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Report

Feature-Based Attention Elicits Surround Suppression in Feature Space

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Summary

It is known that focusing attention on a particular feature (e.g., the color red) facilitates the processing of all objects in the visual field containing that feature [1–7]. Here, we show that such feature-based attention not only facilitates processing but also actively inhibits processing of similar, but not identical, features globally across the visual field. We combined behavior and electrophysiological recordings of frequency-tagged potentials in human observers to measure this inhibitory surround in feature space. We found that sensory signals of an attended color (e.g., red) were enhanced, whereas sensory signals of colors similar to the target color (e.g., orange) were suppressed relative to colors more distinct from the target color (e.g., yellow). Importantly, this inhibitory effect spreads globally across the visual field, thus operating independently of location. These findings suggest that feature-based attention comprises an excitatory peak surrounded by a narrow inhibitory zone in color space to attenuate the most distracting and potentially confusable stimuli during visual perception. This selection profile is akin to what has been reported for location-based attention [8–10] and thus suggests that such center-surround mechanisms are an overarching principle of attention across different domains in the human brain.

Results

Observers viewed overlapping sets of colored dots in the left visual field (e.g., blue among red dots) and the right visual field (e.g., green among red dots) (Figure 1A). Each dot moved in a random, haphazard fashion. Observers concurrently attended to one of the dot arrays in each visual field to detect brief intervals of coherent motion in the target colors. The colors of the dot arrays varied randomly from trial to trial. A target color for one side of the display was determined by choosing a random hue on a color wheel from CIELAB color space. The target color for the opposite side of the display was determined by rotating this hue, such that in a given trial, it could match the other side's target color (0° apart) or differ from that target color in steps of 10° on the color wheel (up to 60°). The distractor color for both sides was always 180° apart from one of the target colors and was identical across both hemifields.

We found that it is more difficult to select two colors that are similar (but not identical) to each other than it is to select two distinct colors. Detection accuracy was highest when the two target colors were identical, and it decreased as the difference in color increased, reaching a minimum at 30° (0° versus 30°; $t(19) = 3.7$; $p = 0.002$; $\eta^2 = 0.42$). Performance gradually increased when the target colors became more distinct from each other (30° versus 60°; $t(19) = 2.7$; $p = 0.01$; $\eta^2 = 0.28$), with performance at 60° no worse than when attending to a single color ($p = 0.87$; Figure 1B). To better understand the magnitude of the performance decrease at 30°, we compared accuracy in that condition to a condition in which participants attended to opposing colors in each hemifield (e.g., blue among red on one side and red among blue on the other side), which eliminates any benefits of feature-based attention [2]. Performance at 30° was similar to this baseline ($p = 0.23$).

These behavioral data suggest that feature-based selection contains an inhibitory surround in color space: selecting two targets nearby in color space places those targets within each other's suppressive zones, interfering with the selection of both target colors. In contrast, selecting two targets far apart in color space places them outside of those zones, enabling both targets to be selected without interference. Although this experiment did not reveal the exact nature of this interference, it is possible that suppression either reduced the motion response of the target dots or increased confusability between targets and distractors. We found the same results using a visual search task (see Figure S1 and Supplemental Experimental Procedures available online).

Direct Measure of Center-Surround Activation in Feature Space with SSVEPs

In a second experiment, we measured the neurophysiological response to colors in unattended regions of the visual field that were perceptually close or far from a to-be-attended color. Participants performed a task similar to experiment 1 but attended to only one color in either the left or the right hemifield. An array of colored dots that was task irrelevant was presented in the unattended visual field at the same time. The colors of these unattended dots matched the target color, diverged 30° or 60° from the target color, or matched the distractor color in the attended visual field. During each trial, target and distractor dots flickered at distinct frequencies (7.1 Hz and 8.5 Hz or vice versa), and the task-irrelevant dots flickered at yet another frequency (10.7 Hz; Figure 2A). Thus, each dot array elicited distinguishable steady-state visual evoked potentials (SSVEPs). The SSVEP is the oscillatory response of the visual cortex to flickering stimuli: it has the same frequency as the driving stimulus, and its amplitude is larger for attended stimuli relative to unattended stimuli [11].

