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Attention-modulated alpha-band oscillations protect against intrusion of irrelevant information

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Abstract

Combining high-density scalp EEG recordings with a sensitive analog measure of short-term memory's fidelity, we characterized the temporal dynamics of intentional ignoring, and related those dynamics to the intrusion of task-irrelevant information. On each trial of the task, two study Gabors were briefly presented in succession. A green or red disc preceding each Gabor signified whether that Gabor should be remembered or ignored, respectively. With cue-stimulus intervals of 300, 600, or 900 ms presented in separate sessions, we found that the onset of posterior, pre-stimulus alpha oscillations varied with the length of the interval. Although stimulus onset time was entirely predictable, the longer the cue-stimulus interval, the earlier the increase in pre-stimulus alpha power. However, the alpha-band modulation was not simply locked to the cue offset. The temporal envelopes of posterior alpha-band modulation were strikingly similar for both cued attending and cued ignoring, and differed only in magnitude. This similarity suggests that cued attending includes suppression of task irrelevant, spatial processing. Supporting the view that alpha-band oscillations represent inhibition, our graded measure of recall revealed that when the stimulus to be ignored appears second in the sequence, peri-stimulus alpha power predicted the degree to which that irrelevant stimulus distorted subsequent recall of the stimulus that was to be remembered. These results demonstrate that timely deployment of attention-related alpha-band oscillations can aid short-term memory by filtering out task-irrelevant information.

INTRODUCTION

Cortical oscillations within the alpha band (8–14 Hz) are markers of task-related engagement or disengagement of specific brain regions. For example, during visual target detection tasks, when a cue directs attention to a lateralized spatial location where an upcoming stimulus may be presented, contralateral brain regions exhibit an anticipatory decrease in alpha activity relative to pre-cue levels (Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Huang & Sekuler, 2010a). Moreover, increases in alpha activity ipsilateral to the target location have been reported to occur when there are distracting stimuli within the uncued space (Kelly, Lalor, Reilly, & Foxe, 2006) and also when there were no distracting stimuli in the unattended space (Rihs, Michel, & Thut, 2007). Similarly, in the somatosensory domain, increased alpha activity ipsilateral to a cued location suppresses detection of stimulation of the uncued hand (Haegens, Luther, & Jensen, 2012). Moreover,

the hand's representation in somatosensory cortex shows decreased power after a cue to attend to that hand, but shows increased power after a cue to attend to the foot (Jones et al., 2012). These results suggest that spatial location is itself a distracter, and an important function of directed attention is to suppress processing of unattended space regardless of whether or not there exists an experimentally defined, irrelevant stimulus in that space.

Modality-specific changes in alpha activity are also seen during feature-based selection when subjects are cued to attend to input from one particular sensory modality of a compound stimulus. In tasks utilizing audio-visual stimuli, alpha amplitude increases selectively over parietal-occipital regions when subjects are cued to attend to the auditory feature, indicating the suppression of visual processing in order to attend to the auditory information (Foxe, Simpson, & Ahlfors, 1998; Fu et al., 2001). A double-dissociation between feature dimensions was observed when subjects were cued to attend either the color or the motion of a dot array (Snyder & Foxe, 2010). Alpha power over dorsal regions encoding motion increased when color was cued, and alpha power over ventral regions encoding color increased when motion was cued. Therefore, it is thought that cued attentional processes entail not only a decrease in alpha activity over regions of active encoding, but also an increase over regions whose potentially distracting processing should be suppressed. In this view, alpha oscillations reflect an active inhibitory mechanism, and alpha desynchronization promotes stimulus processing (for review, see Klimesch, Sauseng, & Hanslmayr, 2007; Foxe & Snyder, 2011).

Despite these successful manipulations of cued attention, there is still little known about the timing of attention modulation. A number of results have indicated that sustained, attention-related changes begin approximately 400 to 600 ms after cue onset (Worden, Foxe, Wang, & Simpson, 2000; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Rihs, Michel, & Thut, 2007). In most of those examples, the onset of differential alpha activity is also approximately 400 to 600 ms before the stimulus onset making it difficult to interpret the timing of attention modulation. Specifically, increased alpha preceding the stimulus that was to be ignored could have been adaptive or anticipatory in nature, the product of subjects' expectation that the stimulus would occur at a predictable time after the cue; alternatively, the pre-stimulus increase in alpha could simply be time-locked to the cue's offset, reflecting the time required to respond to the cue. To select between these very different accounts of the pre-stimulus increase in alpha, we manipulated the interval between cue and stimulus with sessions of either 300, 600, or 900 ms intervals. Each trial sequence consisted of two cue-stimulus pairs. A red cue signaled that the following distracting nonTarget was to be ignored and a green cue signaled that the subsequent Target was to be remembered and reproduced after a brief retention period. If the first cue of a trial instructed subjects to attend, then the second cue would necessarily be the instruction to ignore, and vice versa. In this way, this design also allowed the comparison of alpha signal onset between conditions in which the cue must be completely processed versus a condition in which the cue would be completely predictable.

