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Exogenous capture of medial–frontal oscillatory mechanisms by unattended conflicting information

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ABSTRACT

A long-standing debate in psychology and cognitive neuroscience concerns the way in which unattended information is processed and influences goal-directed behavior. Although selective attention allows us to filter out task-irrelevant information, there is a substantial number of unattended, yet relevant, events that must be evaluated in a flexible manner so that appropriate behaviors can succeed. Here we inspected the extent to which unattended conflicting visual information, which cannot be consciously identified, influences behavior and activates medial prefrontal cortex (mPFC) mechanisms of action-monitoring and regulation, traditionally associated with conscious control processes.

To that end, we performed two experiments using a novel variant of the Eriksen flanker task in which spatial attention was manipulated, preventing the conscious identification of unattended visual events. The first behavioral experiment was conducted to validate the efficacy of the novel paradigm. In the second experiment, we evaluated electrophysiological correlates of mPFC activity (a frontocentral negative ERP component and medial–frontal theta oscillations) in response to attended and unattended conflicting events. The results of both experiments demonstrated that attended and unattended conflicting stimuli altered subjects' behavior in a similar fashion, i.e. slowing down their reaction times and increasing their error rates. Importantly, the results of the EEG experiment showed that unattended conflicting stimuli, similarly to attended conflicting stimuli, led to an increase in theta-related frontocentral ERP activity and medial–frontal theta power, irrespective of the degree of conscious representation of the sources of conflict. This study provides evidence that medial–frontal theta oscillations represent a neural mechanism through which the mPFC may suppress and regulate potentially inappropriate actions that are automatically triggered by conflicting environmental stimuli to which we are oblivious.

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1. Introduction

There are many situations in everyday life in which we have to rapidly monitor relevant unattended information, sometimes without a clear conscious perception,[1] so that appropriate behaviors can succeed. To illustrate this idea, imagine yourself driving your car home and suddenly a dog on the sidewalk starts running into the street. With most of your attention deployed to the oncoming traffic you barely register the dog. However, even without being able to explicitly identify the dog's presence, you find yourself automatically adjusting your speed and trajectory.

There is now a wealth of evidence that monitoring and regulation of erroneous and conflicting (i.e., error-prone) events is accomplished by a neural system sourced in the medial prefrontal cortex (mPFC) (Botvinick et al., 2001; Carter et al., 1998; Ridderinkhof et al., 2004; Ullsperger et al., 2014). EEG studies, for instance, have consistently described cortical responses with negative polarity in frontocentral electrodes of the scalp that indicate the activation of the mPFC during the occurrence of response conflict, the N2 component (van Veen and Carter, 2002; Yeung et al., 2004) and response errors, the error-related negativity (ERN) (Gehring et al., 1993; Rodriguez-Fornells et al., 2002; Yeung et al.,

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[1] In the present manuscript by conscious perception we mean explicit knowledge about the visual representation of a given object, which can be further used for verbal reporting (see Lamme, 2003; Block, 2005).

2004). Considerable evidence supports the idea that these mechanisms are at least partially orchestrated by on-going theta oscillatory activity (4–8 Hz), as errors and response conflict consistently modulate theta power activity in the mPFC (Cavanagh et al., 2009; Cohen, 2011; Cohen and Donner, 2013; Marco-Pallares et al., 2008; Pastotter et al., 2013). Recently, it has been suggested that theta oscillatory activity reflects a generic mechanism of action-monitoring and regulation through which the mPFC interacts with motor and other top-down control networks in order to prompt us to implement fast behavioral adjustments such as canceling or slowing down on-going inappropriate response tendencies or implementing compensatory behaviors after actual erroneous actions (Cavanagh et al., 2012; Cohen and Donner, 2013; Luu et al., 2004; Marco-Pallares et al., 2008; Narayanan et al., 2013).

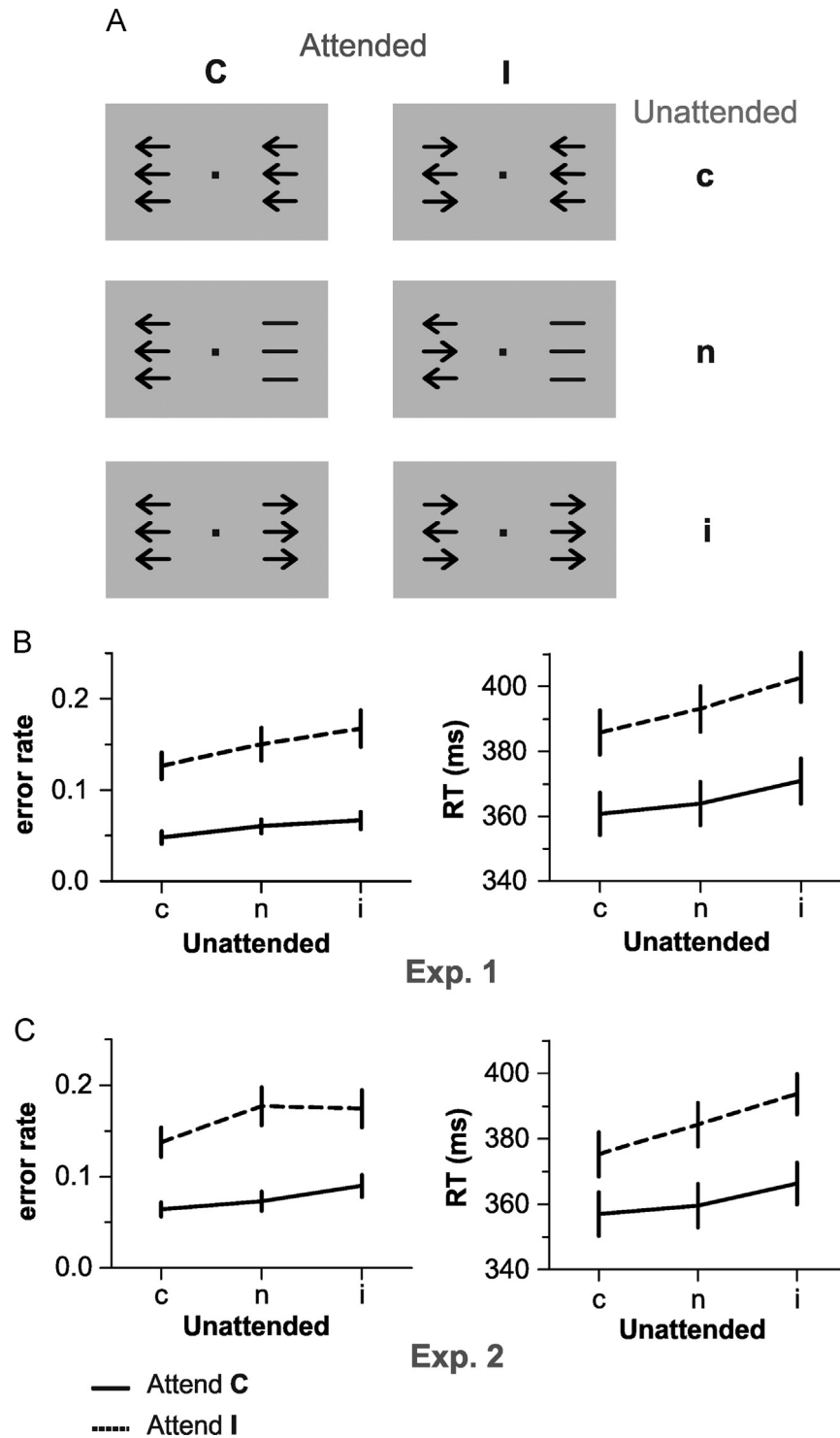However, the extent to which the mPFC action-monitoring

