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The neural markers of an imminent failure of response inhibition

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ABSTRACT

In his novel *Ulysses*, James Joyce wrote that mistakes are the "…portals of discovery". The present study investigated the pre-stimulus oscillatory EEG signatures of selective attention and motor preparation that predicted failures of overt response inhibition. We employed a trial-by-trial spatial cueing task using a go/no-go response paradigm with bilateral target stimuli. Subjects were required to covertly attend to the spatial location cued on each trial and respond to most of the number targets (go trials) at that location while withholding responses for one designated number (no-go trials). We analyzed the post-cue/pre-target spectral patterns comparing no-go trials in which a response occurred in error (False Alarms, FA) with trials in which participants correctly withheld a response (Correct Rejections, CR). We found that cue-induced occipital alpha (8–12 Hz) lateralization and inter-frequency anti-correlations between the motor beta (18–24 Hz) and pre-frontal theta (3–5 Hz) bands each independently predicted subsequent failures of response inhibition. Based on these findings, we infer that independent perceptual and motor mechanisms operate in parallel to contribute to failures of response inhibition.

Introduction

Elucidating the neural underpinnings of behavior is a central goal of cognitive neuroscience. A fruitful approach to understanding brain-behavior associations has been to investigate successes and failures in goal-directed behavior. Studies of action errors, such as executing a motor action when an action was not appropriate, have proven informative in this regard. For example, studies of the brain's responses to errors led to the discovery of the error-related negativity (ERN) in the signal-averaged event-related potentials (ERPs) extracted from the ongoing electroencephalogram (EEG) (e.g., Gehring et al., 1993; for a review see Gehring et al., in press). Although a large literature addresses the neural processes associated with error commission, there is only a modest amount of research on the neural antecedents of errors just before they occur. Most prior research has explored either the evoked neural consequences of errors, or has investigated the averaged behavioral and physiological responses for trials preceding an error (Hajcak, et al., 2005; Nieuwenhuis et al., 2007; Ridderinkhof et al., 2003; Eichele et al., 2008). An alternate approach has been to use the ongoing oscillations present in the EEG to reveal the momentary (within trial) patterns of brain activity immediately preceding actions (Haegens, et al., 2011; Mazaheri, et al., 2009; O'Connell et al., 2009). The present work goes beyond such findings by examining specific spectral dynamics of the EEG that precede failures of response inhibition in a go/no-go task (O'Connell, et al., 2009b; Robertson et al., 1997) within the context of both selective attention and motor-preparation. The EEG spectral dynamics of interest include the hemispheric lateralization of specific frequency bands, and the cross-frequency power coupling of activity across distant regions of the cortex.

The ongoing EEG contains oscillatory activity that can be divided into frequency bands that vary with specificity in response to the cognitive demands of a particular task. The three of interest in the present study are the alpha (8–12 Hz), beta (18–24 Hz) and theta (3–5 Hz) bands. Recent evidence supports a role of the alpha rhythm in the functional disengagement of a brain region for a particular task (for reviews see Klimesch et al., 2007; Jensen and Mazaheri, in press). For example, a number of studies have reported that the task-specific disengagement of the visual system is achieved by an increase in oscillatory alpha activity (Jokisch and Jensen, 2007; Medendorp et al., 2008; Rihs et al., 2007; Romei, et al., 2007; Thut et al., 2006; Jensen et al., 2002). These findings suggest that increases in localized alpha activity serve as a mechanism by which task-irrelevant information is gated (Jensen and Mazaheri, in press; Kelly, et al., 2006; Thut, et al., 2006; Rihs et al., 2009). Furthermore, the functional role of attentionally induced alpha-band power modulation has been demonstrated by showing that the speed of overt task performance is related to occipital alpha lateralization (Thut, et al., 2006).

Whereas alpha is predominantly reported over the occipital cortex, suggesting a role for visual perception, the beta rhythm has been

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shown to be localized over somatosensory and motor cortical regions and has been related to movement preparation or suppression. A number of studies have reliably demonstrated that voluntary movement is preceded by an attenuation of beta activity over sensorimotor areas contralateral to the response hand (see Pfurtscheller and Lopes da Silva, 1999).

