Electrophysiological correlates of block-wise strategic adaptations to consciously and unconsciously triggered conflict

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ABSTRACT

The role of consciousness in conflict adaptation has been a topic of much debate. The purpose of the current study was to investigate the neural correlates of block-wise conflict adaptations elicited by conscious and unconscious conflicting stimuli in a meta-contrast masked priming task. Event-related potentials (ERPs) were recorded while individuals responded to prime-target pairs in mostly congruent (80% congruent trials, 20% incongruent trials) and mostly incongruent blocks of trials (20% congruent trials, 80% incongruent trials). Mean response times and error rates revealed that the conflict effect (incongruent trials–congruent trials) was reduced in mostly incongruent blocks relative to mostly congruent blocks. Furthermore, conflict related ERP signals (the amplitude difference between congruent and incongruent trials) for three ERP components (early occipito-parietal negativity, the fronto-central N2 and the centro-parietal P3) were attenuated in mostly incongruent blocks compared to mostly congruent blocks, reflecting block-wise adaptation to the frequency of conflict. The conflict-related frontal N2 component differentiated most strongly between visibility conditions. These results further specify the electrophysiological correlates of block-wise strategic adaptations to consciously and unconsciously elicited conflict.

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1. Introduction

Cognitive control is an umbrella term that refers to the ability to organize thoughts and actions to accomplish or optimize goal-directed behaviors, including flexibly selecting task-relevant information and initiating, monitoring and adjusting actions (Clayson & Larson, 2011; for reviews see Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). There is a long-lasting debate on the necessity and role of consciousness for cognitive control (for reviews see Desender & Van Den Bussche, 2012; Kunde, Reuss, & Kiesel, 2012; van Gaal, De Lange, & Cohen, 2012), although recent studies suggest that at least some forms of cognitive control, such as response inhibition (Hughes, Velmans, & De Fockert, 2009; van Gaal, Lamme, Fahrenfort, & Ridderinkhof, 2011; van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008; van Gaal, Ridderinkhof, Scholte, & Lamme, 2010) and task-switching (Lau & Passingham, 2007; Reuss, Kiesel, Kunde, & Hommel, 2011) can be influenced unconsciously. In the domain of conflict control, two types of conflict adaptation have been identified:

trial-by-trial adaptations to conflict and block-wise conflict adaptations, also referred to as micro- and macro-adjustment respectively (Ridderinkhof, 2002b). Here, we will address a simple question: What are the behavioral and electrophysiological correlates of block-wise adaptations to consciously and unconsciously elicited conflict?

Previous studies have convincingly demonstrated that unconsciously presented conflict-inducing stimuli can delay responses to subsequent target stimuli and lead individuals to make more errors when the prime-target pairs are incongruent than when they are congruent, a phenomenon also referred to as the congruency or conflict effect (Desender, Van Lierde, & Van den Bussche, 2013; Francken, Gaal, & de Lange, 2011; Jaśkowski, Skalska, & Verleger, 2003; Kunde, 2003; for a review see Van den Bussche, Van den Noortgate, & Reynvoet, 2009; van Gaal, Lamme, & Ridderinkhof, 2010; Wolbers et al. 2006). Interestingly, the magnitude of the congruency effect varies depending on the proportion of congruent and incongruent prime-target pairs within an experimental block, in some reported cases even if the conflict-inducing prime stimuli remain undetected (Bodner & Masson, 2001; Bodner & Mulji, 2010; for a review see Desender & Van Den Bussche, 2012; Jaśkowski et al., 2003; Klapp, 2007; Wolbers et al., 2006). That is, the congruency effect is smaller in blocks with a high proportion of incongruent trials than in blocks

with a low proportion of incongruent trials. For example, Jaśkowski et al. (2003) found that in blocks in which the prime was masked the conflict effect decreased when the proportion of incongruent trials was 80% compared with when it was 20% (see Bodner & Mulji, 2010; Klapp, 2007; Wolbers et al., 2006 for similar results).

A number of studies have been performed on conscious block-wise conflict adaptation effects, using various paradigms, such as Eriksen flanker task (e.g. Gratton, Coles, & Donchin, 1992; Purmann, Badde, Luna-Rodriguez, & Wendt, 2011; Purmann, Badde, & Wendt, 2009), the Stroop task (e.g. Carter et al., 2000; Fernandez-Duque & Knight, 2008; West & Bailey, 2012) and the Simon task (e.g. Stürmer, Leuthold, Soetens, Schroter, & Sommer, 2002). In such conflict studies, several ERP effects have been observed that might reflect conflict processing/ monitoring, with different latencies and scalp distributions. Most prominently, the fronto-central N2 is generally larger for conflict (incongruent) trials compared to no-conflict (congruent) trial (Van Veen & Carter, 2002). The N2 is a negative deflection in the ERP peaking approximately 200–400 ms (Folstein & Van Petten, 2008) after conflict processing and previous source reconstruction suggests that it's neural generator is located in the medial frontal cortex, most likely the anterior cingulate cortex (ACC) (for a review see Ridderinkhof et al., 2004). The N2 is typically associated with conflict monitoring/resolution or inhibition of the incorrectly activated response (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Van Veen & Carter, 2002; Yeung & Cohen, 2006). Further, often, a more centro-parietal and spatially broader P3 component, a positive deflection peaking approximately 300–500 ms after the stimulus (Desender & Van Den Bussche, 2012; Purmann et al., 2011), is also observed during the processing of conflict. The specific functional significance of this component is less clear and it has been suggested to reflect processes such as response inhibition, error monitoring, and response evaluation (Clayson & Larson, 2011; Polich, 2007). Finally, relatively early sensory differences have also been observed when comparing conflict and no-conflict trials. These results are interpreted as being related to the increased attentional demands during conflict processing (Abrahamse, Duthoo, Notebaert, & Risko, 2013; Johnstone, Barry, Markovska, Dimoska, & Clarke, 2009; van Gaal et al., 2011).