In the attended visual field, SSVEP amplitudes over occipital cortex were larger for targets relative to distractors ($t(15) = 3.34$; $p = 0.004$; $\eta^2 = 0.43$; Figure 2B), consistent with research showing that early visual processing of attended features is facilitated [3, 12–14]. In the unattended visual field, we found substantial differences in SSVEP amplitudes depending on the perceptual similarity to the target color ($F(3,45) = 6.92$; $p = 0.001$; $\eta^2 = 0.32$; Figure 2C). Amplitudes were largest for dot arrays matching the target color, and they were decreased for arrays 30° apart from the target color (0° versus 30°: $p = 0.002$; $\eta^2 = 0.48$) and for arrays matching the distractor color (0° versus 180°: $p = 0.0002$; $\eta^2 = 0.61$), with no difference between the latter two (30° versus 180°: $p = 0.57$; $\eta^2 = 0.02$). SSVEPs elicited by dot arrays 60° apart from the target color showed an intermediate amplitude, which was significantly larger relative to the 30° and 180° conditions

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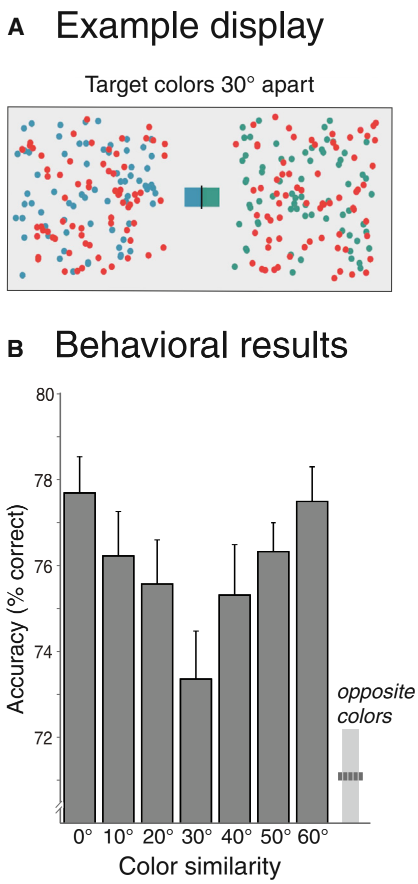

Figure 1. Example Display and Behavioral Results from Experiment 1

(A) Participants attended to colored sets of dots in the left and right visual field to detect brief intervals of coherent motion. Two colored boxes in the center of the screen indicated which colors to attend to on which side (in this example, the cues indicate to attend blue on the left side and turquoise on the right side).

(B) Accuracy is lowest when the two target colors are 30° apart, and it is high both when attending identical colors (i.e., 0°) or when attending two colors that are not similar (i.e., 60° apart). When attending to opposing colors on each side (e.g., blue among red on the left side and red among blue on the right side), performance is also low and not different from the 30° condition. Error bars correspond to within-subject SE of the mean.

(60° versus 30°: $p = 0.02$; $\eta^2 = 0.29$; 60° versus 180°: $p = 0.01$; $\eta^2 = 0.33$). The difference between the 60° and 0° conditions was not reliable across subjects ($p = 0.13$; $\eta^2 = 0.14$), consistent with the hypothesis that feature-based attention is realized largely by suppressing unattended features rather than solely by enhancing target features [15]. However, the (nonsignificant) tendency for higher amplitudes in the identical color relative to the 60° condition suggests that there may be some degree of facilitation.

This pattern of results mirrors the behavioral data from experiment 1, revealing an inhibitory surround extending to about 30° in color space. In addition, these data demonstrate that surround suppression emerges automatically and proliferates throughout the visual field, at least in tasks that involve high competition of different features. The global nature of the inhibitory surround appears similar to the facilitatory effects proposed in the feature similarity gain model [4, 16]. According to this account, attention globally enhances the sensory gain of feature-selective neurons throughout the visual field, regardless of target location. Our results suggest a similar global mechanism of surround suppression in feature space that affects sensory processing independent of location.