In contrast to the alpha and beta activity present in the sensory systems, an increase in lower frequency activity in the theta-band recorded over frontal regions has been associated with executive functions such as focused attention (Gevins et al., 1997; Ishii et al., 1999), error processing (Cohen, 2011; Cavanagh, et al., 2009; Luu and Tucker, 2001; Trujillo and Allen, 2007 please also insert), memory processes (Klimesch et al, 2001; Scheeringa et al, 2009), action adjustment (Vijver et al., in press), and inter-regional coordination of distant brain regions (Jensen and Lisman, 2000). Because theta is a high amplitude, low frequency signal, it might be particularly important for coordinating brain regions across differing frequency bands during task performance. For example, the work of Lisman and Idiart (1995) suggested that a phasic coupling between frontal theta and posterior gamma oscillations might provide the mechanism by which items are stored in working memory. Thus, in addition to the frequency-specific analysis of the roles of alpha, theta and beta bands in response inhibition, we also explore the role of theta in response inhibition in terms of its relationship to other frequency bands via cross-frequency correlational coupling (de Lange et al., 2008; Mazaheri et al., 2009, 2010). Given that alpha modulation is indicative of attentionally induced changes in the sensitivity of the visual system, we hypothesize that frontal theta may be the mechanism by which attention directs the lateralization of occipital alpha activity, and that this inter-frequency interaction is a signature of spatial attention. Furthermore, we explore the inter-frequency interactions between frontal theta and lateralized beta over the motor cortex under the hypothesis that the coordination of motor and executive processes is a critical determinant of the likelihood of generating a motor response.

Materials and methods

Participants

Ten healthy young right-handed adults (7 males) participated as subjects. All had normal or corrected-to-normal vision. Data from an additional four subjects were eliminated due either to systematic confounding eye movements (±2 μV to the left or right in their averaged electrooculograms) to the attention cues, and three were rejected due to excessive artifacts from movement, muscle activity and blinks. The artifact rejection criteria are described in more detail in the EEG Preprocessing section.

Task and stimuli

Fig. 1 illustrates an example trial sequence. Target stimuli consisted of a bilateral display consisting of two numbers from the set 1 through 5, presented 11.5° to the left and right of a central fixation point and 3.5° below the horizontal meridian. Numbers were counterbalanced so that over all trials each number appeared evenly on the left and right side of the screen and also evenly on the attended versus unattended side of the screen. Also, each number was paired with each other number an even number of times over all trials and within attended versus unattended hemifields. In order to ensure the cue-induced lateralization of attention, no trials contained the same number on both sides of the screen. Preceding each target number display, an arrow was presented at fixation, and participants were instructed to direct their covert attention in accord with the arrow direction; eye fixation on a central crosshairs was required (see below for the details of gaze monitoring). Following a jittered 1700–2000 ms stimulus onset asynchrony (SOA), the bilateral numbers were presented (100 ms duration), and participants were instructed to respond as quickly as possible to each number on the cued side (go trials) except for the number "3", in which case they were instructed to withhold a response (no-go trials). False Alarms were defined as responses to a cued-location "3", and Correct Rejections were defined as trials where the participants were able to successfully withhold responses to the cued-location "3's".

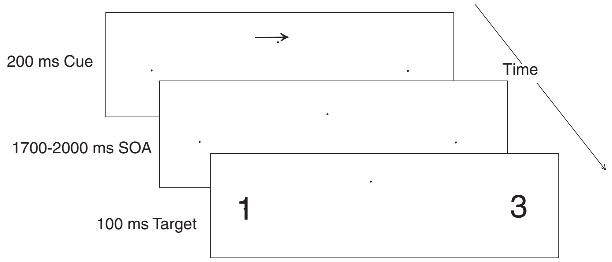

Fig. 1. Example trial. Target stimuli consisted of a bilateral display comprising of two numbers ranging from 1 to 5, presented 11.5° to the left and right of a central fixation point, and 3.5° below the horizontal meridian. Preceding each target number display, an arrow was presented at fixation, and participants were instructed to direct their covert attention in accord with the arrow direction; eye fixation on a central crosshairs was required.