With respect to block-wise adaptations to the frequency of conflict, Purmann et al. (2011) recently observed that the fronto-central N2 ERP component was larger, and the latency of the more central P3 ERP component later, in incongruent than in congruent

trials. More interestingly, both effects were reduced when conflict was frequently experienced compared to when it was infrequently experienced. Wolbers et al. (2006) also explored the underlying brain mechanism of strategic block-wise behavioral adaptations and the relation to conscious awareness of conflict-inducing stimuli using fMRI. They observed that the pre-SMA was more active in high conflict blocks (80% incongruent) than in low conflict blocks (20% incongruent). Further, psychophysiological interaction analyses demonstrated a stronger coupling between the pre-SMA and the putamen, and the Pre-SMA and the lateral occipital complex (LOC), in frequent conflict blocks compared to infrequent conflict blocks. This have led the authors to conclude 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 block-wise conflict adaptation.

To further examine the neural correlates of block-wise conflict adaptation effects and the role of consciousness therein, we measured ERPs in a typical arrow version of the meta-contrast masking paradigm. In this task, a briefly presented prime arrow was presented, which was followed after a short delay (29 ms) by a meta-contrast target arrow (129 ms) upon which participants had to make a left/right decision (Fig. 1A). When the duration of the prime was sufficiently short, the briefly presented prime arrow was strongly masked by the target arrow. However, when the prime was presented for a longer duration (129 ms) prime visibility was much higher. The proportion of incongruent and congruent trials was manipulated in a block-wise manner. In mostly congruent blocks, 80% of the trials were congruent and 20% incongruent, while in the mostly incongruent blocks the proportions were reversed.

Based on these previous studies, we hypothesized that block-wise conflict manipulations would directly impact the conflict effect in behavior and EEG. Behaviorally, we expected the conflict effect (incongruent trials–congruent trials) to be smaller (for RTs as well as errors) in frequent conflict blocks compared to infrequent conflict blocks (Jaśkowski et al., 2003; Purmann et al., 2011; Wolbers et al., 2006). Further, block-wise conflict manipulations would potentially be reflected in three ERP modulations evolving across time: an early sensory event, a somewhat later fronto-central N2 and finally a centro-parietal P3 modulation (Abrahamse et al., 2013; Bartholow, Riordan, Saults, & Lust, 2009; Jaśkowski et al., 2003; Purmann et al., 2011; van Gaal et al., 2011). More specifically, we predicted that the conflict effect for these components would be smaller under mostly
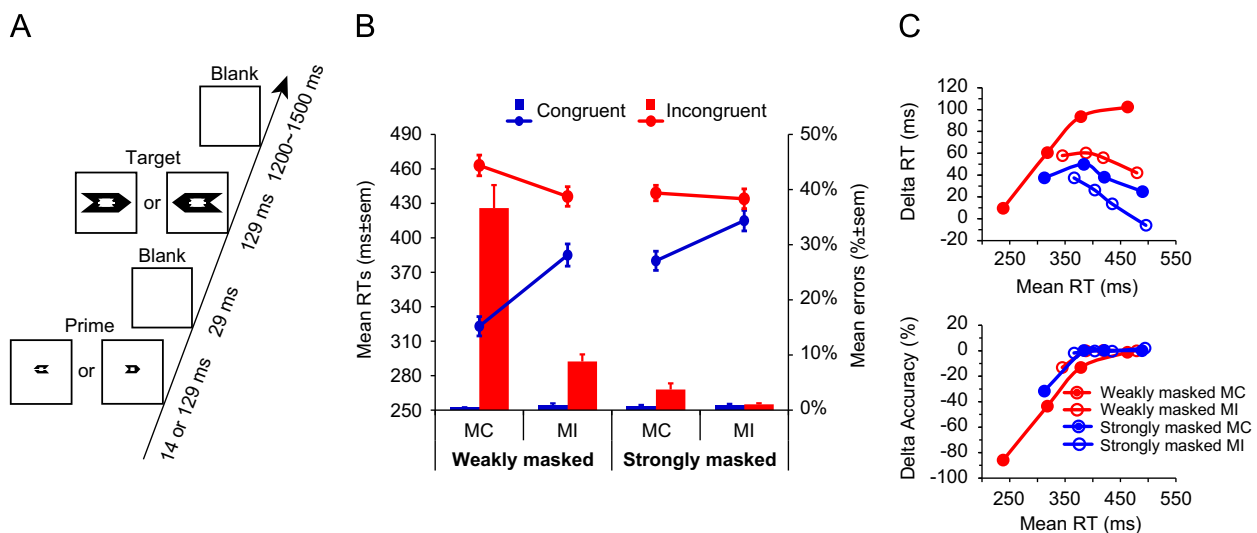

Fig. 1. Experimental design and behavioral results. (A) Schematic representation of the experimental procedure and event timing. (B) Mean response times and error rates for congruent and incongruent trials in mostly congruent (infrequent) blocks and mostly incongruent (frequent) blocks under weakly masked and strongly masked conditions. (C) The delta plots (upper panel) and CAFs plots (lower panel) for the different conflict frequency blocks, separated by masking strength. Bar graphs represent the mean error rates in each experimental condition. MC=mostly congruent blocks; MI=mostly congruent blocks; error bars represent the standard error of the mean (± SEM).

incongruent (MI) blocks than under mostly congruent (MC) blocks, regardless of whether the primes were strongly or weakly masked. A direct comparison between visibility conditions also allows us to explore whether conflict awareness modulates one of these ERP components more than others (Del Cul, Baillet, & Dehaene, 2007; Holcomb, Reder, Misra, & Grainger, 2005; Jaskowski, van der Lubbe, Schlotterbeck, & Verleger, 2002; van Gaal et al., 2011; Verleger & Jaskowski, 2007; Yun et al., 2011).

