

# Feature-based attention modulates feedforward visual processing

Weiwei Zhang<sup>1</sup> & Steven J Luck<sup>1,2</sup>

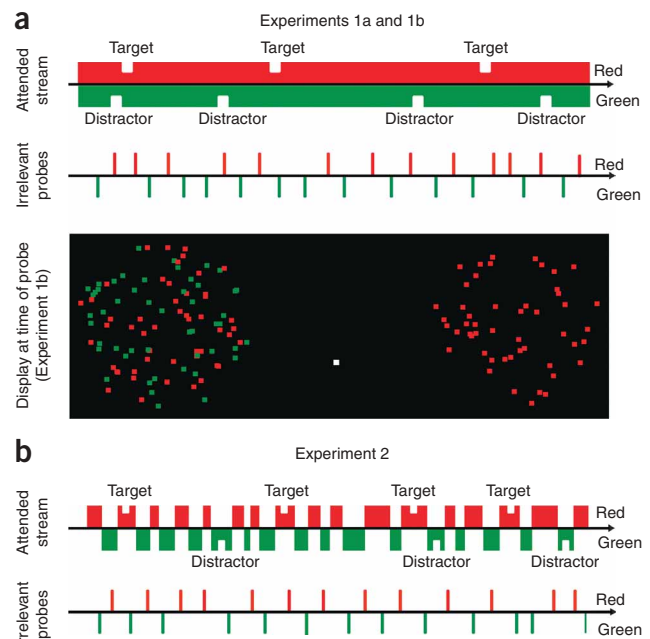
**It is widely believed that attention selects locations at an earlier stage than it selects nonspatial features, but this has been tested only under conditions of minimal competition. We found that, when competition was increased, color-based attention was able to influence the feedforward flow of information in humans within 100 ms of stimulus onset, even for stimuli presented at unattended locations. Thus, color-based attention can operate as early as, and independently from, spatial attention.**

Relevant information in the visual environment is often defined by nonspatial features, such as the shape of a face or the color of an apple. However, many researchers have argued that attentional selection of relevant information ultimately occurs on the basis of location<sup>1,2</sup>, with nonspatial features being used to determine which locations should be attended. This has been clearest in studies of event-related potentials (ERPs), in which spatial attention enhances the amplitude of the sensory-evoked P1 component within 100 ms of stimulus onset, with feature-based attention effects typically occurring between 150 and 300 ms post-stimulus and probably reflecting feedback signals<sup>3–5</sup>. In addition, these feature-based attention effects are typically eliminated for stimuli presented at unattended locations<sup>4,5</sup>. These findings suggest that spatial attention precedes featural attention and that featural attention is applied only to stimuli selected by spatial attention.

However, ERP studies of featural attention have typically presented the attended and ignored feature values one at a time, minimizing direct competition between them. Attentional selection is strongly dependent on competition. Both spatial attention<sup>6</sup> and feature-based attention<sup>7</sup> effects may be much stronger when attended and ignored stimuli simultaneously compete for access to perceptual processing

resources. Moreover, single-unit, functional imaging and steady-state ERP studies using simultaneous presentation of attended and ignored feature values have found featural attention effects in extrastriate visual cortex for stimuli that are presented at ignored locations<sup>8–10</sup>. However, these studies did not address the timing of the attentional modulation or the question of whether attention was influencing feedforward or feedback activity.

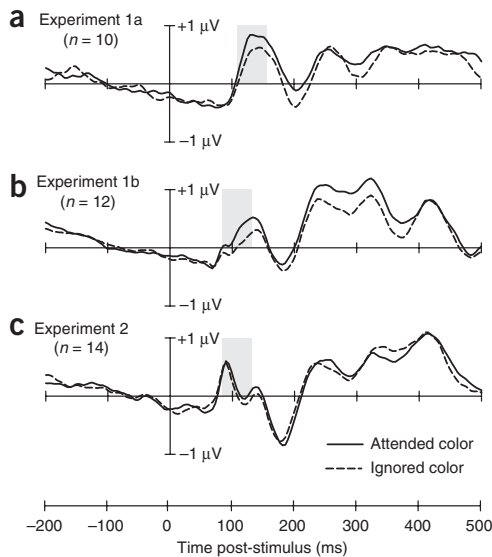
Using ERP recordings, we found that feature-based attention can influence feedforward sensory activity, as reflected by the P1 wave, under conditions of simultaneous competition between attended and ignored feature values. A continuous stream of intermixed red and green dots was presented in one visual field, and observers attended either to the red or green dots to detect occasional luminance decrements in the attended color (Fig. 1a,b and **Supplementary Methods** online). To probe the selectivity of the visual system for the attended and ignored colors, we flashed all-red or all-green probe arrays in the opposite visual field. The task was sufficiently difficult to require continuous attention to the task-relevant stimulus stream, but subjects were able to maintain central fixation (**Supplementary Results** online). If featural attention can influence feedforward sensory processing independently of spatial attention, then the task-irrelevant probes should elicit a larger P1 wave when presented in the attended color than when presented in the unattended color, even though they were presented at an unattended location. We tested this hypothesis at



