Feature-selective attention enhances color signals in early visual areas of the human brain

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We used an electrophysiological measure of selective stimulus processing (the steady-state visual evoked potential, SSVEP) to investigate feature-specific attention to color cues. Subjects viewed a display consisting of spatially intermingled red and blue dots that continually shifted their positions at random. The red and blue dots flickered at different frequencies and thereby elicited distinguishable SSVEP signals in the visual cortex. Paying attention selectively to either the red or blue dot population produced an enhanced amplitude of its frequency-tagged SSVEP, which was localized by source modeling to early levels of the visual cortex. A control experiment showed that this selection was based on color rather than flicker frequency cues. This signal amplification of attended color items provides an empirical basis for the rapid identification of feature conjunctions during visual search, as proposed by "guided search" models.

electrophysiology | feature-based attention | steady-state evoked potential | visual search

When we search for a target item having a unique color (e.g., red) within an array of distracter items of a different color (e.g., green), the target appears to "pop-out" from the background of distracters. This pop-out effect is seen when targets are distinguished from uniform distracters by virtue of an easily discriminated visual feature such as color, orientation, size, curvature, etc. (1, 2). Under conditions where the pop-out effect occurs, the time to detect target presence is rapid and does not vary with the number of background distracters. In contrast, when a target is defined by a particular combination of two or more features (e.g., color and size) and is intermingled with distracter items having different combinations of those features, target detection is typically slower and increases as a function of the number of distracters. These findings have led to proposals that feature conjunctions must be identified by serially examining each item in the display (3), although parallel models of search can also account for the sloping set-size functions of conjunction search (4).

Under certain conditions, it has been found that visual search for conjunction targets may be highly efficient and yield flat rather than sloping set-size functions (4). Such efficient search is possible when the two features defining the conjunction are highly discriminable from the distracter features. To account for such findings, Wolfe and colleagues (5) have proposed a "guided search" model, according to which the sensory representations of items having the relevant features are facilitated by attention, and target items having both attended features stand out by virtue of having a double-dose of facilitation. An alternative proposal is that items having the nontarget features are suppressed, again leading to pop-out of the targets (6). The evidence is mixed, however, as to whether attention can produce a global facilitation (or suppression) of a particular feature such as color across an entire array of stimuli, which these proposals require. Summarizing early studies of this question, Treisman (1) concluded that "attention cannot be distributed over a subset of items (e.g., the red ones) when these are spatially scattered among other items in a randomly mixed display." Similarly, Shih and Sperling (7) found no evidence that irrelevant stimuli could be suppressed or filtered out solely on the basis of color when location could not serve as a cue. On the other hand, there is evidence that paying attention to items of a particular color can amplify the figure-ground salience (8) and improve the discriminability (9) of those items, perhaps by guiding search processes to their locations (7). A key question that remains unanswered, however, is whether attending to items of a particular color can selectively enhance the signal strength of the neural representations of those items across an entire display, regardless of their location.

The present study investigated this question through noninvasive scalp recordings of the steady-state visual evoked potential (SSVEP), which allowed measurement of the relative signal strengths of items of attended and unattended colors interspersed at random in a visual display. The SSVEP is the oscillatory response of the visual cortex to a flickering stimulus, which has the same fundamental frequency as the driving stimulus. Importantly, the amplitude of the SSVEP may be substantially increased with attention (10–12). In the present design, the SSVEP provided frequency-coded neural signals elicited by separate red and blue dot populations that were flickering at different temporal rates while they moved at random within the same zone of visual space. Paying attention to the items of one color was found to substantially increase the signal strength of those items in early visual cortical areas, thereby providing an empirical basis for guided search and related models of visual search.

Results

In the main experiment, subjects were marginally better at detecting the blue targets flickering at 11.67 Hz (mean $d' = 2.89$) as opposed to the red targets flickering at 7.0 Hz [mean $d' = 1.95$, $F(1, 9) = 5.06$, $P < 0.06$], with no significant differences between the colors in reaction times (blue: mean = 659 ± 24 ms; red: mean = 702 ± 26 ms).

