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The importance of ignoring: Alpha oscillations protect selectivity

Lisa Payne and Robert Sekuler

The Volen Center for Complex Systems, Brandeis University

Abstract

Selective attention is often thought to entail an enhancement of some task-relevant stimulus or attribute. We discuss the perspective that ignoring irrelevant, distracting information plays a complementary role in information processing. Cortical oscillations within the alpha (8–14 Hz) frequency band have emerged as a marker of sensory suppression. This suppression is linked to selective attention for visual, auditory, somatic, and verbal stimuli. Inhibiting processing of irrelevant input makes responses more accurate and timely. It also helps protect material held in short-term memory against disruption. Furthermore, this selective process keeps irrelevant information from distorting the fidelity of memories. Memory is only as good as the perceptual representations on which it is based, and on whose maintenance it depends. Modulation of alpha oscillations can be exploited as an active, purposeful mechanism to help people pay attention and remember the things that matter.

Keywords

attention; alpha oscillations; ignoring; distraction

“Pay attention!!” These two words are uttered countless times each day, by teachers, by parents, and by automobile passengers trapped alongside a distracted driver. We present the view that enhanced focus is only half the story when it comes to effective processing. As William James (1890) noted, selective attention has a dual nature, as it “implies withdrawal from some things in order to deal effectively with others.” Withdrawal from background distraction is fundamental to cognition, so fundamental that it accounts for many of the individual differences in I.Q. (Melnick, Harrison, Park, Bennetto, & Tadin, 2013).

There is compelling evidence that cortical oscillations within a frequency band of 8–14 Hz – the alpha band– are key in controlling the impact of task-irrelevant sensory information. Discoveries from multiple perceptual (Worden, Foxe, Wang, & Simpson, 2000; Kelly, Lalor, Reilly, & Foxe, 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006) and short-term memory tasks (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999; Jensen, Gelfand, Kounios, & Lisman, 2002; Sauseng et al., 2005; Tuladhar et al., 2007) converge on the view that alpha oscillations are markers of sensory suppression. We will discuss the

significance of this suppression for accurate perception, for keeping irrelevant information from squandering memory's limited resources, and for preventing distortion of information on which memory depends.

PERCEPTION AND ALPHA OSCILLATIONS

You may have noticed the waning and waxing of your ability to pay attention. This variation in attention is thought to reflect ongoing cortical alpha oscillations (Busch, Dubois, & VanRullen, 2009; Hanslmayr, Gross, Klimesch, & Shapiro, 2011). Variability in stimulus detection (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009) and in the speed of perceptual discrimination (Vanrullen, Busch, Drewes, & Dubois, 2011) seem correlated to the portion of an alpha oscillation (peak or trough) with which the stimulus coincides. Also, spontaneous changes in the strength of alpha oscillations explain variability in the accuracy of discriminations. For example, in a task requiring that subjects respond differently to each of four letters in streams of trials, correct discrimination increased as pre-stimulus alpha power decreased. Additionally, subjects who performed at high level exhibited lower alpha power compared to those who performed at chance-level (Hanslmayr et al., 2005, 2007).

Spontaneous perceptual fluctuation can be regulated in order to promote selectivity for the stimuli that are most relevant while ignoring those that are irrelevant. To visualize this regulation, imagine that a cue directs your attention to a particular location in your left visual hemifield, where a target stimulus is about to be presented. Because of the visual system's contralateral organization, this left-lateralized stimulus would be processed in the right hemisphere. A robust cortical response follows a directional cue for attention: Alpha oscillations following the directional cue decrease in the hemisphere that would process the upcoming stimulus, but increase in the other hemisphere, the one not implicated in processing (Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006). There is an analogous effect of lateralized alpha modulation when auditory attention is cued to the left or right of space (Kerlin, Shahin, & Miller, 2010; Banerjee, Snyder, Molholm, & Foxe, 2011). In addition to suppressing input from a particular location, increased alpha oscillations are associated with feature-based selectivity such as ignoring the color of a stimulus in order to attend to its direction of motion, or vice versa (Snyder & Foxe, 2010). These results, and others, helped lead to the hypothesis that alpha oscillations comprise a suppression mechanism to gate irrelevant stimuli –what James meant by “withdrawal from some things.”