Fig. 1. (A) Experimental task design. Example of the experimental conditions in blocks in which attention was deployed to the left side of the screen. On the Attended side (left) trials are categorized as Congruent (C) or Incongruent (I). On the Unattended side stimuli are congruent (c), neutral (n) or incongruent (i) with the target on the Attended side. (B)Mean error rate and RTs across all conditions (experiment 1: *behavioral experiment*). (C) same as (B) regarding the experiment 2 (*EEG experiment*). Error bars represent SEM.

system is sensitive to conflicting unattended visual events which cannot be consciously identified is a question that has remained unresolved. On the one hand, earlier theories emphasized that cognitive control functions of the mPFC rely almost exclusively on attentive and conscious control processes (Dehaene et al., 2003; Jack and Shallice, 2001; Posner, 1994; Posner and DiGirolamo, 1998; Ridderinkhof et al., 2004). However, new findings have challenged these traditional views by showing that 'high-level' functions of the prefrontal cortex such as conflict-monitoring, response inhibition and error detection can unfold without conscious awareness (D'Ostillio and Garraux, 2012; Nieuwenhuis et al., 2001; Sumner et al., 2007; van Gaal et al., 2008, 2011). To examine the influence of unconscious processing on cognitive control functions most studies have used masked-prime paradigms (see review by van Gaal et al. (2012)). Generally, in these tasks participants have to respond to a target that is rapidly followed by a prime stimulus that can either facilitate or interfere with the response to the target. Because the prime is masked and presented very briefly its visibility is prevented. In an EEG study by van Gaal et al. (2011), for example, it was shown that invisible (masked) stop stimuli slowed down subjects' response times and triggered frontal negative ERP activity which correlated with the magnitude of slowdown during masked stop trials. Similar frontocentral ERP signals have also been described in response to both unmasked and masked incongruent-conflicting stimuli (Wang et al., 2013; Jiang et al., 2013). Altogether, these studies support the idea that the monitoring of conflicting stimuli and the initiation of inhibitory control can take place irrespective of conscious awareness.

In the present study, however, we used a different experimental approach to explore whether unattended (non-conscious) conflicting events can modulate theta oscillatory mechanisms of action-monitoring and regulation in the mPFC. We conducted a behavioral experiment (experiment 1) and an EEG experiment (experiment 2) while participants performed a novel variant of the Eriksen flanker task (Eriksen and Eriksen, 1974) in which spatial attention was manipulated. Using this novel design we aimed to simulate a complex visual environment in which participants had to prioritize visual information that was more relevant to the task on-hand (as when we focus our attention when driving on the oncoming traffic) at the expense of other items that although visible remained oblivious to them (as in the given example, the dog on the sidewalk). Here, participants were instructed to covertly attend either to the left or right visual fields while bilateral flankers were parafoveally displayed at both visual fields. Participants had to respond as fast as possible to the direction of a target arrow presented on the attended side and to ignore the set of flankers exhibited at unattended parafoveal locations – which were congruent, neutral or incongruent with the attended target (see Fig. 1). The spatial arrangement of the flankers prevented participants from accurately discriminating the nature of the stimuli located at unattended parafoveal locations (Block, 2005; Cohen et al., 2012; Lamme, 2003). This paradigm differs from previous studies of masking-priming in one critical point. Here all stimuli remained visible so that subjects were not deprived of the phenomenal visual experience of the conflicting stimuli as in the case of subliminal priming (Lamme, 2003). Therefore, our effort was to simulate an experimental paradigm closer to real-life visual scenarios whereby environmental stimuli, including task-irrelevant stimuli, remain visible but potentially hindered from conscious awareness due to limited attentional resources.

We predicted that even when unattended conflicting stimuli were not accurately identified they could still be causally effective in affecting participant's behavior (experiments 1 and 2) and influencing the amplitude of frontocentral ERP signals and the power of medial–frontal theta oscillatory activity associated with

action-monitoring and regulation mechanisms of the mPFC (experiment 2).

2. Methods

We conducted two experiments in order to examine to what extent unattended conflicting information which cannot be accurately identified influences participant's behavior and modulates electrophysiological mechanisms of action-monitoring and regulation of the mPFC. In experiment 1 we performed an initial *behavioral experiment* to validate the efficacy of the novel variant of the Eriksen flanker task used in the EEG experiment. In experiment 2 we performed an *EEG experiment* to examine ERP components and oscillatory mechanisms of action-monitoring and regulation.

2.1. Participants

Twenty-seven right-handed students (5 men; age range: 18–23 years) participated in the behavioral experiment (Exp. 1). For the EEG experiment (Exp. 2), we recruited 20 right-handed students (7 men; age range: 18–29 years). All participants had normal or corrected-to-normal vision. All participants gave written informed consent before the experiments and were paid for their participation.

2.2. Experimental design and procedure for the behavioral and EEG experiments

The stimuli were presented on a 19-in. color monitor (frequency 60 Hz) against a gray background (178,178,178 RGB) at a viewing distance of 65 cm. Bilateral stimuli consisting of three black arrows oriented horizontally (4.8° × 2.1°) were displayed on the left and right sides of the screen along the horizontal meridian at a distance of 5.5° from a central fixation point. The duration of the stimuli presentation was 130 ms with stimuli onset asynchrony (SOA) set to 870 ms.

At the beginning of each block participants were instructed to attend to the stimuli presented on one side of the screen while ignoring the group of flankers presented on the unattended side. On the attended side stimuli were formed by one central target and flankers above and below. Attended stimuli were categorized as *Attended Congruent*, when the target and flankers pointed in the same direction, and *Attended Incongruent*, when target and flankers were oriented in opposite directions. The unattended stimuli comprised 3 flankers oriented in the same direction that were congruent, *neutral or incongruent* with the direction of the target on the attended side (Fig. 1A). Participants were required to respond as fast as possible to the direction of the central arrow (target) presented on the attended side by pressing one of two buttons assigned to the direction of the target, using both hands (e.g. 'press right button with the index finger of the right hand if the target is pointing to the right'). It was stressed that irrespective of the attended side the fixation point should be maintained throughout all experimental blocks. The experiment followed a 2 × 3 factorial design with factors *congruency on the Attended side* (Congruent, C; Incongruent, I) × *congruency on the Unattended side* (congruent, c; neutral, n; incongruent, i).

2.2.1. Experiment 1. Behavioral experiment

The behavioral experiment included 6 blocks (50% attending to the left side and 50% to the right, counterbalanced) of 156 trials each. Each condition was randomly presented an equal number of times (156 trials per condition). To examine whether participants were able to discriminate the type of visual stimuli presented on

both Attended and Unattended parafoveal locations they performed a two-alternative forced-choice discrimination task throughout the behavioral experiment. Participants were informed that during the experimental blocks there would be questions evaluating their degree of attention during the task. Specifically, participants were asked to discriminate the direction of the central arrow presented on the Attended and Unattended sides. In each block 16 questions (8 regarding the Attended stimuli and 8 the Unattended stimuli) appeared in random order so that participants could not predict the presentation of the question. These questions appeared only on trials in which the Unattended stimuli were congruent or incongruent with the target. In total, 48 questions in reference to the Attended and the Unattended stimuli were presented.

