

Rapid Feature-driven Changes in the Attentional Window

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Abstract

■ Spatial attention must adjust around an object of interest in a manner that reflects the object's size on the retina as well as the proximity of distracting objects, a process often guided by nonspatial features. This study used ERPs to investigate how quickly the size of this type of "attentional window" can adjust around a fixated target object defined by its color and whether this variety of attention influences the feedforward flow of subsequent information through the visual system. The task involved attending either to a circular region at fixation or to a surrounding annulus region, depending on which region contained an attended color. The region containing the attended color varied randomly from trial to trial, so the spatial distribution of attention had to be adjusted on each trial. We measured

the initial sensory ERP response elicited by an irrelevant probe stimulus that appeared in one of the two regions at different times after task display onset. This allowed us to measure the amount of time required to adjust spatial attention on the basis of the location of the task-relevant feature. We found that the probe-elicited sensory response was larger when the probe occurred within the region of the attended dots, and this effect required a delay of approximately 175 msec between the onset of the task display and the onset of the probe. Thus, the window of attention is rapidly adjusted around the point of fixation in a manner that reflects the spatial extent of a task-relevant stimulus, leading to changes in the feedforward flow of subsequent information through the visual system. ■

INTRODUCTION

Attention enables the completion of everyday tasks by biasing neural processing toward behaviorally relevant information. Although the earliest visual sensory inputs are available from across the field of view, a subset must be selected to allow for higher level processes and action. Dynamic and coordinated behavior requires the integration of an observer's current goals with the incoming bottom-up stimulus, such that different parts of the visual field receive a competitive bias from attention as they become relevant over time (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997).

Because retinal size varies enormously depending on the size of an object, its distance from the retina, and the presence of occluders, feature-based guidance often plays a large role in facilitating shifts of spatial attention to a target (e.g., Leonard & Egeth, 2008). Feature-based guidance has been shown to increase neural activity at locations containing task-relevant features (Zhang & Luck, 2008; Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004; Saenz, Buracas, & Boynton, 2002). Although many studies have examined differential neural responses between objects with or without a relevant feature, much less is known about how this transitions into a more general form of spatial attention that facilitates a location. Here,

we examine how the presence of a task-relevant feature leads to the adjustment of the "attentional window" around the point of fixation.

Consider, for example, the task of searching for a poppy in a field like the one shown in Figure 1A. When viewed from a few centimeters away (Figure 1A), a single poppy may subtend well over 10° of visual angle on the retina, whereas the same poppy will subtend a fraction of a degree from a distant viewpoint (Figure 1B). Consequently, the exact retinal size of a search target in the real world will be difficult to predict unless its precise distance is known in advance. To find a poppy (or some other target) amid other scene information, an observer would presumably use a distinguishing feature (e.g., its distinctive color) to adjust the attentional window so that it includes the object of interest and excludes the surrounding information. This expansion or contraction of the attentional window is needed even when the eyes are pointed at the center of an attended object. For example, when an observer fixates the center of the image shown in Figure 1C, the allocation of spatial attention would differ depending on whether the observer was examining the leaves or the flower.

This concept of adjusting the spatial extent of attention has previously been discussed in the context of the well-known spotlight (Posner, Snyder, & Davidson, 1980) and zoom lens (e.g., Eriksen & St. James, 1986) models of attention. Many studies used paradigms that tested the size of the attentional window around a peripheral object,

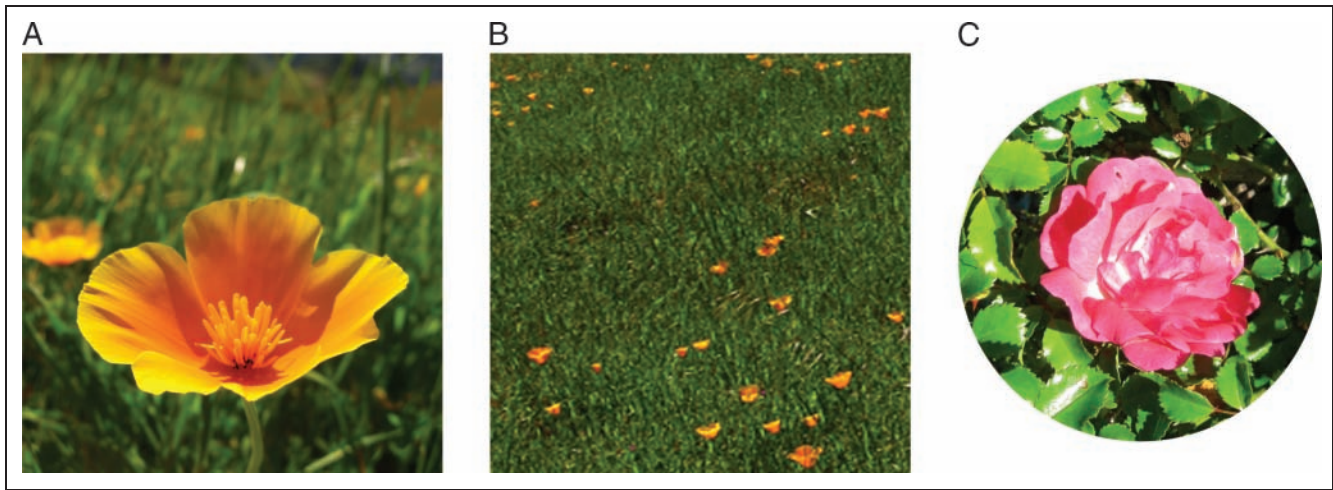


Figure 1. Natural examples of the need to adjust the size of the window of attention. The retinal image of a single poppy flower may be many degrees when viewed from a few centimeters (A) or a fraction of a degree when viewed from many meters away (B). In addition, when an observer is fixated at the center of a rose (C), the appropriate attentional window will differ depending on whether the observer is trying to discriminate the flower or the surrounding leaves. Photo credits to Brian Michelsen (A and B).

not the size of the window around an object being fixated. Some behavioral studies have examined the size of the attentional window around fixation (e.g., LaBerge, 1983), but less is known about the locus at which this attentional modulation influences the visual processing of a subsequent stimulus. This act of expanding and contracting an attentional window around a potential target at fixation occurs frequently during natural vision—perhaps every time a new target object is fixated—and yet the nature and time course of this type of attentional modulation has received relatively little study compared with situations in which covert shifts of attention are made to the periphery.

