

Effects of Search Efficiency on Surround Suppression During Visual Selection in Frontal Eye Field

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Schall, Jeffrey D., Takashi R. Sato, Kirk G. Thompson, Amanda A. Vaughn, and Chi-Hung Juan. Effects of search efficiency on surround suppression during visual selection in frontal eye field. *J Neurophysiol* 91: 2765–2769, 2004. First published January 28, 2004; 10.1152/jn.00780.2003. Previous research has shown that visually responsive neurons in the frontal eye field of macaque monkeys select the target for a saccade during efficient, pop-out visual search through suppression of the representation of the nontarget distractors. For a fraction of these neurons, the magnitude of this distractor suppression varied with the proximity of the target to the receptive field, exhibiting more suppression of the distractor representation when the target was nearby than when the target was distant. The purpose of this study was to determine whether the variation of distractor suppression related to target proximity varied with target-distractor feature similarity. The effect of target proximity on distractor suppression did not vary with target-distractor similarity and therefore may be an endogenous property of the selection process.

INTRODUCTION

This report continues a series of investigations of the neural basis of saccade target selection (reviewed by Schall 2002). In monkeys who shift gaze to the singleton in a visual search array, visually responsive neurons in the frontal eye field (FEF) exhibit a modulation of activation by which the location of the target is distinguished from distractors. This modulation occurs through a suppression of the representation of the distractors (Sato et al. 2001, 2003; Schall et al. 1995; Thompson et al. 1996). Subsequent work has shown that the magnitude of this distractor suppression depends on the visual similarity of the distractor to the target (Bichot and Schall 1999; Sato et al. 2001, 2003). In the original study using efficient search (e.g., green among red), a fraction of neurons exhibited another characteristic of the modulation of the distractor suppression. For these neurons, the magnitude of distractor suppression varied with the proximity of the target to the receptive field with greater suppression when the target was closer to the receptive field (Schall et al. 1995). The purpose of this experiment was to determine whether the effect of target proximity on distractor suppression varies with the visual similarity of the target and distractors. Preliminary results have appeared in abstract form (Vaughn et al. 2001).

METHODS

The behavioral training, data acquisition, and analysis procedures have been described in detail (Sato et al. 2001; Schall et al. 1995). Monkeys were cared for in accordance with the National Institute of

Health's Guide for the Care and Use of Laboratory Animals and the guidelines of the Vanderbilt Animal Care Committee. Monkeys performed singleton visual search for a target presented at one of eight iso-eccentric locations equally spaced around the fixation spot. The remaining seven locations were occupied by the distractors. The target and distractors were distinguished by either color or direction of motion (Fig. 1). Low similarity (efficient) and high similarity (inefficient) search trials were randomly interleaved, and color and motion searches were blocked. For motion search, each stimulus was a circular aperture of randomly positioned dots, a proportion of which translated coherently in a specified direction whereas the remainder were replotted at random locations every three video frames. The apertures were scaled from 1.5° at 6° eccentricity to 2.5° at 10° eccentricity. The stochastic motion stimulus corresponds to those used in earlier studies (Kim and Shadlen 1999). The direction of motion was either left or right, and the direction of motion of the target was the opposite from that of the distractors. The target and distractor were made less discriminable by reducing the proportion of coherent dots in the target and distractors from 100 to 50%. For color search, the target was green and the distractors were either red or yellow-green. The stimuli were scaled from 0.6° of visual angle at 6° eccentricity to 1° at 10° eccentricity. For one monkey (F), the green was Commission Internationale de l'Eclairage (CIE) $x = 283$, $y = 612$, red was CIE $x = 655$, $y = 327$, and yellow-green was CIE $x = 363$, $y = 552$, all with a luminance of 11.1 cd/m². For the other three monkeys, the green was CIE $x = 281$, $y = 609$, red was CIE $x = 632$, $y = 338$, and yellow-green was CIE $x = 375$, $y = 538$ with a luminance of 13.4 cd/m².

