Slow Fluctuations in Attentional Control of Sensory Cortex

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Abstract

■ Top–down control of visual sensory cortex has long been tied to the orienting of visual spatial attention on a rapid, moment-to-moment basis. Here, we examined whether sensory responses in visual cortex are also modulated by natural and comparatively slower fluctuations in whether or not one is paying attention to the task at hand. Participants performed a simple visual discrimination task at fixation as the ERPs to task-irrelevant probes in the upper visual periphery were recorded. At random intervals, participants were stopped and asked to report on their attentional state at the time of stoppage—either "on-task" or "off-task." ERPs to the probes immediately preceding these subjective reports were then examined as a function of whether attention was in an on-task versus off-task state. We found that sensory-evoked responses to the probes were significantly attenuated during off-task relative to on-task states, as measured by the visual P1 ERP component. In two additional experiments, we replicated this effect while (1) finding that off-task sensory attenuation extends to the auditory domain, as measured by the auditory N1 ERP component, and (2) eliminating state-dependent shifts in general arousal as a possible explanation for the effects. Collectively, our findings suggest that sensory gain control in cortex is yoked to the natural ebb and flow in how much attention we pay to the current task over time. ■

INTRODUCTION

One of the idiosyncrasies of human cognition is that the amount of attention we pay to task performance naturally ebbs and flows over time (e.g., Smallwood & Schooler, 2006). During some periods, our attention will be tightly focused on what we are doing, yet during other periods, our thoughts will inevitably drift off-task without any conscious intent to do so. Notably, the practical consequences of this natural human quirk are nontrivial. For example, when attention is in an off-task phase, we are more prone to making errors and slip-ups in what we are doing (e.g., Carriere, Cheyne, & Smilek, 2008; Smallwood, Beach, Schooler, & Handy, 2008; Weissman, Roberts, Visscher, & Woldorff, 2006). Should this happen at the wrong time and place—such as when driving or using power tools—the outcome can be serious.

Given the ubiquity and importance of these attentional cycles in everyday life, there has been growing interest in understanding their neurocognitive underpinnings. Most prominent have been the efforts to identify the neural networks in cortex controlling these transient shifts in attention to task performance (e.g., Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Mason et al., 2007; Sonuga-Barke & Castellanos, 2007). While debate continues over the specific brain areas involved in these networks (e.g.,

Christoff, Gordon, Smallwood, Smith, & Schooler, 2009), a critical and related question concerns how task-related attention alters the initial cortical processing of incoming sensory information.

The question is of interest because it directly recalls the classic debate in selective attention research regarding whether the attentional gating of visual inputs occurs relatively early or relatively late in the afferent visual processing stream (e.g., Deutsch & Deutsch, 1963; Treisman, 1960; Broadbent, 1958). In particular, selective attention is known to facilitate the perceptual processing of visual inputs by biasing the sensitivity of sensory-evoked responses in visual cortex (e.g., Woldorff et al., 1997; Heinze et al., 1994; Mangun & Hillyard, 1991). In an analogous manner, if the cognitive processing of visual stimuli is attenuated when attention drifts off-task, do we dampen or bias the sensory signal itself in cortex when in an off-task state? If so, it would suggest that attentional control of sensory activity in cortex is yoked to at least two distinct control systems operating in parallel—one associated with rapid shifts of selective visual attention (e.g., Hopfinger, Buonocore, & Mangun, 2000; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991), and a second associated with slower temporal fluctuations in attention to task performance (e.g., Dosenbach et al., 2008).

Toward addressing this issue, recent ERP evidence has demonstrated that the extent to which we cognitively engage or evaluate visual stimuli is reduced when attention drifts off-task, as indicated by subjective reports of attention (Smallwood et al., 2008), and an objective measure using

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error rate (O'Connell et al., 2009). Yet, in both of these studies, no corresponding effect of task-related attention was found in the sensory-evoked responses elicited by visual stimuli. Given that attenuation of these sensory responses is the ERP signature of early attentional selection (e.g., Mangun & Hillyard, 1991; Van Voorhis & Hillyard, 1977), this would seem to suggest that task-related attention may not actually affect sensory-evoked responses in cortex.

However, the paradigm used in both of these studies (O'Connell et al., 2009; Smallwood et al., 2008) may not have provided a sensitive test of whether task-related attention can modulate sensory-level processing in visual cortex. To the point, whereas selective visual attention is well known to modulate sensory responses to parafoveal stimuli (e.g., Mangun & Hillyard, 1991; Van Voorhis & Hillyard, 1977), sensory responses to foveated stimuli appear to be much less susceptible to attention-related modulation (e.g., Handy & Khoe, 2005). Given that these previously used stimuli were all presented at fixation (O'Connell et al., 2009; Smallwood et al., 2008), this indicates that these paradigms were less than optimal for assessing whether task-related attention can, in fact, bias sensory responses in visual cortex. Accordingly, the goal of the present study was to examine this issue using a version of Smallwood et al.'s paradigm specifically adapted to allow for measuring parafoveal sensory responses as a function of task-related attentional state.

That task-related attention may affect visual sensory gain is supported by a recent study by Weissman et al. (2006). Using fMRI, they found decreases in hemodynamic activity in visual cortex when people's attention lapsed on a trial-by-trial basis during a target discrimination task, as defined by slower versus faster RTs to the targets. However, whether visual sensory processing—and visual sensory gain, in particular—is affected by the comparatively slower fluctuations in attention to task as under study here remains an open question. If we find such effects here, in conjunction with the aforementioned ERP studies of attention and visual sensory gain, the findings of Weissman et al. only underscore our central point that visual sensory processing may be subject to multiple controlling inputs with different time courses of influence.

EXPERIMENT 1

Methods

Participants

Twenty-two participants (10 men, 12 women) completed the experiment in exchange for CAN$20. They were all right handed, with no history of neurological problems, and had normal or corrected-to-normal vision. Participants provided written informed consent to the experimental procedure, according to the guidelines of the UBC Clinical Review Ethics Board.