2. Materials and methods

2.1. Participants

In this experiment, 22 undergraduate students (15 females) aged between 20 and 22 ($M = 20.67$, $SD = 1.15$) from Southwest University participated for monetary compensation. All participants were right-handed with normal or corrected-to-normal vision, and had no history of head injury or physical and mental illness. This study was approved by the local ethics committee of Southwest University, and written informed consent was obtained from all participants after the explanation of the experimental protocol.

2.2. Apparatus and stimuli

Stimuli were presented against a gray background at the center of a 17-inch View-Sonic CRT monitor (frequency 70 Hz, resolution 1024 × 768) with the E-prime 1.1 software package (Psychology Software Tools, Pittsburgh, PA). Participants were seated 70 cm away from the computer screen. An arrow version of the meta-contrast priming task, similar to Kiesel et al., 2006 was used. The left and right arrows (subtended a visual angle of 0.98° × 0.49°) served as primes, and the somewhat larger left and right arrows (visual angle of 2.87° × 1.23°) served as targets (see Fig. 1A). The primes fitted exactly within the inner contour of the target.

2.3. Design and behavioral procedures

Based on the prime and target correspondence, trials were categorized as either being congruent or incongruent. Two types of blocks were included in this study. MC blocks consisted of 80% congruent trials and 20% incongruent trials, whereas MI blocks consisted of 20% congruent trials and 80% incongruent trials (Wolbers et al., 2006). The stimulus presentation was as follows: First, the prime stimulus appeared for 14 ms (strongly masked) or for 129 ms (weakly masked), which was followed by a blank screen for 29 ms. Then the target stimulus was presented for 129 ms. Finally, a post-target blank screen was presented for a variable duration between 1200 and 1500 ms (see Fig. 1A). Thus, in half of the trials the prime was strongly masked, and in the other half they were weakly masked. Participants were instructed to ignore the prime and to respond to the direction of the target as quickly and accurately as possible by pressing a key on the standard QWERTY keyboard (left target: press "F" with the left index finger; right target: press "J" with the right index finger).

Before the actual experiment, participants performed one practice block with 24 full-feedback trials, in which the mean RT and percentage correct was displayed on the computer screen after each trial. Thereafter, they performed 10 experimental blocks of 120 trials each. To examine the visibility of the primes, three force-choice discrimination blocks were performed at the end of the experiment. These blocks had the same sequence and timing events with the exception that in each trial a screen was inserted after the target to ask the participants to discriminate the direction of the prime arrow. To exclude the possibility that the participants discriminate the prime arrow direction only based on the target arrow direction, the target arrow was replaced by a neutral arrow, which was made by overlapping the left and right target arrows. The ratio of left vs. right pointing prime arrows was 1:1 in all three discrimination blocks. All trials were presented randomly, and the strongly and weakly masked trials were mixed in each block in the EEG experiment as well as the discrimination task.

2.4. Behavioral data analysis

Incorrect trials and correct trials of RTs < 100 and > 1000 were excluded from all analyses. Repeated measures ANOVAs were performed using the mean RTs on correct trials and mean error rates under strongly and weakly masked conditions with block type (MC vs. MI) and congruency (congruent vs. incongruent) as within-subject variables. A one sample t-test on d' was used to analyze the prime visibility (Bodner & Mulji, 2010; Desender et al., 2013; Hughes et al., 2009). A two-tailed significance level of 0.05 was used for all statistical tests.

To further explore whether interference control varied as a function of response time, delta plots (RT) and conditional accuracy functions (CAFs) were calculated (Burle, Possamaï, Vidal, Bonnet, & Hasbroucq, 2002; Ridderinkhof, 2002a; Wylie, Ridderinkhof, Bashore, & van den Wildenberg, 2010). For these analyses, miss trials (without a response) were excluded. For delta plots, RTs of correct and incorrect trials were rank-ordered for each condition and then divided into four bins (quintiles) with equal numbers of trials. Next the mean RT of each RT bin was calculated (Ridderinkhof, 2002a). Delta plots for the conflict effect (incongruent–congruent) were then plotted (Fig. 1C). The slopes of the delta values provide a measure of the conflict effect across the RT distribution. In the activation–suppression model the build-up of suppression should be maximal at the slow end of the RT distribution. Therefore, we focused our analysis on the slope connecting the slowest two RT bins (for discussions of the rationale for this choice, see Forstmann et al., 2008; Ridderinkhof, 2002a; Wylie et al., 2010). For the CAFs, all trials (correct and incorrect) were included, rank-ordered for each condition, divided into four bins with equal numbers, and then corresponding accuracy of each RT-bin was calculated. The strength of automatic response activation is inferred from the pattern of fast errors present at the fastest two RT bins (first slope of the CAF function). Stronger initial response capture is associated with a higher percentage of fast errors (Ridderinkhof, 2002a).

2.5. EEG measurements and analysis

Participants were seated in a dimly lit and electrically shielded room and were instructed to avoid eye blinks and movements during stimulus presentation. EEG activity was recorded from 64 scalp sites using tin electrodes mounted in an elastic cap (Brain Products, Munich, Germany) with the references on FCz and a ground electrode on AFz. The vertical electro-oculogram (EOG) was recorded from an electrode below the right eye. The horizontal EOG was collected from an electrode located at the outer canthus of the right eye. EEG and EOG signals were filtered using a 0.01–100 Hz band-pass and continuously sampled at 500 Hz/channel for off-line analysis. All electrode impedance was kept below 5 kΩ by careful preparation.

All analyses were conducted offline in MATLAB (R2009a, The MathWorks, Inc.) using in-house written MATLAB scripts supported by EEGLAB (Delorme & Makeig, 2004), an open source software package. Continuous EEG data were re-referenced offline to the average of the activity recorded at the left and right mastoids, and then were digitally filtered with band-pass between 0.5 and 20 Hz (van Gaal et al., 2011). The ERP epoch included −200 to 800 ms of data around target onset, including a −200 to 0 ms baseline. Following removal of trials with erroneous responses, two artifact rejection methods were used: (a) epochs with data deviating more than 5SD from the mean probability distribution were excluded, and (b) independent component analysis (ICA) was computed to isolate artifacts contained in the EEG signal (Danielmeier, Wessel, Steinhauser, & Ullsperger, 2009). With the EEGLAB plugin ADJUST (Mognon, Jovicich, Bruzzone, & Buiatti, 2011), ICs representing eye blinks, eye movements, muscle artifacts, or other types of noise were rejected from the signal (Delorme, Sejnowski, & Makeig, 2007). Finally, grand averages were obtained for each subject and relevant conditions. The mean number of trials before and after trial rejection for all conditions are presented in the supplementary Table 1.