**Figure 1** Experimental design. (a) Stimuli and timeline for the attend-red condition in Experiments 1a and 1b. The red and green dots were randomly intermingled throughout each 15-s trial, and subjects detected occasional luminance decrements (notches) in the attended color. Task-irrelevant all-red or all-green probe stimuli were flashed intermittently. The background was gray for Experiment 1a and black (as shown) for Experiment 1b. (b) Timeline for the attend-red condition in Experiment 2, in which the task-relevant stimuli were all-red or all-green at any given moment. Movies of the stimuli are presented in **Supplementary Videos 1–3** online.

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**Figure 2** Grand average waveforms at contralateral occipital electrode sites. Waveforms are shown for attended-color (solid lines) and unattended-color probes (broken lines) for Experiment 1a (a), Experiment 1b (b) and Experiment 2 (c). Shaded areas indicated the ERP amplitude measurement windows.

different stimulus contrast levels in Experiments 1a and 1b and found that the timing of the attention effect depended on the timing of the stimulus-evoked sensory response.

As would be expected from prior research, sensory-evoked activity began approximately 30 ms earlier for the high-contrast experiment than for the low-contrast experiment (**Supplementary Results**). For both experiments, P1 amplitude over the cortex contralateral to the probe (**Fig. 2a,b**) was significantly larger for probes presented in the attended color than for probes presented in the unattended color (Experiment 1a, 110–160 ms,  $P = 0.05$ ; Experiment 1b, 80–130 ms,  $P = 0.02$ ; see **Supplementary Results** and **Supplementary Fig. 1** online for ipsilateral waveforms). This effect was evident within 100 ms of stimulus onset for the high-contrast stimuli used in Experiment 1b (80–100 ms,  $P = 0.04$ ) and was observed across the lateral occipital electrode sites. Thus, color-based attention can influence the flow of feedforward sensory information within 100 ms of stimulus onset, even for stimuli presented at an unattended location.

Previous studies of color-based attention have not typically yielded P1 attention effects and, in Experiment 2, we tested the hypothesis that P1 amplitude was influenced by color-based attention in Experiments 1a and 1b because of the simultaneous competition between the attended and ignored colors. To test this hypothesis, the red and green elements of the task-relevant stimuli were presented sequentially, rather than simultaneously, in Experiment 2, and were thus never in direct competition (**Fig. 1b** and **Supplementary Methods**). We used high-contrast stimuli, as in Experiment 1b, and task difficulty was similar across experiments (**Supplementary Results**).

Color-based attention did not influence P1 amplitude in Experiment 2 (80–130 ms,  $P = 0.23$ ; 80–100 ms,  $P = 0.72$ ; **Fig. 2c**). Thus, in the absence of simultaneous competition, attention did not influence early feedforward sensory activity. A previous study using sequentially presented attended and ignored colors found an enhanced positivity

from 100–140 ms for attended stimuli<sup>11</sup>, and we found the same effect with approximately the same scalp distribution (100–140 ms,  $P = 0.05$ ). The previous study concluded that this effect did not reflect a modulation of the sensory-evoked P1 wave, and the delayed onset of the effect relative to the onset of the P1 wave in the present experiment supports this conclusion.

These results provide, to the best of our knowledge, the first unambiguous demonstration that, under conditions of simultaneous competition between attended and ignored feature values, feature-based attention can influence feedforward sensory processing, even at an ignored location. In the domain of spatial attention, previous research has shown that task instructions lead to top-down signals from prefrontal and parietal cortex that create a tonic change in gain for the attended location in visual cortex<sup>12</sup> and that this leads to enhanced feedforward transmission when a stimulus appears at that location<sup>4,6</sup>. Top-down signals have also been shown for feature-based attention<sup>13</sup> and our results demonstrate that these signals lead to enhanced feedforward transmission for stimuli presented in the attended color, even when they are presented at an unattended location.

