

Effects of Feature-selective and Spatial Attention at Different Stages of Visual Processing

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Abstract

■ We investigated mechanisms of concurrent attentional selection of location and color using electrophysiological measures in human subjects. Two completely overlapping random dot kinematograms (RDKs) of two different colors were presented on either side of a central fixation cross. On each trial, participants attended one of these four RDKs, defined by its specific combination of color and location, in order to detect coherent motion targets. Sustained attentional selection while monitoring for targets was measured by means of steady-state visual evoked potentials (SSVEPs) elicited by the frequency-tagged RDKs. Attentional selection of transient targets and distractors was assessed by

behavioral responses and by recording event-related potentials to these stimuli. Spatial attention and attention to color had independent and largely additive effects on the amplitudes of SSVEPs elicited in early visual areas. In contrast, behavioral false alarms and feature-selective modulation of P3 amplitudes to targets and distractors were limited to the attended location. These results suggest that feature-selective attention produces an early, global facilitation of stimuli having the attended feature throughout the visual field, whereas the discrimination of target events takes place at a later stage of processing that is only applied to stimuli at the attended position. ■

INTRODUCTION

Research on visual selective attention has mainly focused on three levels of selection: space, objects, and features. Models of spatial attention stress the importance of stimulus location as the main property for stimulus selection and feature binding (Treisman, 1988; Eriksen & Yeh, 1985; LaBerge, 1983; Posner, 1980; Treisman & Gelade, 1980), whereas object-based models propose selection on the basis of whole objects irrespective of spatial information (Schoenfeld et al., 2003; O'Craven, Downing, & Kanwisher, 1999; Duncan, 1984). Selection based on features as observed in single-cell recordings in monkeys is well accounted for by the feature similarity gain model (Maunsell & Treue, 2006; Treue & Martinez-Trujillo, 1999), which proposes that attention increases the gain of visual neurons that are sensitive to the behaviorally relevant target feature. Importantly, feature similarity not only is defined in terms of nonspatial features such as color but also includes spatial location (i.e., selection of location produces an analogous gain increase as does attention to nonspatial features of an object). In this model, attentional effects along different feature dimensions are combined in an additive manner. Relevant dimensions include direction of motion, spatial location, color, and orientation. Importantly, attending to a particular feature facilitates processing of that feature throughout the visual field.

This global effect of feature-based attention has been demonstrated in single-cell recordings of monkeys (Hayden & Gallant, 2005; McAdams & Maunsell, 2000; Treue & Martinez-Trujillo, 1999), in human fMRI (Liu, Stevens, & Carrasco, 2007; Serences & Boynton, 2007; Saenz, Buracas, & Boynton, 2002), and in recordings of human ERPs (Zhang & Luck, 2009; Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004).

Only rarely, however, have the underlying neuronal mechanisms been investigated when spatial and feature-selective attention were combined. For example, the studies by Zhang and Luck (2009) and Saenz et al. (2002) employed asymmetric displays, in which overlapping stimuli were only presented on the attended side and the magnitude of feature-selective attention was only measured on the unattended side. Although these studies clearly demonstrated the existence of a global effect of feature selection, they fail to show how feature-selective and spatial attention is combined. Some indirect evidence for an additive combination of spatial and nonspatial attention was obtained in monkeys (Treue & Martinez-Trujillo, 1999), but this study lacked a condition in which the location of the stimulus was attended but its direction of motion was not. One imaging study reported higher modulation in human MT when attention was directed toward both location and motion of a stimulus as compared to when only location of the stimulus was attended (Beauchamp, Cox, & DeYoe, 1997). However, that study did not examine whether attentional effects of location and motion were additive in nature

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and, in addition, did not employ a full factorial design of feature and space, that is, there was no condition in which direction of motion but not location of the stimulus was attended.

Here we employed a full factorial design to examine how spatial and feature-selective attention are combined. Additive facilitation of location and color—as predicted by the feature similarity gain model—would result in main effects of spatial and feature-selective attention but no interaction between the two. As depicted in Figure 1A, two completely overlapping square-shaped random dot kinematograms (RDKs) of different colors were presented on both the left and the right side of a central fixation cross. Participants attended to each of these four RDKs in randomized order on different trials. They were instructed to press a button upon detection of short periods of coherent motion (targets) in the attended RDK. The allocation of attention to all four RDKs was measured by recording steady-state visual evoked potentials (SSVEPs). The SSVEP is a continuous oscillatory response, which has the same temporal frequency as the driving stimulus. Its amplitude is substantially increased both by spatial (e.g., Müller, Malinowski, Gruber, & Hillyard, 2003; Müller & Hillyard, 2000; Morgan, Hansen, & Hillyard, 1996) and by feature-selective attention (Andersen, Müller, & Hillyard, 2009; Andersen, Hillyard, & Müller, 2008; Müller et al., 2006). When multiple stimuli that flicker at different frequencies are presented within the same display, the allocation of attention to each of them can be assessed by recording their respective frequency-tagged SSVEP. In the present design, the SSVEP provided an objective electrophysiological measure of sensory amplification for each combination of color and location: (1) attended color and attended side (c+s+); (2) attended color and unattended side (c+s-); (3) unattended color and attended side (c-s+); and (4) unattended color and unattended side (c-s-). An additional analysis of ERPs evoked by coherent motion targets and distractors was performed in order to assess the allocation of attention to these transient events and, thereby, reconcile the differences observed in the analysis of SSVEP amplitudes and behavioral data. This analysis focused on the amplitude of the P3, which is a late-occurring ERP component that is sensitive to attentional resource allocation (see Polich, 2007, for a recent review). The P3 is a robust component with a broad temporal distribution and can therefore easily be extracted from the concurrently recorded SSVEPs (e.g., Müller & Hillyard, 2000).