To improve signal-to-noise ratio and based on previous literature and visual inspection of the topography of the components of interest (Bartholow et al., 2009; Del Cul et al., 2007; Holcomb et al., 2005; Jaśkowski et al., 2003; Jaskowski et al., 2002; Purmann et al., 2011; van Gaal et al., 2011; Verleger & Jaskowski, 2007; Wolbers et al., 2006; Yun et al., 2011), three spatial regions of interest (ROI) were created: (1) an occipito-parietal ROI for the early component, including electrodes O1, O2, PO3, PO4, PO7, PO8, P5, P6, (2) a fronto-central ROI for the N2 component, including electrodes Fz, F1, F2, FCz, FC1, FC2, Cz, C1, C2, and (3) a centro-parietal ROI for the P3 component, including electrodes Cz, C1, C2, CPz, CP1, CP2, Pz, P1, P2) (van Gaal et al., 2011).

First, to examine the conflict effect in MC and MI blocks during weakly masked and strongly masked conditions, difference waves were calculated by subtracting congruent trials from incongruent trials. We focused our analysis on the three previously defined ERP components and specifically tested each of them at their corresponding ROI. Sample-by-sample t-tests (two-tailed) were performed on the difference wave (incongruent–congruent) to calculate the precise time frame at which each component differed significantly from zero (van Gaal et al., 2011, 2008). The time-windows of significance were defined by all bordering significant samples (Figs. 2 and 3B and C) for each component.

To establish the time frame at which each conflict-related component was modulated by block type (conflict-frequency) sample-by-sample paired t-tests (two-tailed) were conducted on the difference wave of mostly congruent blocks and on the difference wave of mostly incongruent blocks, separately for weakly masked and strongly masked conditions (Figs. 2 and 3D). For this analysis, time-windows for analysis were restricted to all significant samples of B and C together, for each component and visibility condition separately.

Finally, to compare the three ERP effects between the strongly and weakly masked conditions (Fig. 4), we extracted the effect per ERP event per subject (the effect highlighted in Figs. 2 and 3D, mostly congruent blocks difference wave—mostly incongruent blocks difference wave) and compared those directly between visibility conditions. Although the time at which the components peaked might differ slightly between visibility conditions due to task timing parameters (SOA between prime and target), these effects could still be reliably compared in this manner (e.g., the effects had a very similar spatial profile).

Generally, we only highlighted the significant effects for the spatial ROI (in Figs. 2 and 3B–D) at which the ERP effect (component) peaked, although some effects might have been significant at a different (overlapping) spatial ROI as well.
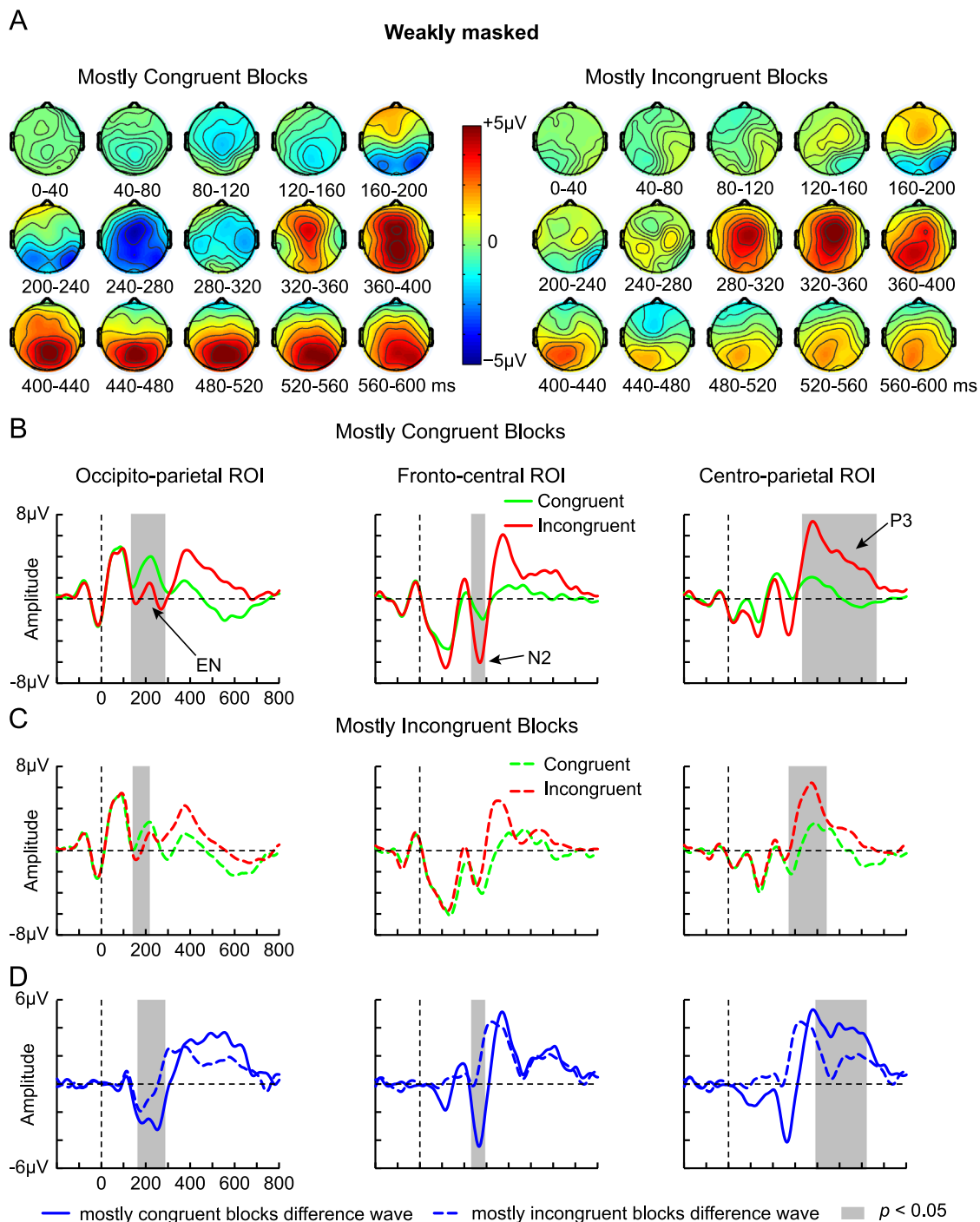
Fig. 2. Time course of activity associated with block-wise strategic adaptations to consciously triggered conflict. (A) The difference scalp spatial distribution: mostly congruent blocks are depicted in the left panel, mostly incongruent blocks are depicted in the right panel. (B) The ERP waves in mostly congruent blocks and in mostly incongruent blocks (C). (D) The difference waves (incongruent–congruent) in mostly congruent and mostly incongruent blocks. The gray shadowed areas highlight the significant time-windows ($p < 0.05$) for each component (early negativity (EN), N2, P3), specifically tested at the ROI at which the component peaked.