Although compelling evidence suggests that alpha oscillations reflect the suppression of irrelevant processing, subjects were actually cued to attend toward a spatial location or stimulus dimension during these tasks. Even if subjects were explicitly instructed to ignore the unattended space or feature, the cue indicated the direction of attention, and any ignoring

of distracters occurred simultaneously. Intentional ignoring of a stimulus as a stand-alone trial event was first addressed with a working-memory task during which a centrally presented stream of sixteen everyday objects were shown, each following a cue to either attend or ignore the upcoming stimulus (Freunberger, et al., 2009). After a brief retention period, a probe object was displayed and subjects indicated whether or not it had been in that trial's stream of attended objects. Objects that followed an ignore cue never appeared as the probe in order to encourage actual ignoring of the irrelevant stimuli, thereby reducing the number of objects in memory. As hypothesized, a cue to ignore an upcoming stimulus elicited higher posterior alpha power than a cue to attend to the stimulus. Although not attending to the irrelevant stimuli would reduce the number of objects to be held in memory and make the task easier, there was no way to determine if those stimuli had been successfully ignored.

A direct link has not been demonstrated between alpha activity and the success with which task-irrelevant information can be kept out of working memory. This potential link is important, as the intrusion of task-irrelevant information is a major cause of failures in working memory, particularly in older adults (Hasher & Zacks, 1988). To examine the link between alpha oscillations and intrusions into working memory, we used sinusoidal luminance grating stimuli (Gabor), together with a recall technique in which subjects adjusted a stimulus to match the item held in memory. To enable reproduction of the Target from memory, a Gabor patch was displayed with a slider bar that increased or decreased the spatial frequency as subjects clicked along the bar. In this way, subjects' reproductions of the spatial frequency of the remembered stimulus yield a sensitive, trial-by-trial continuous measure of accuracy. This information-rich measure of accuracy made it possible not only to gauge whether there was an error in memory, but more importantly to gauge the degree to which errors reflected the influence of the task-irrelevant stimulus (Dube, Zhou, & Sekuler, under review; Huang & Sekuler, 2010b). Many factors during each trial may contribute to the total error including pure error of reproduction, but, as explained below, the use of Gabor stimuli and the recall technique made it possible to disentangle the influence of other stimuli seen during the experiment, particularly each trial's nonTarget stimulus. Our hypothesis is that when a task-irrelevant stimulus is accompanied by higher alpha power, the brain will more effectively filter out that task-irrelevant stimulus so that its influence on memory is curtailed.

METHODS

Subjects

Fourteen subjects gave written informed consent and completed the experiment. Of these, two subjects' data had to be excluded from our analysis because of excessive EEG artifacts (epoch rejection rate > 50%). Seven of the 12 remaining subjects were female. Subjects' ages ranged from 18–30 years (Mean = 22, SD = 3.54). All were right-handed as determined by the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal or corrected-to-normal vision as measured with Snellen targets. All subjects denied psychological or neurological disorders. Subjects were naive to the purpose of the experiment, and were paid for participation.

Apparatus and stimuli

Gabor stimuli were generated and displayed using Matlab 7 (Mathworks), supplemented by extensions from the Psychophysics Toolbox (Brainard, 1997). Each Gabor comprised a vertical sinusoidal luminance grating windowed by a circular Gaussian carrier with a space constant of 1.14 degrees. Each Gabor subtended 4.65 degrees. The contrast of a stimulus' sinusoidal component was fixed at 0.2, a value well above detection threshold. To undermine the possibility that subjects might base their judgments on some local correspondence(s) between stimuli, the absolute phase of each Gabor's sinusoidal component was perturbed on each trial by adding a random sample from a uniform distribution whose range was 0 to $\pi/2$. Stimuli were presented on a 21-inch cathode ray tube monitor with a refresh rate of 99.8 Hz and a screen resolution of 1280×960 pixels. Screen luminance was linearized by means of software adjustment, with the mean luminance of the screen held at 32 cd/m². The red and green discs used to cue attention were equiluminant with the display's mean luminance. During testing, subjects viewed the computer display binocularly from a distance of 57 cm.

Preliminary measurements

To take account of individual differences in visual discriminability, each subject's spatial frequency discrimination threshold was measured for the same type of Gabor that would be later used in testing short-term memory. Each individual's discrimination threshold was then used to scale the spatial frequencies of stimuli used in the memory test. The discrimination thresholds were used also to normalize the recall errors that individual subjects made. Spatial frequency discrimination thresholds were estimated by two-alternative forced choice trials controlled by QUEST, an adaptive tracking algorithm (Watson & Pelli, 1983). On each trial, two Gabors were presented in sequence for 500 ms each. This replicated the temporal and spatial conditions that would be subsequently used in our study of working memory. A subject used keys on a computer keyboard to identify which Gabor, the first or second, had the higher spatial frequency. The higher spatial frequency Gabor was equally likely to occupy the first or second positions in the sequence. A computer-generated tone provided feedback about response correctness during these preliminary, threshold measurements.

The lower spatial frequency of each trial's pair was chosen randomly from a uniform distribution that spanned 0.5–5 cycles/degree. This covered the range of spatial frequencies that was used later to test working memory. The QUEST algorithm controlled trialwise differences in the two Gabors' spatial frequencies. As implemented here, QUEST estimated the difference in spatial frequency that produced correct judgments on 80% of attempts. Each subject's discrimination threshold was estimated in three separate, successive runs of QUEST. The lowest of the three resulting threshold estimates was used to represent the subject's discrimination threshold. Subjects' discrimination thresholds ranged from 9 to 20% (Mean = 13.25, SD = 3.41).