METHODS

Participants

Twenty-one subjects (9 women, 4 left-handed, age range = 19–32 years, average = 24.3 years), with normal color vision and normal or corrected-to-normal visual acuity, participated in the experiment. Informed consent was obtained

from all subjects prior to electrode application. Two participants were subsequently excluded from the sample, one because of excessive artifacts in the EEG and the other due to poor task performance (100% false alarms in one condition).

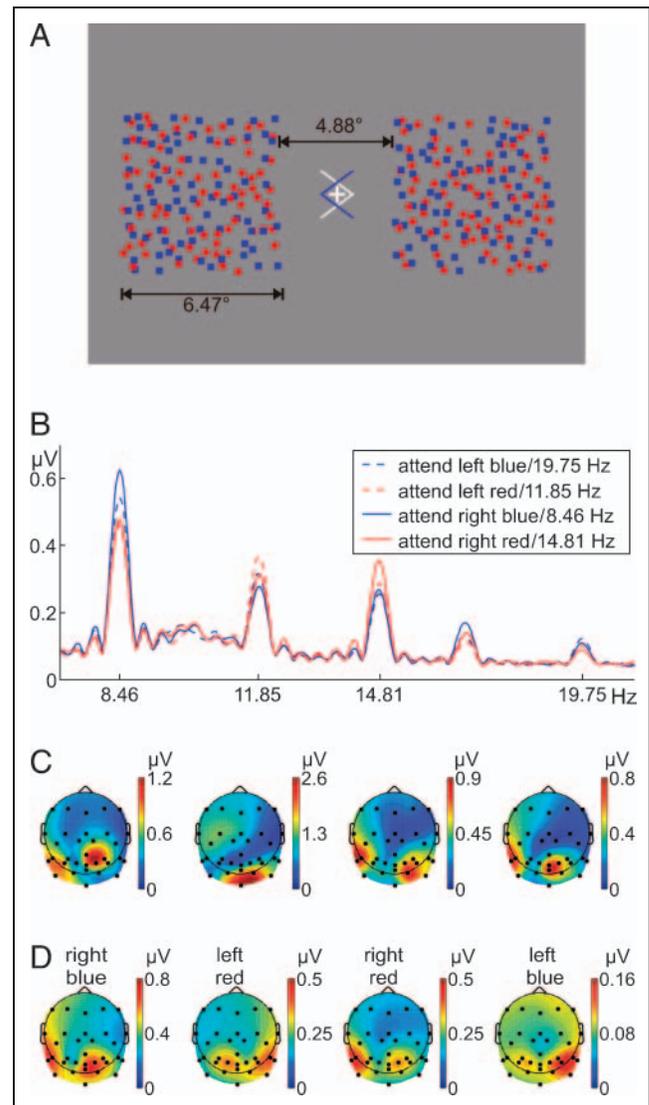


Figure 1. (A) Stimulus display. Black arrows and numbers indicate sizes in degrees of visual angle and were not present in the experiment. (B) Grand-average spectrum obtained by Fourier analysis of SSVEP waveforms for all four attention conditions averaged across a broad cluster of 11 occipital, parietal, and temporal electrodes. Peaks are located at the four stimulation frequencies and the first harmonic of 8.46 Hz. (C) Spline-interpolated voltage maps from four individual subjects of SSVEP amplitudes evoked by the right blue stimulus (8.46 Hz) averaged over the four experimental conditions. The two subjects to the right display a topographical distribution very similar to the grand average for that stimulus (displayed leftmost in D), whereas the two subjects to the left display more dissimilar distributions. (D) Spline-interpolated voltage maps of SSVEP amplitudes for each RDK (i.e., stimulation frequency) averaged across all subjects and the four experimental conditions.