In a series of experiments, Romei and colleagues (Romei, Rihs, Brodbeck, & Thut, 2008; Romei, Brodbeck, et al., 2008; Romei, Gross, & Thut, 2010) put the alpha suppression hypothesis to a direct test. In one experiment, they used transcranial magnetic stimulation (TMS) to artificially boost oscillations in the cortex directly beneath the stimulation site (Thut, Schyns, & Gross, 2011). While subjects tried to detect a near-threshold visual target, TMS was applied to the scalp over either the right or the left parietal-occipital cortex (Romei et al., 2010). Pre-stimulus TMS impaired detection of targets contralateral to the site of stimulation, but only when the TMS was modulated in the alpha band. This result directly supports the hypothesis that increased cortical alpha activity can suppress processing.

Appropriate and timely response to relevant information requires the suppression of irrelevant processing. Haegens, Handel, and Jensen (2011) manipulated somatosensory attention, cuing subjects to attend to either the left or the right hand in order to make a tactile discrimination. Accuracy and speed of response improved with greater alpha lateralization over somatosensory cortex (Figure 1A). Haegens, Luther, and Jensen (2012) extended this observation by simultaneously presenting a task-irrelevant stimulus to the unattended hand. As expected, the irrelevant stimulus reduced the accuracy with which stimuli delivered to the cued hand could be discriminated. Although performance was impaired, there were trials on which subjects made a correct response. On these correct trials, pre-stimulus alpha activity was greater contralateral to the uncued hand than it was on incorrect trials. Thus, a localized increase in alpha activity was able to mitigate the potential effects of distracting stimuli.

MEMORY ENCODING AND ALPHA OSCILLATIONS

Research on short-term memory demonstrates that increased alpha activity during the retention period seems to suppress irrelevant stimuli in order to protect items in memory from interference (Klimesch et al., 1999; Jensen et al., 2002; Sauseng et al., 2005; Tuladhar et al., 2007; Payne & Kounios, 2009). In one such study (Bonnefond & Jensen, 2012), subjects judged whether or not a probe letter had been among the set of letters that had just been presented and were being held in memory. On each trial, a distracter stimulus was presented at a fixed time during retention. Alpha activity during the retention period increased just prior to the onset of the predictable distracter. Moreover, this anticipatory adjustment of alpha power was greater for highly distracting letters than for less distracting symbols.

Of course, short-term memory depends on more than just protecting relevant material from distraction during retention. It also depends on successfully filtering out irrelevant material during encoding (Zanto & Gazzaley, 2009). Sauseng and colleagues (2009) demonstrated that after subjects were cued to remember either the right or the left set of colored squares, alpha power during the retention period decreased over the contralateral cortex (the hemisphere responsible for processing the relevant objects) and increased over the ipsilateral cortex (the hemisphere responding to the irrelevant half of the display). Furthermore, alpha power related to the irrelevant half of the memory set increased with the number of objects that were to be ignored. This increase in lateralized activity was directly correlated with the number of relevant items that subjects could hold in short-term memory. In other words, excluding irrelevant information can maximize the functional use of short-term memory's limited capacity.

The success of excluding irrelevant information is often inferred from recall for relevant information. To directly test memory for the unattended stimuli in a cued visual attention task, Handel, Haarmeier, and Jensen (2011) occasionally asked subjects to report on the stimulus they had not been cued to attend. In their experiment, two separate clusters of dots, each cluster moving in a different direction, were displayed simultaneously to the left and right visual hemifields. Subjects were instructed to attend to either the right or left half of the display. After a brief retention period they were cued to report on the direction of motion of

the attended dots. On the trials that required reporting the direction of motion for the unattended dots, subjects with higher pre-stimulus alpha power over the hemisphere that would have processed the unattended side of the display were worse at remembering the direction of motion. This study linked pre-stimulus alpha power to ignoring behavior, and helped confirm that subjects were, in fact, inhibiting distraction.