The SSVEPs elicited by the moving flickering dots were generally sinusoidal, with fundamental frequencies at the driving flicker rates (Fig. 1*b*). As in our previous studies (11, 13), overall SSVEP amplitudes were considerably smaller in response to the higher frequency (blue) flickering dots [frequency: $F(1, 9) = 16.00$, $P < 0.005$], although the color difference may also have contributed to this effect. Importantly, for both the red and blue dots, SSVEP amplitudes across 16 posterior electrodes were significantly enlarged when attention was directed to the respec

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Abbreviation: SSVEP, steady-state visual evoked potential.

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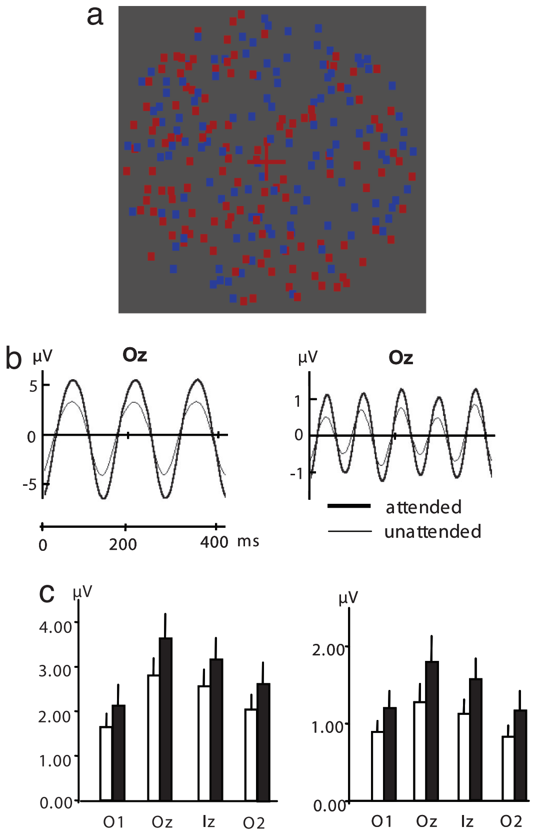

Fig. 1. Feature-based attentional modulation of the SSVEP. (*a*) Example of the stimulus display (not to scale). Stimuli were 125 each of isoluminant red and blue dots that were spatially intermingled and in continuous motion throughout each trial. Red dots flickered at 7.0 Hz and blue dots at 11.67 Hz. The color of the central fixation cross indicated the color to be attended. (*b*) Typical SSVEPs of one subject at electrode Oz elicited by attended (bold line) and unattended (thin line) red (*Left*) and blue (*Right*) flickering dots. (*c*) Mean and SE of SSVEP amplitudes across all subjects for attended (filled bars) versus unattended (open bars) red (*Left*) and blue (*Right*) dots at occipital recording sites.

tive color [condition: $F(1, 9) = 32.68$, $P < 0.0005$]. The greatest amplitudes were found at electrode sites O1, O2, Oz, and Iz (Fig. 1*c*) [condition × electrode: $F(15, 135) = 2.90$, $P < 0.05$].

For both colors, the SSVEP amplitude increase with attention had a tightly focused voltage maximum over the central occipital scalp (Fig. 2*a*). The statistical parametric mapping of the cortical current density giving rise to the SSVEP amplitude increase was localized to the posterior, medial occipital cortex, a region that includes visual areas V1, V2, and V3 (Fig. 2*b*). The Talairach coordinates of the maximum modulations with attention were as follows: for blue dots, single maximum at $x = -1$, $y = -95$, $z = -2$, and for red dots, two maxima at $x = 14$, $y = -102$, $z = -7$ and $x = -8$, $y = -99$, $z = -2$.