2.2.2. Experiment 2. EEG experiment

The EEG experiment included 14 blocks (50% attending to the left side and 50% to the right, counterbalanced) of 120 trials. Each condition was randomly presented an equal number of times (280 trials per condition). In contrast to Exp. 1, in the EEG experiment the control force-choice discrimination task was administered after the experiment was completed. This change was applied to influence participant's decisions as little as possible and to ensure that they were mostly focused on the main task. In this case they performed two additional blocks of 156 trials (one attending to the left and the other to the right, randomly ordered) with the same stimuli and trial timing. They were instructed to perform the control experiment exactly as the EEG experiment. As in the first behavioral experiment 16 questions were introduced randomly in each block (8 questions regarding the Attended stimuli and 8 the Unattended stimuli). In total, 16 questions in reference to Attended and Unattended stimuli were presented.

2.3. Behavioral data analysis for the behavioral and EEG experiments

Trials following resting periods, error responses and trials with RTs shorter than 200 ms or longer than 2 standard deviation of the individual RT mean were excluded from the behavioral (Exp. 1 and 2) and EEG (Exp. 2) analyses. Repeated ANOVAs were performed on the mean proportion of error responses (error rate) and mean RT of correct responses with the factors congruency Attended side (Congruent, Incongruent) × congruency Unattended side (congruent, neutral, incongruent).

Performance on the forced-choice discrimination task (percentage of correct responses to Attended and Unattended stimuli) in both behavioral (Exp. 1) and EEG (Exp. 2) experiments was tested for each individual using a binominal test evaluated at a p-value of 0.05 (two-tailed). We expected that participants could not accurately discriminate the stimuli presented on the Unattended side above chance (50%) since covert attention to those stimuli was limited (Cohen et al., 2012; Lamme, 2003).

2.4. Experiment 2: Eye-movement recording and pre-processing

In the EEG experiment participants' eye movements were also recorded to ensure that participants did not look directly at the Attended and Unattended stimuli. Participant position of gaze was monitored using a binocular EyeLink II eye-tracking system (SR Research System, Ontario, Canada). To compensate for any head movements, we used a chin rest. Eye recordings were coordinated with the EEG recording using the Prexel (Visual Attention Lab, UMass Boston, USA) eye-tracker extension toolbox for Presentation (Neurobehavioral Systems). The eye tracking equipment was calibrated for each participant at the beginning of each experimental block (standard 9 point calibration). The data were recorded with a 500 Hz sampling rate. Eye recordings were used to

filter out those trials in which eye gaze and fixation point coordinates did not match and trials in which participants did not maintain a stable fixation. A stable fixation was defined as eye movements smaller than 0.2° and slower than 0.2°/s during the time window of 1 s around the onset of the stimuli presentation. Trials in which eye gaze deviated from fixation were excluded from the behavioral and EEG analysis of experiment 2. On average 13 ± 7% (mean + SD) of all the trials were rejected offline. All participants had a rejection rate lower than 25%.

2.5. Experiment 2: EEG recording and analysis

EEG was recorded from tin electrodes mounted in an elastic cap and located at 28 standard positions (Fz, Fcz, F7/8, F3/4, Fc1/2 Fc5/6, Cz, C3/4, T3/T4, T5/T6 CP1/2, CP5/6, Pz, P3/4, PO1/2, O1/2). All scalp electrodes were referenced offline to the mean activity of the left mastoid. EOG was recorded with electrodes located below the right eye (vertical EOG) and electrodes placed on the outer canthus of each eye (horizontal EOG). Both vertical and horizontal EOG were used for artifact rejection. Impedances were kept below 5 kΩ. The EEG signals were filtered with band-pass of 0.1–70 Hz (half-amplitude cutoffs) and digitized at a rate of 250 Hz.

Only those trials in which the fixation was maintained (trials pre-selected using the eye movement analysis) were analyzed. ERP effects associated with action-monitoring (response conflict and response errors) were studied by extracting epochs from −1000 ms to 1000 ms locked to response onset (baseline period was defined from −400 to −200 ms prior to response onset). ERP responses associated with spatial attention mechanisms were also inspected by extracting epochs of 1000 ms locked to the onset of the stimulus presentation (baseline corrected from −100 ms to the onset of stimulus presentation).

For both stimulus-locked and response-locked analysis, trials exceeding ± 75–100 μV in both EEG and vertical EOG during the epoch window were rejected offline (thresholds were adjusted individually for each participant). Trials with horizontal eye movements that exceeded 2 standard deviations relative to baseline activity were also removed. For the ERP analysis the EEG was low-pass filtered offline at < 14 Hz in order to clean up EEG artifacts.

2.5.1. ERP analysis on spatial attention effects

To examine whether participants consistently maintained their attention on the instructed target stimuli on the Attended location we started by exploring effects of spatial attention on visual evoked ERPs. We analyzed the amplitude of the P1 and N2pc components which have been interpreted as a neural index of visual attention (Luck, 2012; Mangun et al., 1993). Trials in which attention was directed to the left side were separated from trials in which attention was directed to the right side. No difference between the number of trials analyzed attended left (M+SEM: 501 ± 18) and attended right (M+SEM: 505 ± 22) was seen (t(17) < 1). For statistical analysis we selected two ROIs of three sensors over posterior regions of the scalp: on the right hemisphere (RH: P4, PO2, T6) and on the left hemisphere (LH: P3, PO1, T5) (the selected ROIs are highlighted on the topographical map of Fig. 2B, left panel). Statistical effects were tested by repeated ANOVAs with factors Attended side (Right, Left) × hemisphere recording site (ipsilateral, contralateral) on the mean amplitude of the P1 and N2pc components. Greenhouse–Geisser correction was used when necessary.

2.5.2. ERP analysis on action-monitoring effects (response-conflict and response-error monitoring)

To examine ERP markers of action-monitoring in the mPFC in Attended and Unattended conflicting events we first conducted an
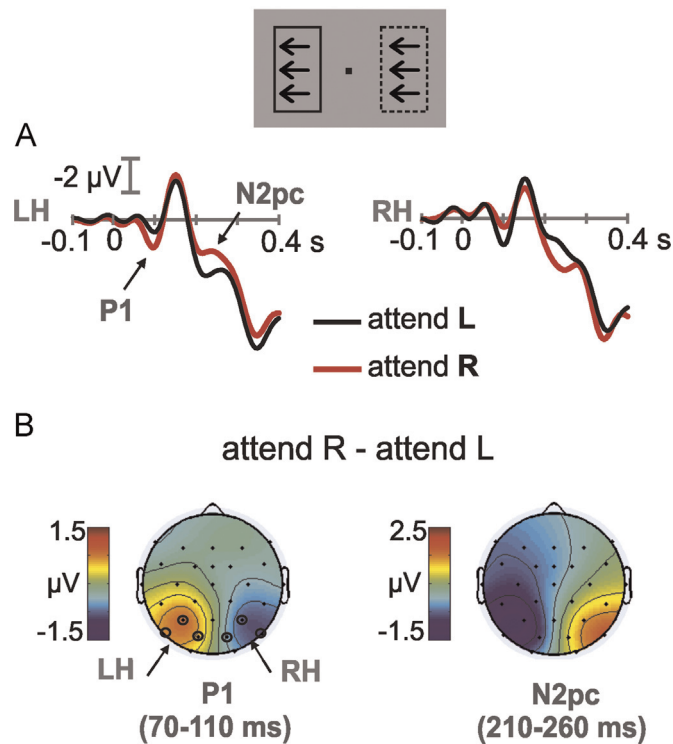
Fig. 2. (A) Stimulus-locked ERPs regarding spatial attention effects. Spatial attention to one side of the screen was associated with an increase in the P1 and N2pc components on the contralateral posterior sites of the scalp. (B) Scalp distribution of the ERPs for the difference attend Right-attend Left. Black disks on the topographical maps denote the ROI of parietal–occipital recording electrodes on the right (RH) and left hemisphere (LH).

analysis of conflicting correct responses. The grand-average waveforms for the contrast Attended Incongruent–Attended Congruent (average across Unattended c, n and i conditions), which at the behavioral level showed greater congruency effects in both experiments (see Figs. 1B and 1C), revealed a negative waveform in frontocentral electrodes (Fz and Fcz) extending from 150 to 80 ms before the response onset (Fig. 3). To inspect conflict-related ERP effects on Attended and Unattended conflicting stimuli we performed repeated ANOVAs with the factors *congruency Attended side* (Congruent, Incongruent) x *congruency Unattended side* (congruent, neutral, incongruent) on the mean amplitude of this negative ERP over the Fz/Fcz electrodes (mean activity) during the time window of maximal activity (-150 to -80 ms).