Stimulus Material and Procedure

Stimulation was presented on a 19-in. computer monitor set to a resolution of 640×480 pixels, 8 bits per pixel color mode, and a refresh rate of 59.25 Hz. Each of the four RDKs flickered at an individual frequency synchronized to the screen's refresh rate: *blue dots left* = 19.75 Hz; *blue dots right* = 8.46 Hz; *red dots left* = 11.85 Hz; *red dots right* = 14.81 Hz. Prior to EEG recordings, equiluminance of dots and gray background was adjusted for each subject by means of heterochromatic flicker photometry (e.g., Wagner & Boynton, 1972; Kaiser, Herzberg, & Boynton, 1971). The to-be-adjusted color (i.e., red or blue) was flickered at a rate of 15 Hz against the gray background, which had a fixed luminance of 5.8 cd/m^2 . Participants individually adjusted the luminance of the red or blue color until the perceived flicker became minimal (i.e., the point of subjective isoluminance).

Each RDK consisted of 80 randomly and independently moving dots. At a viewing distance of 80 cm, each RDK formed a square with edges having a visual angle of 6.47° . The squares' inner edges were situated 2.44° from fixation, centered at the horizontal meridian (see Figure 1A). Each dot subtended 0.28° and changed its position in a random direction by 0.041° per frame of screen refresh. To prevent systematic overlapping of dots of different colors, which might induce a depth cue, all dots were drawn in random order.

Each trial started with the onset of a white fixation cross and a symmetric double arrow cue. One of two arrows was always white, whereas the other was either blue or red, thereby indicating which side (left/right) and which color (red/blue) had to be attended. For example, a blue arrow pointing to the left indicated the subject to attend to the blue dots in the left visual hemifield (example in Figure 1). Side and color were cued on a random basis for each trial. All four RDKs appeared after a random interval of 300 to 600 msec following cue onset and were presented for 3050 msec, followed by an inter-trial interval of 1450 msec, during which only the gray background was presented.

All dots moved in random directions (0% coherence) except for brief intervals (500 msec) of 75% coherent motion in either upward or outward direction. These intervals of coherent motion could occur randomly in either the attended RDK (targets) or in one of the three unattended RDKs (distractors). A total of up to three such targets or distractors could appear during a single trial, and their onsets were separated by at least 900 msec. The earliest onset of targets or distractors was 400 msec after RDK onset. Participants were instructed to press a button whenever they detected a target while ignoring distractors. Responding hand was changed half way through each recording session, and the sequence of hand usage was counterbalanced across participants. Responses occurring within an interval from 350 to 1200 msec after onset of a target or distractor were counted as hits or false alarms, respectively. False

alarm rates were averaged over the four stimuli and subjected to a repeated measures ANOVA with the factor of *distractor type*: $c+s-$, $c-s+$, and $c-s-$.

The whole experiment consisted of 600 trials distributed over 10 blocks of 60 trials each. Targets or distractors occurred on a random one-third of all trials resulting in a total of 25 targets and 75 distractors (25 in each RDK) in each of the four attentional conditions. Prior to recordings, subjects performed a training session of two or more blocks until stable performance was reached.

SSVEP Recordings and Analysis

During EEG recordings, participants were seated in a comfortable chair in a dimly lit electrically shielded chamber. A chin rest was used to avoid head movements. Brain electrical activity was recorded at a sampling rate of 512 Hz from 32 Ag/AgCl electrodes mounted in an elastic cap using a BioSemi ActiveTwo amplifier system (BioSemi, Amsterdam, The Netherlands). Except for the built-in anti-aliasing filter of the amplifier, no additional filtering of the signal was performed in any of the subsequent analyses. Electrodes were placed at positions F3, F7, Fz, F4, F8, C3, Cz, C4, CT5, CT6, T3, T5, T4, T6, TP9, TP10, TO1, TO2, CP1, CP2, P3, Pz, P4, PO1, POz, PO2, O1, O2, INz, IN3, IPz, and IN4 of the extended International 10–20 System. During recordings, all scalp channels were referenced to an electrode placed next to position Cz. Lateral eye movements were monitored with a bipolar outer canthus montage (horizontal electrooculogram). Vertical eye movements and blinks were monitored with a bipolar montage positioned below and above the right eye (vertical electrooculogram).

Processing of EEG data was performed using the EEGlab toolbox (Delorme & Makeig, 2004) in combination with custom written procedures in MATLAB (The Mathworks, Natick, MA). Analysis epochs began 600 msec before stimulus onset and extended for 3900 msec thereafter. This time range included the onset of the cue, and thus, allowed to control for eye movements after cue presentation but prior to stimulation onset. Only trials without targets or distractors were included in the SSVEP analysis to ensure that attentional selection was based solely on color and location with no influence of coherent motion. Trials with lateral eye movements exceeding $12 \mu\text{V}$, which according to calibration recordings in our lab correspond to roughly 0.5° of visual angle, were rejected. Furthermore, all trials with blinks or other artifacts occurring during stimulation were manually rejected, leading to a total rejection rate of 20.1% across trials and 19 participants. After subsequent algebraic transformation of the data to average reference, all epochs within the same attentional condition were averaged for each participant.