A previous study using simultaneous competition between attended and unattended colors found a similar attention effect for stimuli at an attended location<sup>14</sup>, although it was not clear whether it was based on color or apparent depth. Considered together, our results and those of the previous study suggest that, under conditions of simultaneous competition, color-based attention operates throughout the visual field in a global manner (see **Supplementary Discussion** and **Supplementary Fig. 2** online), independently of spatial attention, as proposed by the similarity gain model<sup>9,15</sup>. Spatial attention may still be unique, however, because only spatial attention appears to influence early sensory processing in the absence of high levels of competition.

*Note: Supplementary information is available on the Nature Neuroscience website.*

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#### AUTHOR CONTRIBUTIONS

W.Z. and S.J.L. conceptualized and designed the experiments. W.Z. collected the data and performed the data analyses. W.Z. and S.J.L. wrote the paper.

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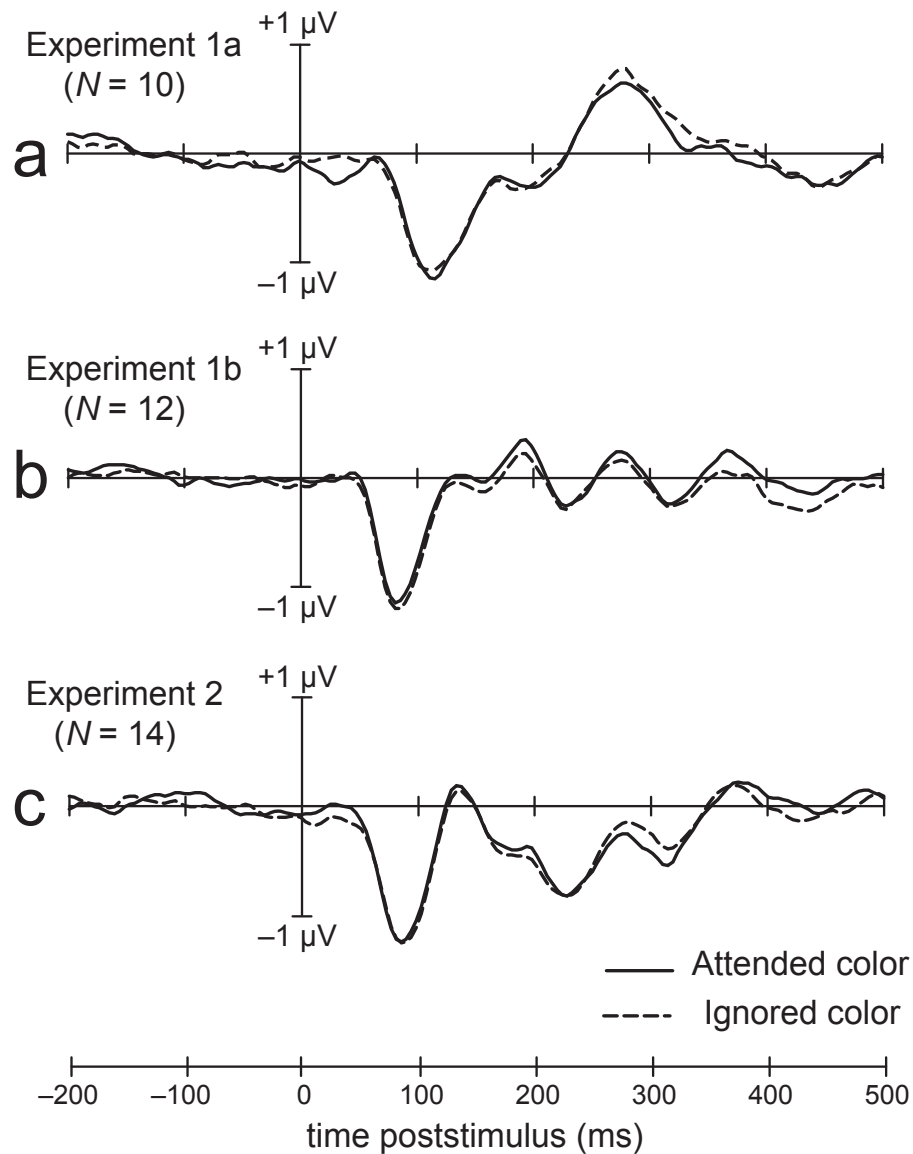