ERP experiments have provided clear evidence that covertly shifting attention to a task-relevant location in the periphery increases the sensory response generated by a stimulus at that location (e.g., Martinez et al., 1999; Eimer, 1997; Mangun & Hillyard, 1988). In particular, the occipital P1 component is larger for stimuli presented at attended locations than for stimuli presented at unattended locations. This component is observed over occipital-temporal electrode sites, typically onsetting around 60-msec poststimulus, and appears to be generated mainly in dorsal extrastriate cortex (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002). The earliest effect of spatial attention on the ERP is typically a modulation of this P1 component, beginning within the first 100 msec after stimulus onset and occurring within the P1 generator location (Di Russo, Martinez, & Hillyard, 2003). The overall pattern of results indicates that these effects reflect a modulation of feed-forward sensory processing in extrastriate visual cortex (Hillyard, Vogel, & Luck, 1998). Almost all previous ERP studies of spatial attention have examined covert attention to locations in the periphery, and little is known about how adjustments of the attentional window around the cur-

rently foveated location influence sensory-evoked brain responses.

Several previous ERP studies have examined related issues. For example, consistent with the zoom lens model and previous behavioral results (e.g., Castiello & Umiltà, 1990), there is a trade-off between the strength and spatial extent of attention as measured by target-elicited P1 responses (Fu, Caggiano, Greenwood, & Parasuraman, 2005; Luo, Greenwood, & Parasuraman, 2001). Other work has compared the allocation of attention at the fixated location relative to that at a peripheral region (Frey, Kelly, Lalor, & Foxe, 2010; Handy & Khoe, 2005; Miniussi, Rao, & Nobre, 2002) or between several peripheral regions (Eimer, 1999). However, most of these studies used experimental designs in which participants were precued to a largely empty region of space, and then an ERP-eliciting target stimulus was presented either in the cued region or an uncued region. This differs from the typical situation in the natural environment, in which a target object itself defines the to-be-attended region of space. We developed a controlled laboratory analog of the perceptual task illustrated in Figure 1C, asking how attention is allocated either to the foveated region or the surrounding region when the observer does not know in advance which region will contain the relevant feature information.

We were specifically interested in whether changes in the attentional window driven by the task display would effectively modulate early sensory processing of a subsequent stimulus, as do covert shifts of spatial attention to a peripheral location. We were also interested in examining the amount of time required for a task-relevant feature to guide the adjustments of the attentional window. Our experimental design took advantage of the fact that the P1 component is increased for a stimulus occurring at an attended location compared with an unattended

location regardless of whether that stimulus is a target or a nontarget stimulus (Heinze, Luck, Mangun, & Hillyard, 1990). Specifically, we used a “probe” design analogous to prior visual search experiments in which a target of a specific color appeared at an unpredictable peripheral location, surrounded by distractors. When a probe square was flashed at the location of the target 200–400 msec after the onset of the search array (allowing time for attention to shift to the target location), the P1 elicited by the probe was enhanced compared with when the probe was presented at a nontarget location (Luck & Hillyard, 1995; Luck, Fan, & Hillyard, 1993).

To adapt this approach for examining the allocation of attention to regions centered on fixation, we used displays containing sets of red dots and blue dots, with one color in the central region and one color in an annular outer region (see Figure 2A). Participants were instructed to attend either to the red dots or to the blue dots and make a judgment about the number of dots of the attended color. The attended dots appeared unpredictably in either the inner or outer region, requiring the observer to use color information to adjust the window of attention on each trial. A task-irrelevant probe stimulus was presented at a variable delay, either in the inner region or the outer region, and the sensory response evoked by this probe stimulus was used to assess sensory processing within the probed region at the time of probe onset. If attention enhances sensory processing in a given region, then the probe-evoked P1 wave should be greater for a probe in this region when the region is attended than when the other region is attended. An important benefit of this approach is that sensory activity can be assessed at both attended and unattended locations without requiring an explicit response to stimuli at the unattended location, which might distort the distribution of attention.

The SOA between the task display and the probe was varied to examine the temporal evolution of the adjustment of the spatial window of attention on the basis of the featural information in the task display. Specifically, at early SOAs, when the attentional window has not yet been adjusted to the task-relevant region, the probe-evoked P1 should not differ depending on whether it appears in the task-relevant or task-irrelevant region on that trial. The onset of spatial selection can be defined as the earliest SOA at which the probe-elicited P1 is modulated, indicating that spatial attention has been differentially allocated to the task-relevant and task-irrelevant regions.