We tested pre-stimulus alpha activity's influence on memory for an unattended attribute of auditory stimuli (Dubé Payne, Sekuler, & Rotello, 2013). This study manipulated subjects' attention to an auditory attribute of spoken words and to an orthographic attribute of printed words. In each trial, an English word was presented twice, once printed and then once spoken. A colored cue preceded each presentation. In half the trials, a red cue signaled subjects to ignore the font of the printed word, and a subsequent green cue signaled subjects to attend to the gender of the speaker of the spoken word. Subjects were then prompted to indicate whether the gender was male or female. In other trials, the green cue signaled that font was to be attended, and the red cue signaled that the speaker's gender was to be ignored. Subjects were then prompted to indicate whether the font of the printed word was italics or Roman. Strikingly, when subjects were cued to ignore a printed word, alpha activity increased over left frontal-temporal cortex (Figure 1B). A key structure in this region of the brain is Broca's area, which is implicated in the silent reading of words (Huang, Carr, & Cao, 2002) and in processing orthographic information (such as the font) of printed words (Montant, Schon, Anton, & Ziegler, 2011). This result reveals the importance of alpha activity in the inhibition of higher-order processing such as written language. In contrast, following a cue to ignore a spoken word, alpha activity increased in the posterior portion of the right-hemisphere (Figure 1C), a region consistent with ignoring auditory input (Banerjee et al., 2011). During a word recognition test tens of minutes after all trials had been completed, subjects demonstrated successful recall of speaker gender for attended spoken words, but performed only at chance for spoken words that they had been cued to ignore. These subjects had successfully prepared to ignore the supposedly task-irrelevant stimulus, and were therefore less able to recall the information it had contained.

In addition to maximizing use of limited resources, the exclusion of irrelevant information prevents distortion of relevant information that is being remembered. To measure the intrusion of irrelevant stimuli into subjects' recall of an attended visual stimulus, we (Payne, Guillory, & Sekuler, 2013) extended a sensitive assay of memory that had been introduced by Huang and Sekuler (2010a, 2010b). In that assay, subjects were tested for how well they remember Gabor patches, gratings comprising light and dark stripes. The gratings' stripes varied in spatial frequency (number of stripes per unit area). In our study, each trial consisted of one grating whose spatial frequency subjects are cued to remember and one they are cued to ignore. Both gratings were presented sequentially to the same area in the center of a computer screen. Note that our vision task did not rely on lateralized stimuli, which would cause attended and unattended stimuli to be processed in opposite hemispheres. Instead, by presenting both attended and unattended stimuli in central viewing, as Freunberger, Fellingner, Sauseng, Gruber, and Klimesch (2009) did, we were able to examine the impact of alpha dynamics when the brain could not restrict processing to one hemisphere. Thus, this design also isolates ignore-related alpha activity from a simultaneous requirement to attend. After holding the grating's spatial frequency in memory for one

second, subjects reproduced the spatial frequency of the attended stimulus by adjusting a comparison Gabor until they believed it matched the attended stimulus. We then calculated how accurately subjects had reproduced the to-be-remembered stimulus, which also allowed us to tell whether errors were shifted toward the direction of the to-be-ignored stimulus or not.

Combining EEG recordings with this analog measure of short-term memory's fidelity, we related alpha activity to the intrusion of task-irrelevant information (Payne et al., 2013). We found that the stronger the posterior alpha activity (Figure 1D) immediately preceding a to-be-ignored stimulus, the less it warped the reproduction of the attended stimulus (Figure 2). It is clear that the ability to modulate selective attention in order to ignore irrelevant information affects the precision of memory for task-related information.

THE PREPARED MIND

One interesting result is common to many of the selective attention experiments we have discussed: Cortical oscillations prior to the onset of a stimulus predict the subsequent behavioral response. Why is anticipating an irrelevant stimulus marked by increased alpha activity such as that shown in Figure 3? According to several researchers (Klimesch, Sauseng, & Hanslmayr, 2007; Jensen & Mazaheri, 2010; Mathewson et al., 2011), the answer lies in the mechanism of inhibition. Simply told, increased alpha activity shrinks the time window within which a stimulus can be processed. Therefore, strong pre-stimulus alpha activity is preventive; limiting neural computation to a brief period reduces the opportunity for unwanted information to reach awareness. This theoretical framework is consistent with the fact that, although the human brain is the most powerful processor known, it could not possibly deal with the complete, never-ending torrent of detailed input from our environment. Some regulation of incoming information is needed. Exploiting this system to willfully inhibit irrelevant information is essential to effective and successful selectivity.