Data acquisition

Scalp potentials (EEGs) were recorded using a 64-channel electrode cap containing tin electrodes (Electro-cap, Int.). All scalp channels were referenced to the right mastoid during recording; electrode impedances were kept below 5 kΩ for all participants. Data were recorded in DC mode with an online low-pass filter of 100 Hz, using a Synamps II amplifier with Scan 4.2 software. Data were digitized at a rate of 1000 samples per second and down-sampled to 250 samples per second offline. To monitor eye position, electrodes were placed on the outer left and right ocular canthi and these were referenced to each other to create a bipolar recording. Blinks were monitored with a bipolar electrode pair located above and below the left eye.

Preprocessing

The Fieldtrip software package (http://fieldtrip.fcdonders.nl) was used for the analysis of EEG data. A semi-automatic routine was used to delete trials containing artifacts. This step involved rejecting trials based on an amplitude threshold of 70 μV and then visual inspection to ensure the quality of the data. Independent component analysis (Bell and Sejnowski, 1995) was used to remove any eye artifacts not rejected by the semiautomatic routines (Jung et al., 2000). A second step, after artifact rejection, was used to eliminate residual contamination from eye movements by removing those subjects whose eyes deviated by more than ±2 μV to the left or right in their averaged electrooculograms at any time point during the cue-target period ($N=4$). Such a strict criterion ensured minimal contribution from cue-induced eye-movements given that a 3 μV change in amplitude corresponds to a change in eye position of 0.2° (Lins et al., 1993). For a discussion of this method, see Mangun and Hillyard (1991). Any subject with less than 30 trials per condition were excluded from further analysis.

Oscillatory analyses

Time-frequency representations (TFRs) of power were calculated for each trial (1.5 s pre/post-stimulus onset) using sliding Hanning tapers having an adaptive time window of three cycles for each frequency ($\Delta T = 3/f$). Similar approaches were used by Jokisch and Jensen (2007), Osipova et al. (2006), and Mazaheri et al. (2009). Our classifications of frequency bands were based on the main frequency bands used to classify the spontaneous EEG (IFSCN 1974), and prior literature (Mazaheri et al., 2009; Mazaheri and Picton, 2005; Thut et al., 2006; Van Dijk et al., 2008; Yordanova, et al., 2003). To analyze theta band-power and the trial-by-trial cross-frequency coupling between frontal theta and the lateralization of the occipital alpha and sensori-motor beta oscillations, we chose the frontal electrode site (Fz) as a seed site for analysis. For each subject and condition, the trial-by-trial correlation (Pearson) between frontal theta power and lateralized occipital alpha (contral-ipsi relative to spatial cue) and beta (left-right relative to right hand) power were calculated. The correlations values were then z-transformed using Fisher's r to z transformation to allow for statistical comparison between conditions across subjects (same procedure used in Mazaheri et al., 2009, 2010). Within-samples paired t-tests were used to assess the statistical differences in correlations between FA and CRs (see Mazaheri et al., 2010). Furthermore, to further classify the predictors that best encapsulated the probability of a failure of response inhibition and to provide unique parameter estimates for each predictive ($p<0.05$) neural measure, we included each in a modified regression model derived from Zeger and Liang (1986) that accounts for both correlated measurements within subjects (typical of a repeated-measures design) and for the non-Gaussian nature of the binary outcome variable: FA's vs. CR's.

ERP analysis

The target locked ERPs data were averaged with the sweep beginning 500 ms before the stimuli and lasting until 1000 ms after stimulus onset. ERPs were baseline corrected using the 500 ms prior to target onset. The visual P1 and N1 were measured as the mean peak amplitude between 50 and 150 ms and 150 and 250 ms post-target, respectively. These latencies were chosen by looking at the grand-averaged target-locked ERP, collapsed across conditions and response type (see Fig. 4A). Moreover, these latency intervals were consistent with previous studies looking at ERPs evoked by bi-lateral stimuli (e.g. Heinze et al., 1990).

