

Under review, July 2012

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

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## Abstract

Combining high-density scalp EEG recordings and 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 entails some suppression of task irrelevant 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.

Cortical oscillations within the alpha band (8-14 Hz) are markers of task-related engagement or disengagement of specific brain regions. For example, when attention is directed to a lateralized visual stimulus, ipsilateral brain regions exhibit a relative increase in alpha activity (Worden, Foxe, Wang, & Simpson, 2000; Kelly, Lalor, Reilly, & Foxe, 2006; Thut, Nietzel, Brandt, &

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Many thanks to Abigail Noyce and Stefan Berteau for help with this project. Supported in part by CELEST, a National Science Foundation Science of Learning Center (NSF OMA-0835976), NIH grants MH068404 and T32-NS07292.

Pascual-Leone, 2006; Rihs, Michel, & Thut, 2007; Huang & Sekuler, 2010a). Additionally, modality-specific changes in alpha activity are seen when subjects are cued to ignore input from one particular sensory modality (Foxye, Simpson, & Ahlfors, 1998; Fu et al., 2001; Snyder & Foxye, 2010; Jones et al., 2010; Haegens, Luther, & Jensen, 2012). It is thought that such attentional processes entail not only a decrease in alpha activity over regions of active encoding, but also an increase in regions whose function is to be reduced. In this view, alpha oscillations reflect an active inhibitory mechanism, and alpha desynchronization promotes stimulus processing (for review, see Klimesch, Sauseng, & Hanslmayr, 2007; Foxye & Snyder, 2011).

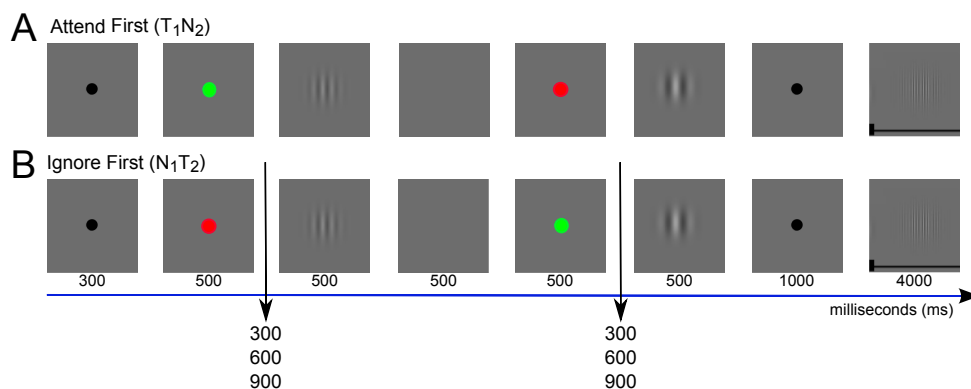
With a working-memory task, Freunberger, Fellingner, Sauseng, Gruber, and Klimesch (2009) demonstrated that a cue to ignore an upcoming stimulus elicits higher alpha power than a cue to attend to the stimulus. Interestingly, this ignoring-related increase in alpha power preceded the stimulus by several hundred ms, and lasted only for the initial 100-150 ms of the entire 1000-ms stimulus presentation. Because Freunberger et al.'s experiment consisted of one fixed delay between the offset of each cue and the onset of the next stimulus, it is not possible 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 in a modification of Freunberger et al.'s core task.

In addition, although increased alpha activity is related to cued-ignoring of spatial locations and task-irrelevant information, 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 exploited a recall technique in which subjects adjusted a stimulus to match an item held in memory. Subjects' reproductions of the spatial frequency of the remembered stimulus yields 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). 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 ( $\bar{X} = 22$ ,  $SD = 3.54$ ). 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.



*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 order as  $T_1N_2$ ). 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,  $N_1T_2$ ).

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  $1.14^\circ$ . Each Gabor subtended  $4.65^\circ$ . 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  $1280 \times 960$  pixels. Screen luminance was linearized by means of software adjustment, with the mean luminance of the screen held at  $32 \text{ cd/m}^2$ . 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 used subsequently 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. Trialwise differences in the two Gabors' spatial frequencies was controlled by the QUEST algorithm. 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% ( $\bar{X} = 13.25$ ,  $SD = 3.41$ ).