The present study demonstrates that feature-based attention elicits a narrow inhibitory surround in feature space, similar to what has been observed for spatial attention [8–10]. This suggests that surround suppression is a unifying principle underlying visual selection, as previously proposed by computational models [17]. This selection profile appears to be optimized to resolve competition between inputs that overlap in their neural representations by attenuating the activity of irrelevant stimuli nearby in feature space, presumably within the same cortical map. Given the map-based organization of the cortex (e.g., [18–20]), a selection mechanism with a narrow inhibitory surround would be beneficial across all dimensions, possibly reflecting a canonical computation that sharpens selective processing across different domains.

Experimental Procedures

Participants

All participants gave written informed consent and had normal or corrected-to-normal vision and normal color vision, assessed with Ishihara's test for color deficiencies [21]. Twenty observers (18–28 years old) participated in experiment 1, and eighteen observers (18–28 years old) participated in experiment 2; data from two participants in experiment 2 had to be excluded from the analysis because >30% of their trials were rejected as a result of artifacts in the electroencephalogram (EEG). The study was performed in accordance with Harvard University regulations and was approved by the Committee on the Use of Human Subjects in Research under the Institutional Review Board for the Faculty of Arts and Sciences.

Stimuli and Procedure

Experiment 1

Two overlapping fields of randomly moving dots in different colors were presented concurrently in both the left and the right visual field. Each dot array consisted of 70 circles (radius = 0.24°). The lightness factor of the colors was kept constant (D65; 26–29 cd/m^2 across all colors). The stimuli were presented on a gray background (186 cd/m^2), within 6° × 6° rectangular regions that were centered to the left and right of the vertical midline at an eccentricity of 4°. Each trial started with the presentation of a color cue in the center of the screen and motionless fields of dots. The cue consisted of two colored squares in the center of the screen (0.5° × 0.5°), with the left square indicating which color to attend to on the left side (e.g., blue) and the right square indicating which color to attend to on the right side (e.g., green). After 1.6 s, all dots started moving randomly for 1.2 s. The color cue remained on the screen throughout the trial.

During the movement period, each dot changed its position in a random direction every four to seven frames (47–82 ms, random). Occasionally, the target dots of one field could move coherently in one of four directions (up, down, left, or right) for 230 ms. Only 80% of the dots moved coherently to prevent observers from tracking single dots. The coherent motion occurred randomly in the interval between 200 ms and 1,100 ms after movement onset. Coherent motion parameters were manipulated independently for each hemifield; thus, in any given trial, a coherent motion could appear on both sides. For each side (left or right), in ½ of the trials, the target colored dots moved coherently; in ¼ of the trials, the distractor colored dots moved coherently; and in the remaining ¼ of the trials, no coherent motion occurred. Which dot array moved coherently and motion direction were randomized across the experiment.

Observers were instructed to concurrently attend to one of the dot arrays in each visual field and to detect brief intervals of coherent motion of the dots in the to-be-attended colors (targets). Observers were instructed to keep their eyes on the color cues in the center of the screen throughout each trial. At the end of each trial, a question mark appeared on one side of the screen, and the observer had to indicate whether the target dots moved coherently on that side of the display. Once a response button was pressed, the observer had to make the same response for the other side. When a coherent motion was detected, the observer had to indicate its direction (up, down, left, or right) by pressing one of the arrow keys on the keyboard. Otherwise, the observer pressed the control key. The order