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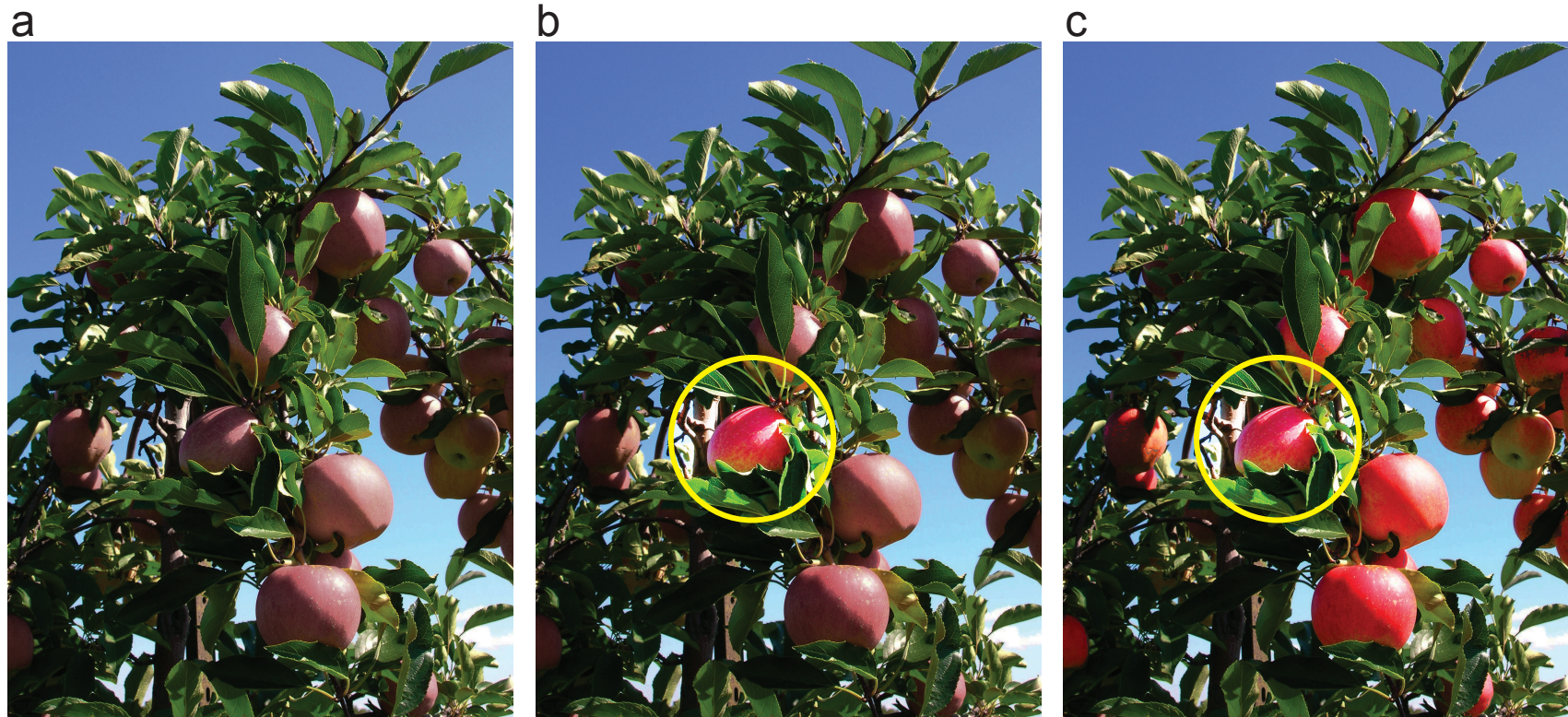
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Supplementary Fig. 1 Grand average waveforms at ipsilateral occipital electrode sites. Waveforms are shown for attended-color (solid lines) and unattended-color probes (broken lines) for Experiment 1a (a), Experiment 1b (b), and Experiment 2 (c).



Supplementary Fig. 2 Hypothesized interplay between spatial attention and featural attention in natural vision. A natural scene (a) contains many potentially relevant objects that share common features (the red apples here). Spatial attention can increase the gain in one region of space (b), which may aid in the perception of one of the relevant objects (the apple inside the yellow circle). The simultaneous application of featural attention to objects with relevant features at unattended locations (e.g., the other apples) increases the gain for those objects (c), highlighting them so they may directly influence behavior or become the next target of spatial attention. Based on photo from <http://www.flickr.com/photos/wxmom/1359996991/>, licensed under the Creative Commons license (<http://creativecommons.org/licenses/by-sa/2.0/deed.en>).