Procedure

As Figure 1 illustrates, two study Gabors were presented in sequence on each trial. A green or red disc immediately before a Gabor signified whether that Gabor was to be remembered (•) or ignored (•). The presentation of the two Gabors was followed by a one-second,

retention period. Then, the presentation of a comparison Gabor and slide-bar signaled the subject to adjust the spatial frequency to match the remembered spatial frequency of the Target Gabor. For half of the subjects, the initial spatial frequency of the comparison Gabor was at the low end of the spatial frequency range; for the other half, the initial spatial frequency of the comparison Gabor was at the high end.

In order to quantify the fidelity of working memory, the two Gabors were presented in sequence, as had been the case during the preliminary threshold determinations. To minimize confusion between the study item that was to be remembered and the one that was to be ignored, the difference between the spatial frequencies of the two Gabors was fixed at a large value, four just noticeable differences (JNDs). The actual frequencies presented on each trial were randomized using the methods described by Huang & Sekuler (2010b).

On each trial, the sequence of the cues (•, •) was randomized. For terminological convenience, the word Target will be used for the Gabor that was to be remembered, and nonTarget for the Gabor that was to be ignored. On half of the trials, the Target appeared first, followed by the nonTarget (T₁N₂); for the remaining trials, the sequence was reversed, with the nonTarget Gabor appearing first, followed by the Target (N₁T₂).

Accuracy of recall was tested under three main conditions, which differed in the length of the interval separating cue offset from stimulus onset. Each subject participated in three sessions on separate days, each comprising a single block of trials with either 300, 600, or 900 ms cue-stimulus timing. The order of the three conditions was counterbalanced across subjects. For each condition, the first 16 trials were excluded from analysis as practice trials, leaving 160 trials per condition for analysis.

Behavioral analysis

The raw error on each trial is defined by the difference between (1) the spatial frequency of that trial's Target Gabor and (2) the spatial frequency produced by the subject's adjustment of the comparison Gabor. Following a method described in Huang and Sekuler (2010b, 2010a), we normalized each raw error relative to the subject's Weber fraction for spatial frequency, which we had already ascertained. Let x be the subject's Weber fraction, f_T be the spatial frequency of target Gabor on some trial, and f_R be the comparison Gabor's final adjusted frequency. The raw error in reproduction $f_R - f_T$ is normalized by the subject's Weber fraction, yielding what we call normalized reproduction error (nRE).

$$nRE = \log_{(1-x)} \left(\frac{f_R}{f_T} \right) = \frac{\ln f_R - \ln f_T}{\ln(1-x)} \quad (1)$$

Huang and Sekuler (2010b) showed that each nRE could be thought of as a sum of multiple influences, including two that arise from stimuli other than the Target stimulus. To start the process of disentangling those influences, the sign of each trial's nRE was adjusted relative to the trial's nonTarget: a plus sign signified an nRE that was displaced toward the nonTarget, and a minus sign signified an nRE that was displaced away from the nonTarget. From these sign-adjusted values of nRE, we used an algebraic manipulation to extract (1)

one component that reflects the influence of the spatial frequency of a trial's task-irrelevant, nonTarget Gabor, and (2) a second component that reflects the influence of the prototypical spatial frequency defined by the mean frequency of all stimuli that a subject had seen (including both Target and nonTarget) on the preceding trials within the same condition.

Because of planned trial-to-trial variation in the nonTarget stimulus' spatial frequency, there would be some trials on which the two putative influences would operate synergistically, both pulling the reproduction in a common direction, and other trials on which the two influences would work in opposition to one another. Thus, for each subject we separated trials (1) on which the two influences would work in the same direction (e.g., both values were higher than target's frequency, or both were lower) from trials (2) on which the two influences would oppose one another (e.g., one value was higher, and the other was lower than target's frequency). As an nRE value with a positive sign signified a bias toward the nonTarget stimulus, the difference between the two components' influences can be found by subtracting $Bias_{Proto}$ from $Bias_{NonTarget}$.

$$Error_{Sdir} = Bias_{Non-Target} + Bias_{Proto} \quad (2)$$

$$Error_{Odir} = Bias_{Non-Target} - Bias_{Proto} \quad (3)$$

Equation 4 isolates the contribution of the nonTarget, nullifying the contribution from the prototypical stimulus, whereas Equation 5 does the opposite, isolating the effect of the prototypical stimulus while nullifying the contribution of nonTarget stimulus.

$$Bias_{Non-target} = 0.5(Error_{Sdir} + Error_{Odir}) \quad (4)$$

$$Bias_{Proto} = 0.5(Error_{Sdir} - Error_{Odir}) \quad (5)$$

This detailed decomposition of errors is especially important as our hypothesis holds that alpha oscillations will be associated in our task not with errors generally, but with one particular kind of error, namely the nonTarget effect.

EEG recording and analysis

Electroencephalographic (EEG) signals were recorded from the scalp using a high-density, 129-electrode array (Electrical Geodesics Inc.) and high-impedance amplifiers. All channels were adjusted for scalp impedance < 50kΩ. Sensor signals were sampled at 250 Hz with a 0–125 Hz analogue bandpass filter, and stored for offline analysis. Bipolar periocular channels were recorded from above and below each eye, and from a location near the outer canthus of each eye.