Most people would agree that it is easier to say, "pay attention!" than it is to actually do it. Remarkably, mindfulness-based-stress-reduction (MBSR) training increases the alpha activity that marks the inhibition of irrelevant information. Kerr and colleagues (2011) devised a somatosensory attention task in which subjects were cued to attend either to their hand or their foot over intermixed trials. Alpha activity in the hand representation of somatosensory cortex decreased when attention was cued to the hand, but increased when attention was cued to the foot (Jones et al., 2010). Half the subjects then underwent training in MBSR, a type of meditation that directs attention to experiences in the present moment, emphasizing attention to bodily sensations. Finally, all subjects were tested again in the attention task. The mindfulness training enhanced alpha activity over the unattended, irrelevant region (over the hand region when cued to attend to the foot).

In summation, intentional ignoring can be enhanced if we learn to harness the mechanism of suppression that is embodied in cortical alpha oscillations. By improving our ability to inhibit irrelevant information, we can more effectively focus our attention.

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Figure 1.

Ignore-related, pre-stimulus alpha activity over modality-specific regions of the cortex. The length of the pre-stimulus interval between cue offset and stimulus onset varied per experiment. A) Relative increase in alpha power in left somatosensory cortex when cued to attend to left stimulation; relative decrease in alpha power in right somatosensory cortex when cued to attend to left stimulation. B) Alpha power over left frontal-temporal regions involved in language processing was greater in the ignore-font condition than in the attend-font condition for printed words. C) Alpha power over right posterior regions involved in auditory attention was greater in the ignore-voice condition than in the attend-voice condition for spoken words. D) Alpha power over posterior regions involved in visual attention was greater in the ignore-visual condition than in the attend-visual condition for non-verbalizable Gabors. A) Data adapted from "Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task" by S. Haegens, B.F. Handel, and O. Jensen, 2011, *Journal of Neuroscience*, 31(14), p. 5197. The original figure scale reflected p-values. The author's adapted the scale to the corresponding t-scores in order to match the other three plots in this figure. B) and C) Reprinted from "Paying attention to attention in recognition memory: Insights from models and electrophysiology" by C. Dubé L. Payne, R. Sekuler, and C. Rotello, 2013, *Psychological Science*, (In press), Copyright 2013 by Sage. D) Data adapted from "Attention-modulated alphaband oscillations protect against intrusion of irrelevant information" by L. Payne, S. Guillory, and R. Sekuler, 2013, *Journal of Cognitive Neuroscience*, 25:9, p.1463–1476, Copyright 2013 by MIT Press. The original figure scale was from 4 to +4 t-scores. It was adapted to the 0 to 4 scale to match C) and D) in this figure.

Figure 2.

Alpha power predicts the intrusion of the irrelevant (nonTarget) information. The relationship shows that as alpha power increases, the amount of error biased toward the nonTarget decreases. Eight bins of approximately equal numbers of trials were sorted according to the ongoing alpha power across the cluster of posterior electrodes in (Figure 1D). Bin 1 comprises trials with the lowest alpha amplitude, and bin 8 includes trials on which alpha amplitude was highest. (Left panel) pre-stimulus 100 ms time window; (Right panel) 100 ms time window following nonTarget onset. Adapted from "Attention-modulated alpha- band oscillations protect against intrusion of irrelevant information" by L. Payne, S. Guillory, and R. Sekuler, 2013, *Journal of Cognitive Neuroscience*, 25:9, p.1463–1476, Copyright 2013 by MIT Press.

Figure 3.

An example of greater pre-stimulus alpha activity when cued to ignore visual stimuli. Time-frequency representations are grand-averages of the cluster of posterior electrodes in Figure 1D. A cue to Ignore or Attend (red or green circles, respectively) starts at -1400 ms and ends at -900 ms. Following the cue, at $t=0$, a stimulus is displayed at the center of the display for 500 ms. Adapted from "Attention-modulated alpha-band oscillations protect against intrusion of irrelevant information" by L. Payne, S. Guillory, and R. Sekuler, 2013, *Journal of Cognitive Neuroscience*, 25:9, p.1463–1476, Copyright 2013 by MIT Press.