Stimuli and Paradigm

Participants performed a sustained-attention-to-response task (SART) adapted from Smallwood et al. (2008). The task involved presenting a serial stream of stimuli at fixation. Participants were asked to make a manual button press for numbers (0–9, which we will refer to as targets and which were presented frequently), and they were asked to withhold a response when presented with a letter ("X," which we will refer to as nontargets and which were infrequent). The timing and sequence of stimuli are shown in Figure 1. Within each block of stimuli, nontarget probability was quasi-randomized, with the constraints that (1) one to two nontargets were presented during each block, and (2) for blocks having two nontargets, the nontargets would be separated by at least ten target events. Each testing session lasted approximately 2 hr.

To assess possible effects of task-related attention on sensory-evoked responses in cortex, a small, yellow square-wave grating (1° × 1°, 2 cycles per degree) was temporally interspersed between each target/nontarget stimulus. This "probe" was presented approximately 3° above fixation on the vertical meridian. Participants were informed that these probes were irrelevant to the task, and therefore, their presence could be ignored with no decrement to task performance.

To measure task-related attention, participants were instructed to report their "attentional state" at the end of each trial block. Specifically, they were asked to identify their state immediately prior to the block termination as either being "on-task" (fully attentive to task performance at block's end), or "off-task" (unattentive to the task at block's end). Importantly, participants were provided with
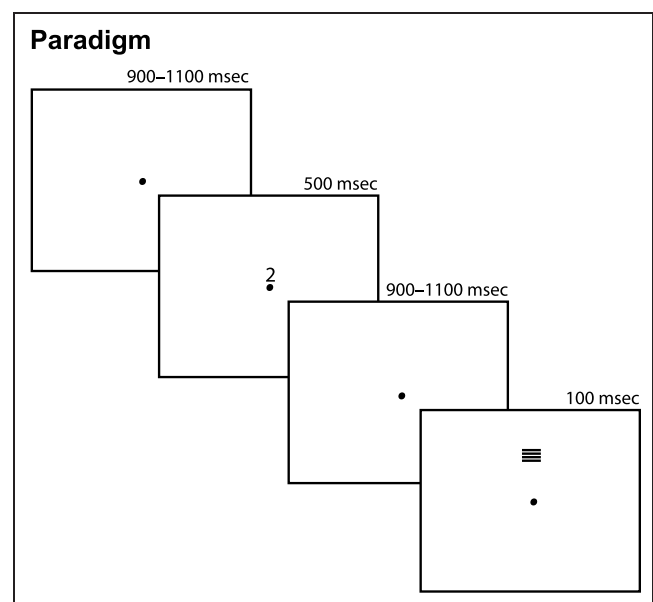

Figure 1. Task paradigm. Timing and sequence of stimuli in Experiment 1.

verbal descriptions and examples of these two "attentional states" prior to starting the testing session. On-task states were defined as when one's attention was firmly directed towards the task, whereas off-task states were described as when one is aware of other things than just the task. Examples of these attentional states were given in the context of reading, during which "one may be fully attentive to the content of the reading material, or thinking about something completely unrelated to the content, reflective of on-task and off-task states, respectively." Attentional reports were recorded by the investigator at the conclusion of each trial block, and these reports were then used to sort ERP data based on on-task versus off-task states as described below. The block duration itself was randomly varied between 30 and 90 sec in order to (1) minimize predictability of block completion and (2) maximize variability of attentional state at the time of block completion.

Electrophysiological Recording and Analysis

Scalp potentials were recorded from 28 tin electrodes (Electro-Cap International, Eaton, OH) mounted in a custom elastic cap: standard sites were O1, O2, Oz, T5, T6, T3, T4, P1, P2, P3, P4, P5, P6, Pz, C3, C4, Cz, F3, F4, F7, F8, Fp1, Fp2, Fz, along with PO1 and PO2, OL and OR (midway between O1/O2 and T5/T6); an additional channel recorded potentials from the right mastoid to use for later re-referencing of the ERP waveforms. All EEG activities were amplified (Model 12 Neurodata Acquisition System; Grass Technologies, West Warwick, RI) with a bandpass of 0.1–30 Hz (1/2 amplitude cutoffs), digitized on-line at a sampling rate of 256 samples-per-second, and recorded relative to a left mastoid reference. To ensure proper eye fixation, vertical and horizontal EOGs were also recorded, the vertical EOGs from two electrodes inferior to both eyes, and the horizontal EOGs from two electrodes on the right and left outer canthus. The electrode under the left eye was used as ground. EOG recordings were calibrated as reported in Handy and Khoe (2005). All electrode impedances were kept below 5 kΩ.

Off-line, computerized artifact rejection was used to eliminate trials during which detectable eye movements (>1°), blinks, muscle potentials, or amplifier blocking occurred. Trials with eye movements, blinks, and muscle potentials were removed if they exceeded the minimum-to-maximum threshold within the artifact rejection time window, whereas trials with amplifier blocking were eliminated when there were more than 10 continuous time points with the same data value. An average of 13% of the total number of trials across participants was rejected due to these signal artifacts. The number of trials rejected in each of the two conditions did not significantly differ from each other in all three experiments ($p > .21$). For each participant, ERPs for each condition of interest were then averaged into 3000 msec epochs, beginning 1500 msec before stimulus onset. Subsequently, all ERPs were algebraically re-referenced to the average of the left and right mastoid signals, and filtered with a low-pass Gaussian filter (25.6 Hz half-amplitude cutoff) to eliminate any residual high-frequency artifacts in the waveforms. All ERP data analyses were performed using custom scripts, and they were all based on mean amplitude measures using repeated measures ANOVAs, with specific time windows of analyses identified below as per each reported ANOVA. These analysis time windows were centered on the peak of the relevant component as identified at each electrode site in the grand-averaged waveform. A −200 to 0 msec prestimulus baseline was used for all ERP component analyses and displays.