#### *Procedure.*

In order to quantify the fidelity of working memory, two Gabors were presented in sequence, as had been the case during the preliminary threshold determinations. Then, after a one-second retention interval, the subject used a matching procedure to reproduce one of the Gabor's spatial frequency from memory. 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). Of the two study items on each trial, the Gabor whose frequency was the lower appeared first or second in the sequence with equal probability. The actual frequencies presented on each trial were randomized using the method described by (Huang & Sekuler, 2010b). On each trial, the order 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 (T<sub>1</sub>N<sub>2</sub>); for the remaining trials, the order was reversed, with the nonTarget Gabor appearing first, followed by the Target (N<sub>1</sub>T<sub>2</sub>).

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 served in three sessions, one devoted to each of the three intervals between cue and stimulus. The order of the three conditions was counterbalanced orders across subjects. For each condition, the first 16 trials were excluded from analysis as practice trials, leaving 160 trials per condition for analysis.

As Fig. 1 shows, 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 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.

### *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. This normalization produces what we call a normalized raw error (nRE).

As with most types of errors, the value of nRE on any trial is likely to arise from multiple sources. With that in mind, Huang and Sekuler (2010b) developed a computational procedure for extracting from an nRE two sources of error, which reflected the influence of stimuli other than the target stimulus. They demonstrated that an nRE can be analyzed into one component that reflects the influence of that trial's nonTarget, and a second component that reflects the influence of the aggregate of spatial frequencies seen on preceding trials. These components can be described as a nonTarget effect and a Prototype effect, respectively. Applying the same computational procedures, we extracted nonTarget and Prototype effects from the nRE values produced by our subjects. 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  $< 50k\Omega$ . 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. Blink artifacts were identified by visual inspection of independent component analysis (ICA) and eliminated. Epochs containing artifacts were excluded from analysis. 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. Topographic plots of peri-stimulus (200 ms window centered around stimulus onset) activity show strongest alpha activity in posterior electrodes (Fig. 4). Wavelet alpha power for all electrodes was calculated for this peri-stimulus epoch. 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.

Electrode 84 showed the highest alpha power, and was selected for further statistical analysis. This slightly right-lateralized posterior-occipital electrode does not have a direct nomenclature correlate in the 10/20 international system. However, its surrounding nearest neighbors in that system would be P8, P4, PO4, PO8, and O2. The close proximity to electrode PO8 is especially noteworthy; PO8 was the electrode that showed the largest ignoring-related signals in Freunberger et al.'s experiment.

## 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. Calculation 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 sessions regardless of the order in which the cue-stimulus intervals were presented ( $F_{(2,22)} = 0.069$ ,  $p = 0.929$ ). For session 1,  $\bar{X} = 1.536$  and  $SD = 0.331$ ; for session 2,  $\bar{X} = 1.5$  and  $SD = 0.33$ ; for session 3,  $M = 1.52$  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 Order ( $T_1N_2$ ,  $N_1T_2$ ) and Cue-stimulus Interval (300, 600 and 900 ms) on three dependent measures, nRE, the nonTarget effect, and Prototype effect. As shown in Fig. 2, order of stimulus presentation, that is  $T_1N_2$  vs.  $N_1T_2$ , significantly affected nRE, with  $T_1N_2$  trials producing larger mean reproduction errors than  $N_1T_2$  trials ( $F_{(1,11)} = 135.38$ ,  $p < 0.001$ ). However, Order influenced neither the Prototype nor the nonTarget 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 power.* A three-way, repeated measures ANOVA with factors cue-stimulus Interval (300, 600 and 900 ms), Cue (Ignore, Attend), and order ( $1^{st}$  Gabor,  $2^{nd}$  Gabor) was calculated. There was a significant main effect of Cue in that Ignore-related alpha was stronger than Attend-related alpha ( $F_{(1,11)} = 17.2$ ,  $p = 0.002$ ). There was also a significant main effect of Order, with alpha related to the second stimulus in a trial being reduced compared to alpha power related to the first stimulus in a trial ( $F_{(1,11)} = 7.9$ ,  $p = 0.017$ ). There was no significant main effect of Interval ( $F_{(1,11)} = .454$ ,  $p = 0.609$ ). There were no significant interactions. Fig. 3 shows the result of a wavelet analysis on signals taken from posterior-occipital electrode 84. 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 first study Gabor.