METHODS

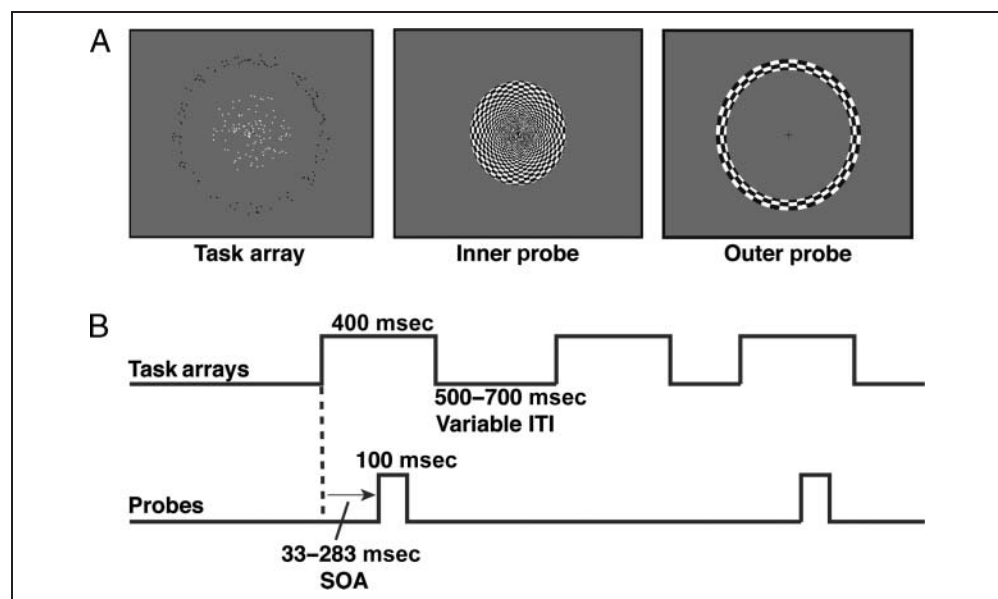
Participants

Twelve neurologically normal participants from the University of California, Davis, community volunteered for the study (mean age = 20.7 years, 10 women). They all reported normal or corrected-to-normal visual acuity and normal color vision. Informed consent was obtained from each participant before taking part in the study, and the protocol was approved by the institutional review board at the University of California, Davis.

Stimuli

The stimuli (see Figure 2A) were created and presented using Matlab in conjunction with PsychToolbox 3 (Brainard, 1997; Pelli, 1997). They were presented on a 53-cm CRT monitor positioned at a viewing distance of 70 cm from the participant, who was seated comfortably such that gaze was easily directed at the center of monitor (which was enclosed in a Faraday cage; see Luck, 2005). All

Figure 2. (A) Examples of the task array and probe stimuli used in this paradigm. Note that black and white in the task array represent red and blue in the actual display. On probe-present trials, either an inner or outer probe appeared behind the task array for 100 msec, with an SOA that varied between 33 and 283 msec. (B) Schematic representation of the timing of the task array and probes. Note that a probe was not present on one third of trials (e.g., the second trial in the timeline shown here). A fixation cross remained on the screen at all times. ITI = intertrial interval.



stimuli were presented on a moderate-intensity gray background (9.1 cd/m^2 ; CIE coordinates: $x = 0.28, y = 0.27$).

On every trial, two simultaneous sets of dots were shown, one in an inner region and one in an outer region. One set was blue (3.8 cd/m^2 ; $x = 0.17, y = 0.11$) and the other was red (3.8 cd/m^2 ; $x = 0.44, y = 0.27$), with the location of the colors randomly determined on each trial. Each dot was approximately 0.1° in diameter. The inner dots were distributed across a circular region with a radius of 3° , centered at fixation. The outer dots were distributed across an annulus-shaped region, with an inner radius of 5° and an outer radius of 5.83° , centered at fixation. The areas of the inner and outer regions were equal. On a given trial, dots were distributed within a region by randomly choosing the eccentricity and angular offset for each individual dot from independent uniform distributions.

The probe stimuli were radial checkerboards composed of alternating black (0.3 cd/m^2) and white (51.4 cd/m^2) wedges, scaled for eccentricity according to the cortical magnification factor (Horton & Hoyt, 1991). There were 48 wedges at each eccentricity of this circular checkerboard, and both the inner and outer probes were created by using portions of the checkerboard that matched the size and shape of the corresponding inner and outer regions of the display, as described above. At the middle eccentricity of the inner probe, each check was approximately 2.5 cycles/degree. At the middle eccentricity of the outer probe, each check was approximately 0.75 cycles/degree. When a probe occurred, the dots were drawn on top so that the probe appeared to onset behind the task array. The small dots we used in this study have essentially equal power across all spatial frequencies, so differences in sensitivity to different spatial frequencies should not influence the perception of these stimuli. This avoids confounding the spatial frequency content of the stimuli with the eccentricity of the stimuli.

Procedure

Each trial block consisted of a sequence of task arrays, in each of which the inner and outer regions were presented simultaneously for 400 msec, followed by an intertrial interval of 500–700 msec (rectangular distribution). A probe stimulus could appear either behind the inner dots (1/3 of trials) or behind the outer dots (1/3 of trials), beginning 33–283 msec after the onset of the task-relevant array (in increments of one screen refresh, 16.7 msec) and lasting for 100 msec. No probe was presented on the remaining trials. Each participant performed 12 blocks with 300 trials per block. Participants were in the laboratory for approximately 2 hr, with about 1 hr of this time used to perform the task.