The ERP waveforms for each condition of interest were, themselves, based on averaging together the EEG epochs for the six probes preceding each of the two attentional state conditions (on-task vs. off-task). Although we had no knowledge as to how long participants had actually been in a particular attentional state at the time a subjective report was given, our analyses were based on the assumption that the 12 sec prior to each report would, on average, reliably capture the given attentional state. In fact, recent evidence has suggested that the time course of off-task thinking approximates this time window (e.g., Christoff et al., 2009; Sonuga-Barke & Castellanos, 2007). Moreover, given our prior use of this window (Smallwood et al., 2008), we wanted to facilitate comparison of results between studies by adopting the same window here. Although a shorter premarker time window for averaging nontarget EEG epochs would more accurately capture attentional state, it would also reduce the number of events included in the ERP analysis. The choice of how many premarker events to include in the averages was therefore an attempt to maximize the number of events per each waveform average while not extending the window back so far in time as to consistently capture the preceding attentional state or transition period between states.
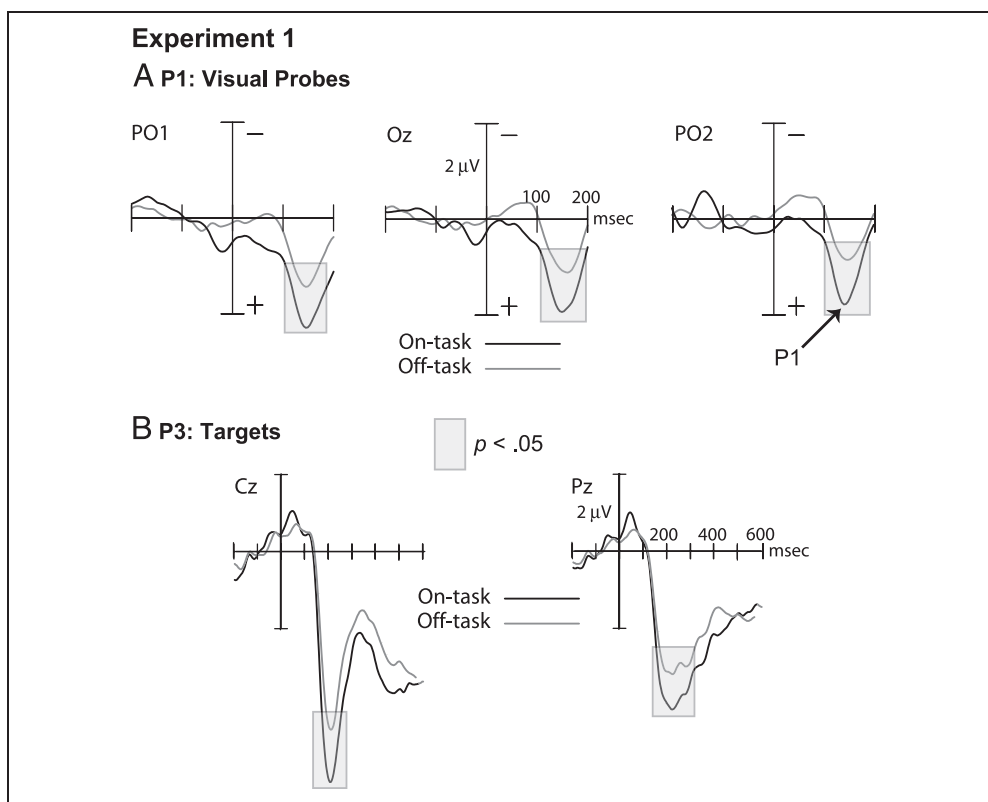
Results

Subjective Reports

Participants completed an average of 37.3 trial blocks, of which 65.6% (*SEM* = 3.58) ended with an off-task report and 34.4% ended with an on-task report. The average reaction times for on-task trials was 339.26 msec (*SEM* = 11.12 msec) and was 346.59 msec (*SEM* = 13.01 msec) for off-task trials; the difference was nonsignificant [$t(42) = -0.43, p = .67$].

ERPs

The primary focus of ERP data analysis was to assess sensory-level effects of task-related attention via mean amplitude measures of the lateral occipital P1 component elicited by the parafoveal probe stimuli. A secondary aim was to assess whether task-related attention affected the cognitive analysis of stimuli, as measured via the P3 component elicited by the targets. In both cases, ERP waveforms for

Figure 2. Results from Experiment 1. (A) Sensory effects: visually evoked P1 ERP component at lateral occipital scalp sites, as a function of on-task versus off-task state. The amplitude of P1 was significantly reduced during periods of off-task relative to periods of on-task attention (significant results highlighted in box). (B) Cognitive effects: P3 ERP component elicited by targets at midline scalp sites as a function of attention state. The P3 amplitude was significantly greater when attention was in on-task versus off-task state.

on-task and off-task states were based on probes/targets presented within the last 12 sec of each trial block, as described above. All statistical analyses were based on repeated measures ANOVAs with factors of attentional state (on- vs. off-task) and electrode location; in the interest of brevity and of relevance to our aim, we only report effects associated with the former.

Sensory effects. The P1 elicited by probe stimuli as a function of attention state are shown in Figure 2A, and was examined at lateral occipital scalp electrode sites, Oz, PO1, and PO2, where the amplitude of the P1 to vertical meridian stimuli tends to be maximal (e.g., Handy & Khoe, 2005; Handy, Soltani, & Mangun, 2001). Mean amplitude measures were taken across a 130–150 msec poststimulus time window. We found a significant main effect of attention state [$F(1, 21) = 7.35, p = .01$], such that the amplitude of the P1 was greater when attention was in an on-task versus off-task state.