EEG signals were preprocessed using the EEGLAB toolbox (Delorme & Makeig, 2004) for Matlab (Mathworks). The recorded signals were re-referenced to the grand average. A 0.5 Hz Butterworth high-pass filter and a 60 Hz Parks-McClellan notch filter were applied. Eye blinks were identified by visual inspection of independent component analysis (ICA) and

eliminated. Epochs containing muscle artifacts or saccades, identified through ICA and visual inspection, were rejected. Wavelet analysis and plotting were performed using the FieldTrip Matlab toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). Time-frequency representations were computed using Morlet wavelets with a width of 4 cycles per wavelet at center frequencies between 1 and 70 Hz, in 1 Hz steps. To ensure equivalent resolution at any given time point for comparison, wavelets for each of the three Cue-stimulus intervals (300, 600 and 900 ms) were made to the same length.

Alpha amplitude was defined by the mean oscillatory power in the band 8–14 Hz. Wavelet alpha power for all electrodes was calculated for this epoch extending from cue onset through stimulus offset. Alpha power values were log transformed to approximate a normal distribution, and then to eliminate between-subject differences in power were converted to standard scores (*z*-scores) for each subject collapsed across the three cue-stimulus intervals. Topographic plots of stimulus-onset activity (100 ms window from stimulus onset) show strongest alpha activity in posterior electrodes (Figure 3). A cluster-based, non-parametric, randomization test (Maris & Oostenveld, 2007) between all Target and all nonTarget conditions was performed in order to establish a group of EEG electrodes to be used for all subsequent analysis. The cluster-based test statistic was calculated by comparing 8–14 Hz power for the two conditions at every electrode, leaving the time window open from cue offset to stimulus offset. All electrodes for which the *t*-value of the difference between conditions exceeded the threshold value of $p < 0.025$ were clustered on the basis of spatial adjacency. The sum of *t*-values from the cluster with the maximum sum was then used as the test statistic, thereby avoiding the problem of multiple comparisons in the significance test. A reference distribution of test statistics was generated by randomly permuting the data across the two conditions 1000 times. A cluster was characterized as significantly different between Target and nonTarget conditions if the proportion of randomized values larger than the observed test statistic was less than alpha-level, $p = 0.01$.

RESULTS

Our findings are presented in three sections. The first section includes our principal behavioral results; the second section presents the analysis of EEG recordings. The final section describes the relationships between alpha oscillations and behavioral measures of memory fidelity. Throughout, results of analyses of variance are reported as Greenhouse-Geisser corrected values. Calculations of within-subject errors are based on the method presented by Cousineau (2005).

Behavioral results

There was no difference in reproduction error (nRE) between the three experimental conditions regardless of the session order in which the cue-stimulus intervals were presented ($F(2,22) = 0.069$, $p = 0.929$). For session 1, Mean = 1.536 and SD = 0.331; for session 2, Mean = 1.5 and SD = 0.33; for session 3, Mean = 1.52 and SD = 0.335. This outcome suggests that the order of testing with the three conditions is not consequential, and need not be included as a factor in our subsequent analyses.

A repeated-measures multivariate analysis assessed the influence of main factors trial Sequence (T_1N_2 , N_1T_2) and Cue-stimulus Interval (300, 600 and 900 ms) on three dependent measures, nRE, the nonTarget effect, and Prototype effect. As shown in Figure 2, the sequence of stimulus presentation, that is T_1N_2 versus N_1T_2 , significantly affected nRE, with T_1N_2 trials producing larger mean reproduction errors than N_1T_2 trials ($F(1,11) = 135.38$, $p < 0.001$). Follow up t-tests reveal that this difference was significant between T_1N_2 and N_1T_2 across each of the three Cue-stimulus intervals (300 ms ($t_{11} = 5.178$, $p < 0.001$), 600 ms ($t_{11} = 4.786$, $p = 0.001$), and 900 ms ($t_{11} = 4.075$, $p = 0.002$)). Stimulus sequence influenced neither the Prototype nor the non-Target effect ($F(1,11) = 0.733$, $p = 0.41$), $F(1,11) = 2.378$, $p = 0.151$, respectively). Interval had no significant effect on any of the three dependent measures in the multivariate analysis: nRE ($F(1,11) = 1.034$, $p = 0.364$), the Prototype effect ($F(1,11) = 0.604$, $p = 0.551$), or the nonTarget effect ($F(1,11) = 0.834$, $p = 0.422$). Thus, the behavioral impact of cued attention was constant despite a three-fold variation in the interval separating cue and stimulus. No interactions were statistically significant.

Alpha oscillations

Alpha cluster—Results of the cluster-based, permutation test reveal a posterior cluster of 26 electrodes that showed higher alpha power during a peri-stimulus epoch of -100 ms to $+150$ ms surrounding onset for nonTarget versus Target stimuli. Correlation analyses between alpha power at this posterior cluster and the intrusion of the nonTarget into short-term memory were performed separately for 100 ms pre- and 100 ms post-onset epochs in an effort to distinguish effects due to pre- and post-stimulus alpha activity. As described below, post-onset alpha activity drove the relationship between alpha activity and the intrusion of the nonTarget into the subsequent Gabor reproduction. Therefore, alpha power during the 100 ms onset epoch across this posterior cluster of electrodes (Figure 4) will be used for all subsequent analyses.