Participants were instructed by means of both a verbal and visual cue at the beginning of each block to attend a single color (red or blue) and make a numerosity judgment about the attended dots in the task array. Specifi-

cally, they were instructed to press a button with the right index finger when the task display contained fewer than 100 dots of the attended color (target displays, 10% of trials), with no response when the display contained more than 100 dots of this color (nontarget displays, 90% of trials). The relevant color was equally likely to occur at the inner and outer regions of the display, making it impossible for participants to predict whether attention should be directed to the inner or outer region for the next trial. The number of dots of the unattended color was also varied, with <100 dots in 10% of displays and >100 dots in 90% of displays. The number of attended and unattended dots was uncorrelated, with the target numerosity (<100) occurring simultaneously in both regions on only 1% of trials. We alternated between attend-red and attend-blue blocks, with the starting color counterbalanced across participants.

To equate task difficulty and, therefore, phasic arousal (Posner, 1978) for the attend-inner and attend-outer trials, the magnitude of the difference between the target and nontarget numerosities was determined separately for the inner and outer regions in each participant before the main task. Specifically, a staircase procedure was used to determine the numerosity difference that would yield 85% accuracy (with separate but concurrent staircases for the inner and outer regions). This yielded a mean of 83 dots versus 117 dots in the inner region and 79 dots versus 121 dots for the outer region, which was a marginally significant difference ($t(11) = 2.16, p = .054$). Note that the same number of dots was used in each region regardless of whether that region was currently to be attended or not.

EEG Recording and Analysis

The EEG was recorded inside a shielded chamber using a Biosemi ActiveTwo EEG recording system (Biosemi B. V., Amsterdam, Netherlands). Thirty-two electrodes were affixed in an elastic cap at a subset of locations from the extended 10–20 System (FP1, FP2, F3, Fz, F4, F7, F8, C3, Cz, C4, P1, P2, P3, Pz, P4, P5, P6, P7, P8, P9, P10, T7, T8, PO3, POz, PO4, PO7, PO8, O1, Oz, O2, Iz). The horizontal EOG was recorded at sites placed at the external canthi and used to monitor for horizontal eye movements. Blinks were detected by recording the vertical EOG above and below the right eye. The single-ended voltage was recorded between each electrode site and a common mode sense electrode. The signals were low-pass filtered with a fifth-order sinc filter (half-power cut-off at 208 Hz) and digitized at 1024 Hz.

Offline signal processing and analysis was performed using EEGLAB Toolbox (Delorme & Makeig, 2004), ERPLAB Toolbox (erpinfo.org/erplab), and custom Matlab scripts. All scalp electrodes were referenced to the average of the left and right mastoids, and the peri-ocular electrodes were rereferenced into bipolar horizontal and vertical EOG signals. The continuous data were then

band-pass filtered using a noncausal Butterworth filter (12 dB/oct) with a half-amplitude bandpass of 0.01–36 Hz. The data were then segmented into epochs from –200 to +800 msec relative to onset of the probe stimulus.

Standard artifact rejection procedures were used to remove trials that contained large voltage deflections or blinks (see Luck, 2005, for a detailed description). Trials with saccades were rejected by means of a step-function algorithm that eliminated trials in which a saccade exceeded $\sim 1.8^\circ$ (Lins, Picton, Berg, & Scherg, 1993; see Chapter 6 in Luck, 2005). In total, an average of 4% of trials were rejected across participants (min: 1%, max: 7%). Because the task-relevant stimuli were distributed over a large area, the participants should have had no motivation to make eye movements. However, even small differences in eye position between attention conditions during the task could change the sensory ERP of the probe. Consequently, we carefully examined the EOG data to ensure that there were no systematic eye movements remaining after trials with artifacts were rejected (see Supplemental Figure 1).

To isolate the probe-elicited sensory ERP response from the ERP elicited by the task-relevant dot array, the probe-absent waveforms were subtracted from the probe-present waveforms. This subtraction approach has been used successfully in other experiments to isolate the response to the probe (Vogel, Luck, & Shapiro, 1998; Luck & Hillyard, 1995; Luck et al., 1993). The data from each probe-absent trial were time-locked to an imaginary probe onset at each possible SOA. We then calculated the average probe-absent waveforms for both the attend-inner and attend-outer conditions for each SOA. Each of these averages provides the time course of activity driven by the task display, time-locked to when a probe would appear in the matched probe-present trials at that SOA. For each probe-present trial condition, the average probe-absent waveform at the equivalent attention condition and SOA is subtracted from the task display + probe waveform to isolate the transient response driven by the probe. This was done separately for each participant at each electrode site. An illustration of this subtraction procedure is provided in Supplemental Figure 2. The probe ERP measures were taken from these difference waves, using the 200-msec period before the probe as the baseline.

Data from the attend-red and attend-blue blocks were collapsed to eliminate any potential sensory differences. The data were divided into eight SOA bins, each representing probes occurring over a range of two screen refresh cycles (e.g., 33–50 msec, 67–83 msec, etc.). P1 amplitude was quantified as the mean voltage from 60 to 120 msec after probe onset at posterior scalp sites (O1, O2, Oz, PO3, PO4, PO7, PO8, POz). This time window was selected in an unbiased manner as the interval between ± 30 msec from the P1 peak in the average waveform across all conditions (~ 90 msec). These amplitude measures were entered into a within-subject ANOVA. The reported p values reflect the Greenhouse–Geisser

epsilon correction for nonsphericity where appropriate (Jennings & Wood, 1976).

RESULTS

Behavioral Results

The stimuli were presented rapidly (one task-relevant array every 900–1100 msec), which was necessary to present the large number of stimuli needed for the averaged ERPs but led to a slight ambiguity in the behavioral results. Specifically, the response on trial n sometimes occurred shortly after the onset of the stimulus for trial $n + 1$. Consequently, any response faster than 3 SD from a given participant's mean RT was assigned to the previous trial. Using these adjusted response assignments, we computed the d' measure of sensitivity for distinguishing between arrays with more or fewer than 100 dots.