Cognitive effects. The P3 elicited by target stimuli as a function of attention state are shown in Figure 2B, and was examined at midline scalp electrode sites, Cz and Pz, where the amplitude of the P3 is typically maximal (e.g., Coles & Rugg, 1995). Mean amplitude measures were taken across a 200–250 msec poststimulus time window. We found a significant main effect of attention state [$F(1, 21) = 7.60, p = .01$], such that the amplitude of the P3 was

greater when attention was in an on-task versus off-task state. Table 1 provides the values of mean P1 amplitudes for probes and mean P3 amplitudes for targets by attentional state.

Discussion

The data from Experiment 1 indicate that the sensory-evoked responses to parafoveal visual stimuli were reduced when attention was in an off-task state, as measured by the amplitude of the P1 ERP component. This finding suggests that task-related attention can, indeed, bias the initial sensory-level processing of visual stimuli. In the second experiment, we thus sought to replicate this result from Experiment 1, while examining whether sensory attenuation during off-task attention states extends to other sensory domains.

In particular, the sensory-evoked midline N1 ERP component elicited by auditory stimuli has been shown to reduce in amplitude when selective attention is oriented away from the ERP-eliciting stimulus (Woldorff & Hillyard, 1991; Hackley, Woldorff, & Hillyard, 1987). This effect directly parallels the attenuated P1 amplitude observed for unattended visual stimuli (Mangun & Hillyard, 1991). Hence, the goal of Experiment 2 was to examine whether the effect of task-related attention on sensory-level cortical processing extends to the auditory domain, as measured via the midline N1 ERP component. If so, it would suggest that task-related effects of attention are not restricted to the visual domain.

EXPERIMENT 2

Methods

We tested another 15 right-handed participants (4 men, 11 women) with normal or corrected-to-normal vision. All procedures and methods were identical to Experiment 1, except that each interval between each target/nontarget included two task-irrelevant probe stimuli: one visual and one auditory. The auditory probe was a brief tone beep (1200 Hz, 75 dB SPL) presented through an external speaker placed directly on top of the video monitor along the vertical midline. The visual probe was identical in form and location to that used in Experiment 1. The order of presentation of these two probes was randomized, but with the constraint that half the time the visual probe appeared first and half the time the auditory probe came first. Similar to the first experiment, each target or nontarget stimulus was presented for 500 msec. This was followed by an interstimulus interval, which varied between 550 and 750 msec. The first probe was then presented for 100 msec, followed by another interstimulus interval, and the second probe appeared for 100 msec. The intertrial interval also randomly varied between 550 and 750 msec.

Results

Subjective Reports

Participants completed an average of 38.2 trial blocks, of which 57.5% (*SEM* = 3.54) ended with an off-task report and 42.5% ended with an on-task report. The difference in reaction times between on-task trials (*M* = 308.86 msec, *SEM* = 9.66 msec) and off-task trials (*M* = 321.34 msec, *SEM* = 11.06 msec) was statistically nonsignificant [$t(28)$ = $-0.85, p = .40$].

ERPs

Sensory effects. The ERP waveforms for visual and auditory probes are shown in Figure 3A and B, respectively.

Table 1. Experiment 1: Mean P1 Amplitudes (and Standard Errors) for Probes (Top) and Mean P3 Amplitudes for Targets (Bottom) by Attentional State (On-Task vs. Off-Task)

Component	Electrodes	Attentional State	
		On-Task	*Off-Task*
Visual P1 (probes)	Oz	1.77 (0.44)	0.95 (0.28)
	PO1	2.15 (0.54)	1.34 (0.34)
	PO2	1.61 (0.43)	0.76 (0.28)
P3 (targets)	Cz	5.20 (0.71)	3.96 (0.73)
	Pz	3.93 (0.61)	3.01 (0.64)

Mean amplitudes were taken across a 130–150 msec poststimulus time window for probes, and across 200–250 msec poststimulus time window for targets, both measured relative to a −200 to 0 msec baseline.

