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Prestimulus Oscillations in the Alpha Band of the EEG Are Modulated by the Difficulty of Feature Discrimination and Predict Activation of a Sensory Discrimination Process

Daniel M. Roberts, John R. Fedota, George A. Buzzell, Raja Parasuraman, and Craig G. McDonald

Abstract

■ Recent work has demonstrated that the occipital–temporal N1 component of the ERP is sensitive to the difficulty of visual discrimination, in a manner that cannot be explained by simple differences in low-level visual features, arousal, or time on task. These observations provide evidence that the occipital–temporal N1 component is modulated by the application of top–down control. However, the timing of this control process remains unclear. Previous work has demonstrated proactive, top–down modulation of cortical excitability for cued spatial attention or feature selection tasks. Here, the possibility that a similar top–down process facilitates performance of a difficult stimulus discrimination task is explored. Participants performed an oddball task at two levels of discrimination difficulty, with difficulty manipulated by modulating the similarity between target and nontarget stimuli. Discrimination processes and cortical excitability were assessed via the amplitude of the occipital–temporal N1 component and prestimulus alpha oscillation of the EEG, respectively. For correct discriminations, prestimulus alpha power was reduced, and the occipital–temporal N1 was enhanced in the hard relative to the easy condition. Furthermore, within the hard condition, prestimulus alpha power was reduced, and the occipital–temporal N1 was enhanced for correct relative to incorrect discriminations. The generation of ERPs contingent on relative prestimulus alpha power additionally suggests that diminished alpha power preceding stimulus onset is related to enhancement of the occipital–temporal N1. As in spatial attention, proactive control appears to enhance cortical excitability and facilitate discrimination performance in tasks requiring nonspatial, feature-based attention, even in the absence of competing stimulus features. ■

INTRODUCTION

Executive control over sensory-related processing, and the ability to discriminate between differing stimuli, is a central aspect of visual cognition. However, the exact mechanism underlying top–down control of the visual discrimination process remains unclear. Several reports have associated the occipital–temporal N1 component with a stimulus discrimination process (Hopf, Vogel, Woodman, Heinze, & Luck, 2002; Vogel & Luck, 2000; Ritter, Simson, Vaughan, & Macht, 1982). In addition, a recent report showed the N1 component to be additionally modulated by the difficulty of the discrimination being made (Fedota, McDonald, Roberts, & Parasuraman, 2012). As Fedota et al. (2012) modulated discrimination difficulty by varying the similarity between serially presented distractor stimuli and physically identical target stimuli, they argue that the increase in N1 amplitude within a hard discrimination context reflects the successful application of increased top–down executive control. However, whether this top–down control process is instantiated proactively (prestimulus) or reactively (poststimulus) remains unknown.

The majority of existing work on the neurophysiology of top–down attention and subsequent task performance has occurred within the domain of visuospatial, rather than feature-based, attention. Specifically, the manipulation of top–down executive control via cued spatial attention tasks has demonstrated that power in the alpha band (an oscillation of approximately 8–12 Hz) of the EEG is enhanced at occipital–parietal sites ipsilateral to the cued target location (Händel, Haarmeier, & Jensen, 2010; Kelly, Lalor, Reilly, & Foxe, 2006; Worden, Foxe, Wang, & Simpson, 2000), suppressed at occipital–parietal sites contralateral to the cued location, and is related to subsequent task performance (Gould, Rushworth, & Nobre, 2011; Kelly, Gomez-Ramirez, & Foxe, 2009; Wyart & Tallon-Baudry, 2009; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). Thus, a strong link between prestimulus alpha power and top–down, spatial attention has been established.

Task-related suppression of alpha oscillations has been suggested to reflect enhanced excitability (Pfurtscheller, 2006) or "release from inhibition" (Klimesch, 2012;

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Klimesch, Sauseng, & Hanslmayr, 2007) of cortical regions involved in task-dependent processes. In line with this interpretation, increases in the magnitude of the alpha rhythm have been observed within regions of cortex that are thought to be irrelevant to a particular task (Foxe & Snyder, 2011). Taken together with previous work on cued spatial attention, this suggests that cortical excitability within the occipital–parietal cortex is subject to top–down control and that failures of such control may impair performance (Gould et al., 2011). Recent work by Snyder and Foxe (2010) has extended the relationship between prestimulus alpha and cued visuospatial attention (Händel et al., 2010; Thut et al., 2006; Worden et al., 2000) to include feature-based attention.

Specifically, it was demonstrated that the locus of alpha suppression shifts from dorsal to ventral visual cortex when participants are cued to attend to either the motion or color of a compound stimulus, respectively (Snyder & Foxe, 2010). Similarly, Min and Herrmann (2007) reported increased parietal alpha magnitude preceding an attend-shape condition relative to an attend-color condition of a combined shape–color task. The attend-shape condition, in which the color dimension of the stimulus had to be ignored, was also associated with increased latency of both the P3 component and behavioral response relative to the attend-color condition. From these findings, Min and Herrmann (2007) suggest that the color dimension of the composite stimulus was of greater salience and argue similarly to Foxe and Snyder (2011) that the increase in parietal alpha power reflects increased inhibition when attempting to ignore the color dimension.

The relationship between prestimulus alpha power and within-subject task performance has been demonstrated for several nonspatial visual tasks in which suppression of the alpha rhythm was related to improved performance. These tasks include detection of a visual stimulus presented at threshold (Van Dijk, Schoffelen, Oostenveld, & Jensen, 2008; Ergenoglu et al., 2004) and detection of an infrequently occurring above-threshold stimulus (O'Connell et al., 2009). In addition, between-subject differences in task performance have also been related to alpha power. That is, the magnitude of prestimulus alpha power has been shown to discriminate between participants who perform at chance (in comparison with those that perform above chance) on a letter discrimination task, an effect that is absent within other frequency bands (Hanslmayr et al., 2007).

Previous work has reported on the relationship between the magnitude of the prestimulus alpha oscillation and the likelihood of detecting a central stimulus presented at detection threshold (Van Dijk et al., 2008; Ergenoglu et al., 2004). However, to our knowledge, no existing report has investigated the relation between prestimulus alpha magnitude and the anticipation of nonspatial visual discrimination difficulty. Although Van Dijk et al. (2008) included a small number of "easy" above-threshold stimuli within their discrimination paradigm (4% of total), presentation of "easy" above-threshold stimuli was randomized with the more frequent at-threshold stimuli (70% of total), and these "easy" trials were not analyzed with respect to prestimulus alpha magnitude or behavioral performance. As these paradigms did not explicitly manipulate task dimensions such as difficulty, it is unclear whether the observed relation between prestimulus alpha magnitude and nonspatial discrimination performance is a function of top–down control or, alternatively, the outcome of a stochastic process.

Considering the consistent observation that modulation in the magnitude of the prestimulus alpha oscillation is related to proactive attention to a region of space or feature dimension of a combined stimulus (Foxe & Snyder, 2011; Händel et al., 2010; Snyder & Foxe, 2010; Min & Herrmann, 2007; Thut et al., 2006; Worden et al., 2000), it is likely that a similar increase in cortical excitability also underlies top–down control processes enacted to maintain performance when presented with difficult visual discriminations. Control processes, which are proactive or instantiated in expectation of task demands, have been suggested to be distinct from those that are reactive or instantiated in response to task demands (Braver, 2012; Braver, Paxton, Locke, & Barch, 2009; Braver, Gray, & Burgess, 2007). As the N1 modulation previously described by Fedota et al. (2012) occurs after stimulus onset, it is unclear whether the putative control processes are enacted proactively or reactively. However, investigation of the neural activity before stimulus onset, such as prestimulus alpha magnitude, may clarify whether this control process is at least in part instantiated proactively.