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## Supplementary Information

### Supplementary Methods

**Participants.** Ten, twelve, and fourteen neurologically normal volunteers between 18 and 35 years old were paid for their participation in Experiments 1a, 1b, and 2, respectively. All had normal or corrected-to-normal visual acuity and reported having normal color vision. Informed consent was obtained at the beginning of each testing session.

**Stimuli.** Stimulus luminance and chromaticity were measured with a Tektronix J17 LumaColor chromaticity meter using the 1931 Commission International d'Eclairage chromaticity space. Stimuli were viewed from a distance of 100 cm on a video monitor with a gray background ( $6.1 \text{ cd/m}^2$ , Experiment 1a) or a black background ( $< 0.1 \text{ cd/m}^2$ , Experiments 1b and 2).

As illustrated in Fig. 1a and Supplementary Video 1, the stimulus display in Experiment 1a was composed of two  $4.0^\circ$  circular regions of random dots centered 8 degrees to the left and right of, and  $2.6^\circ$  above, the central fixation point. One of these regions was task relevant and the other was task irrelevant.

The stimuli in the task-relevant region consisted of a continuous 15-s stream of 50 red dots ( $x=0.62, y=0.32, 8.1 \text{ cd/m}^2$ ) and 50 green dots ( $x=0.26, y=0.58, 8.1 \text{ cd/m}^2$ ). The dots were  $0.2^\circ$  by  $0.2^\circ$  squares that were randomly distributed across the task-relevant region. When red



and green dots overlapped, either could appear in front of the other, promoting the perception of a single surface containing both red and green dots. To minimize the possibility that the observers could focus on the location of a single dot, the dots changed frequently. Specifically, half of the dots disappeared and were replaced by new dots at different random locations every 100 ms. Each dot was therefore replaced every 200 ms. The whole array of dots appeared to scintillate, without any obvious perception of a regular flickering (see Supplementary Video 1).

Luminance decrements occurred unpredictably within this continuous stream. Each luminance decrement consisted of a 500-ms change in all the dots of a single color from 8.1  $\text{cd/m}^2$  to 3.2  $\text{cd/m}^2$ . Between 2 and 5 luminance decrements occurred for a given color on each 15-s trial, with a random period of between 1000 and 7000 ms between decrements (excluding the first and last 500 ms of each trial). The timing of the luminance decrements was independent for the red and green dots.

The stimuli in the ignored region consisted of arrays of 50 dots that were flashed for 100 ms, separated by a blank interval of 300–700 ms (rectangular distribution, varied in increments of the 16.7-ms refresh duration). Each array was composed entirely of red dots or entirely of green dots, and the order of red and green arrays was random. The timing of the flashes was independent of the stimuli presented in the attended region.

Experiment 1b was identical to Experiment 1a, except that a black background was used to increase stimulus contrast (see Supplementary Video 2).

Experiment 2 (Fig. 1b) was identical to Experiment 1b except for the following changes to the task-relevant stimulus stream (see Supplementary Video 3). This stream contained 50 dots of a single color at any given moment, alternating between red and green every 200 to 800 ms

(rectangular distribution, in 16.7-ms increments). A random set of 2–5 of these intervals for each color contained a luminance decrement. Luminance decrements lasted 160 ms and were always preceded and followed by at least 80 ms of the standard luminance.

***Procedure.*** At the beginning of each half of the experiment, subjects were instructed to attend to a particular color (red or green; order counterbalanced across subjects). The attended region was cued with an arrow at the beginning of each 15-s trial. The arrow was presented for 1000 ms and followed by a 500-ms blank period. The 15-s continuous stream of random dots was then presented in the attended region. Subjects were instructed to press a button whenever they detected a luminance change in the dots of the attended color within the cued region. They were further instructed to ignore luminance changes in the dots of the unattended color within the cued region and all stimuli at the uncued location. Each trial was followed by a blank intertrial interval of 800–1200 ms.

Each subject completed eight blocks of 16 trials, with a short break (15 s) in the middle of every block. Subjects were instructed to maintain fixation and avoid blinking throughout each trial, and feedback regarding fixation, blinking, and task accuracy was provided after every 8 trials. It should be noted that any deviations of fixation toward the cued location would influence the attended and unattended colors equally.