For the P1 elicited by visual probes, mean amplitude measures were taken across a 110–120 msec poststimulus time window at electrode sites Oz, PO1, and PO2. We found a significant main effect of attention state [$F(1, 14) = 4.95, p = .04$], such that the amplitude of the P1 was greater when attention was in an on-task versus an off-task state. For the N1 elicited by auditory probes, data analysis was constrained to midline electrode sites Fz, Cz, and Pz, where the N1 amplitude to auditory tones tends to be maximal (Woldorff & Hillyard, 1991). Mean amplitude measures were taken across a 85–95 msec poststimulus time window. A significant effect of attentional state was again observed [$F(1, 14) = 6.02, p = .03$], such that the amplitude of the N1 ERP component elicited by auditory probes was significantly attenuated during periods of off-task relative to periods of on-task attention. Notably, although there was some residual between-condition variance in the −200 to 0 msec baseline portion of the ERP waveforms, analysis of mean baseline amplitude across successive 50 msec time windows revealed no significant main effect of state or significant Window × Attention state interactions.
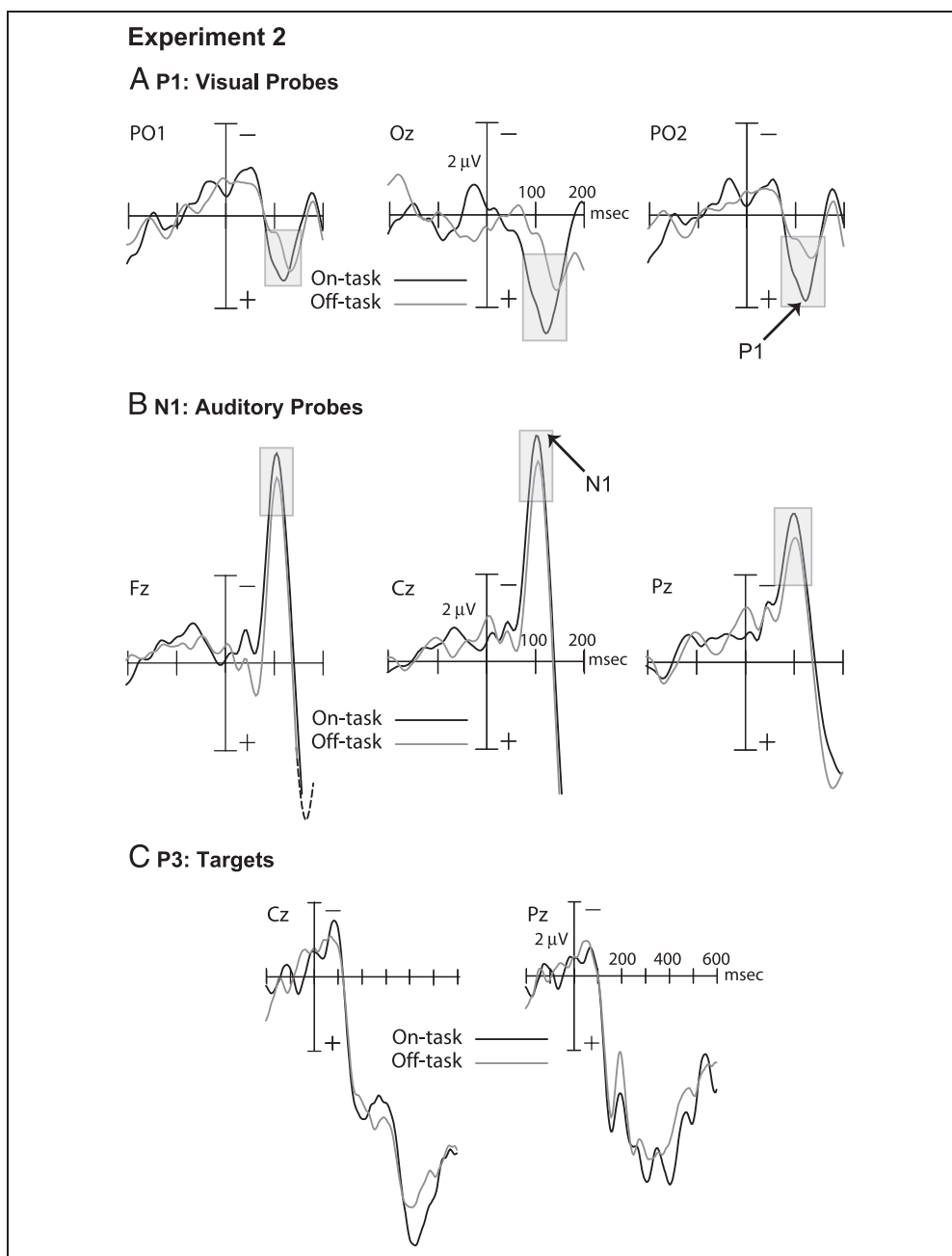
Cognitive effects. The P3 elicited by target stimuli as a function of attention state are shown in Figure 3C. Mean amplitude measures were taken across a 405–440 msec poststimulus time window, again from electrode sites Cz and Pz. Although the amplitude of the P3 was greater when attention was in an on-task relative to an off-task state, the effect only approached significance [$F(1, 14) = 3.51, p = .08$]. See Table 2 for values of mean P1 amplitudes for visual probes and mean N1 amplitudes for auditory probes, as well as mean P3 amplitudes for targets, by attentional state.

Discussion

Two key points emerge from Experiment 2. First, we replicated our finding from Experiment 1 that visual sensory-evoked responses for parafoveal stimuli are reduced during off-task relative to on-task attentional states. Second, we found a corresponding effect in the auditory domain, such that sensory-evoked auditory responses in cortex were also reduced in off-task relative to on-task attentional states. Taken together, these data support the conclusion that when our attention drifts off-task, this can lead to transient reductions in the intensity of sensory-evoked cortical activity across multiple sensory domains.

However, at least two important questions arise from our findings and interpretations. For one, the notion that we reduce the intensity of visual sensory processing in cortex when our attention drifts off-task is seemingly at odds with the fact that although attentional drifts are frequent and ubiquitous in everyday life, we are quite adept at moving and acting in the world even when our minds wander elsewhere. As anyone who has ever mind-wandered while walking down the street knows, how is it that our

Experiment 2

A P1: Visual Probes

PO1   Oz   PO2

2 µV

100   200

msec

On-task ———
Off-task ———

P1

B N1: Auditory Probes

Fz   Cz   Pz

N1

2 µV

100   200   msec

On-task ———
Off-task ———

C P3: Targets

Cz   Pz

2 µV

200   400   600   msec

On-task ———
Off-task ———

motor systems can continue to accurately respond to current environmental contingencies when we are apparently attenuating the sensory inputs critical for these visually guided actions?

A second question to consider is whether there may be an entirely different explanation for our data. As we discuss below, we interpret our results as reflecting a direct influence of task-related attentional control systems on sensory-level cortical processing (see Dosenbach et al., 2008). Yet, an alternative possibility is that these transient shifts in sensory-evoked responses might be due to fluctuations in general arousal rather than reflecting task-related attentional control. The goal in our final experiment was to address these two key questions.

EXPERIMENT 3

Experiment 3 was based on the hypothesis that the lower visual field (LVF) is more salient or important for visuomotor processing, relative to the upper visual field (UVF) (e.g., Previc, 1990). Not only does this stand to reason, given that the hands and feet are typically moving in the lower rather than upper hemifield, but this point is borne out in experimental evidence as well. For example, visually guided actions are more accurate in the LVF versus UVF (e.g., Krigolson & Heath, 2006; Danckert & Goodale, 2001), as is attentional resolution (e.g., He, Cavanagh, & Intriligator, 1996, 1997). The interactions between visual attention and visuomotor processing have also been

Table 2. Experiment 2: Mean P1 Amplitudes (and Standard Errors) for Visual Probes (Top), N1 Amplitudes for Auditory Probes (Middle), and Mean P3 Amplitudes for Targets (Bottom), by Attentional State (On-Task vs. Off-Task)

Component	Electrodes	Attentional State	
		On-Task	Off-Task
Visual P1 (probes)	Oz	2.37 (0.51)	0.59 (0.62)
	PO1	1.35 (0.44)	0.59 (0.58)
	PO2	1.72 (0.33)	0.65 (0.56)
Auditory N1 (probes)	Fz	−3.48 (0.61)	−2.29 (0.55)
	Cz	−4.46 (0.61)	−3.28 (0.67)
	Pz	−3.25 (0.52)	−2.46 (0.58)
P3 (targets)	Cz	7.17 (1.06)	6.10 (1.30)
	Pz	5.17 (0.94)	3.97 (0.94)

These mean amplitudes were taken across a 110–120 and 85–95 msec poststimulus time window for visual and auditory probes, respectively. Mean P3 amplitudes taken across a 405–440 msec poststimulus time window for targets are shown at the bottom. All amplitudes are measured relative to a −200 to 0 msec baseline.

shown to be comparatively stronger in the lower hemifield as well (Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003).