In this study, participants completed an oddball task involving two difficulty levels. As described by Fedota et al. (2012), the hard task condition required greater top–down control over the stimulus discrimination process, relative to the easy task condition. To determine whether this top–down control process was implemented in a proactive (vs. reactive) manner, the magnitude of the prestimulus alpha oscillation was assessed at the occipital–parietal electrode sites where the visual N1 was maximal and compared with both N1 amplitude and subsequent behavioral performance. If the control process previously identified by Fedota and colleagues (2012) is instantiated proactively, then a decrease in the magnitude of the occipital–temporal alpha oscillation preceding stimulus onset should be observed. Specifically, this enhancement is predicted to occur within the region of extrastriate visual cortex generating the occipital–temporal N1 (Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994). In addition, decreases in the magnitude of the prestimulus alpha oscillation are predicted to be related to increases in the amplitude of the subsequent N1 component.

METHODS

Participants

This study is based in part on a reanalysis of existing data (see Fedota et al., 2012) as well as data collected from

three additional participants. Additional participants were collected because it was anticipated that the extended epoch length (required for the analysis of prestimulus alpha power) would increase the likelihood of a given trial containing artifact and possibly prevent the use of all original participants. Following informed consent, 17 individuals participated in the experiment in exchange for course credit. One participant was removed because of insufficient hard-task-context error trials remaining for alpha-contingent partitioning after artifact rejection. The remaining 16 participants (11 women) ranged between 18 and 39 years old (μ = 23.6 years old), were right handed, had normal or corrected-to-normal vision, and had no reported history of neurological illness.

Procedure

The stimuli and procedure are identical to those previously described in Fedota et al. (2012). Participants completed an oddball task with serially presented targets and distractors at two levels of difficulty. Stimuli were Gabor patches (six cycles per image, 2° × 2° visual angle subtended) presented 1.5° above a fixation dot (0.3° × 0.3°) at the center of the screen on a gray background. The fixation dot remained on screen throughout each block. Difficulty was manipulated by alteration of nontarget–target similarity, while maintaining identical target stimuli across blocks. In both task contexts, target stimuli were vertical (no rotation). In the easy task context, nontargets were rotated 10° to the left or right of vertical, whereas in the hard task context, nontargets were rotated 2.5° to the left or right of vertical. During each experimental trial, a single stimulus (target or nontarget) was presented. Examples of rotated nontargets and vertical targets are displayed in Figure 1.

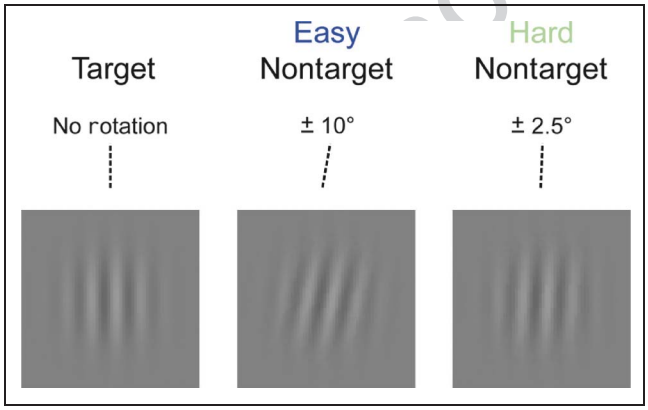

Figure 1. Representative target and nontarget stimuli from the easy and hard task contexts. Target stimuli were equivalent between task contexts and were presented without rotation. Nontarget stimuli were rotated either to the left or right of vertical, here presented rotated to the right, with differing degrees of rotation between task contexts. In the easy task context, nontargets were rotated 10° from vertical. In the hard task context, nontargets were rotated 2.5° from vertical. Dashed lines, rotated to the same degree as each stimulus, are included as a visual aid for the reader and were not presented in the experiment.

Participants were instructed to respond to the vertically oriented target stimuli with their right hand via button box, while withholding any response to the rotated nontarget stimuli. Target stimuli were rare, occurring on 20% of trials, whereas nontarget stimuli were frequent, occurring on 80% of trials, with equal numbers of left and right rotated nontargets. Participants were instructed that speed and accuracy of response were equally important for task performance.

Each trial began with the presentation of either a target or nontarget stimulus (in pseudorandom order) that remained on screen for 100 msec. Response was collected for 700 msec after stimulus onset, followed by an intertrial interval jittered between 500 and 900 msec. Each block in the experiment consisted of 70 trials, with the difficulty of nontargets alternating every four blocks and the difficulty of the starting block counterbalanced across participants. Participants completed 40 blocks throughout the experiment, experiencing 2,800 trials in total, including 560 target trials. The experiment took approximately 90 min to complete, including self-timed breaks between blocks. The experimental procedure was approved by the George Mason University Human Subjects Review Board.

EEG Data Acquisition

EEG was acquired via a SynAmps2 amplifier, 64-channel QuickCap cap, and SCAN 4.3 recording software (Compumedics Neuroscan, Charlotte, NC) at a sampling rate of 500 Hz. Thirty-eight channels were recorded from standard 10–20 sites: Fpz, Fp1, Fp2, Fz, F3, F4, F7, F8, FCz, FC3, FC4, FT7, FT8, Cz, C3, C4, T7, T8, CPz, CP3, CP4, TP7, TP8, Pz, P3, P4, P7, P8, POz, PO3, PO4, PO7, PO8, Oz, O1, O2, M1 (A1), and M2 (A2), with physical reference located approximately 2 cm posterior to Cz. Blinks and vertical and horizontal eye movements were monitored via bipolar-referenced EOG electrodes placed above and below the left eye and lateral to the left and right orbits. EEG was filtered online with a band-pass between 0.1 and 40 Hz.

Data Analysis

Signal processing was performed using MATLAB (vR2011b) in conjunction with the EEGLAB toolbox (Delorme & Makeig, 2004) and custom scripts. Statistics were computed using the R statistics environment v3.0.1 (R Core Team, 2013). All ANOVA models were computed with type III sums of squares. Violations of sphericity were assessed where applicable with Mauchly's test and corrected if necessary with the Greenhouse–Geisser correction.

Behavior

Behavioral trials in which a response was given earlier than 150 msec or later than 650 msec relative to stimulus onset were considered invalid and were excluded

from further analysis. For the remaining trials, percent of accuracy was computed individually for target trials (requiring a response) and nontarget trials (requiring no response), for the easy and hard task contexts. Furthermore, average response time (RT) to correct target trials was computed for the easy and hard task contexts.

EEG Preprocessing

Continuous data were labeled according to task context (easy, hard), stimulus type (target, nontarget), and behavioral accuracy. Epochs were extracted from −500 to 550 msec around stimulus onset. Any epochs containing activity ±75 μV on either vertical or horizontal EOG channels were rejected from further analysis. No offline filtering was performed, following the 0.1- to 40-Hz online filter previously described. Two noisy channels (FC3 and Fp2) were removed from a single participant. For presentation of grand-averaged topographic maps, these two channels were reconstructed using spherical interpolation via the EEGLAB function eeg_interp. EEG and ERP analyses were restricted to target trials only, to maintain identical physical stimulus properties across conditions. As easy misses did not occur with great enough frequency to be analyzed with respect to electrophysiology, EEG and ERP analyses included three conditions: easy hit, hard hit, and hard miss. Identical epochs were used for both ERP and spectral analysis, although signal processing diverged following preprocessing to methods specific to ERP amplitude and spectral power extraction.

ERP Processing: N1 and P1 Amplitude

Following preprocessing, the mean time-domain activity in the portion of −200 to 0 msec of the baseline period was subtracted from each epoch and channel. Both P1 and N1 effects were assessed between difficulty and accuracy conditions. Whereas modulations in N1 amplitude are of direct interest, modulations in the P1 component were additionally assessed to determine the specificity of any N1 effects. Visual inspection of grand-averaged waveforms collapsed across all conditions identified PO8 as the electrode where the N1 is most prominent; PO7 was additionally analyzed to investigate possible lateralization effects of task condition effects. Electrode sites over lateral–occipital cortex, such as PO7 and PO8, have previously been reported as the location where the visual N1 is most prominent (Hopf et al., 2002; Vogel & Luck, 2000).

