The Importance of Ignoring: Alpha Oscillations Protect Selectivity

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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 distracted drivers. 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” (p. 403). Withdrawal from background distraction is fundamental to cognition—so fundamental that it accounts for many of the individual differences in IQ (Melnick, Harrison, Park, Bennetto, & Tadin, 2013).

There is compelling evidence that cortical oscillations within a frequency band of 8 to 14 Hz—the alpha band—are key in controlling the impact of task-irrelevant sensory information. Discoveries from multiple perceptual (Kelly, Lalor, Reilly, & Foxe, 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000) and short-term memory tasks (Jensen, Gelfand, Kounios, & Lisman, 2002; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999; 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 to be 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 prestimulus alpha power decreased. Additionally, subjects who performed at a high level exhibited lower alpha power compared with those who performed at chance level (Hanslmayr et al., 2007; Hanslmayr et al., 2005).

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 (Kelly et al., 2006; Thut et al., 2006; Worden et al., 2000). There is an analogous effect of lateralized alpha modulation when auditory attention is cued to the left or right of space (Banerjee, Snyder, Molholm, & Foxe, 2011; Kerlin, Shahin, & Miller, 2010). In addition to suppressing input from a particular location, increased alpha oscillations are associated with feature-based selectivity, such as that involved in ignoring the color of a stimulus to attend to its direction of motion, or its direction of motion to attend to its color (Snyder & Foxe, 2010). These results, and others, helped lead to the hypothesis that alpha oscillations comprise a suppression mechanism to gate irrelevant stimuli—allowing for what James meant by “withdrawal from some things.”

In a series of experiments, Romei and colleagues (Romei, Brodbeck, et al., 2008; Romei, Gross, & Thut, 2010; Romei, Rihs, Brodbeck, & Thut, 2008) 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). Prestimulus 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 responding 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 responding improved with greater alpha lateralization over the somatosensory cortex (Fig. 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, prestimulus alpha activity contralateral to the uncued hand was greater 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 has demonstrated that increased alpha activity during the retention period seems to suppress irrelevant stimuli in order to protect items in memory from interference (Jensen et al., 2002; Klimesch et al., 1999; Payne & Kounios, 2009; Sauseng et al., 2005; Tuladhar et al., 2007). In one such study (Bonnefond & Jensen, 2012), subjects judged whether or not a probe letter had been among a set of letters that had just been presented and were being held in memory. On each trial, a distractor stimulus was presented at a fixed time during retention. Alpha activity during the retention period increased just prior to the onset of the predictable distractor. 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 presented with bilateral arrays of colored squares and cued to remember only the right or the left set, 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
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 the 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 prestimulus 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 prestimulus alpha power to ignoring behavior and helped confirm that subjects were, in fact, inhibiting distraction.

We tested prestimulus alpha activity's influence on memory for an unattended attribute of auditory stimuli (Dubé, Payne, Sekuler, & Rotello, 2013). In this study, we 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, first printed and then 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 of the speaker 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 italic or Roman.

Strikingly, when subjects were cued to ignore a printed word, alpha activity increased over left frontal-temporal cortex (Fig. 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 the processing of written language. In contrast, following a cue to ignore a spoken word, alpha activity increased in the posterior portion of the right hemisphere (Fig. 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 level 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 the 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 remembered 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 the presentation of one grating whose spatial frequency subjects were cued to remember and one whose spatial frequency they were cued to ignore. Both gratings were presented sequentially in 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 the center of the visual field, as Freunberger, Fellinger, 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 isolated ignoring-related alpha activity from a simultaneous requirement to attend. After holding the grating's spatial frequency in memory for 1 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 electroencephalogram (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 (Fig. 1d) immediately preceding a to-be-ignored stimulus, the less it warped the reproduction of the attended stimulus (Fig. 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 (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Mathewson et al., 2011), the answer lies in the mechanism of inhibition. Simply put, increased alpha activity shrinks the time window within which a stimulus can be processed. Therefore, strong prestimulus

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**Fig. 2.** Alpha power predicts the intrusion of the irrelevant (nontarget) information. As alpha power increases, the amount of error biased toward the nontarget (i.e., the nontarget effect) decreases. Eight bins of approximately equal numbers of trials were sorted according to the ongoing alpha power across the cluster of posterior electrodes observed in Payne, Guillory, and Sekuler (2013; see Fig. 1d); each dot in the graphs represents a bin for the prestimulus 100-millisecond time window (left panel) and the 100-millisecond time window following nontarget onset (right panel). 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, p. 1471. Copyright 2013 by MIT Press. Adapted with permission.
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 to either their hand or their foot over interleaved trials. Alpha activity in the hand representation of the somatosensory cortex decreased when attention was cued to the hand but increased when attention was cued to the foot (Jones et al., 2010). Half of 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 (i.e., over the hand region when subjects were 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.

Recommended Reading

Declaration of Conflicting Interests
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