The SSVEP amplitude at each electrode was calculated by Fourier transformation of a time window from 500 to 2900 msec after stimulus onset. This time window was

chosen in order to exclude the visual evoked response to stimulus onset. Prior to Fourier transformation, data in this time window were detrended (removal of mean and linear trends) in order to correct for any linear drifts. SSVEP amplitudes were quantified as the absolute value of the complex Fourier coefficients at the four stimulation frequencies (see Figure 1B). SSVEP amplitudes showed considerable individual variations of their topographical distributions (see Figure 1C for four examples from different participants at 8.46 Hz). Therefore, appropriate electrodes for further analysis were chosen as follows: the topographical distribution of SSVEP amplitudes averaged across the four attentional conditions was examined for the four stimulation frequencies, respectively (see Figure 1D). This resulted in the selection of 11 electrodes (TO1, TO2, P3, P4, PO1, POz, PO2, O1, O2, INz, IPz). For each frequency and each individual participant, the electrode with the greatest overall SSVEP amplitude from this array of 11 electrodes was chosen for statistical analysis.

Statistical Analysis of SSVEP Amplitudes

The data processing steps described above yielded SSVEP amplitude values for each stimulation frequency (i.e., for each RDK), for each of the four attentional conditions. As an example, SSVEP amplitude in response to the left blue dots flickering at 19.75 Hz was obtained for the conditions when subjects attended the (1) left blue dots (c+s+), (2) right blue dots (c+s-), (3) left red dots (c-s+), and (4) right red dots (c-s-), respectively. The individual electrode out of the array of 11 posterior electrodes (see above) with the greatest overall SSVEP amplitude averaged across these four conditions was chosen for statistical analysis for each participant.

Figure 2A shows SSVEP amplitudes elicited by the four RDKs for the four experimental conditions, respectively. As depicted, the resulting pattern of SSVEP amplitudes as a function of experimental condition was similar for all four RDKs. Based on this similarity, we considered it appropriate to average SSVEP amplitudes across stimulation frequencies for each experimental condition. Given that SSVEP amplitudes decrease at higher stimulation frequencies (Andersen et al., 2008; Müller et al., 2003, 2006) and depicted in Figure 2A, it was essential to normalize amplitudes prior to averaging to avoid lower frequencies being weighted more heavily.

Normalized amplitudes N_{ijk} were calculated by dividing amplitudes A_{ijk} by the mean amplitude across attentional conditions (k : c+s+, c+s-, c-s+, and c-s-) for each participant ($i = 1 \dots 19$) and each frequency ($j = 1 \dots 4$) separately:

$$N_{ijk} = \frac{A_{ijk}}{\frac{1}{4}(A_{ij(c+s+)} + A_{ij(c+s-)} + A_{ij(c-s+)} + A_{ij(c-s-)})} \quad (1)$$

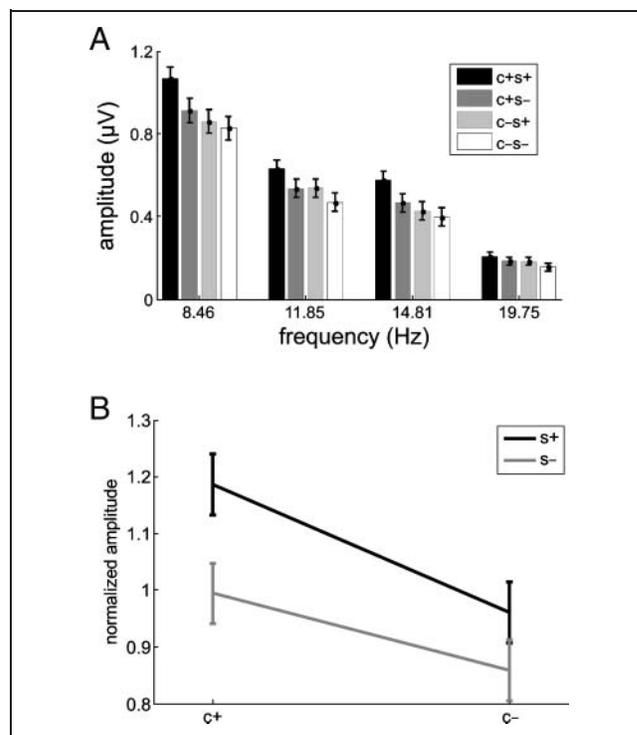


Figure 2. (A) Grand-average SSVEP amplitudes for each RDK and each experimental condition for the individual best electrode (see Methods). Amplitudes decrease at higher stimulation frequency, whereas the modulation pattern remains similar. 8.46 Hz = blue dots right; 11.85 Hz = red dots left; 14.81 Hz = red dots right; 19.75 Hz = blue dots left; (c+s+) = attended color and attended side; (c+s-) = attended color and unattended side; (c-s+) = unattended color and attended side; (c-s-) = unattended color and unattended side. (B) Interaction plot of the normalized grand-average amplitudes for the individual best electrode and experimental condition. Error bars in (A) and (B) correspond to 95% within-subjects confidence intervals of the mean.