Time windows were selected based on visual inspection of grand-averaged ERPs, collapsed across all conditions and channels of interest (PO7 and PO8). P1 amplitude was defined as the mean activity within the window 118-to-158 msec after stimulus onset, whereas N1 amplitude was defined as the mean activity within the window 168-to-208 msec after stimulus onset.

Spectral Processing: Prestimulus Alpha Magnitude

Following preprocessing, the data within the prestimulus period of −500 to −2 msec were selected for each epoch and channel. Each prestimulus segment was linearly detrended using the MATLAB function detrend, then transformed to power spectral density (PSD) via a 256-point hamming-windowed Fourier transform, yielding frequency bins of width 1.953 Hz. Alpha power was defined as the PSD of the frequency bin with center nearest 10 Hz, here 9.766 Hz, with range of 8.789–10.742 Hz. Before aggregation across conditions, the PSD in each trial was converted from units of raw PSD ($\mu V^2/Hz$) to decibel (dB) PSD [$10 * \log_{10} (\mu V^2/Hz)$] because of the positive skewness (right-tailed) distribution of raw PSD values.

Prestimulus Alpha Magnitude and Previous Trial Type

Only target trials were included in the ERP and prestimulus alpha analyses. As previously described, target trials were physically identical in the easy and hard task contexts. However, nontarget trials varied in degree of rotation between easy and hard task contexts. To investigate the possibility that prestimulus alpha modulations between easy and hard hit trials are because of overlap from preceding, physically dissimilar nontarget stimuli, easy and hard hit trials were additionally partitioned contingent on whether the previous trial type was a target or nontarget stimulus.

Component Amplitude Sorted by Prestimulus Alpha Magnitude Bin

The relation between prestimulus alpha and subsequent ERP magnitude was assessed via computation of ERPs contingent on relative prestimulus alpha magnitude. In a procedure adapted from Rajagovindan and Ding (2011), trials from each of the three conditions under analysis for N1, P1, and prestimulus alpha modulation (easy hit, hard hit, hard miss) were independently sorted into two equally sized nonoverlapping bins, according to whether that trial was above or below the median prestimulus alpha magnitude for that condition. Trials were binned according to prestimulus alpha PSD independently for each condition and for each participant. As the two bins were not overlapping, each contained 50% of the total number of trials for that condition, with the first bin (low alpha) containing the first half and the second bin (high alpha) containing the second half of sorted trials. For cases in which a condition contained an odd number of trials, the trial representing the median prestimulus alpha magnitude for that condition was excluded from the binned analysis. N1 and P1 amplitudes were extracted from ERPs composed of trials from each of the two bins, for each of the three conditions, using the same electrode sites (PO7 and PO8) and time windows (118–158 and 168–208 msec) as for the more traditional condition contingent ERPs previously

Table 1. Mean Accuracy (Proportion Correct) and RT (Milliseconds Relative to Stimulus Onset) in Easy and Hard Task Contexts

	Accuracy	*RT*
Easy	0.984 (0.003)	459.613 (8.473)
Hard	0.877 (0.021)	485.935 (9.561)

*SEM*s are given in parentheses.

described. Again, although N1 amplitude relative to prestimulus alpha was of primary interest, the procedure was applied to P1 amplitude as well to assess the specificity of the effect on the N1 component. In addition, as visual inspection of the ERP waveforms split on prestimulus alpha magnitude suggested that other time points may have been modulated by the alpha level preceding stimulus onset, a sample-by-sample analysis of all poststimulus time points was also employed. Specifically, the ERP amplitude at each poststimulus time point was compared for the same ERP waveforms used in the analysis of prestimulus alpha power on subsequent N1 and P1 amplitude. Furthermore, the mean activity in the ERP prestimulus baseline (−200 to 0 msec relative to stimulus onset) was computed for each electrode site, condition, and alpha bin combination. These values were obtained before the standard baseline correction (after which all condition baselines would equal 0 μV by definition) and were collected to assess the presence of a nonspecific linear offset in ERP magnitude that could have resulted from the alpha binning procedure.

RT Sorted by Prestimulus Alpha Magnitude Bin

The relation between prestimulus alpha and subsequent RT was investigated by comparing the average RT in the two prestimulus alpha bins described in the above section. Only the easy hit and hard hit conditions were included in this analysis, as the hard miss trials contain no responses.

RESULTS

Behavior by Task Context

RT

The difference in RT to targets within the easy versus hard task context was assessed via a two-tailed paired-samples t test (Table 1, Figure 2). Participants were faster to respond in the easy task context relative to the hard task context, $t(15) = -3.175$, $p = .006$.

Accuracy

The difference in response accuracy within the easy versus hard task context was assessed via a two-tailed paired-samples t test (Table 1, Figure 2). Participants were more accurate in the easy task context relative to the hard task context, $t(15) = 5.408$, $p < .001$.

Effects of Task Context and Performance on Electrophysiology

The effect of task context (easy, hard), restricted to correct target trials, as well as the effect of performance within the hard task context (hit, miss) were evaluated for N1 amplitude, P1 amplitude, and prestimulus alpha power. Analyses were restricted to target trials, in which physically identical target stimuli were presented across easy and hard task contexts; the dissimilarity in the degree of rotation of nontarget stimuli across task contexts can influence early visual potentials such as P1 and N1. The same trial classes were used for the investigation of prestimulus alpha power to maintain the use of identical trials across analyses.

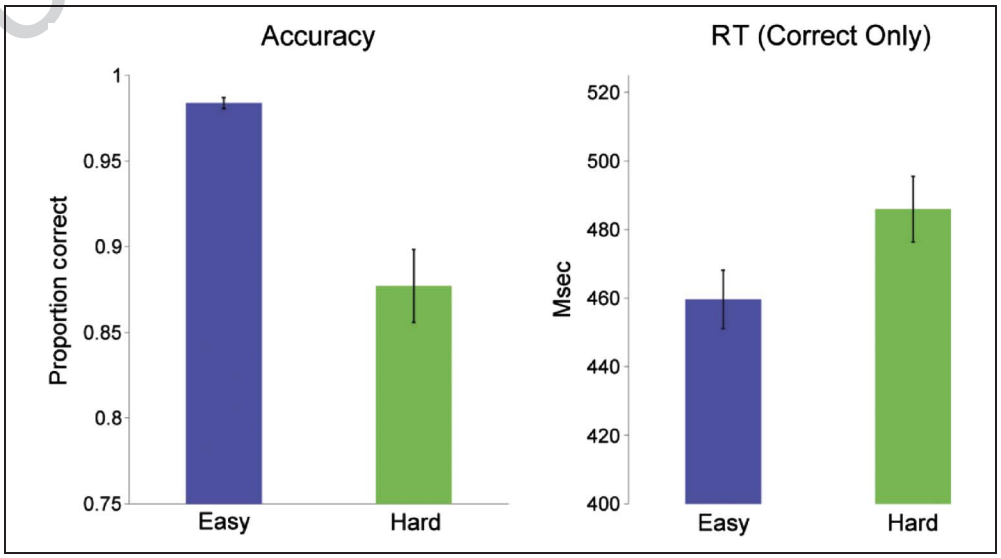

Figure 2. Behavioral accuracy, and correct trial RT, for the easy and hard task contexts. Error bars represent ±*SEM*. Participants were both less accurate and slower to respond in the hard relative to easy task context.

Table 2. Mean P1 Amplitude, N1 Amplitude, and Prestimulus Alpha Magnitude for Electrode Sites PO7 and PO8, at Each of the Three Conditions of Interest

Condition	*Site*	*P1 Amp. (μV)*	*N1 Amp. (μV)*	*Alpha Mag. (dB μV^2/Hz)*
Easy hit	PO7	2.427 (0.539)	0.894 (0.762)	2.808 (1.397)
	PO8	2.990 (0.816)	−0.018 (1.093)	3.907 (1.418)
Hard hit	PO7	2.409 (0.579)	0.521 (0.709)	2.169 (1.171)
	PO8	2.413 (0.978)	−1.170 (1.054)	3.043 (1.120)
Hard miss	PO7	2.290 (0.587)	1.124 (0.645)	3.324 (1.330)
	PO8	2.862 (0.854)	−0.224 (0.931)	3.854 (1.291)

*SEM*s are given in parentheses. Amp. = amplitude; Mag. = magnitude.