The behavioral control experiment provided evidence that flicker rate was not used as a feature to selectively attend to the red or blue dots. No significant differences in reaction times for target detections were found when red and blue dots were presented with identical (mean = 604 ± 9 ms) or different [mean = 597 ± 8 ms, $F(1, 11) = 3.26$, $P = 0.1$] frequencies. The same was true with respect to d' and hit rates. No significant differences were found between the conditions when the dots had identical (mean $d' = 2.37 \pm 0.11$; hit rate = 82.1 ± 2.4%) or different (mean $d' = 2.25 \pm 0.16$; hit rate = 82.8 ± 2.3%) frequencies [for d', $F(1, 11) = 1.98$, $P > 0.1$; for hit rate, $F(1, 11) = 0.001$, $P > 0.9$]. Most critically, the rate of false alarm intrusions from coherent-motion targets of the unattended color was not diminished when the red and blue dots flickered at different frequencies versus identical frequencies [$F(1, 11) = 3.94$, $P > 0.05$]. In fact, a trend in the opposite direction was found (false alarm rates: for different frequencies = 18.3 ± 2.4%; for the same frequency = 14.9 ± 2.0%).

Discussion

The present results provide direct electrophysiological evidence that paying attention to items of a specific color that are spatially intermingled with items of a different color enhances the signal strength of the attended-color items at early levels of the visual cortex. The experimental design made it impossible for subjects to use location as the primary cue for selection, because dots of both colors were rapidly and continuously shifting their positions at random. In addition, a behavioral control experiment showed that the differing flicker frequencies of the two dot populations did not provide an effective cue for selection. If the difference in frequency had improved the selectivity of processing of the two dot populations, it would be expected that the hit rate would be higher and/or the false alarm rate would be lower in relation to when the frequency cue was removed. Because neither effect was observed, we conclude that the relatively enhanced SSVEP amplitudes to items of the attended color reflect a selection based on color that is applied across the visual display. This feature selection could form the basis for the rapid identification of attended feature conjunctions that include color, as proposed by guided search models (3–6).

The neural mechanisms underlying color-selective attention have been investigated previously by using a variety of techniques. Neurophysiological experiments in monkeys have identified a visual-cortical region (area V4) specialized for processing color information (14), and the human homologue of this area (labeled V4 or V8) has been localized in ventral occipital cortex by using hemodynamic neuroimaging techniques (15). Neuroimaging studies have further shown that neural activity in V4/V8 increases when attention is directed to the color of a multifeature object (16, 17). Recordings of event-related potentials and magnetic fields have similarly found that neural responses are enhanced to stimuli of an attended color when presented as a component of a multifeature object (18–20) or in a randomized sequence (21, 22). None of these studies, however, was designed to test whether paying attention to items of a particular color can enhance the neural signals elicited by those stimuli under conditions where items of different colors are randomly intermingled in a dense array as is typical in visual search experiments.

The present results are consistent with psychophysical studies showing that paying attention to a particular color in a multicolored display can amplify its salience with respect to background (8). Our findings are also in line with the feature similarity gain model proposed on the basis of single-cell recordings in monkeys (23, 24). These studies found that attending to the feature of motion-direction in one visual field enhanced the responses of neurons selective to that feature in the opposite visual field. It was proposed that attention can selectively increase the gain of feature selective neurons responding to stimuli throughout the visual field. Using a similar approach, Saenz *et al.* (25) employed fMRI to demonstrate selective processing of color cues in a distributed visual display in humans. They found that paying attention selectively to either red or green dots that were randomly intermixed in a display presented to one visual field resulted in increased neural activity in early visual cortical areas activated by a dot display in the opposite visual field when those dots shared the attended color. The mechanism of this global feature enhancement remains uncertain, however, because of limitations of the fMRI methodology. First, it is not clear whether the increased fMRI signals actually represent enhanced neural signals elicited by stimuli of the