Thus, a normalized amplitude >1 signifies a greater amplitude than the averaged amplitude across attentional conditions for that frequency, whereas a value <1 signifies a smaller amplitude than this average. After normalization, SSVEP amplitudes were averaged across the four frequencies for each experimental condition. These averaged amplitudes were subjected to a repeated measures ANOVA comprising the factors of *color-selective attention* (c+ vs. c-) and *spatial attention* (s+ vs. s-). Single contrasts were compared by means of paired t tests corrected for multiple comparisons by the Bonferroni–Dunn method.

Analysis of P3 Amplitudes

P3 amplitudes elicited by coherent motion targets and distractors were analyzed in order to allow for a comparison with SSVEP amplitudes elicited by sustained flicker. Epochs from 100 msec before to 800 msec after target or distractor onset were extracted from all eye movement free trials. ERPs to targets and distractors were analyzed only if their onsets preceded the offset of steady-state

stimulation by at least 800 msec. The mean amplitude of a window between 100 msec before to target onset served as baseline and was subtracted from each data point in the epoch. After algebraic transformation to average reference, trials with artifacts were manually rejected, and all epochs in the same attentional condition were averaged. P3b amplitudes at electrode Pz were averaged over a time window from 500 to 700 msec poststimulus onset and were statistically compared analogously to SSVEP amplitudes. P3a amplitudes at electrode Fz were averaged over a time window from 300 to 450 msec surrounding the peak and were, subsequently, analyzed analogously. Note that the onsets of coherent motion targets and distractors were not phase-locked to the flicker of the dots, resulting in an attenuation of both SSVEP amplitudes and early ERP components elicited by targets and distractors in this analysis.

RESULTS

SSVEP Amplitudes

Figure 1B depicts the grand-average SSVEP amplitude spectra from all four experimental conditions averaged across a broad cluster of 11 occipital, temporal, and parietal electrodes. Blue lines depict the spectrum when subjects attended to either the left or right blue RDK and red lines depict the spectrum when subjects attended to the left or right red RDK. As can be seen in this figure, attending to the right blue RDK (8.46 Hz) increases SSVEP amplitude elicited by the left blue RDK (19.75 Hz) as well and vice versa. Similarly, attending to the right red RDK (14.81 Hz) increases SSVEP amplitude elicited by the left red RDK (11.85 Hz) and vice versa. This clearly demonstrates the global effect of feature-selective attention. Amplitudes averaged across all experimental conditions were greatest at medial occipital and contralateral occipitotemporal electrodes as depicted in Figure 1D.

The grand-average SSVEP amplitudes prior to normalization and averaging across frequencies are depicted in Figure 2A. The statistical analysis of the normalized and averaged amplitudes revealed an overall enhancement of SSVEP amplitude to stimuli of the attended color [main effect of color-selective attention: $F(1, 18) = 57.842, p < 10^{-6}$] and to stimuli of the attended location [main effect of spatial attention: $F(1, 18) = 21.102, p < .0005$]. The interaction between these two factors approached but did not reach significance [$F(1, 18) = 3.596, p = .07$; Figure 2B]. The total model accounted for $\eta^2 = 59.1\%$ of the variance of the normalized and averaged SSVEP amplitudes. Although factors color-selective attention and spatial attention accounted for $\eta^2 = 34.3\%$ and for $\eta^2 = 22.7\%$ of the variance, respectively, the interaction of both factors accounted for $\eta^2 = 2.2\%$ only.

To further examine the pattern of SSVEP amplitude changes, three specific contrasts were carried out to test: (1) the global effect of color-selective attention (c+s- vs.

c-s-), (2) the global effect of spatial attention (c-s+ vs. c-s-), and (3) the effects of attention to color versus spatial attention (c-s+ vs. c+s-). SSVEP amplitudes to RDKs at the unattended side were greater when their color was attended [c+s- vs. c-s-: $t(18) = 4.13, p < .001$], that is, there was a global effect of color-selective attention. Analogously, there was a global effect of spatial attention, that is, attending to the location of an RDK also increased its SSVEP amplitude, even when its color was unattended [c-s+ vs. c-s-: $t(18) = 3.14, p < .01$]. Amplitudes did not differ between an RDK of the unattended color at the attended side and an RDK of the attended color at the unattended side [c-s+ vs. c+s-: $t(18) = 1.02, p > .1$]. This indicates that the effect of color-selective attention did not differ in magnitude from the effect of spatial attention.