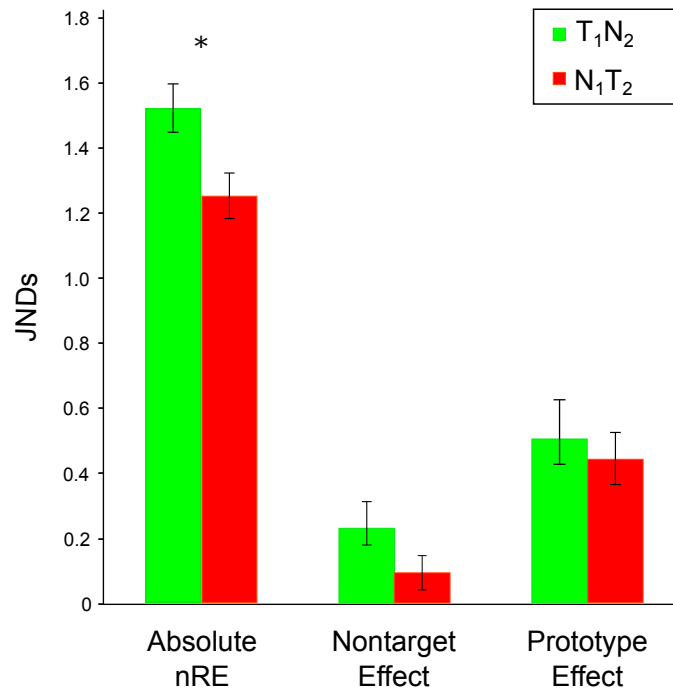


Figure 2. Bar charts showing absolute values of nRE (left pair of bars), the effect of the nonTarget stimulus (middle pair of bars), and the effect of the prototypical stimulus (right pair of bars). In each pair of bars, results for T<sub>1</sub>N<sub>2</sub> and N<sub>1</sub>T<sub>2</sub> conditions are shown separately. Data are means over subjects. Error bars are  $\pm 1$  within-subject standard errors of the mean. A significant difference between two test conditions at  $p < 0.05$  is indicated by the asterisk (\*).

*Alpha latency.* 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. For this reason, towards the aim of identifying the onset latency of the pre-stimulus alpha signal, only the first stimuli were included in this analysis. To further isolate this pre-stimulus signal, the average power at each individual frequency within the 8--14 Hz band from -500 to -100 ms pre-cue was subtracted from the epoch between cue onset to stimulus offset. 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).

A two-way repeated measures ANOVA showed a main effect of Cue-stimulus Interval (300, 600, 900 ms):  $F_{(2,22)} = 62.5$ ,  $p < 0.000$ . 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 ( $t_{11} = -4.674$ ,  $p = 0.001$ ), for 900 vs. 300 ms ( $t_{11} = -10.587$ ,  $p < 0.000$ ), and for 600 vs. 300 ms ( $t_{11} = -6.977$ ,  $p < 0.001$ ). Expressed relative stimulus onset, mean onset