Given these considerations, if transient shifts in general arousal explain our findings, then it predicted that we should see comparable sensory attenuation at both visual field locations during off-task states. Alternatively, if sensory attenuation in off-task states reflects a more adaptive or functional-sensitive cognitive mechanisms, it predicted that sensory attenuation should be less prevalent in the LVF versus UVF, due to the greater importance of preserving visual sensory responses in the LVF as a means of supporting visual–motor processing even when attention drifts off-task. In order to address this issue, Experiment 3 replicated the same basic paradigm used in our prior two experiments, except that two visual probes were presented during each target/nontarget interval, one in the UVF as per Experiments 1 and 2, and the other in the LVF.

Methods

All methods and procedures were identical to Experiment 1, with the exception that an additional visual probe was included in the LVF during each target/nontarget interval. This probe was identical to the one presented in the UVF, and was centered on the vertical meridian approximately 3° below fixation. The timing and ordering of the two probes were identical to that described in Experiment 2. We tested another 12 participants (7 men, 5 women), all of whom were right-handed and had normal or corrected-to-normal vision.

Results

Subjective Reports

Participants completed an average of 39.6 trial blocks, of which 57.6% (*SEM* = 6.77) ended with an off-task report and 42.4% ended with an on-task report. The average reaction times for on-task trials was 331.07 msec (*SEM* = 13.24 msec) and 366.13 msec (*SEM* = 26.84 msec) for off-task trials; the difference was nonsignificant [$t(22) = -1.17$, $p = .25$].

ERPs

Sensory effects. The ERP waveforms for visual probes in the UVF and LVF are shown in Figure 4A and B, respectively. For UVF probes, mean amplitude measures were taken across a 105–115 msec poststimulus time window, and for LVF probes, mean amplitudes were taken across a 105–120 msec poststimulus time window. We found a significant interaction between attentional state and probe location [$F(1, 11) = 4.73$, $p = .05$]. Separate analyses within each location revealed a significant main effect of attentional state for the UVF probes [$F(1, 11) = 6.01$, $p = .03$], but not LVF probes [$F(1, 11) = 0.45$, $p = .52$]. Specifically, there was a significant reduction in the P1 amplitude elicited by probes in the UVF during periods of off-task relative to periods of on-task, however, this was not observed for probes in the LVF.

Cognitive effects. The P3 elicited by target stimuli as a function of attention state are shown in Figure 4C. Mean amplitude measures were taken across a 190–240 msec poststimulus time window, again from electrode sites Cz and Pz. Although the amplitude of the P3 was greater when attention was in an on-task relative to an off-task state, the effect was not significant [$F(1, 11) = 1.79$, $p = .21$]. Table 3 presents the values of mean P1 amplitudes for upper and lower visual probes, and mean P3 amplitudes for targets, by attentional state.

Discussion

We found greater sensory attenuation in the UVF versus LVF during off-task states, as measured by the amplitude of the P1 ERP component. That sensory attenuation was not uniform across the visual field suggests that our findings in the first two experiments were not simply due to attention-related shifts in general arousal. If so, this would have predicted equivalent attenuation in both visual hemifields. Rather, it appears that sensory responses are relatively preserved in the LVF during off-task attentional states. We discuss the broader implications of these results below.

Although the interaction between attentional state and visual field in the P1 is consistent with the hypothesis that UVF effects are not simply being driven by shifts in general arousal, it is also important to consider a possible alternative explanation for the absent P1 effect in the LVF. In