P3 Amplitudes

The averaged ERPs time-locked to targets and distractors at electrode Pz are depicted in Figure 3A. P3b amplitudes were significantly enhanced when either the side [main effect of spatial attention: $F(1, 18) = 52.835, p < 10^{-6}$] or the color [main effect of color-selective attention: $F(1, 18) = 6.255, p < .05$] of the coherent motion was attended. Contrary to the observed pattern of SSVEP amplitudes, however, the interaction of these two factors was significant [Spatial attention \times Color-selective attention: $F(1, 18) = 6.560, p < .05$; see Figure 3B]. Specific contrasts revealed that there was no global effect of color-selective attention on P3b amplitudes; that is, color-selective attention had no influence on P3b amplitudes to distractors on the unattended side [c+s- vs. c-s-: $t(18) = 0.43, p > .1$]. All other contrasts, however, revealed significant differences [all $|t(18)| > 3.7, p < .005$].

P3a amplitudes recorded at electrode Fz showed a similar, but less pronounced, pattern [main effect of spatial attention: $F(1, 18) = 9.118, p < .01$; main effect of color-selective attention: $F(1, 18) = 5.658, p < .05$; interaction Spatial attention \times Color-selective attention: $F(1, 18) = 4.890, p < .05$].

Behavioral Data

False alarm rates differed depending on distractor type [$F(2, 18) = 135.497, p < 10^{-9}$; Table 1]. Two-tailed paired t tests, corrected for multiple comparisons by the Bonferroni-Dunn criterion, showed that distractors on the same side as the attended stimulus produced more false alarms than distractors at the unattended side [c-s+ vs. c+s-: $t(18) = 11.549, p < 10^{-9}$; c-s+ vs. c-s-: $t(18) = 11.798, p < 10^{-9}$]. False alarms to distractors on the unattended side were generally very low (about 1%; see Table 1), with no difference according to whether or not the respective color was attended on the opposite side [c+s- vs. c-s-: $t(18) = -0.015, p > .1$].

DISCUSSION

Amplitude modulations of the SSVEP showed that attending selectively to stimuli of a particular color facilitates the neural response elicited in visual cortex by all stimuli of that color, compared to stimuli of the unattended color, regardless of spatial location. In line with the predictions of the feature similarity gain model, the conjunction of color and location elicited the largest SSVEP response. The effect of attention to color was of about the same magnitude as the effect of attention to spatial location. In both cases, we observed the global effect predicted by the model. Specifically, attending to a particular color resulted in an increase of SSVEP amplitude for the matching RDK at the unattended location, whereas attending to one location resulted in an increase of SSVEP amplitude elicited by the to-be-ignored RDK at the same location, compared to the same-color RDK at the unattended location. Thus, with respect to the global effect of color-selective attention, the present results are in line with previous studies in human visual cortex (Hopf et al., 2004; Saenz et al., 2002). To our knowledge, the present study is the first to demonstrate these effects on stimulus processing using a full factorial design.

We found highly significant main effects of attended color and spatial location on SSVEP amplitudes, but the interaction between these factors only tended toward significance. A previous study (Hayden & Gallant, 2005) reported a small, but significant, interaction between spatial and feature-selective attention in almost half of the recorded V4 cells in macaques. This suggests that any possible deviation from a purely additive combination

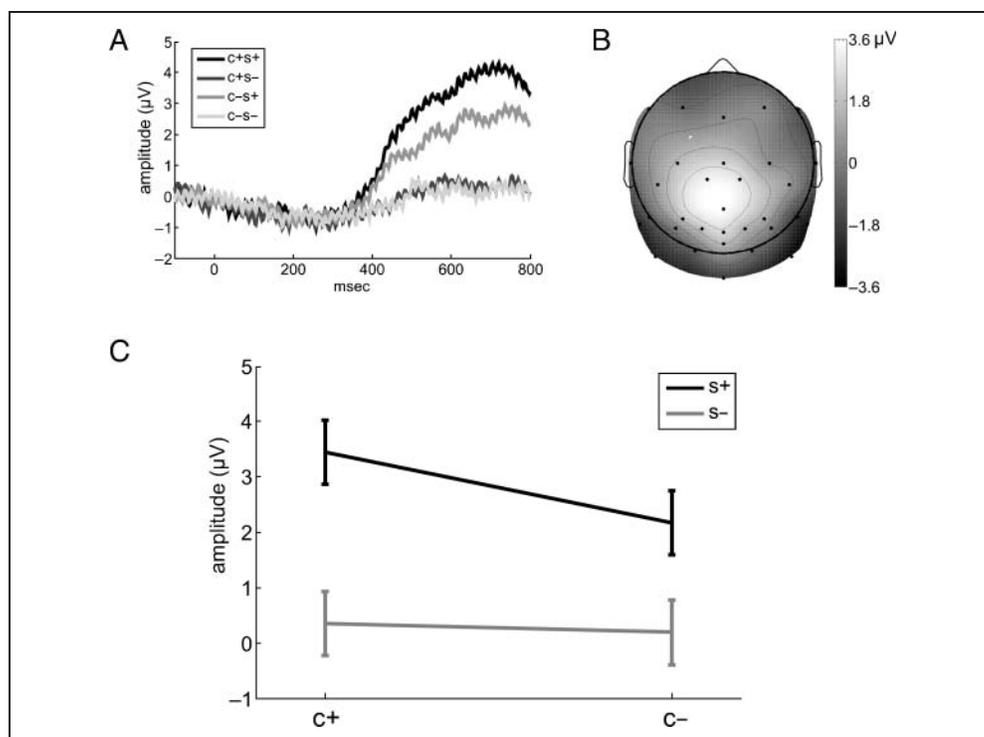
Table 1. Target Hit Rates (First Line; c+s+) and False Alarm Rates (%) for the Three Types of Distractors [Unattended Color and Attended Side (c-s+); Attended Color and Unattended Side (c+s-); and Unattended Color and Unattended Side (c-s-)]