3. Results

3.1. Behavioral frequency modulations

For weakly masked trials, the analysis of RTs revealed a main effect of block type ($F_{1,21} = 20.21$, $p < 0.001$, $\eta_p^2 = 0.49$), and congruency ($F_{1,21} = 229.49$, $p < 0.001$, $\eta_p^2 = 0.92$), as well as an interaction between block type and congruency ($F_{1,21} = 175.87$, $p < 0.001$, $\eta_p^2 = 0.89$). The interaction reflects that the conflict effect was significantly larger during MC blocks ($M = 139$ ms,

$SE = 7.50$) than during MI blocks ($M = 51$ ms, $SE = 6.62$; $t_{21} = 13.23$, $p = 0.018$). Similar results were obtained for errors. There was a main effect of block type ($F_{1,21} = 66.61$, $p < 0.001$, $\eta_p^2 = 0.76$) and congruency ($F_{1,21} = 73.93$, $p < 0.001$, $\eta_p^2 = 0.78$) and an interaction between block type and congruency ($F_{1,21} = 66.95$, $p < 0.001$, $\eta_p^2 = 0.76$), reflecting that the conflict effect for errors was larger in the MC blocks than in the MI blocks ($t_{21} = 8.18$, $p < 0.001$, see Fig. 1B).

For strongly masked trials, the analysis of RTs revealed a main effects of block type ($F_{1,21} = 18.72$, $p < 0.001$, $\eta_p^2 = 0.47$), and
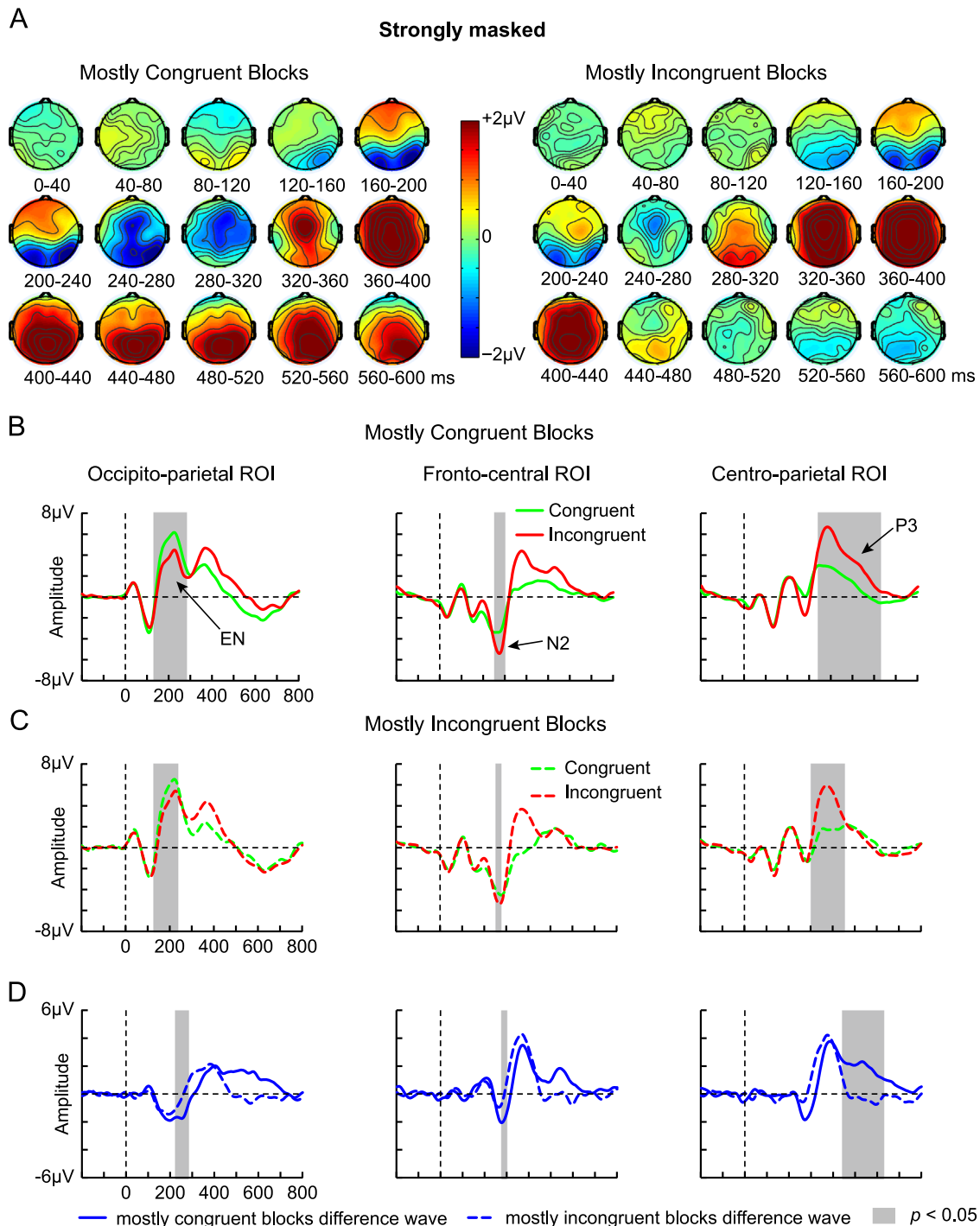
Fig. 3. Time course of activity associated with block-wise strategic adaptations to unconsciously triggered conflict. (A) The difference scalp spatial distribution: mostly congruent blocks are depicted in the left panel, and mostly incongruent blocks are depicted in the right panel. (B) The ERP waves in mostly congruent blocks and in mostly incongruent blocks (C). (D) The difference waves (incongruent–congruent) in mostly congruent and mostly incongruent blocks. The gray shadowed areas highlight the significant time-windows ($p < 0.05$) for each component (early negativity (EN), N2, P3), specifically tested at the ROI at which the component peaked.