Results

Behavior

The proportion of False Alarms to “3's” presented in the cued hemifield was (0.28) for the left hemifield and (0.26) for the right hemifield. No difference was observed between left and right hemifields in the number of False Alarms committed, $t(9)=1.434$, $p=0.185$. Furthermore, a 3 appearing at the uncued location on the trial immediately prior did not influence the ability to withhold a response, $t(9)=1.30$, $p=0.225$ for a given trial, suggesting that our pattern of results is not contingent upon pre-trial uncued 3's and that failures in response inhibition are not influenced by this pre-trial (sequential) contingency.

Electrophysiology

The analysis of the EEG recordings comprised three main aims — 1) the analysis of pre-stimulus occipital alpha lateralization to attention cues prior to FAs and CRs 2) the analysis of the pre-stimulus beta lateralization over the motor cortices, and 3) the comparison of cross-frequency correlations of frontal-theta and the alpha/beta lateralization in the FA and CR trials. In the following, we divide these analyses into separate sections.

Cue-induced lateralization of occipital alpha predicts subsequent False Alarms

As a measure of alpha lateralization, we subtracted the alpha power in the ipsilateral hemisphere (e.g., right occipital alpha when the cue pointed right) from the alpha power in the contralateral hemisphere (e.g., right occipital alpha when the cue pointed left). Fig. 2 displays the power spectra for the 1.5 s interval prior to target presentation for the CR (top) and the FA (bottom) trials. As can be seen in the figure, there is a large negative contra minus ipsi difference for Correct Rejections just prior to and during target onset that is not present for False Alarms. In contrast, the alpha activity preceding the FAs appears lateralized in the opposite direction. For CR, the normalized (log transformed) lateralization index was −0.3141, whereas it was 0.3694 for the trials in which a False Alarm was about to occur; this difference was statistically significant, $t(9)=2.5329$, $p<0.05$.

There were no significant differences in the cross-frequency correlations of frontal-theta and alpha lateralization between FAs and CRs

Next we examined the differences in cross-frequency coupling between power of frontal theta and the cue induced alpha lateralization for FAs and CRs. We chose the frontal Fz electrodes as a seed site for the analysis. The trial-by-trial alpha lateralization (the same posterior scalp sites mentioned above) in the 1.5 s interval prior to target presentation was correlated with the theta power at the Fz site. We did not find a significant difference of this correlation between FAs and CRs (−0.24 vs 0.04, $t(9)=0.98$, $p=0.3$). Moreover, using a one-sample *t*-test, this correlation was not significant for FAs ($t(9)=-1.09$, $p=0.30$) and nor was it significant when we collapsed across all the target types ($r=-0.168$, $t(9)=-0.67$, $p=0.51$).

Pre-stimulus lateralization of beta activity not different for FAs

As a measure of motor related lateralization we subtracted the beta power in electrodes C3 and C4 (electrodes overlying the motor cortex) in the 1.5 s interval prior to target presentation. We found no difference in this lateralization between FAs and CRs (0.0108 vs. 0.0105, $t\ (9)=-0.0399$, $p=0.9$).

Frontal theta activity is differentially correlated with beta lateralization in FAs and CRs

We also examined the cross-frequency coupling between frontal theta activity and lateralized beta power over the motor cortex during the cue-target interval as a function of subsequent errors in response inhibition. The correlation values between frontal theta and beta lateralization across FA and CR trials in single subjects can be seen in Fig. 3. We found that this correlation was different across FA and CR trials with mean correlations of (0.345 vs −0.341, $t(9)=4.2$, $p<0.005$). Specifically, prior to the commission of a FA a reduction in contralateral (relative to ipsilateral to response hand) beta power corresponded with an increase in theta power. In addition, we examined the amplitude of just the frontal-theta in the cue-target interval between FA and CRs and found it was not significantly different ($t(9)=-1.1623$, $p=0.2$). Thus, this result provides a novel application of a measure of inter-frequency coupling across brain regions that differentiates between two conditions despite no power differences in the frequencies between the conditions.

