389$). Thus, gray-matter density in the pre-SMA region did not correlate with some control measures that are unrelated to action selection in the face of conflict.

The absence of any reliable correlations between pre-SMA gray-matter density and discrimination performance already suggests that the reported pre-SMA effects were not related to the visibility of strongly (or weakly) masked primes. As an additional check regarding this latter issue, we only selected the one-third worst detection performers (mean detection performance = 49.9%) and computed the correlation between pre-SMA gray-matter density and the correspondence effect derived from the strongly masked conditions. Across these 20 participants, this correlation was still robust and significant ($\rho = -0.609, p = .004$); if anything, the strength of the correlation even increased. These additional analyses suggest that the reported pre-SMA effects for the strongly masked condition are not related to prime visibility.

Our final set of analyses was more exploratory. To extract the brain areas, other than the pre-SMA, which might be associated with overcoming response conflict, correlations with brain anatomy and the correspondence effects were examined in the whole-brain gray-matter volume. For this analysis, no regions survived multiple comparisons corrections across the whole-brain volume. Further, we were interested whether there were any brain regions that were specifically related to overcoming conscious conflict or unconscious conflict. To this end, we contrasted the conscious and unconscious effects directly (conscious < unconscious as well as unconscious > conscious). Again, no regions survived multiple comparisons corrections across the whole-brain volume or the SFG as a small volume of interest. Next, we checked for cortical regions that passed a threshold of $p < .001$, uncorrected, which revealed only one small cluster, namely, in the anterior part of the thalamus (3 and 16 voxels, respectively; MNI coordinates: 4, −1, 7), for both of the above-outlined analyses (the overall *F* test and the direct comparisons). Structural gray-matter density in the thalamus (for the 16-voxel cluster) correlated marginally positively with the correspondence effect derived from the weakly masked conditions ($\rho = 0.243, p = .066$), and correlated negatively with the correspondence effect derived from the strongly masked conditions ($\rho = -0.289, p = .028$). This suggests that thalamus structure was specifically related to overcoming unconscious conflict, but not conscious conflict. However, the pattern of results in the thalamus was less consistent than observed in the pre-SMA because thalamus gray-matter density did not correlate with error rates in the weakly ($\rho = -0.004, p = .977$) or in the strongly masked condition ($\rho = 0.037, p = .782$). We would like to note that these latter analyses are for descriptive and exploratory purposes only and that future work is required to test the reliability of this effect.

DISCUSSION

We investigated whether structural differences in cortical gray-matter density were related to individual variation in the extent to which people are able to select the appropriate action in the face of distracting alternatives. Participants performed a masked priming task in which conflicting response tendencies were elicited either consciously (weakly masked primes) or virtually unconsciously (strongly masked primes). Consistent with our predictions, VBM analysis revealed a negative correlation between pre-SMA gray-matter density and the size of the RT correspondence effect. Pre-SMA gray-matter density also correlated with the size of the correspondence effect observed in the error rates. These negative correlations indicate that individuals with greater pre-SMA gray-matter density are, on average, better at selecting the appropriate action in the face of response conflict than individuals with smaller pre-SMA gray-matter density. Interestingly, pre-SMA anatomy correlated with individual variability in the ability to select a deliberate response when conflict was triggered consciously as well as (virtually) unconsciously.

Overall, the behavioral conflict effect was larger for conscious primes than for unconscious primes, which is generally the case in these kinds of masked priming studies (see, e.g., Kunde, 2003), however, pre-SMA gray-matter density did not reflect this aspect of the data. We would like to note that this could constitute a problem of interpretation for *functional* MRI, but not necessarily for *structural* MRI. Functionally, we would expect to see greater activation in the pre-SMA when trying to overcome conscious (strong) conflict compared to when trying to overcome unconscious (weak) conflict, thus reflecting the behavioral data pattern. However, with respect to structure, if the pre-SMA is responsible for this process, there is no a priori reason to assume that it is differentially related to the ability to overcome greater versus smaller conflict or conscious versus unconscious conflict (the slopes of both regression lines shown in Figure 2B are comparable).

These present findings confirm and extend previous functional imaging studies (Forstmann et al., 2008; Nachev, Rees, Parton, Kennard, & Husain, 2005), lesion effects studies (Nachev, Wydell, O'Neill, Husain, & Kennard, 2007; Picton et al., 2007), TMS effects studies (Taylor, Nobre, & Rushworth, 2007; Kennerley, Sakai, & Rushworth, 2004), and single-cell recording studies (Isoda & Hikosaka, 2007; Stuphorn & Schall, 2006) that provided support for a crucial role of the pre-SMA in selecting task-relevant information during conflict. However, our results further extend these findings in two important ways: first, by linking structural, instead of functional, correlates to conflict resolution mechanisms in the pre-SMA, and second, by showing that pre-SMA structure is related to overcoming response conflict triggered by conscious as well as (virtually) unconscious stimuli.

The exact origin of structural differences in gray matter is still a matter of debate and might be related to either innate predispositions or environmental factors, or both. Interestingly, recent VBM studies demonstrated rapid learning-dependent structural changes of the brains anatomy over the course of only a few weeks/months of juggling (Driemeyer, Boyke, Gaser, Buchel, & May, 2008; Draganski et al., 2004), extensive studying (Draganski et al., 2006), or mirror reading (Ilg et al., 2008). The precise nature of such gray-matter increase is still unknown, but several mechanisms have been proposed, including a change in cell size of neurons or glial cells, changes in axonal structure, and perhaps, even neurogenesis (Ilg et al., 2008; May & Gaser, 2006; Trachtenberg et al., 2002; Gross, 2000). These results suggest that the brain can alter its shape quickly and that structural neuroplasticity plays a crucial role in adapting our behavior to environmental changes as well as learning. Future studies are required to further elucidate whether individual differences in pre-SMA structure are due to learning (some people might encounter more conflict than others), innate predispositions, or both.