Overall, sensitivity was nearly equivalent for attend-inner and attend-outer trials ($d' = 1.92$ vs. 1.93 , respectively; $t(11) = 0.5$, $p = .95$; these values were equivalent to 91.6% accuracy and 90.4% accuracy, respectively), indicating that our procedure for equating task difficulty was successful. Sensitivity was also calculated independently for those trials on which an irrelevant task probe did and did not occur (see Table 1). Overall, target detection sensitivity was decreased when a probe occurred in the attended region compared with when it appeared in the unattended region or was absent, especially for the attend-outer trials. An ANOVA with factors of Attended Region (attend-inner vs. attend-outer) and Probe Region (attended region vs. unattended region) resulted in no significant effect of Attended Region, $F(1, 11) = 0.18$, $p = .68$. There was a significant effect of probe ($F(1, 11) = 26.9$, $p < .001$), such that performance was decreased when a probe occurred in the attended region. Greater interference by the probe in the attended region during the attend-outer condition was confirmed by a significant interaction, $F(1, 11) = 29.31$, $p < .001$. However, because participants did not have any expectation as to which type of trial was next (inner probe, outer probe, or probe absent) or as to precisely when one might occur, the participants' strategies could not differ across trial types.

ERP Results

The main question addressed in this study is how sensory processing, as indexed by the probe-elicited ERPs, is

Table 1. Mean Probe Detection Sensitivity (with Within-subject Standard Error Shown in Parentheses, following Morey, 2008)

	<i>Inner Probe</i>	<i>Outer Probe</i>	<i>No Probe</i>
Inner region attended	1.89 (0.12)	2.00 (0.16)	2.09 (0.10)
Outer region attended	2.37 (0.15)	1.39 (0.11)	2.36 (0.16)

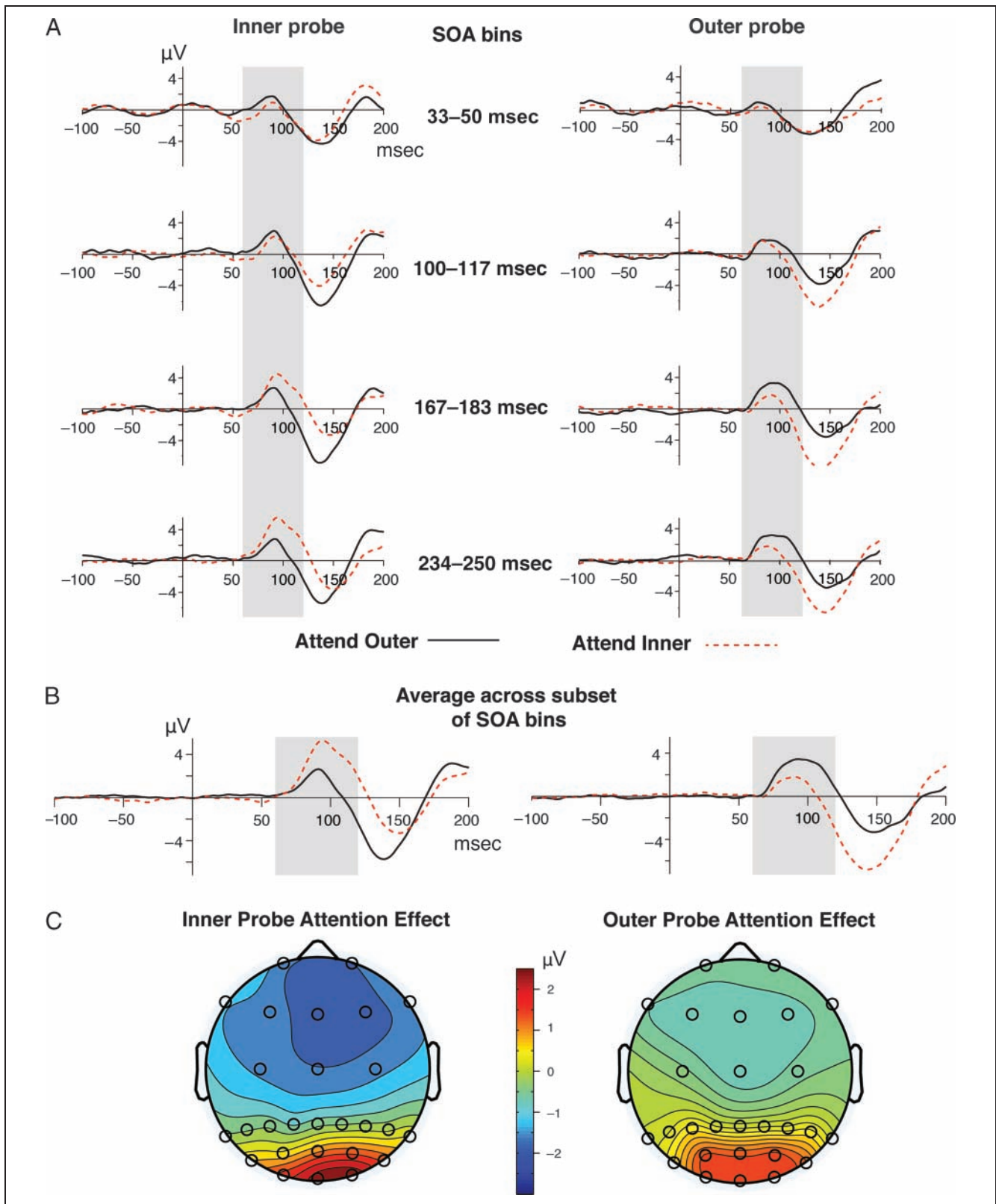


Figure 3. (A) Grand-averaged ERP waveforms to inner probe and outer probe stimuli averaged over posterior sites. Note that these waveforms were created by subtracting the no-probe waveforms from the probe-present waveforms. Each row represents the data averaged over a pair of consecutive stimulus onset asynchronies (SOAs) between the onset of the task array and the probe. Every second pair of SOAs is shown. (B) Average across all SOA bins in which the P1 effect was significant. (C) Scalp voltage maps of the attention effect (trials on which the attended color was in the region of the probe minus trials on which the unattended color was in this region), averaged across the SOA bins after the P1 attention effect became significant. Note that the baseline used for component quantification purposes was -200 to 0 msec.