Additionally, we examined the amplitude of the ERN component after overt errors on Unattended congruent, incongruent and neutral trials in order to compare the timing between the ERPs related to response conflict and response errors during Unattended trials. This analysis was also crucial to examine whether both the ERN and the ERP related to response-conflict stem from overlapping generator structures in the mPFC (*see* electrical source analysis below) (van Veen and Carter, 2002; Yeung et al., 2004). The ERN was calculated as the difference between error and correct responses in Attended Incongruent trials (Unattended c, n, i) within a window of 40–80 ms (peak activity of the ERN). Attended Congruent trials did not enter in this analysis as this condition did not generate enough number of error trials. The mean amplitude of the ERN (difference waveform) was tested with ANOVAs with the factors *congruency Unattended side* (congruent, neutral, incongruent) at Fz/Fcz electrodes. Greenhouse–Geisser epsilon correction was used when necessary.

2.6. Source analysis of conflict and error-related ERP activity

Brain Electric Source Analysis (BESA 2000 version 5.3) (Scherg, 1990) was additionally used to determine the source of the ERP signal observed during conflicting Attended and Unattended events and error trials. BESA algorithm computes the location and the orientation of multiple equivalent dipolar sources by calculating the voltage scalp distribution that would be produced for a given dipole model (forward solution) and comparing it with the original scalp distribution. Source localization analysis was carried out on band-pass filter ERP signals on the theta range (4–8 Hz) resulting from the difference waveforms: (i) error-correct (ERN response), (ii) Attended Incongruent–Attended Congruent, and (iii) Unattended incongruent–Unattended congruent trials. First, we fitted one single dipole in the ACC/pre-SMA areas, which are associated with error and conflict-related fMRI activations in previous studies (Ridderinkhof et al., 2004; Ullsperger et al., 2014), within the ERN component (0–100 ms). Subsequently we tested the strength of this dipole estimating the neural sources of the negative ERP resulting from Attended Incongruent and Unattended incongruent conditions. The final locations of each dipole in the group-average BESA model were projected on mean structural T1 MRI images of 24 individuals and converted into Talairach coordinates in the standard Montreal brain (Talairach and Tournoux, 1988).

2.7. Time-frequency analysis related to response-conflict

In addition to the ERP analysis, time-frequency analysis was performed on the EEG activity for each trial in 4- s epochs (from -2 s to 2 s locked to the onset of the response) using seven-cycle complex Morlet wavelets (Marco-Pallares et al., 2008). The time-varying energy (square of the convolution between wavelet and signal) was computed in the frequencies ranging from 1 to 40 Hz (linear increase of 1 Hz) for each trial and then averaged separately for each participant. The mean increase/decrease in theta power (4–8 Hz) with respect to the baseline for each condition was inspected during the temporal window of -200–0 ms (locked to the response onset) using ANOVAs with factors *congruency Attended side* (Congruent, Incongruent) $\times$ *congruency Unattended side* (congruent, neutral, incongruent) at frontocentral electrodes Fz/Fcz (mean activity).

3. Results

3.1. Experiment 1: Behavioral experiment

The results of the forced-choice discrimination task in experiment 1 revealed that 22 out of 27 participants were unable to discriminate the stimuli located on the Unattended side as evidenced by chance-level performance (binomial test, $p > 0.05$). For these 22 participants the percentage of correct responses to the Attended stimuli was $91.6 \pm 5\%$ and for the Unattended stimuli $52.9 \pm 6.6\%$ ($t(21)=21$, $p < 0.0001$). At the group-level the percentage of correct responses for Unattended stimuli was nearly at chance level (50%) ($t(21)=2$, $p=0.054$).

The behavioral analysis of experiment 1 was conducted on this subsample of 22 participants who were unable to accurately discriminate the Unattended stimuli. A summary of the behavioral results is shown in Fig. 1B.

The mean RT in Attended incongruent trials ($M \pm SD$: 394 ± 33 ms) was higher than Attended Congruent trials (365 ± 31 ms) ($F(1,21)=214.7$, $p < 0.0001$) (Fig. 1b, right panel). Participants' RTs were also affected by the congruency of the Unattended flankers ($F(2,42)=74.9$, $p < 0.001$). Unattended
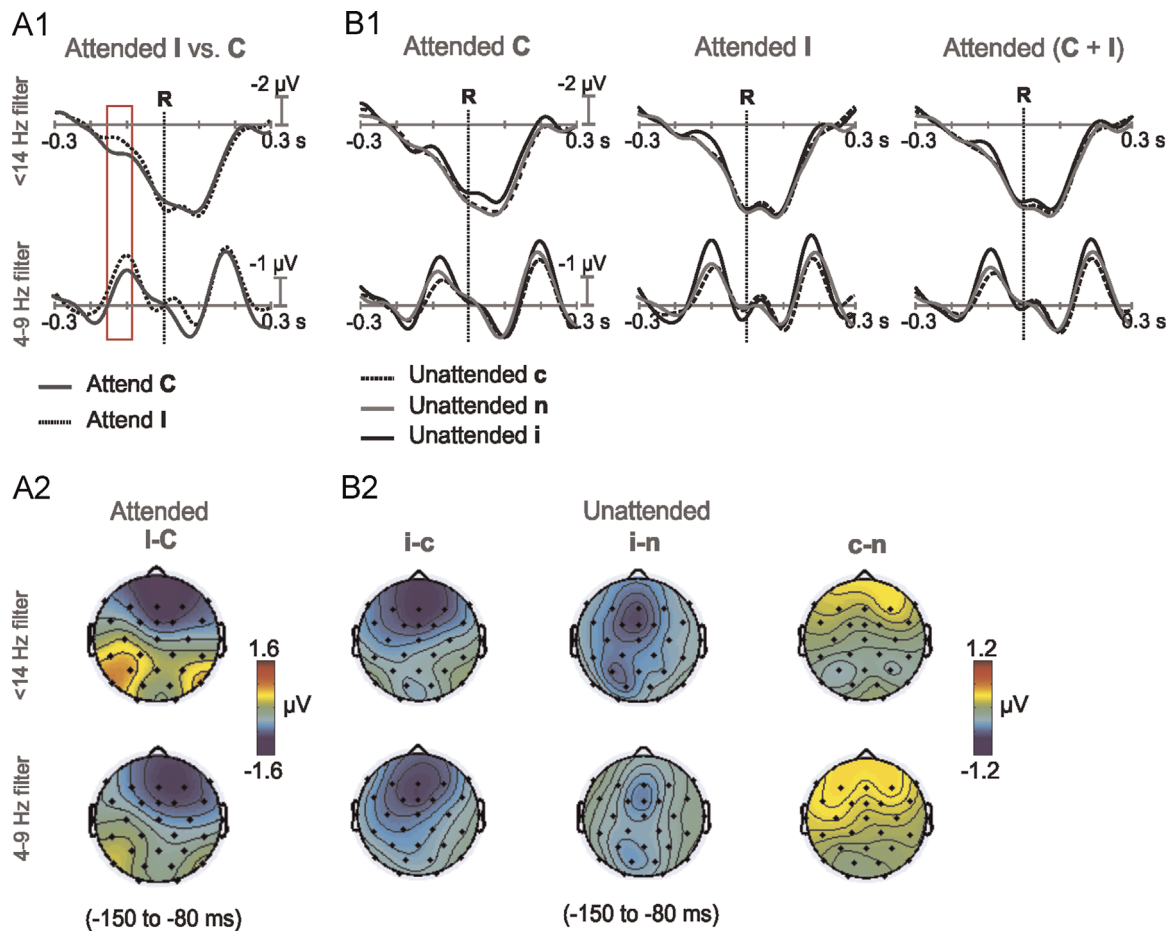
Fig. 3. Response-locked ERPs over frontocentral electrodes (Fz/Fcz) and topographical maps showing negative activity in the pre-response phase (around −150 to −80 ms, signaled by the red box) during Attended (A) and Unattended (B) incongruent (conflicting) events. (A1) Low-pass (top row) and theta-band (3–9 Hz, bottom row) waveforms for Attended Incongruent and Attended Congruent conditions. (A2) Topographical maps for the contrast Attended Incongruent–Attended Congruent. (B1) Low-pass (top row) and theta-band (3–9 Hz, bottom row) grand-average waveforms for Attended Congruent (left), Attended Incongruent (middle), and the average between the two conditions (right) as function of the congruency on the Unattended side (congruent, neutral and incongruent). (B1) Topographical map for the contrasts the Unattended: incongruent–congruent, incongruent–neutral and unattended congruent–neutral. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