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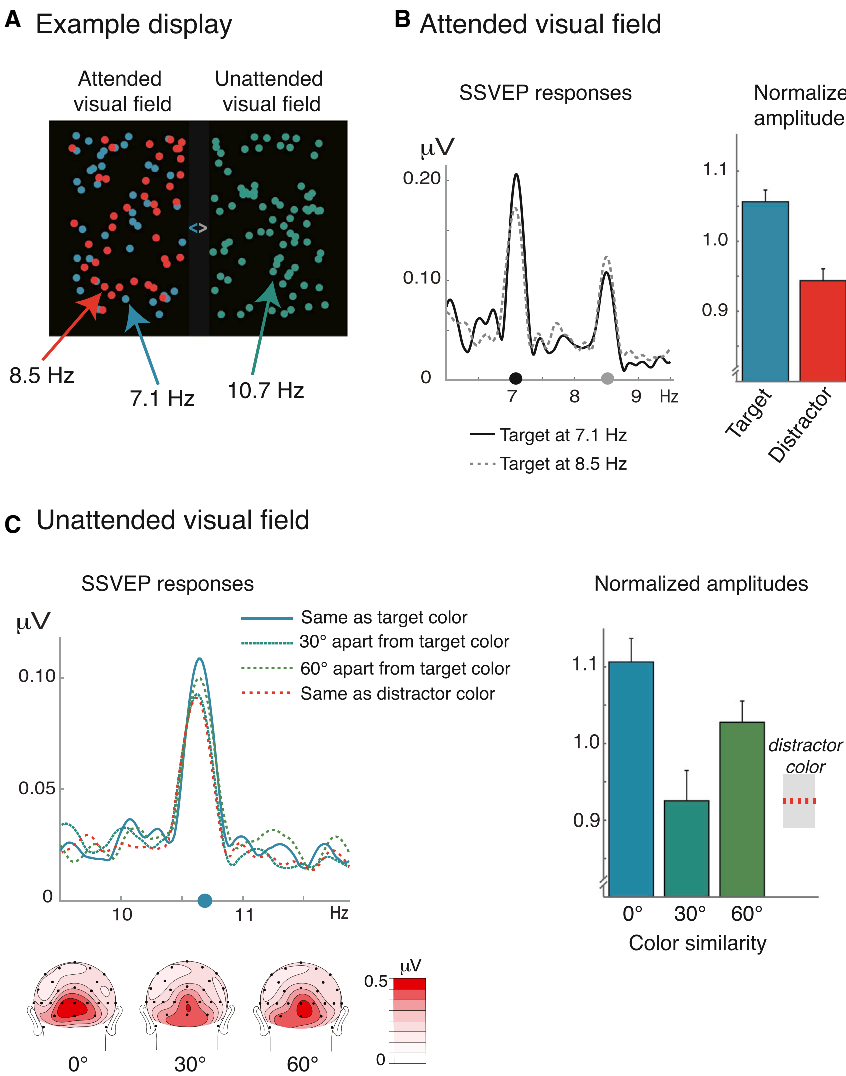

Figure 2. Example Display and SSVEP Responses from Experiment 2

(A) A colored arrow in the center of the screen cued participants to attend to a colored dot field on one side of the screen (here: blue dots on the left side). A dot array was also presented on the unattended side, and its color varied with respect to the target color. Each field of dots flickered at distinct frequencies to separate neural responses for each of them.

(B) Grand-averaged amplitude spectrum obtained by Fourier transformation of the SSVEP waveforms shows clear attentional enhancement for target colors relative to distractor colors at the stimulating frequencies. Error bars correspond to within-subject SE of the mean.

(C) Grand-averaged SSVEP responses for the field of dots in the unattended visual field show the highest responses to colors matching the target color (0°) and the lowest responses to colors 30° distant from the target color and the distractor color, with an intermediate response to colors 60° distant from the target color. Topographical scalp maps show peak amplitudes at occipital scalp sites. Error bars correspond to within-subject SE of the mean.

of the side tested first in each trial (left or right) was counterbalanced across the experiment. Each participant completed 32 practice trials, followed by a total of 512 experimental trials (64 per color condition).