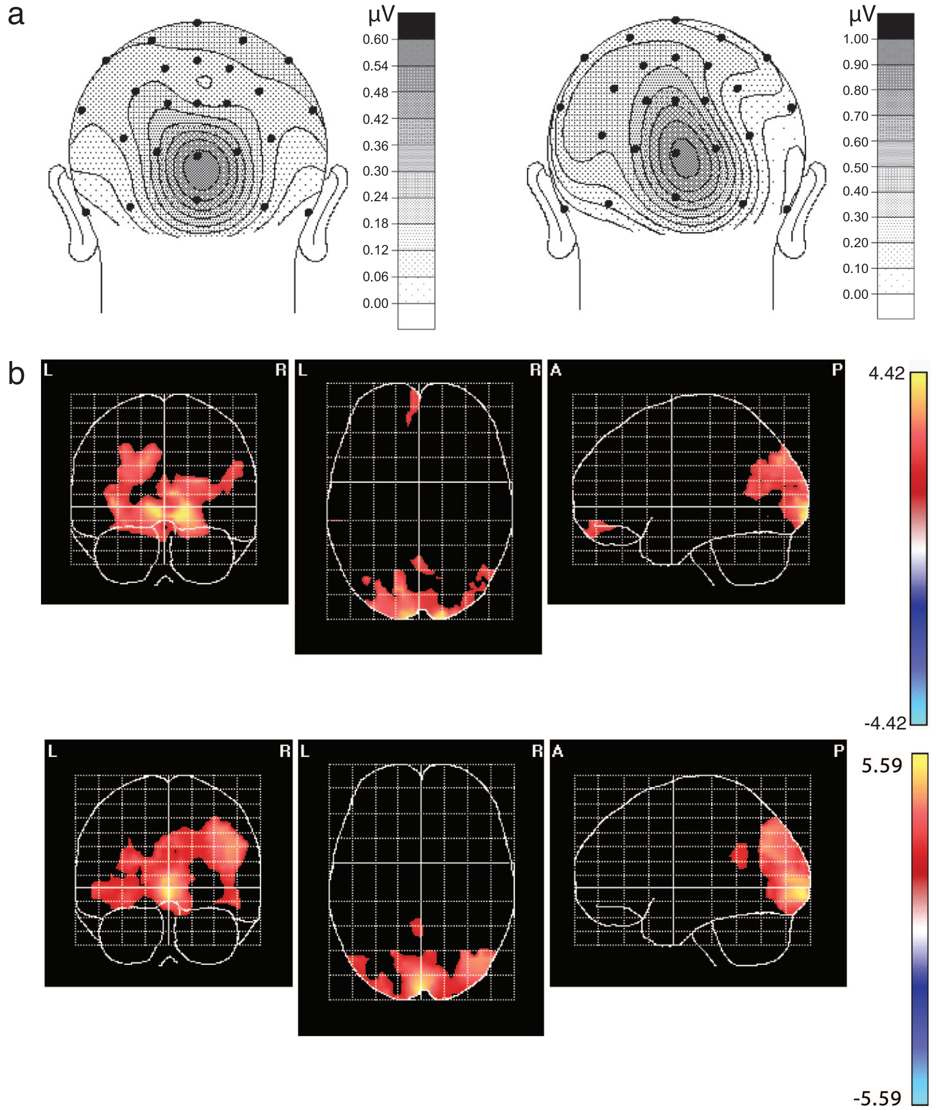

Fig. 2. Topographical distribution and cortical sources of attention-related enhancement of SSVEP amplitude. (*a*) Spline-interpolated isocontour maps of the grand average attended minus unattended amplitudes for red (*Left*) and blue (*Right*) dots. (*b*) Statistical parametric map of the cortical current density distribution giving rise to the SSVEP amplitude increase for attended versus unattended red (*Upper*) and blue (*Lower*) dots. Scale represents *t*-values, and the $P < 0.01$ threshold for the attended versus unattended comparison corresponds to 1.97 for red and 2.32 for blue dots. Thresholds were corrected to account for multiple comparisons.