congruency ($F_{1,21} = 124.80$, $p < 0.001$, $\eta_p^2 = 0.86$), as well as a block type × congruency interaction ($F_{1,21} = 72.26$, $p < 0.001$, $\eta_p^2 = 0.78$). The latter effect reflects that the conflict effect was larger for MC blocks ($M = 59$ ms, $SE = 4.82$) than MI blocks ($M = 19$ ms, $SE = 3.42$; $t_{21} = 8.48$, $p < 0.001$). Again, similar effects were observed for the error rates. The main effects of block type ($F_{1,21} = 18.72$, $p < 0.001$, $\eta_p^2 = 0.22$), and congruency ($F_{1,21} = 8.10$, $p = 0.010$, $\eta_p^2 = 0.29$), as well the block type × congruency interaction ($F(1,21) = 6.54$, $p = 0.018$, $\eta_p^2 = 0.24$) were significant. Error rates for congruent and incongruent trials did not differ significantly in the MI block

($t_{21} = 0.66$, $p = 0.518$), while error rates for incongruent trials were much higher than congruent trials in the MC blocks ($t_{21} = 2.79$, $p = 0.011$, see Fig. 1B).

An ANOVA incorporation the factor Masking condition revealed that strategic block-wise conflict adaptations (3-way interaction between Block type, Congruency and Masking condition) were greater for weakly masked primes than for strongly masked primes, both for RTs ($F_{1,21} = 58.14$, $p = 0.001$, $\eta_p^2 = 0.735$), as well as error rates ($F_{1,21} = 61.47$, $p = 0.001$, $\eta_p^2 = 0.745$).
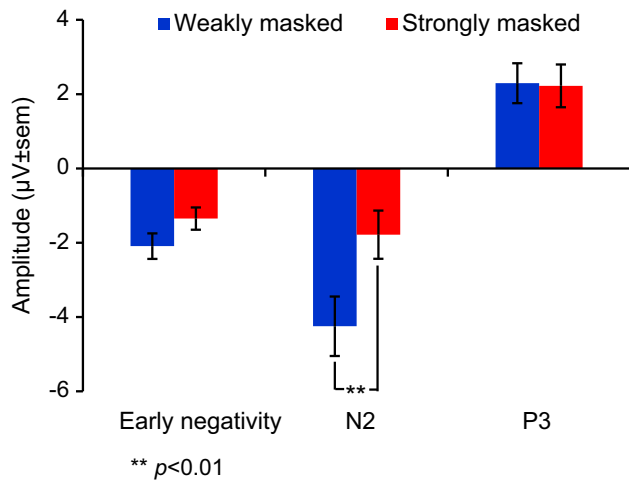
Fig. 4. Strategic block-wise conflict adaptations for all three ERP events for weakly and strongly masked conditions. Error bars represent the standard error of the mean ($\pm$ SEM).

3.2. RT delta plots and conditional accuracy functions

To further explore whether interference control varied as a function of response time, delta plots (RT) and conditional accuracy functions (CAFs) were calculated (Burle et al., 2002; Ridderinkhof, 2002a; Wylie et al., 2010). The slopes of the delta values (Fig. 1C, upper panel) provide a measure of the conflict effect (incongruent RT—congruent RT) across the RT distribution. In the activation–suppression model the build-up of suppression should be maximal at the slow end of the RT distribution. The delta plots show the typical RT conflict profile and the last slope differed significantly between MC blocks and MI blocks in weakly ($t_{21} = 4.01$, $p < 0.001$) and strongly ($t_{21} = -5.11$, $p < 0.001$) masked conditions. This indicates that selective suppression was stronger when conflict was more frequent, for both visibility conditions. Further, an ANOVA on the last slope with Masking condition and Block type as within-subject variables revealed a significant interaction ($F_{1,21} = 22.11$, $p < 0.001$, $\eta_p^2 = 0.51$), indicating that the difference in slopes between frequent and infrequent conflict blocks was larger in the weakly masked condition than in the strongly masked condition.

The strength of automatic response activation is inferred from the pattern of errors present at the fastest two RT bins (reflected in the first slope of the CAF function). Stronger response capture is associated with a higher percentage of fast errors (Ridderinkhof, 2002a), as can be observed in Fig. 1C (lower panel). For the CAFs plot, as illustrated in the right panel of Fig. 1C, the first slope differed significantly between MC blocks and MI blocks in strongly ($t_{21} = 2.31$, $p < 0.05$) masked condition, but not for the weakly masked ($t < 1$) masked condition. An ANOVA on the first slope with Masking condition and Block type revealed no significant interaction between them ($F < 1$).