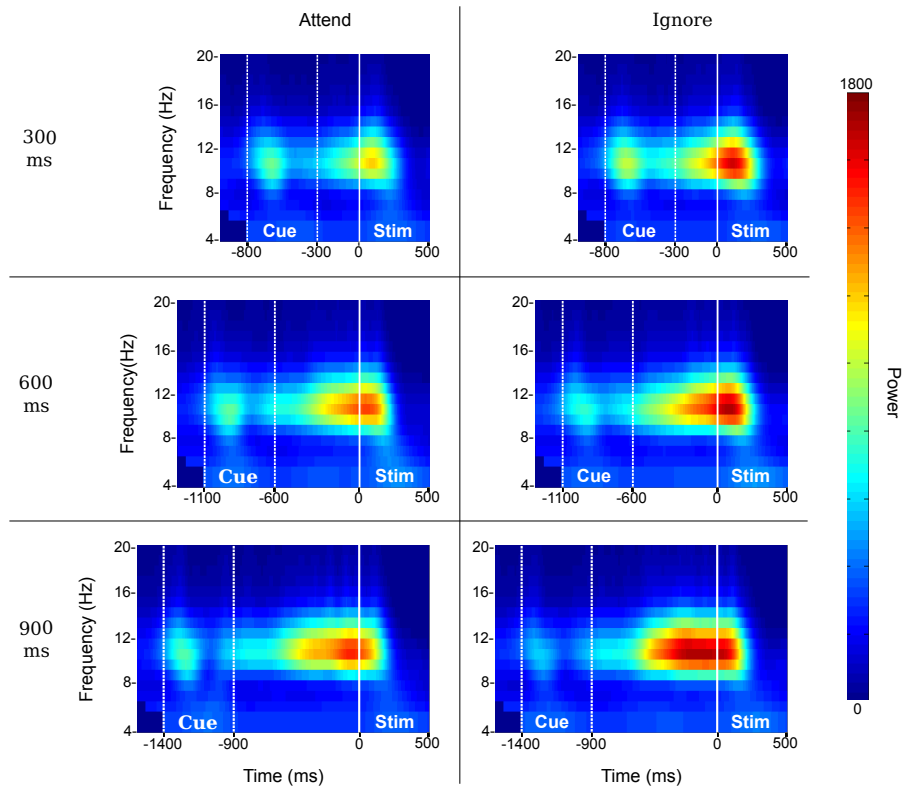
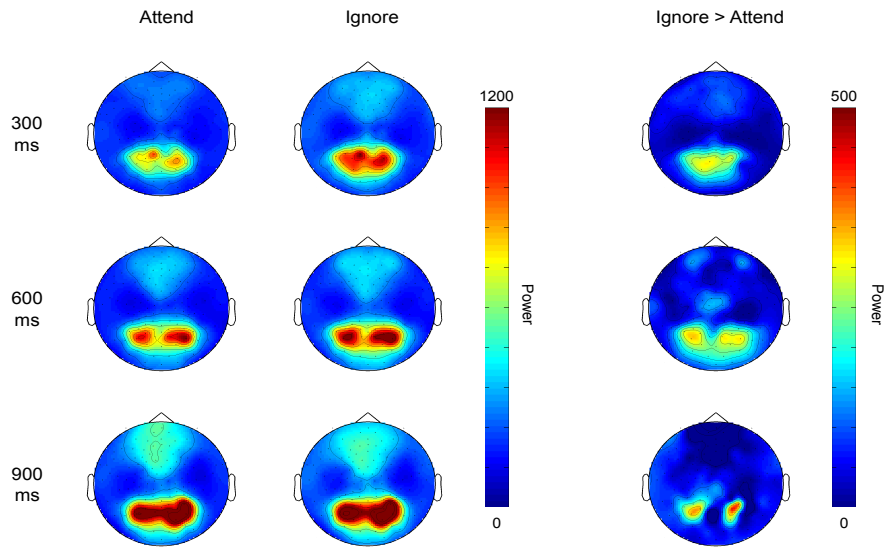


Figure 3. Grand averaged, time-frequency wavelets at a representative posterior electrode 84 for Attend (left panels) and Ignore (right panels) conditions. The time scale is the same for each wavelet (500 ms is the same length on all wavelets). The Attend and Ignore panels are lined up on the stimulus 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.

latencies were:  $\bar{X}_{300ms} = -0.226$ ;  $\bar{X}_{600ms} = -0.479$ ; and  $\bar{X}_{900ms} = -0.673$ . 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 (Fig. 3) and time-power traces (Fig. 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  $\bar{X}_{300ms} = 0.219$ ;  $\bar{X}_{600ms} = 0.178$ ; and  $\bar{X}_{900ms} = 0.179$ , confirming that the offset of alpha power began at approximately 200 ms post-cue, a time several hundred ms before the stimulus disappeared.





*Figure 4.* Grand averaged, topographic maps for Attend (left panels) and Ignore (middle panels) conditions, with the right panel showing Ignore greater than attend. (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 -100 to 100 ms time window centered around the stimulus onset. Rounded ears are to the right and left sides and a triangle nose is at the top of each map.

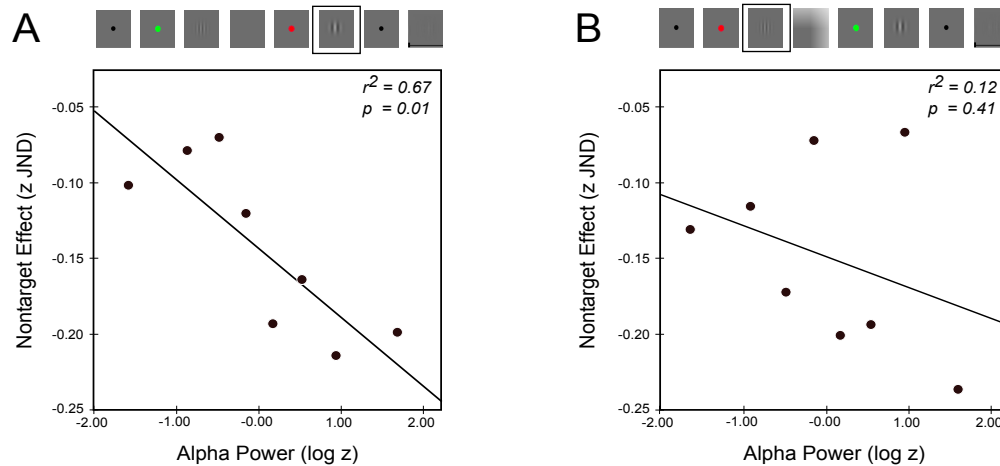
### *Alpha and memory fidelity*

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 the 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.