Targets	c+s+	69.86 ± 3.04
Distractor type	c-s+	33.5 ± 2.70
	c+s-	1.09 ± 0.27
	c-s-	1.09 ± 0.19

Means and standard deviations of the mean are given.

of spatial and feature-selective attention is of small magnitude at best. This conclusion is underlined by the small amount of variance accounted for by the interaction in our data; it was less than one tenth or one fifteenth of the variance explained by the individual factors, respectively. Our results thus demonstrate that color and spatial location are, indeed, facilitated in a parallel and largely additive manner, in accordance with the tenets of the feature similarity gain model (Maunsell & Treue, 2006; Treue & Martinez-Trujillo, 1999). Importantly, this conclusion is based on the fact that the employed data processing steps, such as averaging, normalization, and Fourier transformation, are all linear operations, that is, SSVEP amplitudes are directly proportional to the recorded electrical field. If the analysis was based on the power of the SSVEP, which is a quadratic function of the electrical field, independent additive enhancement

Figure 3. (A) Grand-average ERP elicited by coherent motion targets (c+s+) and distractors (c+s-, c-s+, and c-s-) at electrode Pz. Note that SSVEPs elicited by the flickering stimuli are visible as oscillatory activity. (B) Spline-interpolated voltage map of the grand-average ERP 600 msec post target onset. (C) Interaction plot of P3b amplitudes at electrode Pz averaged over the time range from 500 to 700 msec post target or distractor onset. Error bars correspond to 95% within-subjects confidence intervals of the mean.



in the brain would have led to an interaction in the ANOVA.

To further elucidate any possible interaction between spatial and feature-selective attention, we considered the alternative that both attentional factors are multiplicatively combined. If the amplitude increase for each attentional factor is small, then both additive and multiplicative combinations of the effects yield almost identical results. For example, if both attentional factors produced a 20% enhancement, then an additively combined effect would amount to 40%, whereas a multiplicatively combined effect would amount to 44%. In order to test if a multiplicative model better explains the data, we logarithmized¹ SSVEP amplitudes before subjecting them to the same statistical analysis as before. The size of the main effects was almost identical to the original analysis [color-selective attention: $F(1, 18) = 55.085, p < 10^{-6}$; spatial attention: $F(1, 18) = 20.979, p < .0005$], but the trend toward an interaction disappeared [$F(1, 18) = 1.715, p > .1$] while the amount of variance explained by the total model stayed almost identical ($\eta^2 = 58.4\%$). This suggests that our data can better be described by a multiplicatively independent combination of both attentional factors.

The effects of spatial and feature-selective attention on stimulus processing, as indexed by the SSVEP, were found to be very similar, but the extent to which the mechanisms mediating these effects are the same or different is unclear. A recent fMRI study found a close overlap between regions that represented spatial and feature-based search information during the cue–stimulus interval (Egner et al., 2008). In good accordance with the present results, an additive representation of spatial and feature cue information was found in those regions of top–down attentional control. On the other hand, considerable evidence exists that feature-selective and spatial attention are mediated by different systems. In monkey area V4, Hayden and Gallant (2005) demonstrated a different time course for spatial and feature-selective attention that clearly indicates that these two mechanisms are controlled at least partially by different attentional control systems. Whereas spatial attention was interrupted by stimulus transients, feature-selective attention was not. It has been proposed that spatial attention is closely related to the saccade generation system (Moore, Armstrong, & Fallah, 2003; Corbetta, 1998; Kustov & Robinson, 1996), and that feature-selective attention may rather be related to the maintenance of an internal representation of stimulus features (Bichot, Rossi, & Desimone, 2005; Hayden & Gallant, 2005; Chelazzi, Miller, Duncan, & Desimone, 2001; Motter, 1994). However, a recent fMRI study by Serences and Boynton (2007) found feature-specific attentional modulation in the frontal eye fields that was linked to the spatial attention control system (Moore et al., 2003).