***EEG recording and statistical analysis.*** The EEG was recorded from 15 scalp sites at low impedance ( $< 5\text{K}\Omega$ ) with a bandpass of 0.01–80 Hz and a sampling rate of 250 Hz using the average of the left and right mastoids as the reference. Horizontal and vertical electrooculogram (EOG) recordings were used to detect blinks and eye movements. Individual trials contaminated by artifacts were excluded using our standard methods<sup>1,2</sup>. In addition, to assess the presence of



unrejected eye movements toward the cued side, we computed averaged horizontal EOG waveforms over the course of the entire trial, time-locked to the cue.

Averaged ERP waveforms were computed time-locked to the task-irrelevant probe stimuli, and these were collapsed into attended-color and ignored-color waveforms, averaged across red and green probes. Contralateral waveforms were constructed by averaging the left hemisphere electrodes for right hemifield probe and right hemisphere electrodes for left hemifield probes. Ipsilateral waveforms were constructed by averaging the right hemisphere electrodes for right hemifield probe and left hemisphere electrodes for left hemifield probes.

ERP amplitudes at the O1, O2, OL, OR, P7, and P8 electrode sites were measured as the mean voltage within a given time window relative to the 200-ms prestimulus voltage. ERP onset latencies were measured as the time at which the voltage reached 50% of the peak value, which is typically the most sensitive measure of onset time<sup>3</sup>. Analysis of variance (ANOVA) was used for all statistical tests, and all p values were adjusted with the Greenhouse–Geisser epsilon correction for nonsphericity<sup>2</sup>. An offline low-pass filter was applied to the waveforms for plotting but not for measurement (Gaussian impulse response function, full width at half maximum = 14 ms, half-amplitude cutoff = 30 Hz).

## Supplementary Results

**Behavioral Results.** The luminance detection task was demanding, yielding mean hit and false alarm rates of 83% and 7% for Experiment 1a, 78% and 8% for Experiment 1b, and 79% and 9% for Experiment 2. This level of performance indicates that the luminance detection task was quite challenging, making it unlikely that subjects frequently shifted spatial attention to the location of the task-irrelevant probes.

**Eye Movements.** To assess fixation performance, we computed averaged horizontal electrooculogram (EOG) waveforms, time-locked to the cue and extending over the entire trial duration. The average difference in voltage between left-cue and right-cue trials was less than 3.2  $\mu\text{V}$  in each experiment, corresponding to an average deviation of less than  $0.1^\circ$  toward the cued side<sup>4</sup>. Thus, subjects were able to maintain fixation on the central fixation point quite well. Moreover, even if subjects had moved their eyes toward the attended location, this would have had an equal effect on the attended-color and unattended-color probe flashes.

**Ipsilateral Waveforms.** Supplementary Fig. 1 shows the waveforms recorded at lateral occipital scalp sites ipsilateral to the probe stimuli (and therefore contralateral to the task-relevant stimulus stream). The ipsilateral waveforms were dominated by a C1 wave, which is generated in primary visual cortex and is typically largest at ipsilateral scalp sites owing to the tilt of the generator source<sup>5-7</sup>. The P1 and N1 components were not readily visible in the ipsilateral waveforms, possibly because of inhibition from the task-relevant stimulus stream, which projected directly to this hemisphere. Furthermore, no relevant experimental effects were evident in the ipsilateral waveforms. Thus, we focused our main analyses on the contralateral waveforms.

**Latencies.** Increases in stimulus contrast typically produce faster visual integration times<sup>8, 9</sup> and shorter ERP latencies<sup>8, 10-12</sup>. Consequently, the averaged ERP waveforms from Experiment 1b (high contrast) looked much like those from Experiment 1a (low contrast), but shifted leftward (see Fig. 2a,b and Supplementary Fig. 1). To assess this statistically, we compared the ipsilateral C1 and contralateral P1 onset latencies for Experiments 1a and 1b. The onset latencies of both components were approximately 30 ms earlier in Experiment 2 than in Experiment 1, and these differences were statistically significant for both components (C1:  $F(1,20)=70.50$ ,  $p < 0.001$ ; P1:  $F(1,20) = 91.27$ ,  $p < 0.001$ ). We therefore shifted the amplitude measurement windows by 30 ms for Experiment 1b relative to Experiment 1a. The onset latencies were nearly identical for Experiments 1b and 2, which used identical stimulus contrast levels, and we therefore used the same amplitude measurement windows for these two experiments.