**Figure 5.** 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 distracting stimulus of interest. A) Ignore-second trials ( $T_1N_2$ ) and B) Ignore-first trials ( $N_1T_2$ ) were sorted into eight equally populous bins according to the ongoing alpha power at representative posterior electrode E84 within the -100 to 100 ms time window centered around the nonTarget stimulus onset. Bin 1 comprises trials with the lowest alpha amplitude, and bin 8 includes trials on which alpha amplitude was highest.

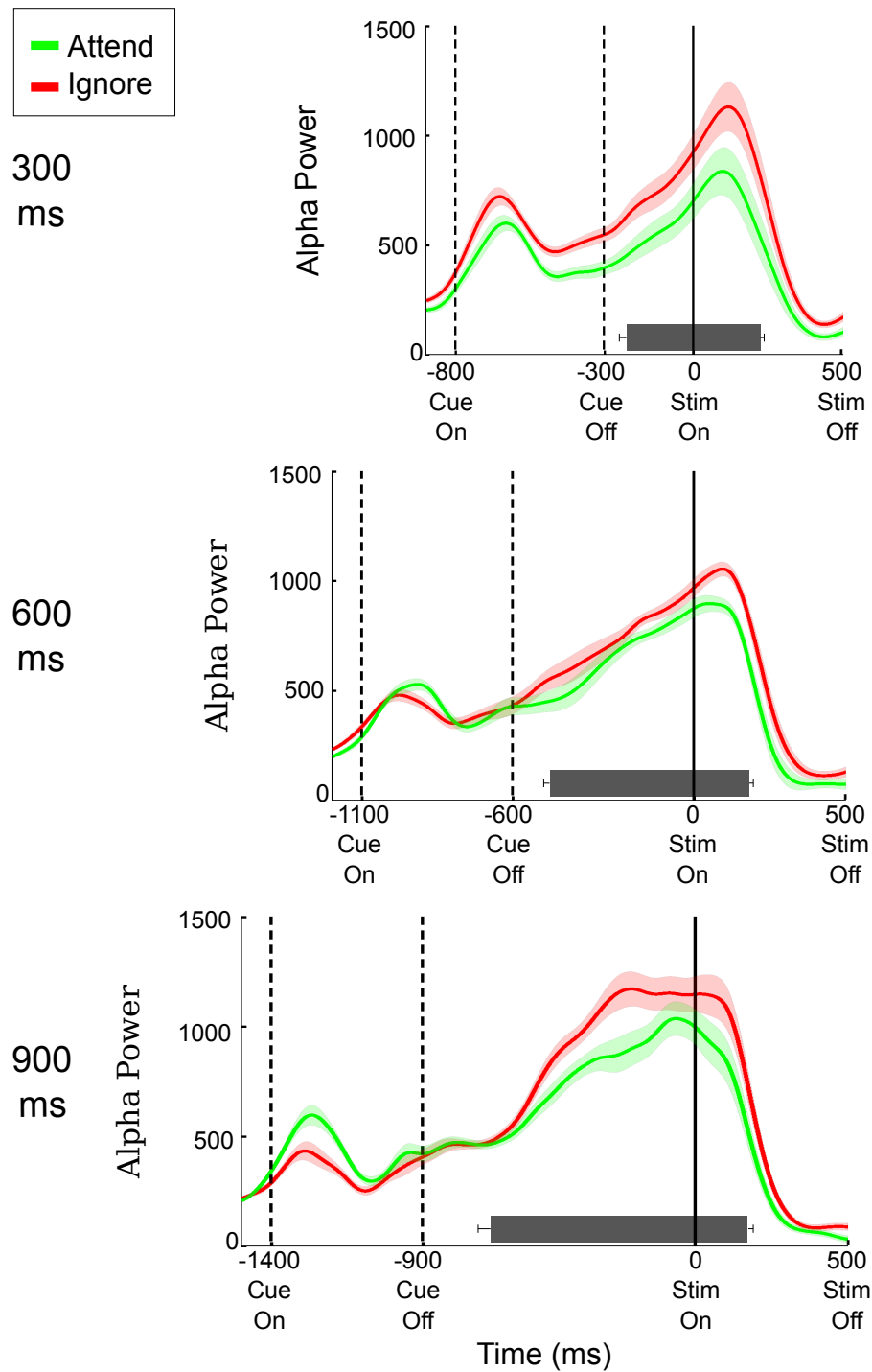
As shown in Fig. 5A, peri-stimulus alpha power is a strong predictor of the nonTarget effect ( $F(1,11) = 12.4$ ,  $p = 0.012$ ) in the  $T_1N_2$  trials, that is, when the nonTarget stimulus appeared second. As alpha power increases, so does the ability to ignore distracting information and so the intrusion of the nonTarget decreases. This linear trend accounts for 67% of the variance in the nonTarget effect across the eight alpha-defined bins. This analysis performed on the peri-stimulus epoch around the nonTarget stimulus in the  $N_1T_2$  trials produced no comparable relationship ( $F(1,11) = 0.792$ ,  $p = 0.408$ ), as can be seen in Fig. 5's panel B.