N1

A two-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8) and (2) task context (easy, hard) was used to assess the effect of task difficulty on N1 amplitude, restricted to correct trials only (Table 2, Figure 3). Target stimuli in the easy task context elicited smaller amplitude N1s relative to target stimuli in the

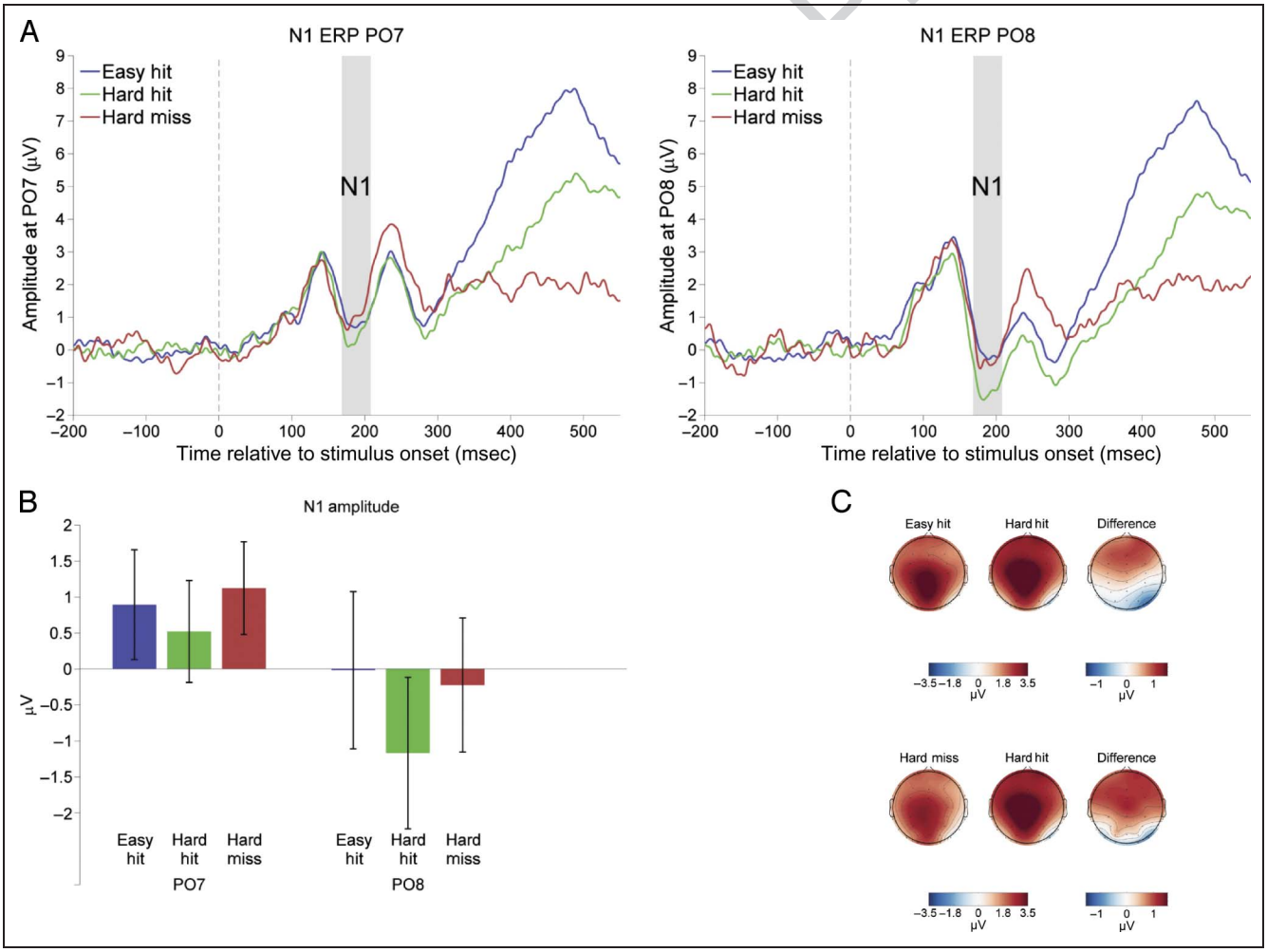

Figure 3. A displays ERP waveforms for the three conditions of interest at electrode sites PO7 and PO8. The region defining the mean N1 amplitude is shaded in gray. B indicates the mean N1 amplitude for each of the three conditions, separately for sites PO7 and PO8, with error bars representing ±*SEM*. C (top) displays the topography of mean N1 amplitude for the easy hit condition, hard hit condition, and hard hit–easy hit condition difference. C (bottom) displays the topography of mean N1 amplitude for the hard miss condition, hard hit condition, and hard hit–hard miss condition difference (bottom).

hard task context, $F(1, 15) = 4.737$, $p = .045$. The main effect of electrode site was not significant ($p > .08$); however, there was a significant interaction between electrode site and task context, $F(1, 15) = 6.803$, $p = .020$, such that the effect of difficulty on N1 amplitude was larger at electrode site PO8.

A two-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8) and (2) performance (hit, miss) was used to assess the effect of task performance on N1 amplitude, restricted to hard target trials only (Table 2, Figure 3). There was a main effect of electrode site, such that N1 amplitude was greater at electrode site PO8, relative to site PO7, $F(1, 15) = 5.236$, $p = .037$. Additionally, there was a main effect of performance, such that target stimuli in hit trials elicited larger amplitude N1s in comparison with target stimuli in miss trials, $F(1, 15) = 21.407$, $p < .001$ (Figure 3). The Site × Performance interaction was not significant ($p = .276$).

P1

A two-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8) and (2) task context (easy, hard) was used to assess the effect of task difficulty on P1 amplitude, restricted to correct trials only (Table 2). Neither the main effect of electrode site ($p = .733$), nor the main effect of difficulty ($p = .324$), nor the interaction between electrode site and difficulty ($p = .080$) reached significance.

A two-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8) and (2) performance (hit, miss) was used to assess the effect of task performance on P1 amplitude, restricted to hard target trials only (Table 2). Neither the main effect of electrode site ($p = .718$), nor the main effect of accuracy ($p = .615$), nor the interaction between electrode site and accuracy ($p = .206$) reached significance.