incongruent conditions caused slower RTs (387 ± 33 ms) compared to Unattended neutral (378 ± 31 ms) ($t(21)=10$, $p < 0.001$) and congruent conditions (373 ± 31 ms) ($t(21)=8.8$, $p < 0.001$). There were also differences between Unattended neutral and congruent conditions ($t(21)=5.2$, $p < 0.001$). A significant interaction congruency Attended side × congruency Unattended side ($F(2,42)=7$, $p < 0.005$) showed that the congruency effects caused by the Unattended flankers (incongruent–congruent) were stronger during Attended Incongruent trials.

The error rates increased in Attended incongruent trials ($M \pm$ SD: 0.15 ± 0.07) compared to Attended Congruent (0.06 ± 0.04) ($F(1,21)=29.9$, $p < 0.001$) (Fig. 1B, left panel) and also varied as a function of the congruency in the Unattended side ($F(2,42)=7.7$, $p < 0.01$). Unattended incongruent conditions caused more errors (0.12 ± 0.05) than Unattended congruent conditions (0.09 ± 0.05) ($t(21)=3.9$, $p < 0.001$), but no differences were found compared to Unattended neutral conditions (0.11 ± 0.05) ($t(21)=1.8$, $p > 0.05$). Unattended congruent flankers caused fewer errors than Unattended neutral flankers ($t(21)=2.1$, $p < 0.05$). The interaction congruency of Attended × Unattended stimuli was not significant ($F(2,42)=1.2$, $p > 0.05$).

The results of the behavioral experiment demonstrated that not only attended sources of conflict, but also unattended conflicting stimuli, which are less likely to be accurately discriminated, can affect behavior, slowing down participants' RTs and increasing

their error rates.

3.2. Experiment 2: EEG experiment

3.2.1. Behavioral results

Regarding experiment 2, 18 of the 20 participants scored at chance level in the forced-choice discrimination task as evidenced by chance-level performance (0.5) (binomial test, $p > 0.05$). All further analyses were conducted on these 18 participants. For these 18 participants the percentage of correct responses for Attended stimuli was $93 \pm 9\%$ and for Unattended stimuli $55 \pm 9\%$ ($t(17)=12.8$, $p < 0.001$). Although the accuracy regarding the Unattended stimuli was low, it was significantly above chance level ($t(17)=2.4$, $p < 0.05$).

The behavioral results regarding experiment 2 are shown in Fig. 1C. Similar to the results of experiment 1, in the EEG experiment it was shown that Attended Incongruent trials caused slower RTs ($M \pm$ SD: 384 ± 27 ms) compared to Attended Congruent trials (361 ± 28 ms) ($F(1,17)=203.3$, $p < 0.0001$) (Fig. 1C, right panel). Participants' RTs were also affected by the congruency of the Unattended flankers ($F(2,34)=56.6$, $p < 0.001$). Paired t-test comparisons showed that Unattended incongruent conditions led to higher RTs (380 ± 26 ms) compared to Unattended neutral conditions (371 ± 28 ms) ($t(17)=7.2$, $p < 0.001$) and Unattended congruent conditions (366 ± 28 ms) ($t(17)=9.5$, $p < 0.001$);

furthermore, Unattended congruent flankers caused less interference than Unattended neutral flankers ($t(17)=4.3$, $p < 0.001$). Again, the congruency effects caused by Unattended flankers were stronger during Attended Incongruent trials as revealed by the significant interaction congruency of Attended × Unattended stimuli ($F(2,34)=11$, $p < 0.005$).

The error rates were also higher in Attended Incongruent trials ($M \pm$ SD: 0.16 ± 0.07) compared to Attended Congruent trials (0.08 ± 0.04) ($F(1,17)=55$, $p < 0.001$) (Fig. 1C, left panel). The main effect of congruency on the Unattended side was also significant ($F(2,34)=9.4$, $p < 0.001$). Unattended incongruent trials led to higher error rates (0.13 ± 0.07) compared to Unattended congruent trials (0.10 ± 0.05) ($t(17)=3.8$, $p < 0.001$), which, in turn, caused fewer errors than Unattended neutral flankers (0.12 ± 0.06) ($t(17)=3$, $p < 0.01$). There were no differences between Unattended incongruent and neutral conditions ($t(17)=1.1$, $p > 0.05$) (Fig. 1C, left panel). The interaction congruency of Attended × Unattended stimuli was not significant ($F(2,34)=2.9$, $p > 0.05$).

3.2.2. Spatial attention ERP effects

In agreement with previous studies (Hillyard and Anllo-Vento, 1998; Luck, 2012; Mangun et al., 1993) it was observed that covert deployment of attention to the Attended stimuli (vs. Unattended stimuli) was associated with increased activity of the P1 and N2pc components on posterior sites of the cortex contralateral to the attended side as revealed by a contralateral lateralization effect (main effect of hemisphere recording site) for the P1 ($F(1,17)=69.4$, $p < 0.0001$) and the N2pc ($F(17)=25.9$, $p < 0001$) components (Fig. 2A). Topographical maps (Fig. 2B) depict this clear enhancement of both components on the parietal–occipital recording sites contralateral to the attended side. For both components neither a main effect regarding the attended side nor an interaction attended side × hemisphere recording site were observed (both $Fs < 1$). These results are important because they show that throughout experiment 2 participants consistently maintained their attention on the instructed target stimuli.

3.2.3. Frontocentral ERP activations during attended and unattended conflicting events

The inspection of the response-locked ERP waveforms revealed that Attended and Unattended conflicting (i.e. incongruent) events elicited a fronto-central negative ERP that reflects on-going oscillatory activity on the theta band (Fig. 3).