Figure 4. Results from Experiment 3. Sensory effects: Visually evoked P1 was elicited by visual probes in the UVF and LVF as a function of attention state. There was significant attenuation of sensory-evoked visual cortical activity indexed by P1 during off-task states in the UVF (A), but no comparable effect in the LVF (B). This indicates that the strength of visual responses is reduced in the UVF but maintained in the LVF when attention is in an off-task state. (C) Cognitive effects: Although the P3 amplitude at midline scalp electrode sites was greater when attention was in an on-task versus an off-task state, this result was nonsignificant.
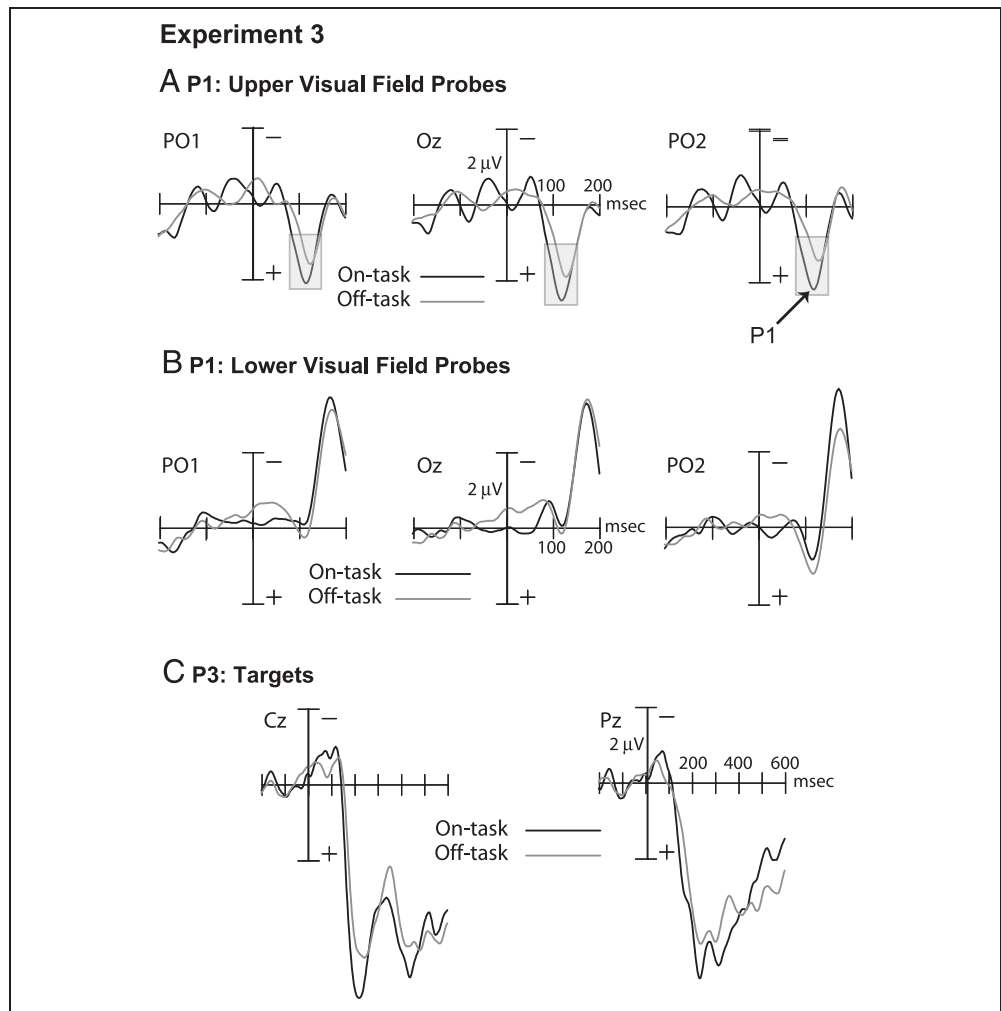

Table 3. Experiment 3: Mean P1 Amplitudes (and Standard Errors) for Upper Visual Probes (Top) and Lower Visual Probes (Middle), and Mean P3 Amplitudes for Targets (Bottom), by Attentional State (On-Task vs. Off-Task)

		Attentional State	
Component	Electrodes	On-Task	Off-Task
Upper visual field P1 (probes)	Oz	2.20 (0.32)	1.14 (0.37)
	PO1	1.93 (0.34)	1.04 (0.26)
	PO2	2.03 (0.40)	0.93 (0.30)
Lower visual field P1 (probes)	Oz	−0.28 (0.85)	−0.04 (0.64)
	PO1	−0.14 (0.45)	0.19 (0.24)
	PO2	−0.67 (0.67)	1.04 (0.40)
P3 (targets)	Cz	5.41 (0.58)	4.24 (0.74)
	Pz	4.37 (0.48)	3.69 (0.60)

These mean amplitudes were taken across a 105–115 and 105–120 msec poststimulus time window for UVF and LVF probes, respectively. Mean P3 amplitudes taken across a 190–240 msec poststimulus time window for targets are shown at the bottom. All amplitudes are measured relative to a −200 to 0 msec baseline.

particular, the overall P1 amplitude is relatively small across attention conditions, relative to the P1 observed for UVF stimuli. One concern here might be that, with a smaller P1 amplitude, it may be less susceptible to changes in sensory gain. Although we cannot rule this possibility out, it remains for future investigations to examine whether there is actually a relationship between overall P1 amplitude and the extent to which sensory gain can affect it.

GENERAL DISCUSSION

Our study addressed the question of whether slow fluctuations in task-related attention can attenuate sensory inputs at a cortical level. In three experiments, we found consistent evidence that both visual and auditory sensory responses in cortex were selectively reduced during off-task relative to on-task states, as measured by the visual P1 and auditory N1 ERP components, respectively. Importantly, we also eliminated the possibility that our results were accounted for by global shifts of arousal, as sensory attenuation was not evident across the entire visual field. Our results thus provide direct electrophysiological evidence suggesting that sensory gain control in cortex is engaged when our minds naturally drift off-task. Given these findings, at least four key issues follow.

First, our data suggest that sensory gain is not yoked to a single, unitary control network. In particular, attention-related control of sensory responses in cortex has long been linked to top–down, strategic decisions about where to orient visual spatial attention on a relatively rapid, moment-to-moment basis (e.g., Mangun & Hillyard, 1991). In turn, this form of attentional control is mediated by a well-established network comprising prefrontal and superior parietal regions of cortex (e.g., Corbetta & Shulman, 2002; Hopfinger et al., 2000; Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta et al., 1991). Our results, however, suggest that sensory gain is also subject to modulation by comparatively slower fluctuations in whether or not one is paying attention to task performance. Not only is this a form of attentional control that is distinct from attentional orienting in terms of its functional purpose, time scale of influence, and control network in cortex (e.g., Dosenbach et al., 2008), but the stability of a dynamic cortical system is optimized when there are multiple controlling inputs operating at multiple scales of time (e.g., Honey, Kötter, Breakspear, & Sporns, 2007). It would thus appear that sensory gain control may have a functional benefit by operating under a dual-control network structure.