Alpha power—A three-way, repeated measures ANOVA with factors cue-stimulus Interval (300, 600 and 900 ms), Cue (Ignore, Attend), and Position of the stimulus within the sequence (1st Gabor, 2nd Gabor) was calculated. There was a significant main effect of Cue in that Ignore-related alpha was stronger than Attend-related alpha ($F(1,11) = 28.495$, $p < 0.001$). There was also a significant main effect of Position, with alpha related to the second stimulus in a trial being reduced compared to alpha power related to the first stimulus in a trial ($F(1,11) = 16.57$, $p = 0.002$). Despite the difference between the mean posterior alpha values between Interval in Figure 3, there was no significant main effect of Interval following Z-score normalization ($F(1,11) = .373$, $p = 0.554$). None of the interactions were significant. Figure 5 shows the result of a wavelet analysis on signals taken from the posterior cluster. Results shown are for oscillations recorded over the interval (i) from onset of the first of the trial's color cues until (ii) the offset of the trial's first study Gabor.

Onset latency and resolution

The onset of increase in alpha power was defined as the first time point at which the power reached 50% of peak power (Luck et al., 2009; Kiesel, Miller, Jolicoeur, & Brisson, 2008; Luck et al., 2006). In order to identify the 50% peak moment, the average power at each

individual frequency within the 8–14 Hz band from –500 to 0 ms pre-cue was subtracted from the epoch between cue onset to stimulus offset, thus bringing power values at the cue epoch onset close to zero. On each trial, subjects were presented with one cue-Target pair and one cue-nonTarget pair. Although the sequence of attend first versus ignore first was randomized and counterbalanced, subjects knew that if the first Gabor was to be attended then the second would be ignored, and *vice versa*. Thus the response to the second cue-stimulus pair was influenced by prior knowledge and existing task demands. The influence of these factors can be seen in the right panel of Figure 6 in the variability of alpha power and temporal resolution. For several subjects in each of the Cue-stimulus interval conditions, there was no time-point at which the power reached 50% peak without being at 50% during the previous time-point. For this reason, in order to identify the onset latency of the pre-stimulus alpha signal, only a trial's first stimulus was included in this analysis.

A two-way repeated measures ANOVA showed a main effect of Cue-stimulus Interval (300, 600, 900 ms): $F(2,22) = 81.93$, $p < 0.001$. Neither Cue type (Ignore, Attend), nor any interaction was significant. Follow-up *t*-tests revealed that for every pairwise comparison for 300, 600 and 900 ms, alpha latency onset was significantly shorter for the longer of the two intervals being compared (earlier for 900 vs. 600 ms ($t_{11} = -5.194$, $p < 0.001$), for 900 vs. 300 ms ($t_{11} = -9.976$, $p < 0.001$), and for 600 vs. 300 ms ($t_{11} = -16.74$, $p < 0.001$). Expressed relative to stimulus onset, mean onset latencies were: 300ms = -0.185 ; 600ms = -0.472 ; and 900ms = -0.699 . So despite the fact that the timing of stimulus onset was constant and entirely predictable trial after trial in a session, the longer the cue preceded the stimulus, the earlier the onset of the alpha-band response.

Visual inspection of the time-frequency wavelets (Figure 5) and time-power traces (Figure 6) indicated that the enhanced peri-stimulus alpha power declined well before the offset of the stimulus. In other words, even though the study item remained on the computer screen, alpha power appeared to have returned to pre-onset levels. With this intriguing phenomenon in mind we carried out an additional post-hoc analysis, in which the end of the signal was defined as the first time point after the stimulus onset at which the power had fallen back to 50% of peak power. A two-way ANOVA with factors cue-stimulus Interval (300, 600 and 900ms) and Cue type (Ignore, Attend) showed no difference in offset times with Cue-stimulus Interval, Cue type, or their interaction. The mean offset latencies were 300ms = 0.220; 600ms = 0.204; and 900ms = 0.184, confirming that the offset of alpha power began at approximately 200 ms post-cue, a time several hundred ms before the stimulus disappeared.

Alpha and memory fidelity

To test the prediction that alpha power would be negatively correlated with the degree to which the nonTarget stimulus intruded into memory, trials across subjects and across cue-stimulus interval conditions were aggregated for the T_1N_2 trials in which the Gabor to be ignored appeared second in the sequence, and the N_1T_2 trials in which the Gabor to be ignored appeared first in the sequence.

For the T_1N_2 trials, each subject contributed on average 204 artifact-cleaned trials ($SD = 17$ trials). Alpha power over a –100 to +100 ms peri-stimulus epoch was log-transformed and

converted to z-scores for each subject across all three cue-stimulus interval conditions. Additionally, nRE values for these trials were converted to standardized scores (z-scores) for each subject across the three conditions in order to mute any impact of between-subject differences in over-all fidelity of recall. The resulting 2,445 total trials were sorted in order of increasing alpha power and divided into 8 bins of 306 trials each, except for bin 8 which held 303 trials. Ordering the bins according to increasing alpha power, bin 1 comprises trials across subjects with the lowest alpha amplitude, and bin 8 includes trials on which alpha amplitude was the highest. The nonTarget effect associated with trials in each of bin was then calculated. The strength of the relationship over the eight ordered bins between the nonTarget effect and alpha power was then evaluated with linear regression.

The same analysis was carried out for the N_1T_2 trials. Each subject contributed on average 196 artifact-cleaned trials ($SD = 20$ trials). The 2,352 total trials resulting from N_1T_2 trials were sorted into eight bins of 294 trials each.