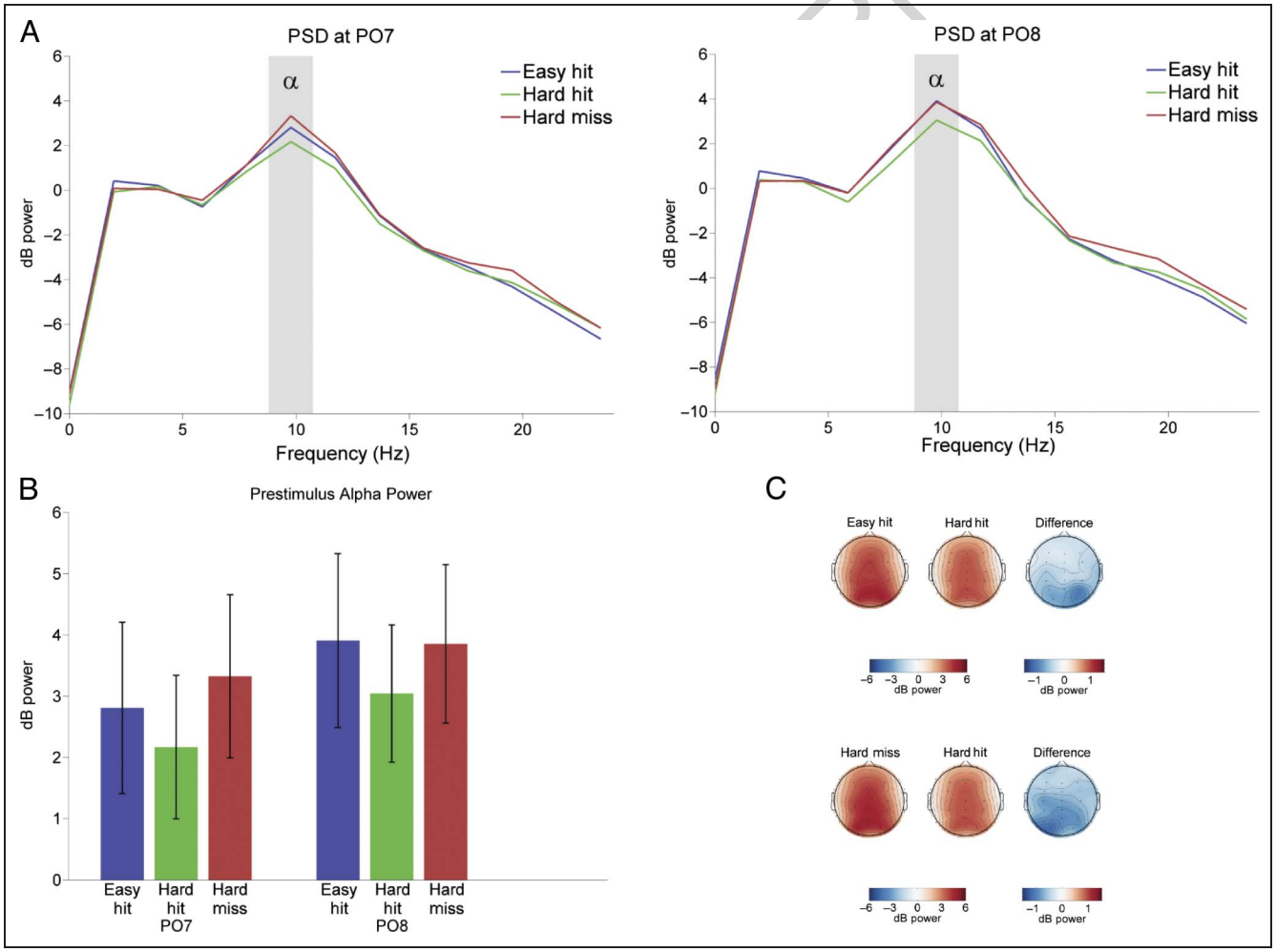

Figure 4. A displays the PSD within the prestimulus period of −500 to −2 msec, for the three conditions of interest at electrode sites PO7 and PO8. The width of the frequency bin defining the alpha oscillation is shaded in gray. B indicates the alpha power for each of the three conditions, separately for sites PO7 and PO8, with error bars representing ±*SEM*. C (top) displays the topography of alpha power for the easy hit condition, hard hit condition, and hard hit–easy hit condition difference. C (bottom) displays the topography of alpha power for the hard miss condition, hard hit condition, and hard hit–hard miss condition difference (bottom).

Table 3. Mean Prestimulus Alpha Magnitude (in dB $\mu V^2/Hz$) for Electrode Sites PO7 and PO8 in Both the Easy and Hard Task Contexts, for Hit Trials That Were Preceded by Either a Target or Nontarget Stimulus Type

	Previous Target	*Previous Nontarget*
PO7		
Easy	1.849 (1.239)	3.160 (1.467)
Hard	1.058 (1.236)	2.471 (1.171)
PO8		
Easy	2.929 (1.400)	4.208 (1.450)
Hard	2.295 (1.253)	3.257 (1.114)

*SEM*s are given in parentheses.

Prestimulus Alpha PSD

A two-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8) and (2) task context (easy, hard) was used to assess the effect of task difficulty on prestimulus alpha PSD, restricted to correct trials only (Table 2, Figure 4). There was a main effect of electrode site, such that the PSD was greater at site PO8, relative to site PO7, $F(1, 15) = 5.401$, $p = .035$. Additionally, there was a main effect of task difficulty, such that target stimuli in the easy task context were preceded by greater alpha PSD relative to target stimuli in the hard task context, $F(1, 15) = 6.300$, $p = .024$. The Site × Difficulty interaction was not significant ($p = .234$).

A two-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8) and (2) performance (hit, miss) was used to assess the effect of task performance on prestimulus alpha PSD, restricted to hard target trials only (Table 2, Figure 4). Target stimuli in hit trials were preceded by reduced alpha PSD in comparison with miss trials, $F(1, 15) = 6.813$, $p = .020$. Neither the main effect of electrode site ($p = .075$) nor the Site × Performance interaction ($p = .308$) was significant.

Effects of Task Previous Trial Type on Prestimulus Alpha Magnitudes

A three-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8), (2) task context (easy, hard), and (3) previous stimulus type (target, nontarget) was used to assess whether prestimulus alpha differences before hit trials in the easy task context relative to the hard task context is driven by overlap from preceding trials, which in some cases contained physically dissimilar nontargets (Table 3, Figure 5). There was a main effect of electrode site, such that alpha power at site PO8 was greater than alpha power at site PO7, $F(1, 15) = 7.512$, $p = .015$. There was a main effect of task context, such that alpha power in the easy task context was greater than alpha power in the hard task context, $F(1, 15) = 6.242$, $p = .025$. Additionally, there was a main effect of previous trial type, such that prestimulus alpha power in trials preceded by a target presentation trial was reduced compared with alpha power in trials preceded by a nontarget presentation trial, $F(1, 15) = 15.325$, $p = .001$. There were no significant interactions between any of the three main effects (all ps > .40); for the most critical interaction effect of task context and previous trial type, $p = .838$.

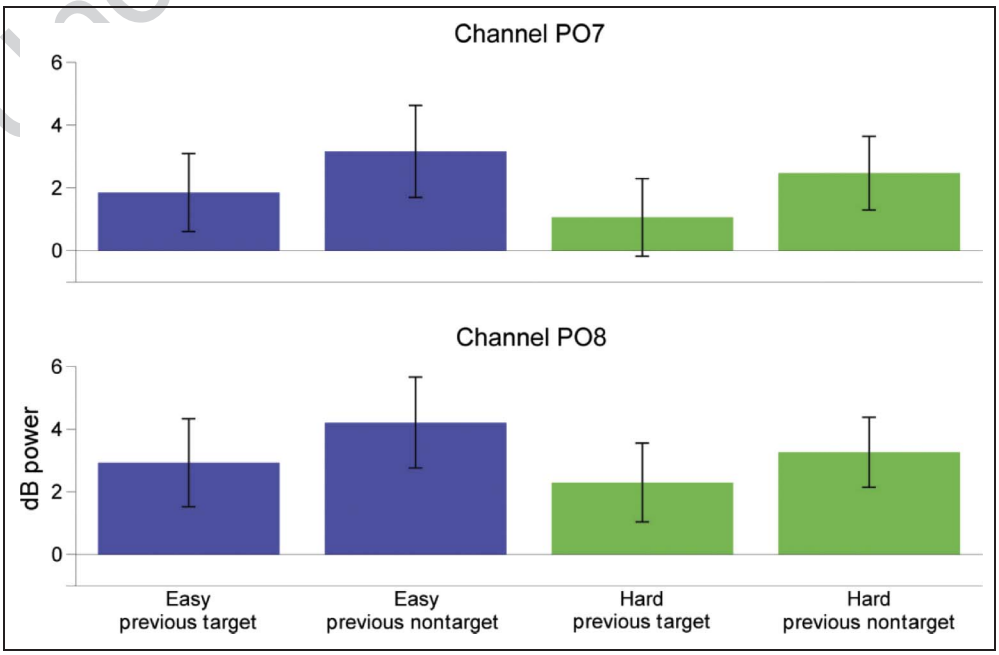

Figure 5. Prestimulus alpha magnitude for hit trials, sorted by electrode site, task context, and previous stimulus type. Error bars represent ±*SEM*.