modulated when attention has been guided to the inner region or the outer region on the basis of the task-relevant color within the task array. To answer this question, we looked at the probe-elicited waveform from the average of the posterior electrode sites for each target-probe SOA. To avoid any response-related activity, the ERP analyses were limited to nontarget trials (i.e., those that contained more than 100 dots in both the inner and outer regions) on which no behavioral response was made. Figure 3A shows these ERPs separately for a subset of SOA bins, and Figure 3B shows the waveform averaged over the SOA bins after the attention effect became significant. The ERPs for all of the SOA bins are available in Supplemental Figure 3.

The P1 wave was present at posterior electrode sites, with an onset latency of approximately 60 msec relative to probe onset. Not surprisingly, the absolute size of the P1 increased as the SOA increased, which reflects a basic refractory effect. In addition, the P1 was larger for inner probes than for outer probes, which presumably reflects the overrepresentation of the fovea in visual cortex.

At the shortest SOA between task-array onset and probe onset, the P1 amplitude for a probe in a given region was similar regardless of whether that region contained the attended color or the unattended color. At later SOAs, however, the P1 was larger when the probe was presented in the attended region compared with the unattended region. That is, the P1 for inner probes was larger when the attended color was in the inner region than when this color was in the outer region, and the P1 for outer probes was larger when the attended color was in the outer region than when this color was in the inner region. This greater positive voltage for the attended region was present throughout the period of the P1 peak (approximately 60–120 msec) and extended into the initial portion of the N1 peak (approximately 120–180 msec). Topographical plots of the attention effect (Figure 3C) indicate that this modulation was largest at posterior electrode sites. When combined with the early latency of the attention effect, the scalp distribution is consistent with the proposal that this attention effect reflects a modulation of the feedforward flow of information through visual cortex rather than being a modulation of, for example, prefrontal activity.

The mean amplitude of the P1 across conditions is summarized in Figure 4. Because the inner and outer probes were different stimuli and therefore elicited somewhat different ERP morphologies, these time course effects were analyzed in separate ANOVAs. First, P1 amplitude for inner probes (Figure 4A) was submitted to an ANOVA with factors of SOA Bin (eight levels) and Attended Region (attend-inner and attend-outer). The main effect of SOA Bin was significant, $F(7, 77) = 8.5, p < .001$, reflecting the increase in P1 amplitude as SOA increased. The main effect of Attended Region was significant, $F(1, 11) = 15.2, p = .003$, reflecting the larger P1 amplitude observed for inner probes in the attend-inner compared with attend-

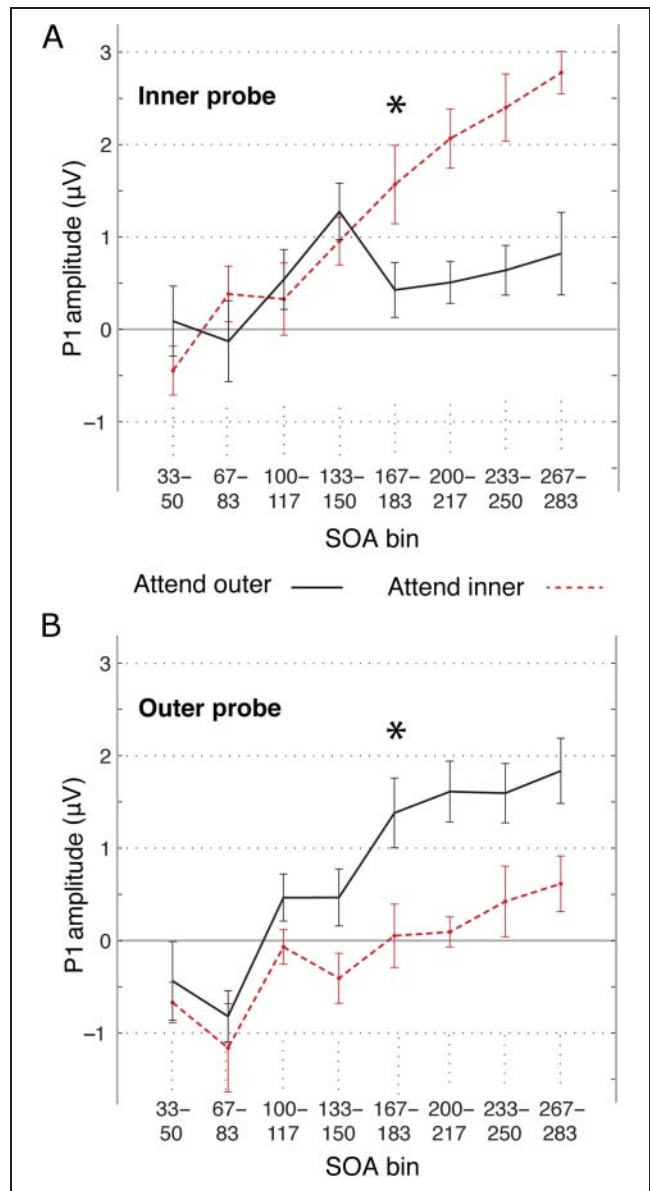


Figure 4. Mean P1 amplitude from 60 to 120 msec at posterior sites as a function of SOA bin and task-relevant region for both the inner probes (A) and outer probes (B). Asterisks indicate the point at which the difference between attention conditions became significant.

outer trials. The interaction was also significant, $F(7, 77) = 7.0, p < .001$, reflecting the fact that the effect of attention did not emerge until longer SOAs between the task array and probe onsets.