As shown in Figure 7B, in the T_1N_2 trials, that is, when the nonTarget stimulus appeared second, alpha power is a predictor of the nonTarget effect during both the pre-stimulus epoch and the stimulus-onset epoch. As alpha power increases, so does the ability to ignore distracting information and so the intrusion of the nonTarget decreases. For the first 100 ms following stimulus onset, this linear trend accounts for 86% of the variance in the nonTarget effect across the eight alpha-defined bins ($F(1,11) = 35.63, p = 0.001$). Alpha power during the 100 ms leading up to the stimulus onset was a significant but weaker predictor of the intrusion of the distracting stimulus ($F(1,11) = 6.02, p = 0.050$). This analysis performed for nonTarget stimuli in the N_1T_2 trials produced no comparable relationship for pre-stimulus ($F(1,11) = 0.438, p = 0.533$) or stimulus onset ($F(1,11) = 0.059, p = 0.817$), as can be seen in Figure 7's panel A.

DISCUSSION

When a stimulus is intentionally ignored rather than attended, the ignored stimulus is preceded and accompanied by a relative increase in posterior alpha power (Figure 5). Importantly, this increase in alpha power is directly linked to the ability to prevent task-irrelevant stimulus from influencing recall of an accompanying task-relevant stimulus (Figure 7). The onset latency, resolution, and modulation of the cued-increase in alpha power provide valuable insights into the nature of the process that serves to protect memory.

Alpha Oscillations

The increase in alpha power we observed over posterior brain regions when subjects attempted to ignore a stimulus (Figure 3) is consistent with previous reports of attentional modulations of alpha during visual (Foxe & Snyder, 2011; Klimesch et al., 2011) and auditory (Banerjee, Snyder, Molholm, & Foxe, 2011) stimulus encoding. Parietal regions are believed to be a part of a fronto-parietal network of attentional control that modulates activity in sensory cortices (Corbetta & Shulman, 2002; Bollimunta, Mo, Schroeder, & Ding, 2011; Greenberg et al., 2012). In line with the view that posterior alpha power reflects an inhibitory mechanism, evidence shows that attentional biasing in visual cortex can suppress competing information (Kastner & Ungerleider, 2000; McMains & Kastner, 2011).

and task-irrelevant information (H. E. Payne & Allen, 2011). A similar, task-related posterior locus of alpha-band activity is also observed during short-term memory retention (Jensen, Gelfand, Kounios, & Lisman, 2002; Klimesch et al., 2007; Michels, Moazami-Goudarzi, Jeanmonod, & Sarthein, 2008) and again seems to reflect the suppression of distracting information in order to protect memory (Jokisch & Jensen, 2007; L. Payne & Kounios, 2009; Freunberger, Werkle-Bergner, Griesmayr, Lindenberger, & Klimesch, 2011; Bonnefond & Jensen, 2012).

The reduced alpha power for the second stimulus of a sequence compared with the first was an unexpected finding (Figure 3). We are uncertain if this reduction occurred because of a relative lack of attentional resources late in the trial's sequence or because the stimulus immediately prior to the retention period was more efficiently modulated. The latter seems more likely, as the dissociation between attend and ignore signals began immediately upon cue processing and the difference between the two is quite exaggerated compared to their first-stimulus counterparts. This early dissociation between attend and ignore for the second cue-stimulus pair likely manifests from participant's prior knowledge given that if the first cue had been to attend, then the second would always be to ignore, and vice versa. Individual differences in the use of this prior knowledge were reflected in the variability in alpha onset during this second pre-stimulus interval (Figure 6). Regardless of this difference in overall strength of alpha power between the first and second cue-stimulus pairs, alpha power was always greater for ignore versus attend across posterior electrodes (Figure 3) and across the same approximate temporal envelope (Figures 3 and 6).

Onset latency

As Figure 6 showed, the onset latency of increased pre-stimulus alpha power tracked the length of the interval separating the cue from the ensuing stimulus. As the cue-stimulus interval grew from 300 to 900 ms, the onset of increased alpha activity led stimulus onset by an increasing amount. Within a session of isochronic trials, the time at which the stimulus would appear was completely predictable, so it is unsurprising that onset latency of increased alpha power would be linked to predictable timing within the subsecond range used in our study. After all, a wide range of behaviors including target-interception and collision-avoidance depend upon being able to predict timing within this range (Zarco, Merchant, Prado, & Mendez, 2009). Moreover, the Weber fraction for intervals within the range covered by our manipulation, 300–900 ms, is ~5 and 15%, which should make each of our three intervals highly distinctive (Thompson, Schiffman, & Bobko, 1976; Merchant, Zarco, Bartolo, & Prado, 2008). Despite this predictability of stimulus onset time, the latency of the pre-stimulus increase in alpha was not, as one might expect, tightly linked to stimulus onset. Instead, the increase in alpha power preceded stimulus onset by as much as several hundred ms, a value many times the Weber fraction for time interval discrimination. When the cue-stimulus interval was varied between sessions, the latency of alpha increase did not occur at a fixed interval before the stimulus. Rather, the temporal relationship between cue and stimulus strongly influenced the timing of anticipatory alpha. Given only scant time to decide whether to attend or ignore, as in our 300 ms condition, modulation of alpha began almost immediately upon cue offset; however, given additional warning time,

as in our 900 ms condition, alpha modulation was delayed until several hundred ms after cue offset.