Effect of Prestimulus Alpha Magnitude on Component Amplitude and Behavior

Trials from the three conditions under consideration—easy hits, hard hits, and hard misses—were independently sorted into two bins of equal size according to whether they were above or below the median prestimulus alpha magnitude for that condition, within each participant. ERPs were computed for trials within each of the two bins to assess the relation between prestimulus alpha power and subsequent N1 and P1 amplitude. Furthermore, as visual inspection of the resulting ERP waveforms binned by alpha level suggested that time points other than those in the latency range of the N1 may have been modulated by prestimulus alpha level, a post hoc exploratory analysis was used to compare the resulting alpha contingent waveforms at each poststimulus sample. Additionally, the mean baseline ERP amplitude (before baseline correction) was examined for each bin to investigate the possibility that the bin procedure was introducing a baseline shift in the time domain. Finally, the mean RT was taken from trials in each bin from the easy hit and hard hit conditions to establish whether the level of prestimulus alpha affected the speed of subsequent behavioral response.

N1

A three-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8), (2) alpha power bin (low alpha power, high alpha power), and (3) condition (easy task hit, hard hit, hard miss) was used to assess the effect of prestimulus alpha power on N1 amplitude (Table 4, Figure 6A–C, Figure 7A). Prestimulus alpha power bin had a significant effect on N1 amplitude, such that N1 amplitude from trials in the low alpha power bin was greater than from trials in the high alpha power bin, $F(1, 15) = 4.784$, $p = .045$ (Figure 5). There was additionally a trend for a main effect of condition on N1 amplitude in the alpha bin analysis, marginal after correction for a violation of sphericity, $F(1.253, 18.801) = 3.795$, $p = .058$. This effect reflects the overall increase in N1 amplitude within the hard hit condition, relative to the easy hit or hard error conditions. Neither electrode site nor any interactions were significant (all ps $> .06$).

P1

A three-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8), (2) alpha power bin (low alpha power, high alpha power), and (3) condition (easy hit, hard hit, hard miss) was used to assess the effect of prestimulus alpha power on P1 amplitude (Table 4). None of the main effects or interactions reached significance (all ps $> .10$).

Sample-by-Sample Poststimulus Analysis

A three-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8), (2) alpha power bin (low alpha power, high alpha power), and (3) condition (easy hit, hard hit, hard miss) was computed at each poststimulus sample, which includes all even-numbered time points from 0 to 550 msec after stimulus onset. The resulting F values for the main effect of alpha power bin are presented in Figure 7D. The red horizontal line indicates the $F(1, 15)$ value, which is significant at a .05 alpha level, uncorrected for

Table 4. Mean Baseline Amplitude, P1 Amplitude, N1 Amplitude, and Prestimulus Alpha Magnitude for Electrode Sites PO7 and PO8, Derived from Trials in Either the Low or High Alpha Bin, for All Three Conditions of Interest

Condition	*Alpha Bin*	*Site*	*Baseline Amp. (μV)*	*P1 Amp. (μV)*	*N1 Amp. (μV)*
Easy hit	Low	PO7	−0.787 (0.265)	1.782 (0.497)	−0.065 (0.602)
		PO8	−0.662 (0.347)	2.196 (0.887)	−0.900 (0.971)
	High	PO7	−1.289 (0.226)	3.057 (0.764)	1.840 (1.132)
		PO8	−1.083 (0.467)	3.730 (0.921)	0.848 (1.313)
Hard hit	Low	PO7	−1.092 (0.249)	1.920 (0.583)	−0.060 (0.604)
		PO8	−0.697 (0.428)	1.807 (1.104)	−2.031 (1.072)
	High	PO7	−1.200 (0.242)	2.992 (0.689)	1.079 (0.897)
		PO8	−1.141 (0.478)	2.960 (0.907)	−0.344 (1.121)
Hard miss	Low	PO7	−0.820 (0.305)	2.005 (0.675)	0.180 (0.651)
		PO8	−1.027 (0.498)	2.399 (1.039)	−0.560 (0.934)
	High	PO7	−1.304 (0.403)	2.558 (0.775)	2.051 (0.961)
		PO8	−0.919 (0.539)	3.330 (0.825)	0.142 (1.084)

*SEM*s are given in parentheses.

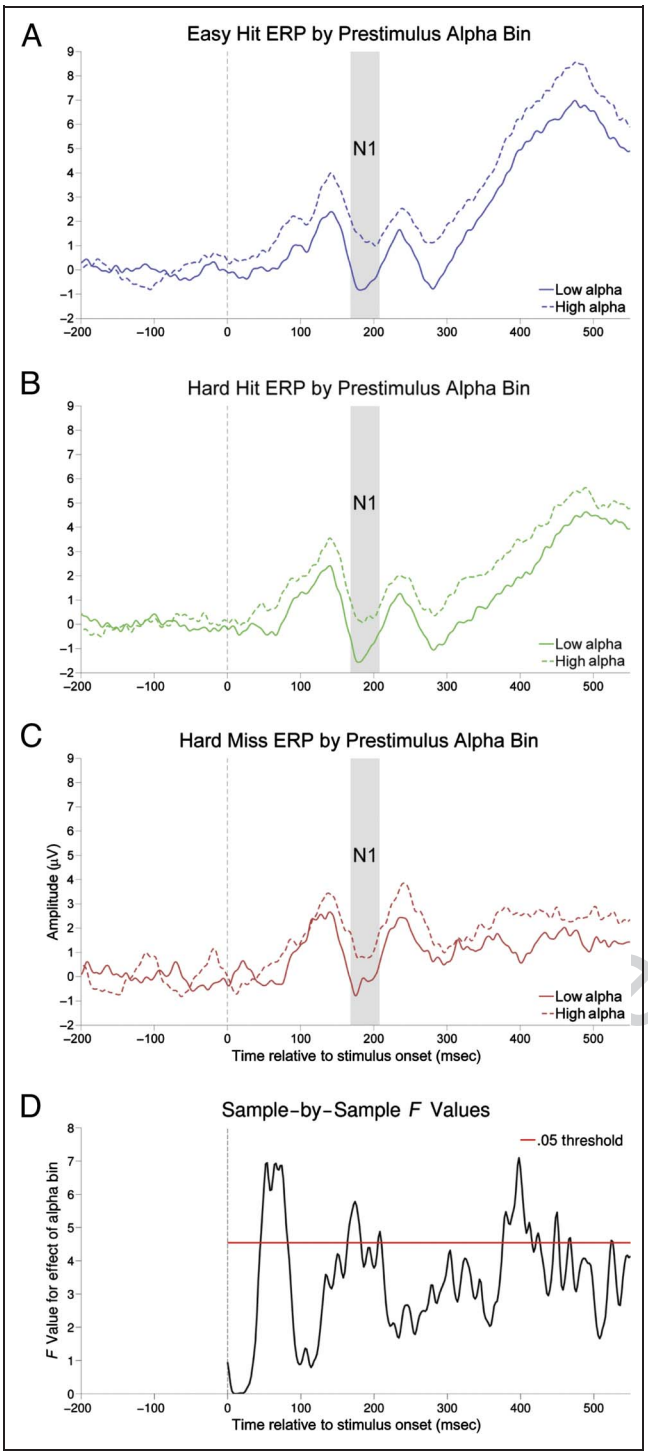

Figure 6. A–C display the ERP waveform for trials partitioned into two groups according to relative prestimulus alpha power, for the three conditions under study. Waveforms represent the average of electrodes PO7 and PO8. The region defining the mean N1 amplitude is shaded in gray. D displays the ANOVA *F* value for the main effect of prestimulus alpha bin, at each poststimulus sample. The red line indicates the *F* value threshold for a *p* value of .05.

multiple comparisons. In addition to the predicted and aforementioned effect within the N1 window, there are additionally above-threshold effects within an earlier, 46- to 82-msec poststimulus-onset window and a later, 376- to 416-msec poststimulus-onset window. This earlier effect is consistent with the time frame of the C1 component, whereas the later effect appears within the P300 time frame, although not at the peak of the P300 wave, which occurred at approximately 475 msec after stimulus onset. However, these additional effects should be interpreted with the caveat that this analysis was computed post hoc and is uncorrected for multiple comparisons.