As can be seen in Fig. 3A1 (the top row shows the grand-average waveforms with a low-pass filter < 14 Hz over Fz/Fcz electrodes) Attended Incongruent compared to Attended Congruent trials elicited a negative ERP component peaking before the response onset which was superimposed on a slow positive waveform. Differences between the two conditions regarding the amplitude of this negative ERP were confirmed by a main effect of congruency on the Attended side ($F(1,17)=5.1$, $p < 0.05$). The fronto-central distribution of this negative ERP for the difference waveform Attended Incongruent–Congruent trials is shown in Fig. 3A2. Importantly, this fronto-central negative ERP was also modulated by the congruency on the Unattended side ($F(2,34)=3.5$, $p < 0.05$) (Fig. 3B1). The amplitude of this negative ERP was greater in Unattended incongruent compared to Unattended congruent ($t(17)=2.3$, $p < 0.05$) and Unattended neutral conditions, although in this case the statistical differences were only marginal ($t(17)=1.96$, $p=0.065$); no differences between Unattended congruent and neutral conditions were observed ($t(17) < 1$). In Fig. 3B2 is shown the scalp distribution of the negative ERP for the pairwise contrasts: Unattended incongruent–congruent, Unattended incongruent–neutral, and Unattended congruent–neutral. The congruency effects by Attended and Unattended flankers were simply additive as demonstrated by the

non-significant interaction between the factors congruency Attended side × congruency Unattended side ($F(2,34)=1.3$, $p > 0.05$).

Furthermore, the EEG data were reanalyzed using a band-pass filter [3–9 Hz] in order to retain theta-band conflict-related EEG activity and to remove the positive waveform in which this negative ERP developed (see for similar approaches Cavanagh et al., 2012). Again we observed an increase in negative ERP before the response onset in Attended and Unattended conflicting trials as confirmed by a main effect of congruency on the Attended side ($F(1,17)=10.5$, $p < 0.05$) (Fig. 3A1, see the bottom row) and on the Unattended side ($F(2,34)=5.7$, $p < 0.05$) (Fig. 3B1, see the bottom row). The interaction congruency Attended side × congruency Unattended side was not significant ($F(2,34)=2.1$, $p > 0.05$). Further pairwise comparisons confirmed the enhanced theta-related negativity in Unattended incongruent trials compared to congruent ($t(17)=2.9$, $p < 0.01$) and neutral Unattended conditions (marginal increase: $t(17)=2$, $p=0.06$). No significant differences between Unattended congruent and neutral conditions were found ($t(17)=1.5$, $p > 0.05$).

3.2.4. Frontocentral ERP activations during overt response errors

In addition we inspected ERN activity following overt response errors (Fig. 4). The ERN during Attended Incongruent trials (Unattended c, n, i) showed a frontocentral distribution maximal at the Fz/Fcz electrodes (see the topographical distribution of the ERN for the difference waveform error-correct responses across the three different conditions in Fig. 4). The ERN was not modulated by the congruency on the Unattended side ($F < 1$).

3.2.5. Source localization of the frontocentral ERPs related to response conflict and response errors

Source localization results showed that a single source in the right ACC (Talairach coordinates (x, y, z): 3.4, 8.2, 45.8) accounted for 88.8% of the variance of the ERN response in overt error trials (temporal window of 0–100 ms post-response) (Fig. 5A). Critically, this single dipole model was found to explain 87.7% of the variance of the negative frontocentral ERP component associated with response conflict in attended Incongruent trials (time window of peak activity: -160 to -100 ms) and 88.2% of the variance in unattended incongruent trials (time window of peak activity: -130 to -70 ms) (Fig. 5). The source waveforms showed similar pre-response peak-latency in both Attended and Unattended conflicting conditions (right panel Fig. 5). Our results confirm our predictions that the theta-related frontocentral negative ERP signals in both Attended and Unattended conflicting events overlap within the same neural networks involved in error-monitoring in the mPFC.
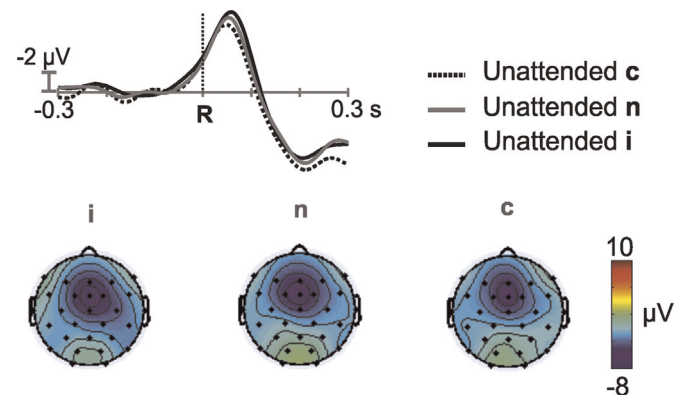

Fig. 4. Response-locked ERPs over frontocentral electrodes (Fz/Fcz) and related topographical maps for overt error responses (difference waveform error-correct) as function of the congruency of Unattended events.
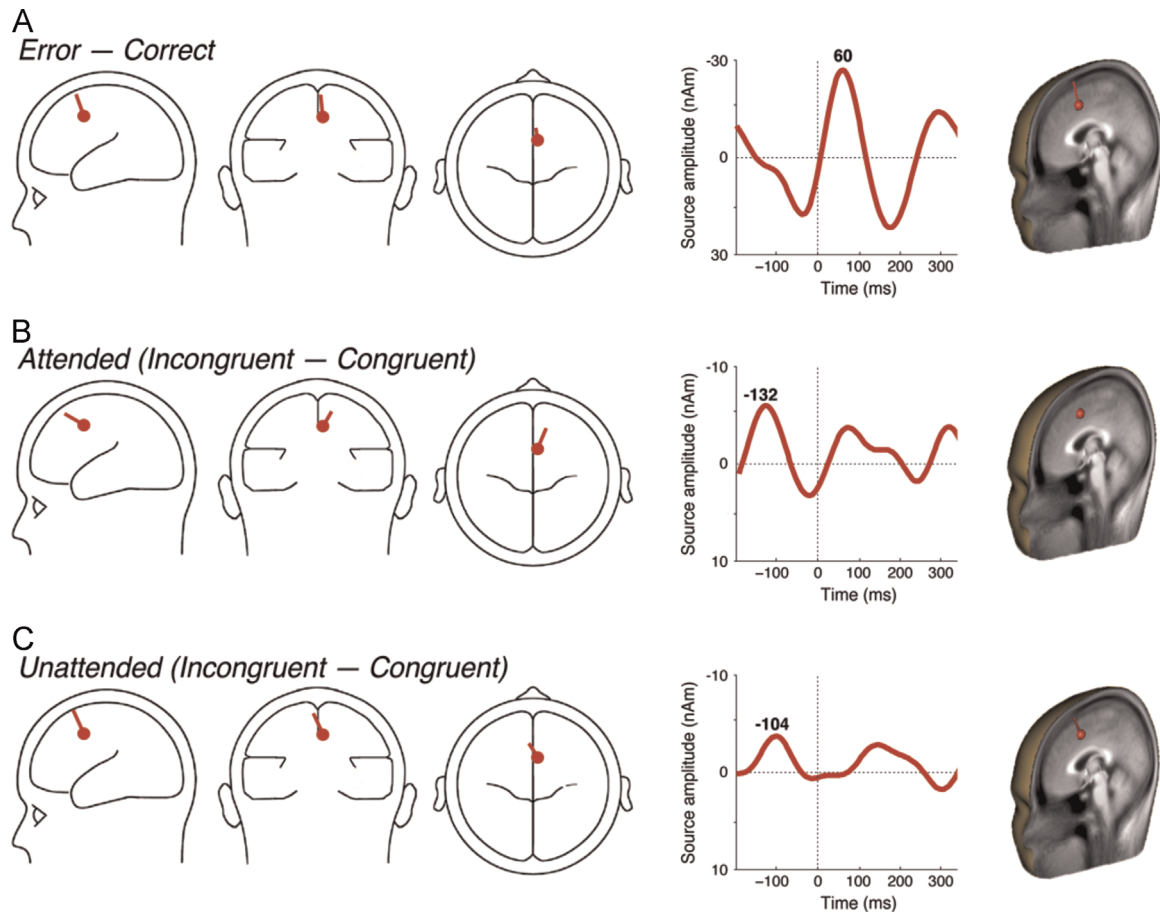
Fig. 5. Source localization analysis revealing a common neural source in the ACC for the monitoring of errors and conflict during Attended and Unattended incongruent conditions. (A) single dipole in the right ACC (red; $x=3.4$, $y=8.2$, $z=45.8$) was found for the ERN response during error trials. The same dipole explained 87.7% of the variance of the negative frontocentral ERP during conflicting Attended trials (B) and 88.2% of the variance during conflicting Unattended trials (C). Time-course of each computed dipole is represented in the source waveform on the right side of the figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2.6. Medial–frontal theta power during attended and unattended conflicting events