**Consistency of Spatial Attention.** One of our main conclusions is that color-based attention can influence sensory transmission even for stimuli presented at unattended locations. Thus, it is important to consider whether the observed P1 effects could have occurred when attention was occasionally attracted to the location of the task-irrelevant probe stimuli.

One possibility is the presentation of an attended-color probe led to contingent capture of attention<sup>13</sup> to the probe's location. This could not have produced a larger P1 amplitude for attended-color probes relative to unattended-color probes, because the shift of attention would have been too late to influence P1 amplitude. However, if attention remained at the location of the probe after being captured, the next probe would have been presented within the focus of spatial attention. This next probe was equally likely to be the attended color or the unattended color, so capture could not have directly produced the observed difference in P1 amplitude

between attended- and unattended-color probes. However, if attention remained at the location of the task-irrelevant probes after being captured by a probe of the attended color, this would call into question our conclusion that the P1 attention effect can occur for stimuli presented at unattended locations. To rule out this possibility, we examined target detection performance during the 1-s period following attended-color versus unattended-color probes. If attended-color probes had captured attention, and attention had remained at the probe location through the time of the next probe, then this should have caused a substantial decline in target detection performance in the period following an attended-color probe. However, we found no significant difference in target detection performance following attended- versus unattended-color probes (Experiment 1a:  $F(1,11)=1.10, p=0.31$ ; Experiment 1b:  $F<1$ ). This is consistent with prior evidence showing that focusing attention on one location can eliminate the capture of attention by stimuli at other locations<sup>14, 15</sup>.

Another possibility is that attention occasionally wandered to the probe location, irrespective of the color of the probe. This is a very unlikely explanation of the results, because it means that the observed P1 attention effect was present on a small subset of trials and yet was visible when these trials were averaged with the large number of trials on which attention was focused on the task-relevant stimulus stream. However, to provide more direct evidence, we conducted a new set of analyses in which probes were included in the averaged ERP waveforms only if behavioral performance was accurate within the preceding two seconds. The pattern of results was identical to that observed in the original analyses, with significant effects of attention on P1 amplitude in both Experiment 1a ( $F(1,9)=4.89, p=0.05$ ) and Experiment 1b ( $F(1,11)=10.62, p<0.01$ ). Thus, the observed P1 effects were not due to a small subset of trials in which attention was directed to the location of the task-irrelevant probes.

## Supplementary Discussion

It is always difficult to be certain that an ERP component observed in one experiment is identical to a component observed in a different experiment, and we cannot be certain that the color-based P1 attention effect observed in the present study is identical to the space-based P1 attention effects observed in prior studies. They both occur in the same general time range and at the same general electrode sites, and both consist of a change in amplitude with no change in latency. However, additional research is necessary to determine if they arise from the same neural generator sources.

A key difference between the color-based and space-based P1 attention effects is that the color-based effect but not the space-based effect appears to require substantial competition between attended and ignored feature values. It is important to note, however, that the conditions of simultaneous competition that seem to be necessary for the color-based P1 attention effect are not an unusual laboratory contrivance. Instead, this sort of simultaneous competition reflects a common situation in natural vision, in which relevant features are distributed across the scene and intermixed with irrelevant features.

Consider, for example, the task of picking apples from an apple tree. As illustrated in Supplementary Fig. 2, apples are typically scattered around a tree, separated by leaves and branches. Although it may be useful to focus spatial attention on one object to identify that object (e.g., to determine whether a given apple is ripe), it may also be useful to obtain information about the entire set of relevant objects (e.g., to determine whether the tree has a large number of ripe apples). Consequently, it may be useful to highlight objects across the scene that contain relevant features. Moreover, the scene-wide feature information may be processed in parallel with information from an attended location (e.g., allowing the observer to evaluate the

ripeness of one apple while simultaneously preparing to reach toward another cluster of apples).

Broadly speaking, feature-based attention may work as means of biasing scene-level perceptual segregation processes to favor scene elements that contain task-relevant features even when spatial attention is focused on a subregion of a perceptual group.

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## **Supplementary Video Captions**

**Supplementary Video 1** Example of a trial from Experiment 1a.

**Supplementary Video 2** Example of a trial from Experiment 1b.

**Supplementary Video 3** Example of a trial from Experiment 2.