Mean Baseline

A three-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8), (2) alpha power bin (low alpha power, high alpha power), and (3) condition (easy hit, hard hit, hard miss) was used to assess the effect of prestimulus alpha power on the mean ERP prestimulus baseline, before baseline correction (Table 4). None of the main effects or interactions reached significance (all *p*s > .25). The most important main effect, that of prestimulus alpha bin, did not approach significance ($p = .394$).

RT

A two-way repeated-measures ANOVA with factors (1) task context (easy, hard), (2) alpha power bin (low alpha

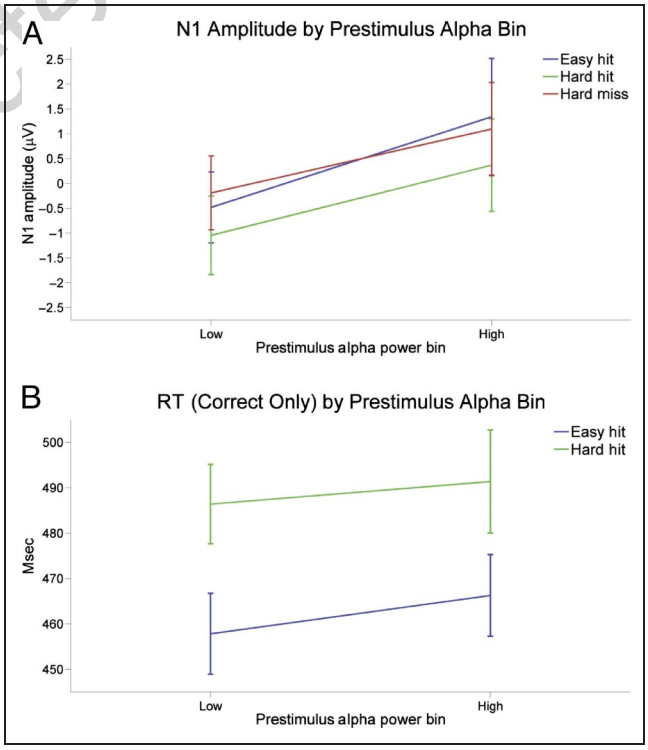

Figure 7. A displays the mean N1 amplitude for waveforms composed of trials from the low and high prestimulus alpha bins, at each of the three conditions of interest. The plotted values represent the average of electrode sites PO7 and PO8. B displays the mean RT to correct trials from the low and high prestimulus alpha bins, in both the easy and hard task contexts. Hard misses are omitted because they are defined by a lack of response. In both A and B, error bars represent ±*SEM*.

Table 5. Mean RT (Milliseconds Relative to Stimulus Onset) to Correct Trials from the Low and High Prestimulus Alpha Bins, in Both the Easy and Hard Task Contexts

	Low Alpha	*High Alpha*
Easy	457.827 (8.927)	466.273 (9.016)
Hard	486.397 (8.758)	491.368 (11.340)

*SEM*s are given in parentheses.

power, high alpha power) was used to assess the effect of prestimulus alpha power on subsequent RT, restricted to correct trials only (Table 5, Figure 7B). Task context had a significant effect on RT, such that response was slowed in the hard task context relative to the easy task context, $F(1, 15) = 9.747$, $p = .007$. Prestimulus alpha bin additionally had a significant effect on RT, such that responses were slowed for trials preceded by high prestimulus alpha, relative to trials preceded by low prestimulus alpha, $F(1, 15) = 7.043$, $p = .018$. The interaction between task context and prestimulus alpha bin did not reach statistical significance ($p = .535$).

Effect of Task Context and Performance on C1 Amplitude

The post hoc sample-by-sample analysis of the ERP waveforms, split by prestimulus alpha bin, suggests modulation of a component within the time frame of the C1 component. Subsequently, the presence of any modulation of the C1 component with respect to task context (easy, hard), restricted to correct target trials, or performance within the hard task context (hit, miss) was evaluated using a 40- to 80-msec poststimulus window. A two-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8) and (2) task context (easy, hard) was used to assess the effect of task context on C1 amplitude. Neither of the main effects nor the interaction was significant (all ps $> .14$). A two-way repeated-measures ANOVA with factors (1) electrode site (PO7, PO8) and (2) performance (hit, miss) was used to assess the effect of task performance on C1 amplitude, restricted to hard target trials only. Again, neither of the main effects nor the interaction was significant (all ps $> .49$).

DISCUSSION

The current study assessed the relationship between proactive, top–down control, as indexed by modulation of the alpha band of the EEG, and the stimulus discrimination process reflected by the N1 component. Discrimination difficulty was manipulated by changing the orientation similarity of serially presented target and nontarget Gabor patches. Participants were slower and less accurate in their responses during the hard task context, relative to the easy task context. As was previously reported in Fedota et al. (2012), a focused effect of top–down control was reflected in the N1 component. Specifically, the N1 was of greater amplitude for hard hits relative to easy hits and, additionally, of greater amplitude for hard hits relative to hard misses. Moreover, prestimulus alpha power was diminished within the condition for which the occipital–temporal N1 was enhanced and elevated within the conditions for which the occipital–temporal N1 was reduced. Furthermore, a relationship between prestimulus alpha power and N1 amplitude was demonstrated by the construction of ERPs contingent on the relative level of prestimulus alpha power, independently for each of the three conditions under study (easy hits, hard hits, and hard misses). At lateral occipital sites, increased alpha power in the period preceding target onset was associated with decreased occipital–temporal N1 amplitude to the subsequent stimulus.

Examination of the mean ERP baseline from each of the low and high alpha bins before baseline correction suggests that the effect of prestimulus alpha on subsequent N1 amplitude cannot be explained by a prestimulus baseline offset. It also seems unlikely that the observed effects between difficulty conditions are because of general fatigue. As the two difficulty conditions were alternated every four blocks, with the starting block counterbalanced across participants, any systematic differences related to time on task should have been reduced. Furthermore, fatigue related to continued task performance has been demonstrated to increase RTs, increase error rates, decrease visual N1 amplitude, and increase alpha power (Boksem, Meijman, & Lorist, 2005). This pattern is inconsistent with the present data, in which the more difficult task condition was associated with longer RTs and greater numbers of errors but also increased visual N1 amplitude and decreased alpha power. These findings are in agreement with the hypothesis that top–down control increases excitability of sensory cortex in the prestimulus period when feature discrimination is difficult and demonstrate that the application of control was related to task performance. Furthermore, these data are interpreted as evidence that top–down control over the discrimination process was instantiated in a proactive manner. It is noted that fatigue cannot be ruled out as a contributor to within-condition effects, as the alpha bin partitions within each condition were not under experimental control. However, the relation between prestimulus alpha level and subsequent N1 amplitude was observed to be similar between and within conditions.

The present task required participants to discriminate between vertical and rotated Gabor patches, with difficulty manipulated via similarity of nontarget to target rotation. As the stimuli in the present task were presented centrally, regardless of task difficulty, the experiment presumably manipulated the demand on feature-based attentional control processes without altering spatial attention. This is supported by the observed modulation of the N1 component, which has previously been associated with a

feature discrimination process in particular (Vogel & Luck, 2000). In addition, the lack of any statistically significant modulation of the P1 component, which is associated with manipulations of spatial attention (Woldorff et al., 1997), supports the notion that feature-based attention was selectively manipulated in the current paradigm.