Medial–frontal theta power modulations to conflicting Attended and Unattended stimuli at frontocentral electrode locations are shown in Fig. 6. We observed greater medial–frontal theta power during the 200 ms prior to the response onset in Attended Incongruent compared with Attended Congruent conditions ($F(1,17)=7.4$, $p < 0.05$) (Figs. 6A and 6C left side). A main effect of congruency on the Unattended side was also found ($F(2,34)=4.2$, $p < 0.05$) (Fig. 6B). Medial–frontal theta power was enhanced in Unattended incongruent compared to Unattended congruent conditions ($t(17)=4$, $p < 0.005$); see the frontocentral topographical distribution of theta power for this contrast in Fig. 4C. No differences between Unattended incongruent and neutral conditions ($t(17)=1.2$, $p > 0.05$) or Unattended neutral and Unattended congruent conditions were observed ($t(17)=1.3$, $p > 0.05$).The interaction congruency Attended side × congruency Unattended side was not significant ($F(2,34) < 1$).

3.2.7. Correlations between medial–frontal theta power and RTs

To further assess the relationship between medial–frontal theta oscillatory activity and behavior regulation during conflicting events we computed Spearmen correlations between the mean theta power at frontocentral locations in Attended (difference Incongruent vs. Congruent) and Unattended (incongruent vs. congruent) conflicting conditions and the congruency RT effects resulting from these contrasts (Fig. 6D). These comparisons revealed significant positive correlations between enhanced medial–frontal theta power in Attended Incongruent trials and the RT slowing during these trials (rho=0.51, $p=0.034$). Notably, medial–frontal theta power and the RT slowing during Unattended incongruent conditions were also positively correlated (unattended i–c: rho=0.47, $p=0.047$).

4. Discussion

In the present study we conducted both a behavioral and an EEG experiment to show that conflicting stimuli presented at unattended locations, which could not be consciously identified, still influenced participants' behavior and modulated mPFC theta oscillatory activity. By combining ERP, time-frequency, and electrical source (BESA) analysis, our results showed that both attended and unattended (non-conscious) conflicting stimuli led to enhanced frontocentral ERP activity, reflecting on-going theta oscillatory activity, and medial–frontal theta power right before the response onset. Source analyses localized the origin of this theta-band specific frontocentral ERP activity in the mPFC. A positive correlation between the conflict-induced medial–frontal theta power and the magnitude of participant's slowdown further suggested that theta oscillations in the mPFC not only participate in the monitoring of attended conflicting events, but also may regulate inappropriate responses triggered by unattended conflicting information presented in the periphery. These findings cast doubts
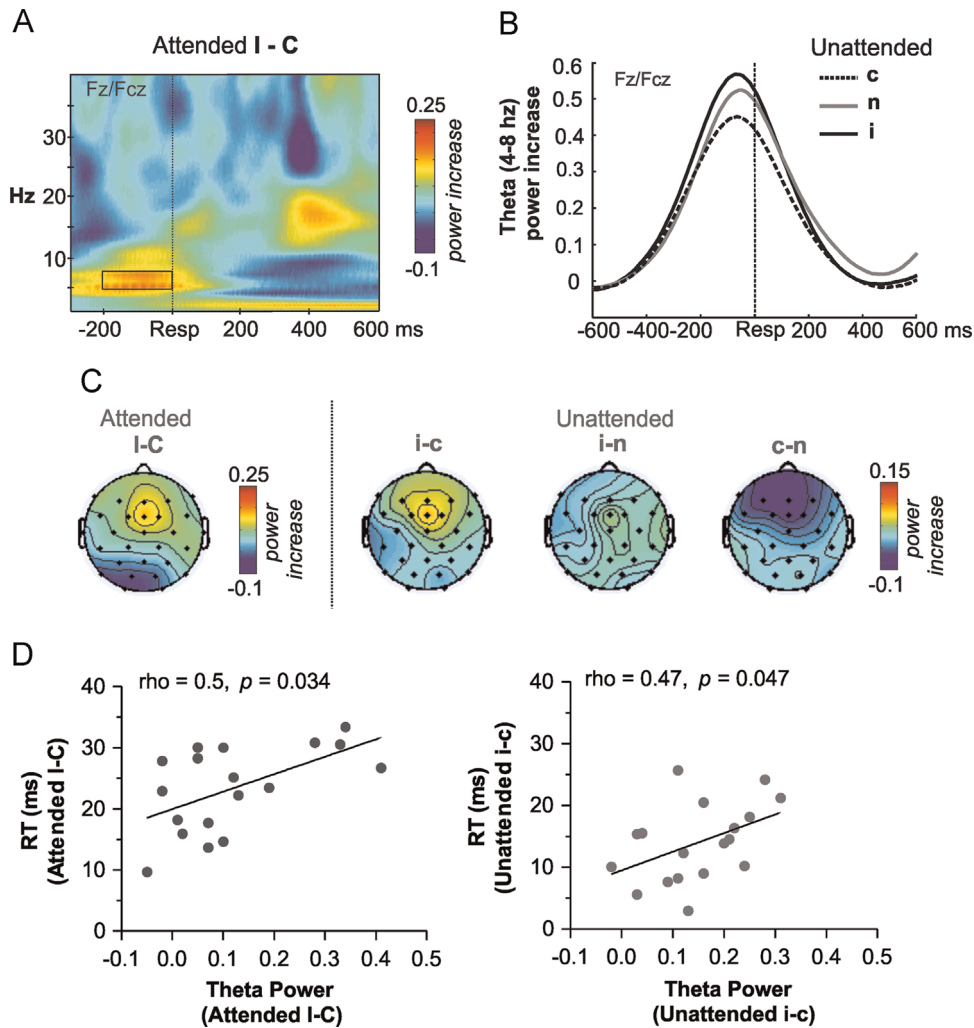
Fig. 6. (A) Medial–frontal theta power increases with respect to baseline at frontocentral electrodes prior to response onset in Attended conflicting trials (difference Attended Incongruent–Congruent). (B) Line plots of theta power activity over time for the different Unattended conditions (incongruent, neutral, congruent). (C) Topographical maps for the contrasts (Attended Incongruent–Congruent; Unattended incongruent–congruent; Unattended incongruent–eutral; Unattended congruent–neutral). (D) Spearman correlations calculated between the medial–frontal theta power (Fz/Fcz) and RTs during Attended (I–C) and Unattended (i–c) conflicting trials.

on traditional views which have stressed that high-level control functions of the mPFC, such as conflict-monitoring, rely exclusively on top-down and conscious processes (Dehaene et al., 2003; Jack and Shallice, 2001; Posner, 1994; Posner and DiGirolamo, 1998; Ridderinkhof et al., 2004) and give support to new evidence suggesting that mPFC control functions can potentially operate without conscious awareness (D'Ostillio and Garraux, 2012; Sumner et al., 2007; van Gaal et al., 2008, 2010b, 2011; Wang et al., 2013).