Second, although we found consistent effects of task-related attention on sensory-evoked activity, a comparable pattern of activity was not observed in the P3 ERP component elicited by target stimuli. Specifically, whereas off-task attention reduced sensory-evoked responses in all three experiments, we only found significant or near-significant effects of off-task attention on the P3 in Experiments 1 and 2, respectively. Why might there have been variability in this P3 response to targets? In our original study that

had no task-irrelevant probes included in the paradigm, we found significant P3 attenuation during off-task states (Smallwood et al., 2008), whereas here we found comparable effects with one probe in the paradigm (Experiment 1) but not two probes (Experiments 2 and 3). What this raises is the possibility that as one adds extra "distracting" elements to the display, it may alter to a degree how targets are processed at a cognitive level—for example, by increasing the complexity and unpredictability of spatial–temporal patterns of stimulation. Indeed, these are precisely the kinds of contextual factors that modulate P3 amplitude (e.g., Donchin & Coles, 1988).

Regardless of what may drive variability in the P3 effect, however, this finding suggests that there may be a decoupling of sensory versus cognitive effects of task-related attention. That is, effects appear to arise in the former without necessarily always co-occurring in the latter. Importantly, this possibility is not without precedence in the attention literature. To the point, although canonical models of visual selective attention have often implicitly assumed that cognitive-level effects of attention positively covary with sensory-level effects (e.g., Mangun & Hillyard, 1995; Luck et al., 1994), more recent evidence has demonstrated that the effects of selective attention on these stages of processing can be independent (e.g., Handy & Khoe, 2005)—and specifically, attention effects can arise in the P3 when none are apparent in the P1. Our data here hint that this same independence of attention effects at sensory versus cognitive levels may apply to task-related attention as well.

In this regard, it is also interesting to note that we found no effect of attentional state on the reaction times to the targets, despite consistent decreases in the sensory responses to task-irrelevant probes. To the point, if the inclusion of task-irrelevant probes was sufficient to alter the cognitive context of target processing relative to when no probes are included (Smallwood et al., 2008) as measured by the P3, it is thus not surprising that no effect of attentional state was observed in reaction times as well. Indeed, this is exactly what the P3 data would predict. When one considers that effects of attentional state were, in fact, reliably observed for task-irrelevant stimuli presented away from the fovea, the implication is that under conditions such as those here, attention drifting away from a task at hand can alter peripheral sensory processing while leaving the cognitive and perceptual processing of foveal information comparatively unchanged. Such spatially mediated effects may help to explain our behavioral functionality in the face of frequent mind wandering episodes such as when driving, walking, and the like.

A third issue of note concerns the apparently adaptive nature of sensory attenuation during off-task states. Namely, we found that sensory-evoked activity remained unaffected in the LVF despite significant attenuation in the UVF— attenuation that was reliably observed in all three experiments. As such, our findings converge on a diverse body of evidence indicating that the LVF plays a specialized

role in visuomotor processing (e.g., Krigolson & Heath, 2006; Handy et al., 2003; Danckert & Goodale, 2001; He et al., 1996, 1997). Although our hypothesis—LVF sensory responses are preserved during off-task attention states in order to support ongoing visuomotor processing—remains to be directly tested, the possibility does have intuitive appeal. That is, the LVF may specifically resist tuning out so that our bodies can respond to current environmental contingencies regardless of where in time and space our mind may have wandered.

Finally, given our findings, an important question concerns how our data relate, if at all, to the recent report of Weissman, Warner, and Woldorff (2009) showing that sensory processing for "task-irrelevant" stimuli actually *increases* during attentional lapses. The critical issue here, as we see it, concerns the nature of the task-irrelevant stimuli used in the two studies. Specifically, the auditory task irrelevant stimuli used by Weissman et al. (2009) were auditory analogs of their visual targets (Xs and Os), and thus, the "irrelevant" stimuli were designed to engender response conflict a la an Eriksen flanker task. As such, optimal performance in their task required actively attending to the visual targets while actively suppressing the auditory inputs. It is thus not surprising that when attention lapsed in their paradigm, sensory processing decreased for visual inputs but increased for auditory inputs. In this manner, their task is consistent with directly and/or consciously engaging sustained attention and then examining what happens to stimulus processing when that attention lapses or wanes.

In our study, however, the nature of the irrelevant stimuli was fundamentally different, in that the square-wave gratings used as visual "probes" had no direct mapping or bearing on the responses required by the task (discriminating letters vs. numbers). As such, there was no need for participants in our study to actively suppress these task-irrelevant stimuli in order to optimize their task performance. Accordingly, what our paradigm captures is not the consequence of lapsed sustained attention, but rather, the consequence of simply having one's mind drift off-task. In this case, with task-irrelevant stimuli that one does not need to actively suppress, the net consequence is that sensory processing can decrease. Within this context, however, one can logically ask how, if at all, "attentional lapses" may relate to attention drifting off-task. From our perspective, these may often be one and the same phenomenon. The key difference is thus not with these two terms per se, but rather, whether a "lapse of attention" or "attention drifting" off-task occurs when one is engaging sustained attention as part of current task goals. In our paradigm, sustained attention was not engaged during the task and that explains our pattern of results relative to Weissman et al. (2009). However, if our understanding here is correct, it predicts that if one monitored "attention to task" during a task that engages sustained attention in a manner similar to Weissman et al., then sensory-level effects should resemble their findings—task-irrelevant stimuli that are ac-

tively suppressed as part of optimal task performance should *increase* when attention drifts off-task.

In conclusion, our findings highlight the value of emerging methodologies that are using subjective reports of cognitive states as a means by which to identify the conditions of interest in a study (e.g., Christoff et al., 2009; Handy, Smilek, Geiger, Liu, & Schooler, 2010; Smallwood et al., 2004, 2008; Mason et al., 2007). In this approach, cognitive states are not placed under direct experimental control, but rather, systems and processes of interest are allowed to operate in their own natural, unconstrained manner. Within this context, experimental paradigms are designed to identify the status of the system or process at various intervals over time, as reported by the participant. Although the reliability of any given subjective report may certainly be open to question, the overall validity of the collection of reports is borne out by state-dependent differences in objectively measured neural-based signals. Having identified that sensory responses in cortex attenuate when people slip into off-task attentional states, our study illuminates the importance of such subjective report methodology in providing unique and useful information, and thus, complementing objective measures.

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