Parameter estimates for alpha lateralization and theta–beta coupling

Given that occipital alpha lateralization preluded failures of response inhibition, and that increased theta–beta coupling preceded such errors, we tested the possibility that these two predictors may be correlated in terms of their predictive utility. Such a finding would suggest that these two neural measures, although frequency-specific and topographically unique, might share a common cognitive process that manifests as a subsequent failure of response inhibition. To explore such a possibility, we included the normalized alpha lateralization measurements and theta–beta correlations for each subject as predictors in a Generalized Estimating Equation (Zeger and Liang, 1986) using a logistic (rather than linear) link function with response category (FA vs. CR) as the binary dependent variable. The inclusion of both neural predictors allows for the predictive variance of each independent variable of interest to be simultaneously estimated, while allowing for the possible shared variance between the two measures to influence parameter estimates. Results of this analysis reveal that each measure significantly predicts subsequent behavior as revealed by significant parameter estimates for alpha lateralization ($B=5.992$, $\chi 2=8.675$, $p<0.01$) and theta–beta coupling (B=

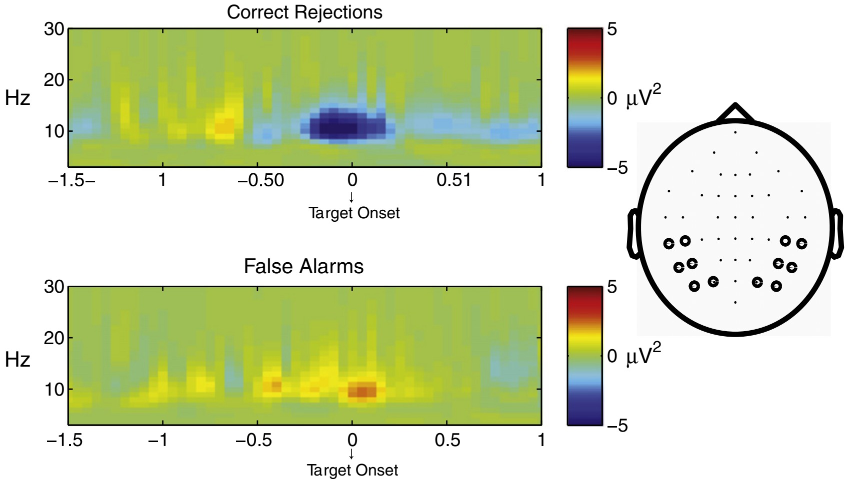

Fig. 2. The time course of cue-induced alpha (8–12 Hz) lateralization (contra-ipsi) in the 1.5 s prior to target stimulus presentation. The alpha power was higher in the ipsilateral hemisphere compared with the contralateral hemisphere for subsequent Correct Rejections. The reverse was true for trials in which a False Alarm occurred.

-5.182, $\chi 2 = 8.327$, $p < 0.01$). The finding that each predictor is strongly associated with subsequent behavior suggests unique predictive utility of alpha lateralization and of theta–beta coupling respectively. Furthermore, we do not observe significant correlation between alpha lateralization and theta–beta coupling across subjects ($p > 0.10$). The results of these analyses when combined with the distinct topographies of each predictor strongly imply modular frequency-specific neural networks that independently operate to contribute to subsequent failures of response inhibition.

Different lateralized event-related responses to targets for False Alarms and Correct Rejections

The onset of the stimulus array elicited a P1/N1 with a maximal amplitude in the occipital electrodes over both hemispheres. The topography of the N1 and P1 component collapsed across condition and response type can been seen in Fig. 4B. We explored the role of the early and late deflections of this bilateral P1/N1 complex in separate 2 × 2 ANOVAs with hemisphere (contra vs. ipsilateral) and subsequent behavior (False Alarm vs. Correct Rejection) as variables. For the P1 component, we found a main effect of laterality, $F(1,9) = 13.346$, $p = 0.005$, showing that the cue induced a greater positivity in the hemisphere contralateral to the cue direction upon target presentation. However, this early sign of selective target processing was not critical to correct behavioral performance, as evidenced by a non-significant hemisphere × subsequent behavior interaction, $F(1,9) = 1.219$, $p = 0.298$. For the N1 component, we also observed a main effect of laterality with a larger negativity in the hemisphere ipsilateral to the cue direction, $F(1,9) = 8.206$, $p = 0.019$.