## Conclusions and 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 (Fig. 3). Importantly, this relative increase in alpha power is directly linked to the ability of the ignored, task-irrelevant stimulus to influence recall of an accompanying task-relevant stimulus (Fig. 5). The onset latency, resolution, and temporal envelope of the cued-increase in alpha power provide valuable insights into the nature of the process that serves to protect memory.

### *Onset latency and resolution*

As Fig. 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 block of isochronic trials, the time at which the stimulus would appear was



*Figure 6.* Grand Averaged alpha power over time for attend (green) and ignore (red) for the 300 ms condition (Top), 600 ms condition (Middle) and 900 ms condition (Bottom). Ribbons indicate  $\pm 1$  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.

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  $\sim 5$  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 blocks, 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.

Regardless of the cue-stimulus interval within a block of trials, the increase in alpha power anticipated stimulus onset and then resolved by  $\sim 200$  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 Fig. 3). 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). In agreement with these reports, successful employment of goal-directed, attentional control limited the interference from task-irrelevant stimuli (Fig. 5). 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). Within approximately 200 ms of a visual stimulus onset, EEG recordings can differentiate between characteristics such as spatial location, category meaning, and task-relevance (VanRullen & Thorpe, 2001). In combination, these findings demonstrate the significance of the timely deployment of alpha-related attentional processes during cued, intentional ignoring.

### *Temporal envelope*

Although there were significant differences in alpha power for attended and ignored stimuli, the temporal envelopes of alpha power during a trial are strikingly similar for the two conditions (see Fig. 6). Interestingly, Freunberger et al. (2009) also noted that the alpha-band response to an “attend” cue resembled a scaled-down version of the response to an “ignore” cue. They speculated that this similarity reflected the initiation of top-down control. It is tempting to ascribe the consistency in alpha’s time course to some general executive function, perhaps one 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. Instead, we propose that modulation of alpha power during cued attention to some stimulus reflects the same suppression mechanism that supports intentional ignoring. Our hypothesis is that attention directed toward a stimulus requires that processing of other irrelevant stimuli be suppressed. This premise that attention directed toward some object or attribute requires simultaneous suppression of other objects or attributes is not new. In fact, William James (1890) wrote about attention in terms of these dual processes: attention “implies withdrawal from some things in order to deal effectively with others.” 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. Consistent with that perspective, our results suggest that selective attention toward a stimulus entails the active reduction of irrelevant processing.

This reliable difference in posterior alpha power between cued ignoring and cued attending has been well documented, both in target detection tasks with visual stimuli (Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006; Rihs et al., 2007) and in short-term visual memory tasks (Huang & Sekuler, 2010a; Freunberger et al., 2009). The match between Freunberger et al. (2009)’s result (their Fig. 3) and our own 600 ms condition (Fig. 3) is particularly striking. In both, posterior oscillatory power in the alpha band increases from cue offset, reaches a maximum 150--200 ms before the stimulus onset, and continues on during the first 100--150 ms of stimulus presentation. Although both Freunberger et al.’s experiment and our 600 ms condition shared the same cue-stimulus timing, the similarity between the two sets of results is remarkable considering the many differences between the protocols: the type of stimuli in the two studies (drawings of nameable, every day objects vs. Gabor stimuli), the type of task subjects performed (recognition versus recall), the duration of the stimuli (1000 vs. 500 ms), and the number of items per trial (16 cue-stimulus pairs vs. 2 cue-stimulus pairs). The reproducibility of alpha power variation during a trial suggests that could be useful as a signature of some general top-down process for visual attention.