Signal resolution

Regardless of the cue-stimulus interval within a block of trials, the increase in alpha power anticipated stimulus onset and then resolved by ~200 ms following stimulus onset. Note that the resolution is essentially complete well before the stimulus would disappear from view. Interestingly, Freunberger et al. (2009) found highly similar timing of alpha signal onset and offset, despite the use of a longer, 1000 ms stimulus (see their Figure 3). Within approximately 200 ms of a visual stimulus' onset, EEG recordings differentiate between characteristics such as spatial location, category meaning, and task-relevance (VanRullen & Thorpe, 2001). Reliable cue-related increases in pre-stimulus alpha power and its resolution before stimulus offset demonstrates the importance of suppressing the onset and early processing of irrelevant information. The sudden onset of a stimulus has been found to be particularly hard to ignore (Yantis, 1993; Ludwig & Gilchrist, 2002), but directed attention can attenuate the response to the onset of task-intrusive stimuli (Yantis & Jonides, 1990; Ludwig & Gilchrist, 2003; Fukuda & Vogel, 2009).

Although the response to nonTarget onset may be attenuated, there is no evidence that the alpha suppression that always occurs in response to visual stimulus onset can be completely prevented during an eyes-open task. Regardless of cued warning to ignore an upcoming stimulus, alpha returns to pre-cue levels within a couple hundred milliseconds of a stimulus onset. Successful attentional modulations of neural activity associated with distracting information are consistently observed during this early epoch of visual processing (Hillyard, Vogel, & Luck, 1998). This concept was illustrated clearly by Zanto and Gazzaley (2009) who demonstrated that poor memory performance was associated with the unsuccessful filtering of distracting information during stimulus encoding, as evidenced by early ERP components N1 and P1. In agreement with these reports, successful employment of goal-directed, attentional control within the first 100 ms of the stimulus presentation limited the interference from task-irrelevant stimuli (Figure 7). Our findings also agree with a number of empirical results demonstrating a relationship between alpha oscillations and early event-related signatures of visual processing (Klimesch, Fellinger, & Freunberger, 2011; Rajagovindan & Ding, 2011).

Attentional modulation

Although there were significant differences in alpha power for attended and ignored stimuli, the temporal envelopes of increased alpha power during a trial are strikingly similar for the two conditions (see Figure 6). Although some reports demonstrate that cueing attention is associated with a desynchronization of alpha activity in advance of a stimulus' presentation (Huang & Sekuler, 2010a; Thut et al., 2006; Sauseng et al., 2005), that result may not be universal (Rihs et al., 2007; Worden et al., 2000). Additionally, as our own results show, alpha synchronization may increase during the interval between the cue offset and the onset of the stimulus (Freunberger et al., 2009). It is tempting to ascribe some general executive function to alpha synchronization, perhaps a function related to timing (Gooch, Wiener, Hamilton, & Coslett, 2011). For example, Min et al. (2008) proposed that posterior alpha

power observed during a cue-stimulus interval represented temporal expectancy. However, temporal expectancy would not differ between nontarget and target stimuli, as the timing is the same for both. Also, temporal expectancy did not differ between studies that report desynchronization rather than synchronization.

Instead, we propose that increased EEG alpha power during cued attention to some stimulus reflects the suppression of processing across the rest of the visual field when it is necessitated by centrally presented stimuli or irrelevant information within the same hemifield. The retinotopic organization of attentional modulation of alpha activity recorded over posterior cortex was demonstrated across the four visual field quadrants (Worden, Foxe, Wang, & Simpson, 2000) and across eight equally spaced locations, placed equidistant around fixation (Rihs, Michel, & Thut, 2007). Recently, retinotopically organized connections between intraparietal sulcus (IPS) and the visual cortex, correlated with attentional biasing, were illuminated in an elegant series of experiments using diffusion spectrum imaging (DS) in human participants (Greenberg et al., 2012). These studies reveal selective attention's spatial specificity. When attention is directed to the location of a stimulus, alpha desynchronizes in cortical areas involved in processing that stimulus. When a target stimulus is localized to one visual hemifield, alpha desynchronizes over the contralateral occipital cortex (Thut et al., 2006), provided the attended stimulus is spatially separated from distracting stimuli. However, alpha synchronization will be prevalent if a stimulus that should be ignored can potentially occupy the same location as an attended stimulus. That is the case for the centrally-presented stimuli in our study and for Freunberger et al. (2009), for multiple locations within the same hemifield (Rihs et al., 2007), and for spatially-overlapping attributes (Worden et al., 2000).

Alpha and the nonTarget effect

Our novel finding is that as alpha power increases, the intrusion of the distracting stimulus decreases (Figure 7). In other words, as alpha power increases, so does the ability to filter out task-irrelevant information. Interestingly, this relationship was true only for the T_1N_2 trials in which the nonTarget stimulus appeared second in the sequence. The total error was greater for these T_1N_2 than for the N_1T_2 trials (Figure 2), however, the nonTarget effect was not significantly different between the two sequences, despite T_1N_2 trials also yielding a greater average nonTarget effect. The combination of Gabor stimuli and the Target reproduction technique used in this experiment enables the dissociation of errors toward stimuli other than the Target. There would also be, on any given trial, errors arising from many other sources such as internal or external distraction, or poor reproduction. Our finding indicates that errors not systematically in the direction of the other stimuli drove the significant difference in total error between the trial types. It seems likely that a major source of error in the T_1N_2 trials that would not bias reproduction toward the nonTarget would be the disruption of Target maintenance due to the sudden onset of the second cue and the subsequent nonTarget stimulus.