Medial Frontal Cortex and Unconscious Conflict Resolution

These results extend the sparse and somewhat contradicting evidence obtained in recent functional imaging studies that looked into how the brain overcomes the interference of unconscious information in conflicting situations. Dehaene et al. (2003) measured behavioral and brain imaging correlates of response conflict induced by conscious and unconscious primes in a masked priming paradigm. Although they observed a typical masked priming effect in behavior (for conscious as well as unconscious primes), fMRI revealed that anterior cingulate cortex (ACC) responded more strongly to incongruent primes than to congruent primes, but only when primes were presented consciously. Therefore, the authors concluded that ACC was only responsive to consciously experienced conflict, but not to unconscious conflict. However, recently, others have demonstrated that ACC is responsive to conflict induced by unnoticed ("unconscious") sequence violations of an implicitly learned rule (Ursu et al., 2009) and "unnoticed" response errors (Klein et al., 2007; Hester, Foxe, Molholm, Shpaner, & Garavan, 2005; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001).

Another interesting study with this respect is one of Lau and Passingham (2007), who designed a masked priming task in which they tested whether an unconscious (masked) stimulus can trigger task preparatory processes. Participants had to prepare to perform either a phonological or a semantic judgment on an upcoming word. On a single-trial basis, participants were instructed which task to perform by a consciously presented cue. On all trials, a prime was presented just before the instruction cue (which also functioned as a meta-contrast mask). Half of these primes triggered the alternative task (incongruent trials), and half of them triggered the same task (congruent trials). Also, half of the primes were strongly masked (unconscious) and half were weakly masked (conscious) by the meta-contrast instruction cue. When participants were unconsciously primed to perform the alternative task (incongruent trials), there was increased activity in the network associated with this task, and decreased activity in the consciously cued task set. Moreover, they observed a main effect of congruency in medial frontal cortex (bordering the paracingulate gyrus and the pre-SMA), indicating that the congruency effect was similar for conscious and unconscious primes. These fMRI results fit nicely with the present VBM findings, in the sense that medial frontal cortex (including the pre-SMA) seems to process conflicting information irrespective of whether it is perceived consciously or unconsciously.

Instead of studying the immediate effects of unconscious conflict-inducing stimuli, Wolbers et al. (2006) studied the strategic control over interfering unconscious information using fMRI. To this end, they varied the number of congruent and incongruent trials in a masked priming block. Behaviorally, strategic effects consisted of longer RTs and fewer errors across incongruent blocks (containing more incongruent trials than congruent trials) compared to congruent blocks (containing fewer incongruent trials than congruent trials), indicative of a changed speed/accuracy balance according to the number of unconsciously presented distractors. The pre-SMA was more active during incongruent than congruent blocks and psychophysiological interaction analyses demonstrated a tight coupling between the pre-SMA and both the putamen and the lateral occipital complex (LOC) on incongruent blocks. The authors concluded that the pre-SMA might have an overarching role in controlling the processing of unconscious primes by modulating perceptual analysis (LOC) and response selection (putamen) during conflict. Although such strategic effects differ slightly from the immediate control operations studied here, the results nicely converge on the role of the pre-SMA in selecting relevant information over irrelevant unconscious distractors. However, here we show that individual differences in structural, instead of functional, properties of the pre-SMA predict individual differences in the ability to overcome (virtually) unconscious response conflict.

Positive vs. Negative Priming

Behavioral studies have demonstrated that masked primes initially facilitate responses (as observed here), but somewhat later, when the delay between prime and target is increased (>100 msec), are followed by inhibition of these responses (Eimer & Schlaghecken, 1998). Although the exact cause of this effect is controversial (Lleras & Enns, 2004; Verleger, Jaskowski, Aydemir, van der Lubbe, & Groen, 2004), it seems that it is (at least partly) caused by an automatic and unconscious process of self-inhibition (Schlaghecken & Eimer, 2006; Klapp, 2005). Recently, Sumner et al. (2007) showed that a patient with a highly specific SMA lesion did not show automatic inhibition of unconscious primes in a manual version of a masked priming task. Interestingly, a patient with a large lesion including the pre-SMA still showed normal automatic inhibition effects, which suggests that the pre-SMA is not necessary for such automatic (unconscious) forms of motor inhibition. In combination with the present results, this suggests that the supplementary motor areas (SMA/pre-SMA) play a key role in voluntary action selection by suppressing irrelevant or premature response tendencies that have been primed unconsciously. However, both areas might contribute differently to this process, which is in line with recent theoretical accounts that have proposed that the SMA is primarily involved in automatic (unconscious) forms of motor control, whereas the pre-SMA might be crucial for more complex higher-level control processes that are experienced as difficult, effortful, and voluntary (Botvinick, Cohen, & Carter, 2004; Lau et al., 2004; Rushworth, Hadland, Paus, & Sipila, 2002).

Conclusion

We report that individual differences in the ability to select the correct action in the face of distracting alternatives are accompanied by structural differences in pre-SMA gray-matter anatomy. Thereby, these results link structural anatomy to cognitive control ability, and extend recent functional imaging and electrophysiological evidence for the role of the pre-SMA in selecting the appropriate action in situations of response conflict, even when conflicting response tendencies are triggered automatically and unconsciously.

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