Previous ERP studies provide further evidence that spatial and feature-selective attention involve very different neural mechanisms (Anllo-Vento, Luck, & Hillyard, 1998). In a design not very different from the one of the present

study, Hillyard and Münte (1984) presented transient red and blue stimuli in random order to both left and right visual field locations. Subjects attended to stimuli of one color at one location at a time (see also Anllo-Vento & Hillyard, 1996). They found that all stimuli at the attended location (regardless of their color) elicited equally enlarged P1 and N1 components (80–200 msec), whereas a subsequent selection negativity (150–300 msec) elicited by attended-color stimuli was markedly greater for stimuli at the attended location. This pattern of results contrasts sharply with the present findings and suggests that feature-selective attention is much attenuated at the unattended location under conditions where stimuli are presented as transient single flashes rather than continuously and together with competing unattended stimuli as in the present SSVEP experiment. This suggests that the global feature enhancement mechanism observed here and postulated by the feature similarity gain model may be contingent upon continuous presentation of both the attended feature and competing unattended features, as was also the case in previous studies using single-unit recordings (e.g., Treue & Martinez-Trujillo, 1999) and fMRI (e.g., Saenz et al., 2002).

Flicker frequencies were confounded with the different types of stimuli in the present experiment. Therefore, it might be possible that flicker frequency served as an attribute for selection. A behavioral control experiment in our previous study (Müller et al., 2006), which employed similar stimuli, showed that different flicker frequencies do not provide a useful cue for the observed attentional selection. Furthermore, if flicker frequencies had served as a cue for selection in the present experiment, then the observed global effects for color and spatial location cannot be explained because they extend to stimuli presented at other frequencies. The existence of these global effects also clearly shows that attentional selection was not object-based in the present experiment.

The pattern of attentional modulation of P3b amplitudes elicited by the targets and distractors differed considerably from the observed modulations of SSVEP amplitudes. For transient coherent-motion stimuli, the effect of feature-selective attention was local (i.e., limited to the attended position) rather than global. This pattern was closely matched by the distribution of false alarms, which were almost exclusively elicited by distractors at the attended location. P3a amplitudes showed a similar, but less pronounced, pattern than P3b amplitudes. The smaller effects observed here might be due to the temporal overlap of the P3a and the 500-msec duration of targets and distractors (i.e., the P3a occurred in a time range), during which new target/distractor information was still being encoded.

Three previous studies that employed similar displays, and in two cases the same task (Andersen et al., 2008, 2009; Müller et al., 2006), located the focus of attentional modulation of SSVEP amplitudes to early visual areas V1–V3. Therefore, although not tested explicitly, the attentional

modulations observed in the present experiment are very likely to stem from the same cortical areas. As in the present experiment, in both prior studies, the SSVEP analysis integrated over a prolonged temporal window. Therefore, they cannot discriminate whether the observed attentional effects in early visual areas result from a modulation of feedforward processing or from an influence of feedback connections. However, a recent ERP study using random dot stimuli reported feature-based attentional modulation of feedforward processing (Zhang & Luck, 2009). Discrimination and selection of the transient targets and distractors, however, appears to be related to a later, location-specific stage of processing that was reflected in P3b amplitudes but not in SSVEP amplitudes. Note that processing of targets and distractors was not reflected in the analyzed SSVEP signals, as all trials with targets or distractors were excluded from the SSVEP analysis. Correct performance in the present task requires not only the detection of coherent motion signals but also assignment of this motion to the correct color and location. Thus, the task requires correct binding of these features, which is proposed to rely on spatial attention (Treisman, 1988; Treisman & Gelade, 1980).

In summary, the present SSVEP results strongly support the view that spatial and feature-selective attention amplify visual inputs in a global and largely additive manner at early stages of processing, in accordance with the feature similarity gain model. However, the findings that false alarms and feature-selective modulation of P3 amplitudes were limited to the attended location indicate that later processing stages related to target discrimination and identification were only applied to stimuli at the attended location. This points to the concurrent operation of multiple levels of attentional selectivity having distinctive properties. Whereas attending to a continuously present nonspatial feature such as color results in the global amplification of that feature throughout the visual field, the discrimination and identification of transient targets appear to be carried out by higher-order networks that are restricted to analyzing inputs at the attended location.

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Note

1. Since $\log(A \times B) = \log(A) + \log(B)$, taking the logarithm of the SSVEP amplitudes converts a multiplicative model to an additive model.

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