The same analysis was performed on P1 amplitude for the outer probes. Significant effects were again observed for SOA Bin, $F(7, 77) = 11.5, p < .001$, and Attended Region, $F(1, 11) = 33.7, p < .001$. The interaction did not reach significance, $F(7, 77) = 1.7, p = .18$. Thus, for both inner and outer probes, the P1 was larger when attention was directed to the region of the probe than when attention was directed to the other region. For the inner probe, this effect did not occur when the probe appeared very

soon after the onset of the task array as indicated by a significant interaction. For the outer probe, there was only a trend for a smaller attention effect when the probe appeared very soon after the onset of the task array (see Figure 4B).

The temporal evolution of the P1 attention effect was further examined via post hoc comparisons that compared attend-inner and attend-outer trials at each SOA bin. For each probe type, paired *t* tests at each SOA were performed, corrected for multiple comparisons using the false discovery rate adjustment (Benjamini, Drai, Elmer, Kafkafi, & Golani, 2001). Effects of the attended region on the P1 became significant starting at the 167- to 183-msec SOA bin for both the inner probe and the outer probe.

An additional follow-up analysis was conducted to compare the time course of the attention effects across the inner and outer probes. The raw P1 measures could be influenced by sensory differences between the inner and outer probes, so we instead analyzed the attention effect (difference in P1 amplitude when attention was directed to the region of the prober vs. when it was directed to the other region). These difference scores were entered into an ANOVA with factors of SOA Bin and Probe Region (inner or outer). Consistent with the systematic time course of the attention effect for both the inner and outer probe trials in Figure 4, there was a significant main effect of SOA Bin, $F(7, 77) = 6.4, p < .01$. However, there was no overall difference in the size of the attention effect between the inner and outer probe, $F(1, 11) = 0.51, p = .49$, nor was there a significant interaction between SOA Bin and Probe Region ($F(7, 77) = 1.9, p = .19$). Thus, although the interaction between Attended Region and SOA was significant for inner probes but not for outer probes, there was no positive evidence that the adjustment of the attentional window differed between the inner and outer regions. Moreover, for both regions, the attention effect became significant in the same SOA bin (167–183 msec).

DISCUSSION

The current results clearly show that feature-driven adjustment of the attentional window around the point of fixation modulates early sensory processing, as indexed by P1 amplitude. A probe stimulus appearing in the outer region produced a smaller sensory response when the attended color was in the inner region than when it was in the outer region, consistent with a shrinking of the attentional window around the inner region when this region contained the attended color. Similarly, the P1 response to a probe appearing in the central region was larger when the relevant information was in the inner region than when it was in the outer region. This attentional modulation of the probe-related response began approximately 60 msec following probe onset and was largest over occipital cortex, consistent with the idea that adjust-

ments of the size of the attentional window around fixation produce changes in the initial processing of incoming sensory information. This adjustment of spatial attention to locations that contain a relevant feature serves to facilitate sensory processing of subsequent visual input at these task-relevant locations.

No significant attention effects were observed if the probe was presented less than 167 msec after the onset of the task-relevant stimuli, indicating that the adjustment of spatial attention was not instantaneous. However, significant attention effects were observed when the probes were presented as early as 167–183 msec after task-array onset. Given that the P1 wave (and the P1 attention effect) began ~60 msec after the onset of the probe stimulus, this suggests that attention was adjusted in response to the task array no later than 227–243 msec after the onset of task array. However, if we assume that the onset latency of the P1 wave reflects the time required for information to arrive in high-level areas of visual cortex, then our results indicate the time required to adjust attention once information about the task array is available in these regions is 167–183 msec.

Interestingly, this is similar to the time typically required for spatial attention to shift to the location of a relevant color at a peripheral location, as indexed by the N2pc component, which typically begins between 150 and 175 msec after the onset of a visual search array (Sawaki, Geng, & Luck, 2012; Girelli & Luck, 1997; Luck & Hillyard, 1994). It is reasonable to suppose that the same mechanisms that produce a shift of attention to a single feature-defined target object in a search array are also responsible for expansions and contractions of spatial attention around the center of gaze.

The present results indicate a rapid transformation of feature-based attention to a more general form of spatial attention that can modulate the sensory response to a task-irrelevant probe that does not contain the to-be-attended feature. Previous studies have found an influence of feature-based attention on the neuronal response to a stimulus by 90 msec in the FEFs and by 130 msec in V4 (Zhou & Desimone, 2011). Electromagnetic measures have also shown evidence of selection between two colors by ~130–180 msec after stimulus onset (Schoenfeld et al., 2007; Hopf et al., 2004) and, under some circumstances, even an increase in P1 response to a stimulus that matches the attended color (Zhang & Luck, 2008). In these previous studies, however, the P1 response to a stimulus is changed depending on whether that stimulus either has or does not have a feature that matches the current attentional set, without specific regard to how attention modulates a location itself. The time estimate in the current study instead measures the time needed to transform the detection of a relevant feature into an adjustment of the spatial window of attention.