attended color as opposed to top-down attentional control or bias influences on ongoing neural activity. Second, with fMRI it was not possible to record the separate neural signals elicited by the intermingled dots of the attended and unattended colors in the display, as could be done by using the SSVEP in the present study. The present results thus provide direct support for the hypothesis that paying attention to the color of a distributed set of items results in an increased gain of the sensory signals encoding those items at early stages of processing in the visual cortex. Because the SSVEP is averaged over time and trials, however, it is not clear whether all of the attended items are facilitated in parallel or whether some more circumscribed allocation of attention takes place.

The cortical generators of the color-selective increase in SSVEP amplitude were localized by a Bayesian modeling technique to the posterior medial occipital lobe, in the region of the calcarine fissure. This region includes visual areas V1, V2, and V3, but the inverse source modeling of event-related potentials, as carried out here, generally lacks the anatomical precision to distinguish among sources in adjacent visual areas unless additional constraints are added (26). Using fMRI, Saenz *et al.* (25) showed an increased color-selective hemodynamic response in areas V1, V2, and V3 (as well as in higher areas such as V4 and MT). The present results are in accord with color-based selection at these early levels, but further studies are needed to pinpoint the precise visual area(s) at which stimuli of the attended color are initially selected. Further work is also needed, perhaps by using methodology like that of the present study, to determine whether simple features other than color can similarly be selected from a distributed set of items within a visual display.

Previous SSVEP studies have generally found that an attended flickering stimulus elicits a larger steady-state response than the same stimulus when unattended across a wide range of flicker frequencies and task conditions (10, 11, 13, 20, 27–30). Such effects have been interpreted as evidence for an enhancement of the signal strength of the attended visual input (10, 13). An opposite effect, with a smaller SSVEP amplitude to a stimulus when attended, has been reported in two studies (20, 31) under certain conditions. Chen *et al.* (20) reported that focusing attention narrowly on the central portion of a flickering stimulus reduced the amplitude of the SSVEP it elicited, perhaps because of a suppressive effect on the larger unattended region of the stimulus. Ding *et al.* (31) found that shifting attention from a foveal to a more peripheral ring of flickering stimuli resulted in decreased amplitude of the SSVEP elicited by the peripheral ring, but only for a narrow frequency band in the low-alpha range (9.2 Hz). This SSVEP amplitude decrease was accompanied by a decrease in non-phase-locked EEG power in the same frequency range, suggesting an interaction of cortical resonance in the low-alpha band with the specific task conditions that involved increased discrimination difficulty. In the present study, where the spatial extent of attention did not differ between conditions and flicker frequencies were outside the low-alpha range, we interpret the increased SSVEP amplitude to flickering dots of the attended color as reflecting an increase in the strength of their sensory representations in the visual cortex.

According to the guided search class of models, paying attention to items sharing a particular feature such as color results in the parallel activation of those items in a feature activation map (5). During conjunction search, there would be separate and parallel activations for each of the features defining the target, with the greatest activation occurring at the location of the target itself. A closely related model achieves the same end by proposing that attention suppresses items having the nontarget distracter features (6). Because these parallel operations of activation (or suppression) can take place rapidly across the entire visual field, the location of the target (if present) can be quickly highlighted regardless of the number of distracters in the field. In the present experiment, the selective modulation of SSVEP amplitudes could be interpreted either as reflecting a relative facilitation of the attended-color information regardless of spatial position (23–25) or as a consequence of the selective allocation of attention to the locations designated by the attended color (8, 9, 32). In either case, however, the greater amplitude of neural activity elicited by the attended-color items demonstrates the operation of a feature-based selection mechanism that can be applied across a visual field cluttered with intermingled attended items and distracters. This demonstration provides critical support for the fundamental mechanism proposed to underlie guided visual search and suggests that this feature selection (at least for color) takes place in early visual cortical areas.