The finding of a positive relationship between alpha power and the nonTarget effect only for T_1N_2 trials implies that although the nonTarget effect did not differ significantly between the two types of trial sequences (T_1N_2 , N_1T_2) these two populations have two distinct

distributions affecting the correlation with alpha power. It is clear that the mean nonTarget effect for the N₁T₂ trials is quite small, near zero, which would hinder efforts to correlate with such a small range of values. Previous work with cued attention to Gabor stimuli located in separate hemifields failed to produce a nonTarget effect (Huang & Sekuler, 2010a), indicating that characteristics of non-Target stimuli that appear in a separate visual hemifield or first in a sequence can be more successfully filtered out of memory. NonTargets that appear in the same visual field as a Target already being maintained have a decreasing influence on Target reproduction with increasing alpha power. When there are even stronger alpha oscillations, as for the first cue-stimulus interval compared to the second cue-stimulus interval (Figures 3, 4, and 6), there is no such linear relationship.

Thus, the ability to ignore distraction is fundamental to perception and memory, and it is correlated with increased alpha oscillations. In combination, our findings demonstrate the significance of the timely deployment of alpha-related attentional processes during cued, intentional ignoring.

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Figure 1.

Schematic diagram illustrating a trial's event structure. Each trial began with a fixation cross that oriented the subject to the region of the computer display within which the trial's stimuli would be presented. The fixation point was replaced either by a green disc or a red disc. The green disc cued the subject that the spatial frequency of the ensuing Gabor stimulus should be remembered; a red disc cued the subject that the next Gabor's spatial frequency should be ignored. A cue-stimulus interval of either 300, 600 or 900 ms followed (blocked design), and then the first of two Gabor stimuli was presented. Immediately thereafter, a second cue was presented. This cue was a disc that was green if the first cue had been red, or red if the first cue had been green. Then a second cue-stimulus interval followed; this interval was always the same as the trial's initial cue-stimulus interval, that is, either 300, 600 or 900 ms. Next a second Gabor stimulus was presented, which was followed by a one-second long retention interval. Finally, a comparison Gabor appeared whose spatial frequency could be adjusted to match the remembered spatial frequency of the Gabor that the subject had been cued to remember. Top row: on half the trials, the target Gabor to be attended appeared first and the nonTarget Gabor to be ignored appeared second (hereafter we refer to this sequence as T₁N₂). Bottom row: on half of the trials the nonTarget Gabor to be ignored appeared first and the Target Gabor to be attended appeared second (hereafter, N₁T₂).

Figure 2.

Bar charts showing absolute values of nRE (left set of bars), the effect of the nonTarget stimulus (middle set of bars), and the effect of the prototypical stimulus (right set of bars) for the 300ms, 600ms and 900ms cue-stimulus interval conditions. In each pair of bars, results for T_1N_2 and N_1T_2 trials are shown separately. Data are means over subjects. Error bars are ± 1 within-subject standard errors of the mean. A significant difference between two test conditions at $p < 0.05$ is indicated by the asterisk (*).

Figure 3.

Grand averaged, topographic maps of alpha power for the first Attend and Ignore stimuli (left panels) and the second Attend and Ignore stimuli (right panels). (Top) Results with 300 ms between cue's end and onset of stimulus; (Middle) results with 600 ms between cue's end and onset of stimulus; (Bottom) results with 900 ms between cue's end and onset of stimulus. Results are averaged over the 0 to 100 ms time window from the stimulus onset. Rounded ears are to the right and left sides and a triangle nose is at the top of each map.

Ignore > Attend

Figure 4. Topographic display of ignore-related alpha power (nonTarget > Target cluster; $p < 0.01$). Electrodes within the cluster showing a significant difference between the two test conditions at $p < 0.025$ are indicated by the asterisk (*).

Figure 5.

Grand averaged, time-frequency wavelets averaged across the cluster of 26 posterior electrodes for the first Attend and Ignore stimuli (left panels) and the second Attend and Ignore stimuli (right panels). The time scale is the same for each wavelet (500 ms is the same length on all wavelets). The Attend and Ignore columns are lined up on the stimulus onset for ease of comparing the timing of the increases in alpha power. (Top) Results with 300 ms between cue's end and onset of stimulus; (Middle) results with 600 ms between cue's end and onset of stimulus; (Bottom) results with 900 ms between cue's end and onset of stimulus.

Figure 6.

Grand Averaged alpha power over time for attend (green) and ignore (red) for the first stimulus (left panel) and the second stimulus (right panel). (Top) 300 ms condition, (Middle) 600 ms condition and (Bottom) 900 ms condition. Ribbons indicate ± 1 within-subject standard errors of the mean. The black rectangles along the time axis mark the duration between the onset and offset of 50% peak power.

Figure 7.

Alpha power predicts the nonTarget effect (intrusion of the nonTarget information) when the nonTarget stimulus follows the Target stimulus. The relationship shows that as alpha power increases, the nonTarget effect decreases. The header depicts the trial type with a box around the nonTarget stimulus of interest. A) Ignore-first trials (N_1T_2) and B) Ignore-second trials (T_1N_2) were sorted into eight equally populous bins according to the ongoing alpha power across the cluster of posterior electrodes. Bin 1 comprises trials with the lowest alpha amplitude, and bin 8 includes trials on which alpha amplitude was highest. (Top) Pre-stimulus 100 ms time window; (Bottom) 100 ms time window following nonTarget onset.