3.3. Electrophysiological frequency modulation effect under weakly masked condition

The difference scalp maps (incongruent trials–congruent trials) for MC blocks (left panel) and MI blocks (right panel) are shown in Fig. 2A. As expected, we observed three ERP components that had different peak times and different spatial properties (see Section 2). In MC blocks, the occipito-parietal early negative event was modulated by conflict between 138 and 284 ms (peak difference = 3.26 µV, peak latency = 250 ms, $t_{21} = -8.36$, $p < 0.001$ across whole significant time-window). Thereafter, at the fronto-central ROI, the amplitude of the N2 was also significantly modulated by conflict (peak difference = 4.46 µV, peak latency = 266 ms, $p < 0.05$ between 232 and 288 ms, $t_{21} = -4.65$,

$p < 0.001$ across whole significant time-window) and at the centro-parietal ROI, a similar conflict effect was observed for the P3 (peak difference = 5.30 µV, peak latency = 380 ms, $p < 0.05$ between 332 and 658 ms, $t_{21} = 5.64$, $p < 0.001$ across whole significant time-window, see Fig. 2B). For MI blocks we observed a similar effect at the occipito-parietal ROI (peak difference = 1.94 µV, peak latency = 176 ms, $t_{21} = -4.57$, $p < 0.001$, between 146 and 214 ms). However, at the fronto-central ROI the N2 was not significantly modulated by conflict between 232 and 288 ms ($t_{21} = 1.04$, $p = 0.309$), but the centro-parietal P3 was (peak difference = 4.43 µV, peak latency = 324 ms, $t_{21} = 6.52$, $p < 0.001$, between 272 and 434 ms, see Fig. 2C).

Next, we tested the effect of conflict frequency for these three ERP events. For all events we tested the exact time-frame of significant difference using sample-by-sample t-tests on the difference waves (obtained from Fig. 2B and C). All three events were significantly modulated by conflict frequency (block type, see Fig. 2D). For the early occipito-parietal event, congruency was significantly modulated by block type between 168 and 284 ms ($t_{21} = -6.09$, $p < 0.001$), for the N2 between 234 and 288 ms ($t_{21} = -5.31$, $p < 0.001$) and for the P3 between 392 and 614 ms ($t_{21} = 4.27$, $p < 0.001$). These interactions reflect that the size of all three conflict-related ERP effects in MC blocks was significantly larger than in MI blocks.

3.4. Electrophysiological frequency modulation effect under strongly masked condition

The difference scalp maps (incongruent trials–congruent trials) in MC blocks (left panel) and in MI blocks (right panel) are shown in Fig. 3A. We observed the same three ERP events as in the weakly masked condition. For MC blocks, the occipito-parietal early negative event was modulated by conflict between 134 and 280 ms (peak difference = 1.90 µV, peak latency = 198 ms, $t_{21} = -7.03$, $p < 0.001$). Thereafter, the amplitude of fronto-central N2 was significantly modulated by conflict (peak difference = 2.06 µV, peak latency = 276 ms, $t_{21} = -3.10$, $p < 0.001$) between 254 and 296 ms. Finally, at the centro-parietal ROI the P3 amplitude of incongruent trials were significant larger than for congruent trials (peak difference = 3.77 µV, peak latency = 384 ms, $t_{21} = 4.95$, $p < 0.001$) between 342 and 624 ms (see Fig. 3B).

For MI blocks, we observed a similar effect of conflict at the occipito-parietal ROI (peak difference = 1.46 µV, peak latency = 194 ms, $t_{21} = -6.84$, $p < 0.001$) between 130 and 234 ms. At the fronto-central ROI, the N2 amplitude of incongruent trials was significantly larger than of congruent trials between 254 and 272 ms (peak difference = 0.96 µV, peak latency = 264 ms, $t_{21} = -3.08$, $p < 0.001$). At the centro-parietal ROI, the P3 of incongruent trials was significantly larger than on congruent trials (peak difference = 4.23 µV, peak latency = 374 ms, $t_{21} = 3.83$, $p < 0.001$) between 302 and 448 ms (see Fig. 3C).

Next, we tested the difference between blocks for these three ERP events. For the early occipito-parietal event, congruency was significantly modulated by block type between 226 and 280 ms ($t_{21} = -4.51$, $p < 0.001$). For the N2, this was the case between 278 and 296 ms ($t_{21} = -2.75$, $p = 0.012$) and for the P3, congruency was modulated by block type between 442 and 624 ms ($t_{21} = 3.86$, $p < 0.001$). Similar to the weakly masked condition, this reflects that the conflict effect for all ERP events was modulated by the frequency of conflict (block type, see Fig. 3D).

3.5. Comparing conflict adaptations between weakly and strongly masked conditions

To compare the difference of the block-wise conflict adaptation between weakly and strongly masked conditions, the mean block-wise conflict adaptation effect (the significant difference shown in Figs. 2 and 3D) were compared directly between both visibility conditions (reflecting an interaction between congruency, block

type and masking strength). For the negative early event, the block-wise conflict adaptation effect in the weakly masked condition ($M = -4.25\ \mu V$, $SE = 0.80$) was not significantly different than in strongly masked condition, although a trend was observed ($M = -1.78\ \mu V$, $SE = 0.65$; $t_{21} = -1.92$, $p = 0.069$). Similar results were obtained for the P3, observed at the centro-parietal ROI: there was no significant difference between weakly masked ($M = 2.30\ \mu V$, $SE = 0.54$) and strongly masked conditions ($M = 2.22\ \mu V$, $SE = 0.58$; $t_{21} = 0.125$, $p = 0.902$). However, most importantly, for the frontal N2, the block-wise conflict adaptation effect in the weakly masked condition ($M = -2.09\ \mu V$, $SE = 0.34$) was significantly larger than in strongly masked condition ($M = -1.35\ \mu V$, $SE = 0.30$; $t_{21} = -3.45$, $p = 0.002$, see Fig. 4).