Methods

Subjects. Eleven subjects (5 female, age range 20–30 years) with normal color vision and normal or corrected to normal visual acuity participated in the main experiment. Twelve different subjects (10 female, age range 18–25 years), also with normal color vision and acuity participated in the behavioral control experiment. All subjects gave informed consent, and the study was approved by the local ethics committee.

Stimuli. The stimulus array was presented on a video monitor and consisted of 250 equiluminant red and blue dots (125 of each) superimposed on a gray circular background with a radius of 5° of visual angle (Fig. 1*a*). Each dot subtended 0.23° of visual angle. Equiluminance of dots and gray background was adjusted for each subject by means of heterochromatic flicker photometry; the background luminance was fixed at 7.2 cd/m^2. The red dots were flickered continuously at 7.00 Hz and the blue dots at 11.67 Hz throughout each trial, which lasted for 4,114 ms. All dots were continuously in motion throughout the trial. Each dot changed its position in a random direction by 0.08° every one to three frames of screen refresh (i.e., every 14.3–42.9 ms, also randomized). As a result, each dot appeared to undergo a jerky, random walk across the screen, and the net effect was an impression of continual Brownian motion throughout the field. On a random 32% of the trials, 75% of either the red or the blue dots were given coherent motion for a period of 586 ms. This coherent movement could take place in one of four directions (up, down, left, or right) at random and could occur once or twice on a given trial, with a minimum separation of 1,100 ms.

Procedure. Subjects were given the task of attending selectively to either the red or the blue flickering dot population on each trial and detecting the coherent motion events of the attended color (targets) while ignoring coherent motion of the unattended color (distracters). The color to be attended was cued on a random basis for each trial by the color of the central fixation cross, which appeared 500 ms before the onset of flicker and lasted throughout the trial. Subjects were required to maintain their gaze on the fixation cross during each trial. Detections of coherent motion targets were signaled by pressing a single button, and only responses occurring between 200 ms and 1,100 ms after target onset were considered correct. For each condition (attend red dots/attend blue dots) 225 trials were administered, distributed over nine blocks of 50 trials each.

SSVEP Recording. Brain electrical activity was recorded from 30 scalp electrodes mounted in an elastic cap (F3, F7, C3, CP1,CP5, P1, P3, PO3, PO7, PO9, O1, F4, F8, C4, CP2, CP6, P2, P4, PO4, PO8, PO10, O2, FZ, CZ, PZ, POZ, OZ, IZ, and the right mastoid of the extended international 10-20 system) all referenced to the left mastoid. Vertical eye movements and blinks were monitored with a bipolar montage positioned above and below the left eye (vertical electrooculogram). Lateral eye movements were monitored with a bipolar outer canthus montage (horizontal electrooculogram). Electrode impedances were kept below 5 kΩ. The EEG was recorded with a sample rate of 250 Hz and a bandpass of 0.05–100 Hz and stored on disk for off-line analysis.

The SSVEP analyses were carried out only for trials without coherent motion (i.e., no targets or distracters) to ensure that selective attention was based on color only, with no interference from the coherent motion. From these trials, epochs of 4,100 ms starting with flicker onset were extracted. Epochs containing blinks or other artifacts exceeding 100 μV were rejected from further analysis. Based on this criterion, one subject had to be excluded because of excessive artifacts, which contaminated 56% of the trials. For the remaining subjects, the mean rejection rate of trials was 30.8%.