The increase in alpha power we observed over posterior brain regions when subjects attempted to ignore a stimulus (Fig. 4) is consistent with previous reports of attentional modulations of alpha during visual (Foxye & Snyder, 2011; Klimesch et al., 2011) and auditory (Banerjee, Snyder, Molholm, & Foxye, 2011) stimulus encoding. We found that as alpha power increases, the intrusion of the distracting stimulus decreases (Fig. 5). In other words, as alpha power increases, so does the ability to filter out task-irrelevant information. Parietal regions are believed to be a part of a frontoparietal 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). Thus, the ability to ignore distraction is fundamental to perception and memory, and it is correlated with increased EEG alpha oscillations.

## References

- Banerjee, S., Snyder, A. C., Molholm, S., & Foxe, J. J. (2011). Oscillatory alpha-band mechanisms and the deployment of spatial attention to anticipated auditory and visual target locations: supramodal or sensory-specific control mechanisms? *Journal of Neuroscience*, *31*(27), 9923--9932.
- Bollimunta, A., Mo, J., Schroeder, C. E., & Ding, M. (2011). Neuronal mechanisms and attentional modulation of corticothalamic alpha oscillations. *Journal of Neuroscience*, *31*(13), 4935--4943.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433-436.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201--215.
- Cousineau, D. (2005). Confidence intervals in within-subject designs: a simpler solution to Loftus and Masson's method. *Tutorials in Quantitative Methods for Psychology*, *1*, 42-45.
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9--21.
- Dube, C., Zhou, F., & Sekuler, R. (under review). Similarity-based distortion of short-term visual memory is perceptual.
- Foxe, J. J., Simpson, G. V., & Ahlfors, S. P. (1998). Parieto-occipital approximately 10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport*, *9*(17), 3929--3933.
- Foxe, J. J., & Snyder, A. C. (2011). The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Frontiers in Psychology*, *2*, 154.
- Freunberger, R., Fellinger, R., Sauseng, P., Gruber, W., & Klimesch, W. (2009). Dissociation between phase-locked and nonphase-locked alpha oscillations in a working memory task. *Human Brain Mapping*, *30*(10), 3417-3425.
- Freunberger, R., Werkle-Bergner, M., Griesmayr, B., Lindenberger, U., & Klimesch, W. (2011). Brain oscillatory correlates of working memory constraints. *Brain Research*, *1375*, 93--102.
- Fu, K. M., Foxe, J. J., Murray, M. M., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001). Attention-dependent suppression of distracter visual input can be cross-modally cued as indexed by anticipatory parieto-occipital alpha-band oscillations. *Brain Research*, *12*, 145--152.
- Fukuda, K., & Vogel, E. K. (2009). Human variation in overriding attentional capture. *Journal of Neuroscience*, *29*(27), 8726--8733.
- Gooch, C. M., Wiener, M., Hamilton, A. C., & Coslett, H. B. (2011). Temporal discrimination of sub- and suprasecond time intervals: a voxel-based lesion mapping analysis. *Frontiers in Integrative Neuroscience*, *5*, 59.
- Greenberg, A. S., Verstynen, T., Chiu, Y.-C., Yantis, S., Schneider, W., & Behrmann, M. (2012). Visuotopic cortical connectivity underlying attention revealed with white-matter tractography. *Journal of Neuroscience*, *32*(8), 2773--2782.
- Haegens, S., Luther, L., & Jensen, O. (2012). Somatosensory anticipatory alpha activity increases to suppress distracting input. *Journal of Cognitive Neuroscience*, *24*(3), 677--685.
- Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: A review and a new view. In G. H. Bower (Ed.), (Vol. 22, pp. 193--225). New York: Academic Press.
- Huang, J., & Sekuler, R. (2010a). Attention protects the fidelity of visual memory: behavioral and electrophysiological evidence. *Journal of Neuroscience*, *30*(40), 13461--13471.
- Huang, J., & Sekuler, R. (2010b). Distortions in recall from visual memory: two classes of attractors at work. *Journal of Vision*, *10*(2), 24.1-24.27.
- James, W. (1890). *The principles of psychology*. New York: H. Holt and Company.
- Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex*, *12*(8), 877--882.
- Jokisch, D., & Jensen, O. (2007). Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *Journal of Neuroscience*, *27*(12), 3244--3251.
- Jones, S. R., Kerr, C. E., Wan, Q., Pritchett, D. L., Hamalainen, M., & Moore, C. I. (2010). Cued spatial

- attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *Journal of Neuroscience*, 30(41), 13760--13765.
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, 23, 315-241.
- Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *Journal of Neurophysiology*, 95(6), 3844--3851.
- Kiesel, A., Miller, J., Jolicoeur, P., & Brisson, B. (2008). Measurement of ERP latency differences: a comparison of single-participant and jackknife-based scoring methods. *Psychophysiology*, 45(2), 250--274.
- Klimesch, W., Fellinger, R., & Freunberger, R. (2011). Alpha oscillations and early stages of visual encoding. *Frontiers in Psychology*, 2, 118.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Research Reviews*, 53(1), 63--88.
- Luck, S. J., Fuller, R. L., Braun, E. L., Robinson, B., Summerfelt, A., & Gold, J. M. (2006). The speed of visual attention in schizophrenia: electrophysiological and behavioral evidence. *Schizophrenia Research*, 85(1-3), 174--195.
- Luck, S. J., Kappenman, E. S., Fuller, R. L., Robinson, B., Summerfelt, A., & Gold, J. M. (2009). Impaired response selection in schizophrenia: evidence from the P3 wave and the lateralized readiness potential. *Psychophysiology*, 46(4), 776--786.
- Ludwig, C. J. H., & Gilchrist, I. D. (2002). Stimulus-driven and goal-driven control over visual selection. *Journal of experimental Psychology. Human Perception and Performance*, 28(4), 902--912.
- Ludwig, C. J. H., & Gilchrist, I. D. (2003). Goal-driven modulation of oculomotor capture. *Perception & Psychophysics*, 65(8), 1243--1251.
- McMains, S., & Kastner, S. (2011, Jan). Interactions of top-down and bottom-up mechanisms in human visual cortex. *Journal of Neuroscience*, 31(2), 587--597.
- Merchant, H., Zarco, W., Bartolo, R., & Prado, L. (2008). The context of temporal processing is represented in the multidimensional relationships between timing tasks. *PLoS One*, 3(9), e3169.
- Michels, L., Moazami-Goudarzi, M., Jeanmonod, D., & Sarnthein, J. (2008). EEG alpha distinguishes between cuneal and precuneal activation in working memory. *Neuroimage*, 40(3), 1296--1310.
- Min, B. K., Park, J. Y., Kim, E. J., Kim, J. I., Kim, J. J., & Park, H. J. (2008). Prestimulus EEG alpha activity reflects temporal expectancy. *Neuroscience Letters*, 438, 270--274.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97--113.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011, 156869.
- Payne, H. E., & Allen, H. A. (2011). Active ignoring in early visual cortex. *Journal of Cognitive Neuroscience*, 23(8), 2046--2058.
- Payne, L., & Kounios, J. (2009). Coherent oscillatory networks supporting short-term memory retention. *Brain Research*, 1247, 126--132.
- Rajagovindan, R., & Ding, M. (2011). From prestimulus alpha oscillation to visual-evoked response: an inverted-U function and its attentional modulation. *Journal of Cognitive Neuroscience*, 23(6), 1379--1394.
- Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by alpha-band EEG synchronization. *European Journal of Neuroscience*, 25(2), 603--610.
- Snyder, A. C., & Foxe, J. J. (2010). Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *Journal of Neuroscience*, 30(11), 4024-32.
- Thompson, J. G., Schiffman, H. R., & Bobko, D. J. (1976). The discrimination of brief temporal intervals. *Acta Psychologica*, 40, 489--493.

- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, *26*(37), 9494--9502.
- VanRullen, R., & Thorpe, S. J. (2001). The time course of visual processing: from early perception to decision-making. *Journal of Cognitive Neuroscience*, *13*(4), 454--461.
- Watson, A. B., & Pelli, D. G. (1983). QUEST: a Bayesian adaptive psychometric method. *Perception & Psychophysics*, *33*(2), 113--120.
- Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *The Journal of Neuroscience*, *20*(6), 1--6.
- Yantis, S. (1993). Stimulus-driven attentional capture. *Current Directions in Psychological Science*, *2*(5), 156-161.
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *Journal of experimental Psychology. Human Perception and Performance*, *16*(1), 121--134.
- Zanto, T. P., & Gazzaley, A. (2009). Neural suppression of irrelevant information underlies optimal working memory performance. *Journal Neuroscience*, *29*(10), 3059--3066.
- Zarco, W., Merchant, H., Prado, L., & Mendez, J. C. (2009). Subsecond timing in primates: comparison of interval production between human subjects and rhesus monkeys. *Journal of Neurophysiology*, *102*(6), 3191--3202.