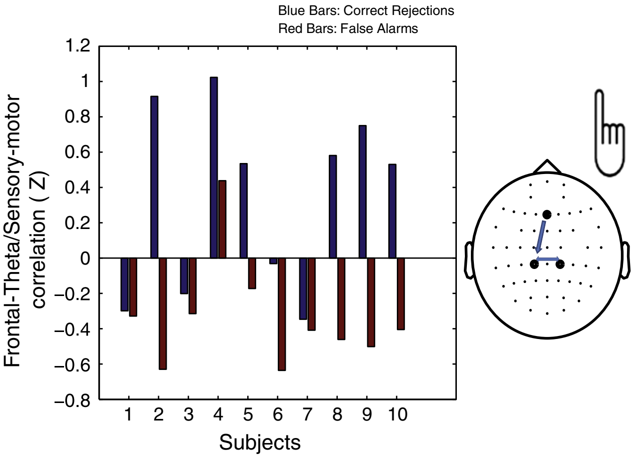

Fig. 3. The trial-by-trial correlations between frontal theta (3–5 Hz) and beta power (18–24 Hz) over the contralateral motor-cortex. There was a negative coupling between frontal theta and lateralized beta power specifically for the trials in which a False Alarm was about to occur (in red).

In contrast to the early positivity, however, the attention-induced modulation of the N1 component was critically related to subsequent behavioral performance with a significant hemisphere × subsequent behavior interaction, $F(1,9) = 5.856$, $p = 0.039$ showing a larger negativity in the ipsilateral hemisphere for those trials in which participants were about to correctly withhold a response compared with those trials in which a False Alarm was about to occur (Fig. 4). Thus, we replicate the sustained attention-induced positivity observed in Heinze et al. (1990), and further demonstrate that the later phase of this attention related positivity over contralateral visual cortex is correlated with subsequent behavior. This within-trial correlation between ERPs and behavior is consistent with previous work which has shown that the behavioral and ERP related contingencies of prior trials can predict performance on the current trial (Hajcak, et al., 2005; Nieuwenhuis et al., 2007; Ridderinkhof et al., 2003; Eichele et al., 2010).

Discussion

Several findings help paint a picture of the network-level and frequency-specific substrates of imminent failures of response inhibition during selective spatial attention. First, we demonstrate that a failure to lateralize occipital alpha activity in response to an attention-directing arrow is predictive of subsequent False Alarms. Moreover, we find a distinct pattern of cross-frequency coupling of frontal-theta and beta-lateralization that also preluded subsequent FAs independent of any shared variance with alpha lateralization.

A number of studies have suggested that the disengagement of sensory structures not relevant for a given task may be achieved by an increase in alpha activity in those sensory structures (Jensen and Mazaheri, in press; Kelly et al., 2006; Klimesch et al., 2007; Medendorp et al., 2008; Mazaheri et al., 2010). In the visual system, occipital alpha lateralization has been shown to be predictive of visual sensitivity (Thut, et al., 2006) and has been shown to play a causal role in visual perception (Romei, et al., 2010). In the present work, we find that attention to a task-relevant stimulus, and the corresponding suppression of an unattended stimulus in the un-cued hemifield (as indexed by alpha lateralization), is critically important for the successful inhibition