Artifact-free EEG epochs were averaged and algebraically re-referenced to averaged mastoids by subtracting one-half of the averaged signal recorded from the right mastoid from the averaged signals at each scalp site. SSVEP amplitudes at the two stimulus frequencies were extracted from the EEG signal by means of complex demodulation at 7.00 and 11.67 Hz, respectively (33, 34). The amplitudes calculated by complex demodulation correspond to the peak-to-baseline amplitudes of the SSVEP. To exclude the visual evoked response to flicker onset, the first 500 ms of the waveforms of each trial were excluded from the analysis. Mean SSVEP amplitudes were subsequently calculated from the complex demodulated waveforms between 750 and 3,750 ms after stimulus onset for each condition and electrode. The attention effect on SSVEP amplitude was analyzed statistically by a repeated-measures ANOVA comprising the factors of stimulation frequency (7 versus 11.67 Hz), condition (attended versus unattended), and electrode location (posterior electrodes: P1/2, P3/4, PO3/4, PO7/8, PO9/10, O1/2, Pz, POz, Oz, and Iz).

Behavioral Data. Target detection (hit) rates, false alarms, and reaction times were analyzed with repeated-measures ANOVAs comprising the factor of attended color (red versus blue). A hit was defined as a response occurring within a window of 200–

1,100 ms after onset of a coherent motion of the attended color (target), and a false alarm was considered as a response occurring 200–1,100 ms after the onset of a coherent motion of the unattended color (distracter). Because subjects only responded to targets of the attended color, the present design did not provide comparative behavioral evidence for more effective processing of the attended items. Such evidence was provided by the SSVEP recordings.

Source Analysis of SSVEP Generators. To gain information about the cortical regions that mediate feature-based attention, a source analysis was carried out based on attention-related changes in the complex coefficients derived from the complex demodulation of the SSVEP waveform at each electrode (see ref. 34 for details). An image of the underlying brain electrical activity (primary current density) for each individual scalp topography was estimated by Bayesian model averaging of different EEG inverse solutions (see ref. 35 for details), each one based on anatomical constraints derived from the Montreal average-brain atlas (36). A model-independent final image of the underlying brain electrical activity in each case was then obtained by averaging all computed primary current densities weighted by the corresponding support that they received from the data. This weighting coefficient is measured in terms of the posterior probability of the corresponding model (anatomical constraint), given the data. A set of difference images was constructed by a voxel-by-voxel subtraction of the magnitudes of the solutions of the attended versus unattended conditions for each subject and each frequency. A statistical parametric map of the difference images was obtained by means of Student's t test.

Behavioral Control Experiment. A control experiment was carried out with 12 subjects to evaluate the possibility that subjects might select between the two dot populations on the basis of their differing flicker frequencies rather than their respective colors. This experiment obtained behavioral target detection data under conditions when the red and blue dot populations had differing flicker frequencies, as in the main experiment, and when they had identical flicker frequencies. The experimental design, stimulus display, and task were the same as in the main experiment, but now target durations were shortened to 429 ms, thereby allowing up to three targets per trial. In addition, the number of trials with coherent motion of the attended or ignored color was increased to about two-thirds of all trials to obtain more target detection data.

On successive trials, the red and blue dots had either identical (both with 7.00 or 11.67 Hz) or different frequencies (red with 7.00 Hz and blue with 11.67 Hz, or the reverse). These trial types were given in random order. For all frequency combinations, subjects were cued to either attend to the red or blue dots, and respond to the coherent movement events (targets) in that color while ignoring the other color. This resulted in eight experimental conditions [same versus different frequency × attended frequency (7.00 versus 11.67 Hz) × attended color (red versus blue)]. For each condition, 75 trails were conducted. Hits and false alarms were defined as in the main experiment.

Target detection accuracy was quantified in terms of hit rates, false alarm rates, and d' scores. Statistical analyses of target detection parameters and reaction times were carried out with repeated-measures ANOVAs comprising the factors of frequency combination (identical versus different frequency), attended frequency (7 versus 11.67 Hz), and attended color (red versus blue). Hit and false alarm rates were normalized by inverse Gaussian transform before testing. For all analyses, the Huynh–Feldt adjustment for nonsphericity was applied whenever appropriate.

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