In the present study we set up a novel experimental design to examine action-monitoring and regulation processes triggered by visual events that were paravofeally processed under conditions of limited visual attention. It is important to mention that subjects were not distracted from a conscious phenomenal visual experience (*see* Lamme, 2003) of the events located at both attended and unattended parafoveal locations. Yet, they showed drastic problems in providing accurate reports about the nature of the stimuli presented at the unattended locations. Participants' performance during the force-choice discrimination task in the behavioral and the EEG experiment was nearly at chance level, suggesting that the monitoring and regulation of the unattended events unfolded, at least partially, without an explicit knowledge or a clear metacognitive representation of the sources of conflict. These findings dovetail with previous suggestions that visual attention is an

important requisite to access conscious representations of perceived stimuli from the outside world, influencing the likelihood of accurate reports (Cohen et al., 2012; Lamme, 2003; Wyart and Tallon-Baudry, 2008). Neurophysiological support for this idea came from the observation that covert deployment of attention towards the target in the attended locations was associated with an increase in the P1 and N2pc components on contralateral posterior brain locations (spatial attention effects on the EEG experiment, Fig. 2). Since both ERP signals have been interpreted as a neural index of visual attention (Hillyard and Anllo-Vento, 1998; Luck, 2012; Mangun et al., 1993), this control analysis suggests that selective attention to the attended target stimuli may have biased perceptual judgments of the unattended stimuli by selectively granting priority in the processing of attended (task-relevant) information (Hawkins et al., 1990; Hillyard and Anllo-Vento, 1998; Posner, 1994).

Even though stimuli presented at unattended locations may have generated weaker representations and therefore remained unavailable for accurate reports, they still influenced participant's behavior. In fact, our two experiments showed that although the accuracy regarding the unattended stimuli was very low (~53% in experiment 1 and ~55% in experiment 2), unattended conflicting events were associated with slower RTs and higher error rates in the same fashion as attended conflicting trials. The present results

are thus in agreement with previous studies showing the difficulty in achieving complete abolishment of the flanker compatibility effect event when conflicting information is presented (i) in unattended and distant (peripheral) locations (Eriksen and Eriksen, 1974; Lavie, 1995; Miller, 1991; Yantis and Johnston, 1990) and (ii) in conditions with reduced visual awareness (e.g., subliminal priming) (van Gaal et al., 2010a).

Of note, electrophysiological results revealed that both attended and unattended conflicting stimuli led to an increase in theta-related frontocentral ERP activity and medial–frontal theta power. For both contrasts Attended Incongruent–Congruent (which exposes conflict effects for fully attended stimuli) and Unattended incongruent–congruent (manifesting conflict effects derived from exogenous unattended stimuli) we observed a frontocentral negative ERP component in the pre-response phase that, by timing and scalp topography, is consistent with a frontal N2 component – an ERP correlate of mPFC conflict-monitoring activity (van Veen and Carter, 2002; Yeung et al., 2004). These ERP results are similar to recent EEG studies which have shown enhanced frontal negative ERP activity in response to both visible (unmasked) and invisible (masked) conflicting stimuli (van Gaal et al., 2011; Wang et al., 2013).

By applying a band-pass filter (3–9 Hz) in the EEG data, we were able to show that these frontocentral negative ERPs reflect ongoing oscillatory activity in the theta band. Further source localization analysis demonstrated that the theta-specific modulation was partially originated in the mPFC, a key structure in error and conflict monitoring and action selection (Botvinick et al., 2001; Holroyd et al., 2004; Ridderinkhof et al., 2004). The observation of enhanced medial–frontal theta power during attended conflicting events replicates earlier electrophysiological findings (Cavanagh et al., 2012; Cohen and Donner, 2013; Pastotter et al., 2013). However, to the best of our knowledge, no previous study has reported medial–frontal theta activity in the mPFC in response to unattended (non-conscious) conflicting stimuli.

It has been proposed that theta oscillations support action-monitoring and consequent compensatory mechanisms by coordinating the mPFC with other control and motor networks supporting flexible and adaptive decision process (Cavanagh et al., 2009, 2012; Luu et al., 2004; Narayanan et al., 2013; Nigburg et al., 2012; van Driel et al., 2012). For instance, a recent study in humans and rodents has demonstrated that post-error compensatory mechanisms strongly rely on the coordination of slow theta oscillations between the mPFC and the motor cortex (Narayanan et al., 2013), extending previous neuroimaging findings showing that increases in mPFC activity and decreases in the motor threshold predict post-error slowing effects (Danielmeier et al., 2011; King et al., 2010). In agreement with these findings, here we showed that the magnitude of medial–frontal theta power increase in both attended and unattended conflicting trials was correlated with the behavioral slowing down. Given the present results, it is very likely that medial–frontal theta activity arising prior to action initiation is involved in the cancellation or slowing down of prepotent erroneous actions even when these actions are activated automatically by stimuli that remain outside the scope of attentional control. As an alternative, but not incompatible explanation, it is possible that the observed enhancement of theta activity is associated with a larger number of partial errors during conflicting unattended trials (Cohen and van Gaal, 2013). Partial errors make reference to subthreshold muscle twitches during correct responses that are ensued by suppressing on-going erroneous response tendencies (Gratton et al., 1988). Although this hypothesis is hard to disentangle since electromyography (EMG) activity was not recorded, our results suggest that theta activity in the mPFC is somewhat involved in some sort of regulatory processes in order to suppress inappropriate response tendencies activated by conflicting and error-prone events.

Importantly, these results further suggest that such regulatory processes are initiated in medial prefrontal networks irrespective of the degree of conscious control (Jackson and Shallice; Posner 1994; Posner and DiGirolamo, 1998). Consequently, it is possible that the mPFC responds to all kinds of non-conscious conflicting and error-prone events in a graded manner depending on the robustness of the representation of the experienced conflict (Horga and Maia, 2012). In agreement with this idea, previous studies using subliminal-priming paradigms have shown that the mPFC is sensitive to response conflict and related compensatory control processes even in conditions of reduced perceptual awareness (D'Ostillio and Garraux, 2012; Sumner et al., 2007; van Gaal et al., 2010b) and is responsive to unaware error responses (Hester et al., 2005; Nieuwenhuis et al., 2001).

Our study, however, is different from previous studies that have used subliminal priming paradigms to study unconscious processes of action-monitoring. Here, even when participants might have remained partially unaware of the specific details of the information presented at the unattended side, stimuli were still visible, which differs from subliminal presentations. We believe that the paradigm presented here is closer to real-life scenarios in which our senses are constantly bombarded by visible information outside the focus of our attention that can influence our behavior and, thereby, activate neural networks related to action monitoring and regulation in a way similar to an exogenous capture of the action-monitoring system by unattended (non-conscious) stimuli.

In summary, the present findings demonstrate that mPFC activity related to response conflict monitoring, classically associated with conscious and attentional control processes, can take place in response to unattended conflicting events, irrespective of the degree of conscious representation of the sources of conflict. The present study provides electrophysiological evidence that oscillatory theta activity in the mPFC is a plausible neural mechanism though which flexible monitoring and compensation are exerted to suppress and regulate potentially inappropriate actions that are automatically triggered by environmental stimuli to which we are oblivious.

Notes

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Conflict of interest

None declared.

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