The prestimulus activity occurring before easy and hard hit trials was additionally partitioned by the previous stimulus type (target or nontarget) to investigate the potential influence of overlapping activity elicited by preceding, physically dissimilar nontargets. This analysis revealed an effect of previous trial type on prestimulus alpha magnitude, such that alpha was reduced within the prestimulus period of trials preceded by a target presentation, relative to the prestimulus period of trials preceded by nontarget presentations. Critically, this effect occurred independent from the effect of task context on prestimulus alpha magnitude, as no interaction was observed between previous trial type and task context. The presence of reduced alpha power in trials preceded by target stimulus presentation suggests that greater cognitive control is exerted following the occurrence of rare, task-relevant stimuli. This notion is consistent with a large literature on the P3 component, which presumably reflects the potentiation of processing of motivationally significant stimuli, showing an inverse relation between its amplitude and the probability of task-relevant stimuli (reviewed in Nieuwenhuis et al., 2005).

In addition to N1 amplitude, RT was affected by prestimulus alpha level. Specifically, responses were observed to be faster in trials from the low alpha group, relative to the high alpha group. Importantly, this effect occurred in addition to the effect of task context on RT, such that responses in the easy task context were quicker than responses in the hard task context, with no observed interaction between prestimulus alpha level and task context on RT. Although Van Dijk et al. (2008) did not observe RT differences with prestimulus alpha level within their threshold-level discrimination task, RT has been reported to be related to prestimulus alpha level within paradigms manipulating cued spatial attention (Gould et al., 2011; Kelly et al., 2009; Thut et al., 2006), such that lower prestimulus alpha level contralateral to the cued location is associated with a speeded response. Given that these paradigms, as in the current report, manipulated attention in a top–down manner, we argue that reduced prestimulus alpha magnitude and speeded RT are two manifestations of a successful application of top–down control.

A post hoc comparison of ERPs from the low and high alpha groups suggests two additional periods of modulation with respect to prestimulus alpha level, at 46–82 and 376–416 msec after stimulus onset. The modulation from 46 to 82 msec is consistent with the time frame of the C1 component (Jeffreys & Axford, 1972a, 1972b). The C1 reflects activity generated within striate cortex (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Clark, Fan, & Hillyard, 1995) with contributions from extrastriate cortex (Foxe & Simpson, 2002). Despite the modulation of C1 as a function of prestimulus alpha level, there was no observed modulation of C1 with respect to either task difficulty or behavioral outcome. This is in line with early studies of the C1, which found this component to be insensitive to manipulation of spatial attention (Martínez et al., 1999; Clark & Hillyard, 1996). However, Kelly, Gomez-Ramirez, and Foxe (2008) report that covert spatial attention may modulate the C1 under some conditions. In addition, others have subsequently noted that the C1 can be modulated by attentional load (Rauss, Pourtois, Vuilleumier, & Schwartz, 2009) and that the C1 may be modulated by attention only when the attentional load is high (Fu, Fedota, Greenwood, & Parasuraman, 2010). The presence of C1 modulation with respect to prestimulus alpha level within task difficulty or behavioral outcome conditions, despite the absence of between-condition modulations, suggests a differentiation in top–down control within and between conditions. It is possible that within-condition variations in prestimulus alpha may contain a stochastic component that is reduced when relating prestimulus alpha and N1 amplitude between conditions. The finding that, in contrast to the N1, the C1 was not significantly modulated between hard hit and hard miss trials suggests that variation in this component is not critical for task performance. The interpretation of modulation from 376 to 416 msec is less clear, as this window is well before the peak of the P3 component. It is possible that this difference may be related to response preparation, as reflected in differing RTs with prestimulus alpha level.

Under the interpretation that the magnitude of the alpha rhythm within a region of cortex is inversely related to excitability (Lange, Oostenveld, & Fries, 2013; Klimesch, 2012; Pfurtscheller, 2006) or attentional gating (Foxe & Snyder, 2011; Foxe, Simpson, & Ahlfors, 1998), the current results suggest that top–down control is at least in part instantiated via an increase in cortical excitability preceding stimulus onset, an increase that later facilitates stimulus discrimination. The timing of this control process, which is instantiated before stimulus onset, suggests that successful performance in the hard task context is at least partly because of the use of a proactive process in anticipation of task demands (Braver et al., 2007, 2009).

Although the spatial resolution of EEG does not allow for strong claims on the cortical locations generating the observed prestimulus alpha and poststimulus N1 modulations, these two electrophysiological effects were likely generated by a similar region of cortex. Although both ipsilateral alpha enhancement and contralateral alpha suppression have been observed with cued spatial attention, recent evidence suggests that these two effects can be dissociated (Capilla, Schoffelen, Paterson, Thut, & Gross, 2012). Using magnetoencephalography and source localization techniques, Capilla et al. (2012) demonstrated that ipsilateral alpha enhancement and contralateral alpha suppression are localized to dorsal parietal–occipital cortex and ventral occipital cortex, respectively. The dorsal

alpha enhancement was suggested to be related to the inhibition of ignored regions of space, whereas the ventral alpha suppression was suggested to be related to enhanced processing of task-relevant stimulus features. Interestingly, only alpha suppression, which was localized to ventral occipital cortex, was related to detection of the low contrast stimuli used by Capilla et al. (2012). Moreover, prestimulus alpha suppression was sustained, whereas alpha enhancement was transient, a finding consistent with the notion that alpha suppression likely reflects proactive control. As this study manipulated processes related to the top–down control of feature-based attention, the observed alpha modulations are consistent with those localized to the ventral stream by Capilla et al. (2012). This is further supported in this study by the relationship of prestimulus alpha to both discrimination difficulty and behavioral outcome, with alpha magnitude being suppressed for hard target trials relative to easy correct target trials and enhanced for incorrect hard target trials relative to correct hard target trials.

Prestimulus alpha power was observed to be inversely related to N1 amplitude, both between task conditions and within each task condition. The lack of any statistically significant relationship between prestimulus alpha power and the P1 component suggests that prestimulus cortical excitability has a selective effect on subsequent stimulus processing. Here, it is suggested that this relationship reflects the application of top–down control processes preceding the correct, hard target trials, relative to both the incorrect, hard target trials and correct, easy target trials. It has previously been demonstrated that top–down control can act to enhance task-relevant mechanisms (Egner & Hirsch, 2005) and that the locus of prestimulus alpha modulations is dependent on the demands of a given task. For example, lateralized occipital alpha suppression has been observed in anticipation of lateralized spatial attention tasks (Thut et al., 2006). Similarly, dorsal or ventral alpha enhancement has been observed in a combined motion–color task, when either motion or color is attended to, respectively (Snyder & Foxe, 2010). Relations between prestimulus alpha power and the amplitude of the subsequent P1, a component thought to reflect spatial attention processes (Woldorff et al., 1997), have additionally been observed within a cued spatial attention task (Rajagovindan & Ding, 2011). In the current task, prestimulus alpha modulation was focused over the temporal–occipital areas previously associated with the stimulus discrimination N1 component (Fedota et al., 2012; Hopf et al., 2002; Vogel & Luck, 2000).

Previous work has established a strong relationship between prestimulus alpha and spatial attention, demonstrating both alpha suppression (excitation) and alpha enhancement (inhibition) depending on the task. However, the use of centrally presented stimuli, in the absence of concurrently presented distracters, is a novel manipulation of the present experiment. These findings suggest that top–down control can serve to enhance discrimination processing by task-relevant enhancement, even when suppression of competing stimuli is not required.

The present experiment provides evidence that top–down control of a stimulus discrimination process occurs proactively via increased cortical excitability preceding stimulus onset, as reflected by prestimulus alpha magnitude. The magnitude of the alpha oscillation preceding stimulus onset was not only related to the difficulty of the discrimination to be made but was also associated with subsequent N1 amplitude, providing evidence for a link between top–down control and stimulus discrimination processing. The present findings extend existing work by demonstrating that alpha suppression is facilitatory for nonspatial, feature-based attention, even in the absence of competition from other concurrently presented features.

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