3.6. Prime visibility

As expected, prime discrimination was high in the weakly masked condition ($d' = 2.01$) and much lower in the strongly masked condition ($d' = 0.34$), and differed significantly between masking conditions ($t_{21} = 5.24$, $p < 0.001$). Although prime visibility was low in the strongly masked condition, it was significantly different from zero ($t_{21} = 2.30$, $p = 0.032$). There are several reasons to assume that prime visibility did not cause the reported effects, however. First, Spearman's rank correlations showed that discrimination performance did not correlate with the observed behavioral conflict effects in the mostly congruent blocks (RT: rho = 0.03, $p = 0.893$, ER: rho = 0.38, $p = 0.084$) or the mostly incongruent blocks (RT: rho = -0.16, $p = 0.487$, ER: rho = -0.14, $p = 0.549$). Further, there were no correlations between d' and the observed EEG results: none of the three ERP components correlated with prime visibility (smallest $p = 0.098$). Finally, it has been demonstrated that prime discrimination is higher with neutral meta-contrast masks than with arrow masks (e.g. Francken et al., 2011; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). Because we used a neutral mask for the discrimination task, but arrow masks in the experimental blocks, we have possibly, if anything, overestimated the visibility of the primes. To rule out the possibility that the results may be caused by some subjects who show above chance performance in discrimination task we further performed a median-split on our subject group (high d' group vs. low d' group) and compared both groups directly. Both groups had similar block-wise conflict adaptation effects, for RTs ($t_{10} = 0.179$, $p = 0.862$) as well as error rates ($t_{10} = 0.081$, $p = 0.937$). Together,, it seems that the reported effects are not due to visibility of the strongly masked primes (Bodner & Mulji, 2010; Kiesel et al., 2006).

4. Discussion

The current study was designed to examine the electrophysiological correlates of block-wise strategic adaptations to consciously and unconsciously triggered conflict in a meta-contrast masking paradigm. The conflict effect, reflected by slower RTs and greater error rates for incongruent than congruent trials, was significantly larger in blocks with mostly congruent trials compared to blocks with mostly incongruent trials, replicating previous findings (Bodner & Mulji, 2010; Klapp, 2007; Wolbers et al., 2006). RT-distributional analyses showed that the selective suppression induced by conflicting stimuli was stronger when conflict was frequent than when it was infrequent (Ridderinkhof, 2002a).

EEG recordings revealed that three ERP components were significantly modulated by block-wise conflict frequency in the current study: an early occipital–parietal event, the fronto-central N2 component, and the centro-parietal P3 component. The conflict-related difference (incongruent trials–congruent trials) of all these events was greatly reduced in MI blocks compared to MC blocks. This pattern of results is consistent with the conflict monitoring theory (Botvinick

et al., 2001), which predicts that the difference between congruent and incongruent trials should be less pronounced in conditions of high overall conflict (Kerns et al., 2004).

Although speculative, the block-wise strategic adaptations observed to unconscious and conscious conflict in the current study may be explained by the allocation of additional top-down attentional resources in the mostly incongruent blocks (Abrahamse et al., 2013; Bartholow et al., 2009; Wolbers et al., 2006). The reduced conflict effect of the early sensory component in mostly incongruent blocks may suggest that participants narrow their attentional focus on the target specifically, in order to reduce conflict from processing the prime. To better prevent or resolve conflict, the amount of (temporal) attention to the target may be increased when conflict is frequently experienced. This explanation is consistent with other work (Wolbers et al., 2006) that showed that adaptation to frequent conflict is related to increased connectivity between medial-frontal cortex (specifically the pre-SMA) and the lateral occipital complex (as well as the putamen).

Although we observed block-wise adaptations in blocks with a high proportion of conflict-inducing primes in both the behavioral and ERPs results, it is worth noting that there were differences between the conscious and unconscious conditions. The N2 component was most strongly and consistently associated with differences between conscious and unconscious conflict effects depending on the block-wise conflict manipulation (Fig. 4). This is interesting because this component is most consistently associated with conflict processing (Van Veen & Carter, 2002; Yeung & Cohen, 2006). One question arising from the differences in neural activity observed here is whether conscious and unconscious conflict is processed by distinct brain networks and whether differences between visibility conditions are mainly quantitative or qualitative (D'Ostilio & Garraux, 2011; van Gaal, Scholte, Lamme, Fahrenfort, & Ridderinkhof, 2011). Future studies should be performed to address this issue more specifically.

Over the years, several authors have highlighted that block-wise adaptations to unconsciously triggered conflict might be caused by meta-cognitive (conscious) processes. During task performance, subjects might become conscious of the *consequence* of conflict, such as increased error rates and reaction times, without being aware of the conflicting-inducing stimuli themselves (the origin of conflict, see Desender & Van Den Bussche, 2012 for an extensive overview on this topic). In mostly incongruent blocks, error rates are higher and RTs slower than in mostly congruent blocks. Subjects might notice this and adapt their behavior accordingly, leading to the observed pattern of results. Kinoshita, Mozer, and Forster (2011) have explained these findings in a so-called adaptation to statistics of the environment (ASE) model, which highlights the importance of the *difficulty-level* of the task (or trial) at hand. Because mostly incongruent blocks contain a majority of difficult trials subjects might adopt a more conservative response strategy after these trials, in the end, leading up to the block-wise response pattern. In our experiment, we mixed weakly masked and strongly masked trials within blocks and therefore focused on the *effect* of overall block-wise conflict manipulations on the subsequent processing of consciously vs. unconsciously triggered conflict. Further, because we cannot be certain that subjects remained unaware of the conflict in masked trials by meta-cognitive processes we consistently refer to unconsciously *triggered* (or elicited) conflict instead of unconscious conflict. Future studies need to be performed to test the relative contribution of conscious metacognitive processes in (block-wise) adaptations to consciously vs. unconsciously triggered conflict.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2013.09.020.

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