One might wonder how the distribution of attention before the onset of the task array might influence the present results. Imagine, for example, that participants

tended to be focused on the inner region at the beginning of the trial. If participants simply maintained attention on the inner region when the target color was present in this region but adjusted attention to the outer region when the target color appeared in the outer region, then we would see a difference in P1 amplitude between attend-inner and attend-outer trials for both probe types at the time when attention was changed in response to the region containing the colored dots. If we instead imagine that attention tended to be focused on the outer region at the beginning of the trial and was adjusted if the attended color appeared in the inner region, we would also see the P1 effect at the time when attention was changed in response to the region containing the colored dots. Thus, because the attention effect in this study was defined as the difference in P1 amplitude for trials in which the attended color appeared in the inner and outer regions, the locus of attention before trial onset could not have influenced the observed attention effect.

It is also possible that the distribution of attention before a given task array was related to whether attention was directed to the inner or outer region on the previous trial. We examined this in additional analyses not reported here, in which we compared trials preceded by the same versus the opposite attended region. No significant influence of the prior attended region was found, suggesting that attention likely returned to a default setting at the beginning of each trial.

Foveal versus Peripheral Attention

The results of this study differ from those of three previous studies that contrasted foveal versus peripheral attention. In one previous study, Handy and Khoe (2005) cued participants to a peripheral location or a central location and then examined the ERPs elicited by an isolated target that was presented at the cued location (80% of trials) or at the uncued location (20% of trials). They found that the P1 elicited by targets at the central location was not influenced by whether the central location or the peripheral location was cued. Similar results were obtained by Miniussi et al. (2002). Eimer (1999) conducted a related study in which two concentric circles were continuously visible in the display, and participants were cued centrally on each trial to attend to the region inside the inner circle, the region between the two circles, or the region outside the outer circle. A target letter was then presented in isolation within the cued region or within an uncued region. The target-elicited P1 wave did not differ for targets presented within the cued and uncued regions. These three studies appear to indicate that the spatial attention cannot be adjusted around the point of fixation in a manner that influences sensory responses, which conflicts with the robust P1 modulations observed in this study.

It is impossible to be certain of the critical factor that was responsible for the P1 effects observed in this study. One possibility is that this study probed attention after

participants had an opportunity to focus on one of two competing sets of stimuli (i.e., after they focused on either the inner or outer dots). Attention often has stronger and earlier effects when attended and unattended stimuli simultaneously compete for processing. For example, single-unit attention effects are typically much stronger when attended and unattended stimuli are present simultaneously inside the receptive field of the neuron being recorded (Luck et al., 1997; Treue & Maunsell, 1996; Moran & Desimone, 1985). Similarly, feature-based attention influences the P1 wave if the attended and unattended features are presented simultaneously (Zhang & Luck, 2008) but not if they are presented sequentially (Anllo-Vento, Luck, & Hillyard, 1998). Thus, attention may have been more strongly focused on the to-be-attended region at the time of the probe stimulus in this study than in the prior studies in which no P1 effects were observed.

Another interpretation is that the presence of a structured object in the visual field, not the competition between objects, is responsible for the P1 effect in our study. For example, the grouped array theory of object perception posits that locations are selected on the basis of their inclusion within the boundaries of an object representation (Vecera & Farah, 1994). In our study, the attentional modulation of the probe may be because of the fact that attention has locked onto the locations that contain the task-relevant object. A recent cuing study has indeed suggested that attention—as measured via the N2pc component—is allocated in the interval between cue and target when a placeholder is present but not when the cued location is empty (Woodman, Arita, & Luck, 2009).

Our finding of attentional modulation of a foveal stimulus is consistent with the results of Frey et al. (2010). In that study, there were always two stimuli on the screen, one of which was fixated. In each block, participants either attended to the fixated object or covertly attended to the peripheral object, monitoring for a rare deviation at the attended location. Throughout the task, the luminance of each whole object was varied continuously in an independent fashion. The visual evoked potential from these transient changes was estimated for each condition, and the results showed that attending to the foveal object rather than the peripheral object increased the ERP amplitude in the P1 time window. This study does not help differentiate between the object structure and competition accounts but does provide further evidence that shifting attention to a single location in the periphery can modulate sensory processing at fixation.

Attention to Ring-shaped Regions

The finding that the P1 wave for inner probes was larger when the relevant stimuli appear in the inner region than when they appeared in the outer region might be taken as evidence that it is possible to attend to a ring-shaped region around fixation, suppressing the inner region when attention is directed to the outer region. However,

these results are also compatible with a zoom lens mechanism, in which attention spreads across both the inner and outer regions when the relevant stimuli appear in the outer region. That is, the P1 for inner probes would be reduced when attention is expanded to include the outer region because processing resources are distributed over a larger region. Indeed, previous data from ERPs (Fu et al., 2005; Luo et al., 2001), fMRI (Müller, Bartelt, Donner, Villringer, & Brandt, 2003), and psychophysics (Egeth, 1977) have provided evidence for a zoom-lens-like account, in which the magnitude of attentional enhancement is decreased as the size of the attentional window increases. However, other behavioral results have suggested that attention can be configured into an annulus shape in which foveal information is ignored (e.g., Egly & Homa, 1984), and steady state ERP studies have shown that attention can be directed to two regions without including the space between them (Muller, Malinowski, Gruber, & Hillyard, 2003). Thus, future work will be needed to determine whether the present pattern reflects the diffusion of processing resources over a larger region or a ring-shaped region of enhanced sensory processing.

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