Experiment 2

The stimuli and experimental procedure were similar to experiment 1. Two overlapping sets of colored dots were presented on one side of the display (e.g., blue and red on the left), and another array of colored dots was presented on the other side of the display (e.g., green on the right). Each dot array in the to-be-attended hemifield consisted of 130 stimuli (260 total), and the dot array in the other unattended hemifield consisted of 260 dots (radius = 0.32°). The stimuli were presented on a black background (0.02 cd/m^2) within 7° × 14° rectangular regions that were centered to the left and right of the vertical midline at an eccentricity of 4°. At the beginning of each trial, a colored arrow in the center of the screen (0.5°) cued observers to which hemifield and color they should attend. The cue appeared together with motionless colored dot arrays for 500–800 ms (jittered) and stayed on the screen throughout each trial. After the cue period, all dots moved randomly for 2.6 s (for details, see Experiment 1), and participants had to detect brief intervals of coherent motion of the target colored dots. In ½ of the trials, target colored dots moved coherently (left, right, up, or down; counterbalanced). In ¼ of the trials, the dots in the distractor color moved coherently, and, in the remaining ¼ of the trials, no coherent motion occurred. The dot array in the unattended visual field never moved coherently, and participants never attended to that side. In ½ of the trials, participants attended to colored dots on left side, and, in the remaining ½ of the trials, participants attended to colored dots on the right side. Participants were instructed to maintain their gaze in the center of the screen throughout each trial. Horizontal eye movements were monitored with electrooculogram (see Electrophysiological Recordings and Analysis).

During the movement period, each of the dot arrays flickered at a distinct frequency. In ½ of the trials, the target colored dots flickered at 7.1 Hz (six frames on, six frames off; mean luminance: 1.6 cd/m^2), and the distractor colored dots flickered at 8.5 Hz (five frames on, five frames off; mean luminance: 1.9 cd/m^2). In the remaining ½ of the trials, this assignment was reversed. The dot array on the unattended side always flickered at 10.7 Hz (four frames on, four frames off; mean luminance: 2.1 cd/m^2).

Colors were picked as in experiment 1, with the exception that the same five color sets were used for all participants (see Supplemental Experimental Procedures) and that only four color conditions were chosen to increase the signal-to-noise ratio. Each color was presented equally often in each attention condition to eliminate any differences in sensory input across conditions. For example, the exact same green was presented on the unattended visual field while participants attended to a target color exactly matching that green, a color 30° apart from that green, or a color 60° apart from that green; thus, any differences observed for the SSVEP responses elicited by that green must be due to differences in which color is attended to in the other hemifield. Participants completed 32 practice trials and 640 experimental trials. Participants performed at 78% correct (±0.07), with no differences between the color conditions ($p > 0.22$).

Electrophysiological Recordings and Analysis

EEG was recorded continuously from 32 Ag/AgCl electrodes mounted in an elastic cap and amplified by an ActiCHamp amplifier (BrainVision). Electrodes were arranged according to the 10-10 system, with three additional electrodes positioned inferior to the occipital sites to ensure adequate spatial sampling from the posterior scalp. Signal processing was performed with MATLAB (MathWorks) using the EEGLAB toolbox [22] and custom-written scripts. A semiautomated procedure was performed to remove epochs from the EEG that were contaminated by eye movements, blinks, and myographic artifacts. Artifact-free data were rereferenced to the average reference. The averaging epochs extended from 400 ms to 2,500 ms after movement onset. The SSVEP amplitudes were quantified as the absolute value of the complex Fourier coefficients for each frequency; that is, for each participant and condition, the maximum absolute value within a small band of the respective stimulation frequency (±0.2 Hz) was chosen and then averaged across 11 posterior electrodes (I3, Iz, I4, O1, Oz, O2, PO3, PO4, PO7, PO8, POz). For the attended visual field, SSVEP amplitudes were normalized for target and distractor color by dividing the amplitude by the mean amplitude of target and distractor color for each frequency separately for each participant [23]. The normalized amplitudes were collapsed across frequencies to reveal amplitude values for targets and distractors. Similarly, the SSVEP amplitudes were normalized for the dot array in the unattended visual field by dividing the amplitude for each condition by the mean amplitude across all four conditions. The same pattern was observed when we analyzed only lateralized electrodes, excluding any possible contribution from the midline responses (see Supplemental Experimental Procedures).

Pairwise t tests were conducted to examine the SSVEP amplitudes for target and distractor colors in the attended visual field. The SSVEP responses in the unattended visual field were analyzed by a repeated-measures ANOVA with the factor color similarity (with respect to the target color). After establishing a main effect of color similarity, pairwise t tests were performed.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and one figure and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.07.030.

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