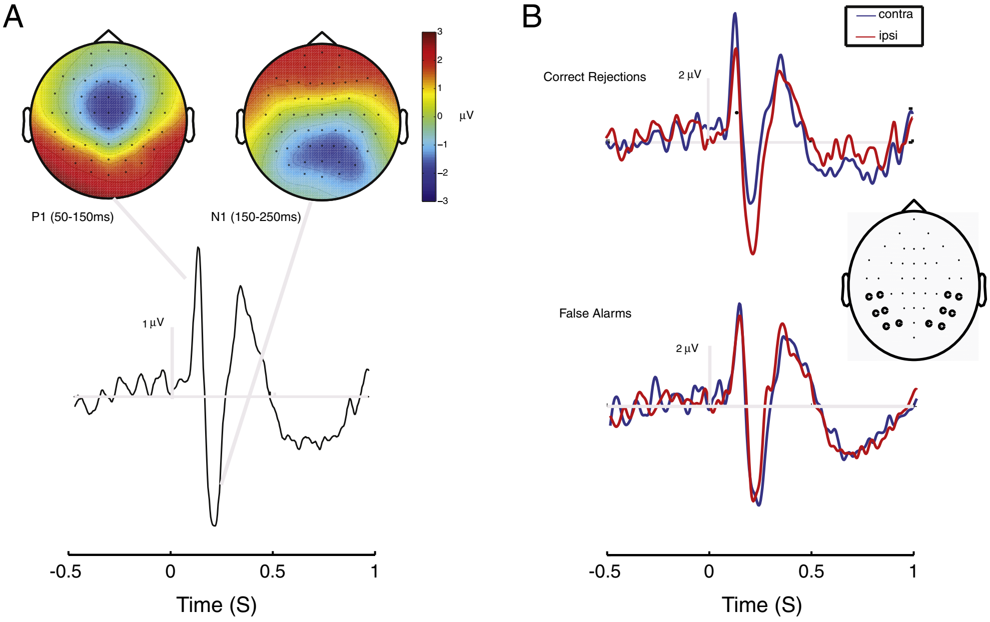

Fig. 4. A) The topography of the average-target P1 (50–150 ms) and N1 (150–250 ms) evoked components, collapsed across conditions and response types. B) The averaged target-evoked response in the Ipsilateral (red) and Contralateral (blue) hemispheres (to cue direction) for False Alarm trials and Correct Rejections. The lateralization of the N1 response (150–250 ms) was particularly relevant for successful subsequent behavior. Waveforms are plotted positive voltage upward, and the recordings are from the marked occipital electrode sites. Target onset is at time = 0 ms.

of a pre-potent motor response. The reduction in alpha lateralization observed prior to FA trials could suggest a misreading of the cue, or failure to process it properly.

Interestingly, despite no power differences in the theta or beta bands between FA and CR trials, we found differences in the cross-frequency correlations, with a negative correlation between beta lateralization and theta power for trials in which an FA was about to occur. Given that lateralized beta suppression over the motor cortex is particularly relevant for motor imagery (Neuper, et al., 1999) and self-paced movements (Stancák and Pfurtscheller, 1996), we conclude that this anti-correlation reflects an independent neural marker of response activation that specifically occurs prior to an imminent failure to withhold a response. It should be noted that in contrast to the studies reported we did not observe a significant beta lateralization in the cue to target interval. One possible explanation for this discrepancy is that some of the previous studies have used cues to initiate movements, and/or have focused on the interval just prior to the movement onset. In contrast, our analysis focused on the activity in the interval prior to a go/no go stimulus that could trigger the motor response. Beta lateralization in this interval might be too subtle to be picked up by comparing average activity across trials. One caveat of the present study is the relatively limited sample size. A study with a larger sample size could further elucidate and quantify the independent contributions of the attentional and motor systems in failures of response inhibition.

Finally, whereas other work has illustrated the evoked amplitude changes of prior trials can predict subsequent behavior (Eichele, et al., 2010; Hajcak, et al., 2005; Nieuwenhuis, et al., 2007; Ridderinkhof et al., 2003), the present work extends these findings to reveal a predictive measure of the attentionally induced lateralization of the evoked response *within* a trial just prior to the execution of an action. Those trials in which a False Alarm occurred did not show the lateralized amplitude difference immediately prior to behavior that was observed in trials where a Correct Rejection was about to occur. It is interesting to note that the present lateralized amplitude difference in the N1 range at the occipital electrodes and the lateralized alpha response, also at the occipital electrode sites, both predict subsequent behavior. Thus, if alpha indexes functional inhibition of cortical regions (Händel et al., 2010; Mazaheri and Jensen, 2010) these two markers might reflect the common task of filtering the unattended input with the pre-stimulus alpha, reflecting a preparatory state of the visual system that might subsequently be expressed as a target-evoked lateralized response. Indeed, it has been previously demonstrated that the trial by trial changes in spectral power might be a causal determinant of evoked amplitude changes (Nikulin et al., 2007; Mazaheri and Jensen, 2008; Van Dijk et al., 2010).

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