To quantify the variation of activity with location when the target was presented alone, the magnitude of response as a function of target direction was fit with a Gaussian function of the form

$$A(\varphi) = B + R \times \exp(-1/2[(\varphi - \Phi)/T_\varphi]^2)$$

where activation (A) as a function of meridional direction (φ) depends on the baseline discharge rate (B), maximum discharge rate (R), optimum direction (Φ), and directional tuning (T_φ). Previous reports have shown that this function effectively characterizes the spatial pattern of responsiveness of FEF neurons (Bruce and Goldberg 1985; Schall et al. 1995). To characterize whether a pattern of central facilitation and surrounding suppression was expressed in the pattern of neural activity, the variation of neural activation as a function of target direction was described with a difference-of-Gaussians (DOG) equation of the form

$$A(\varphi) = B + R_+ \times \exp(-1/2[(\varphi - \Phi_+)/T_+]^2) - R_- \times \exp(-1/2[(\varphi - \Phi_-)/T_-]^2)$$

Positive subscripts denote the central facilitatory component, and negative subscripts denote the broader antagonistic component. We

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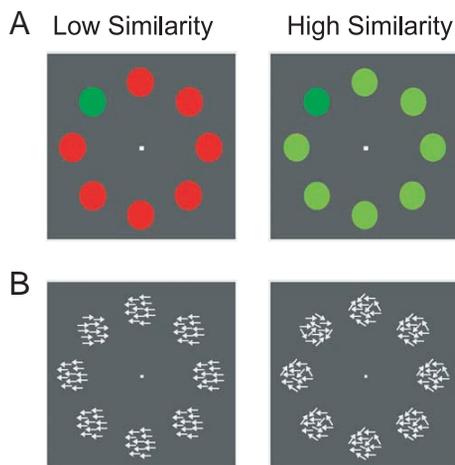
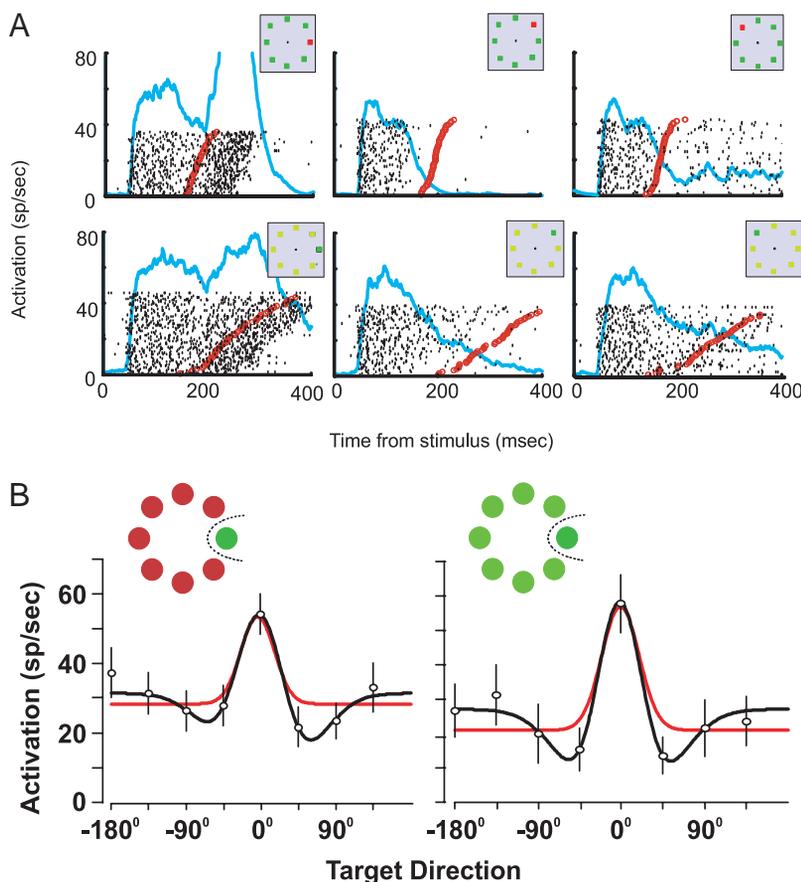


FIG. 1. Visual displays requiring localization of a singleton defined by color (A) or motion (B) with stimuli that support efficient (left) and inefficient (right) search. Efficient and inefficient displays were interleaved. Color and motion search was blocked.

compared the quality of fit of both functions using the Model Selection Criterion (MSC) statistic

$$MSC = \ln \left\{ \frac{\sum_{i=1}^n [a(\phi)_i - \bar{a}]^2}{\sum_{i=1}^n [a(\phi)_i - A(\phi)]^2} \right\} - 2 p/n$$

where $a(\phi)$ is the activity measured for the different target directions, \bar{a} is the average presaccadic firing rate, $A(\phi)$ is the activity expected based on the best fit Gaussian or DOG function, p is the number of free parameters, and n is the number of data points (Akaike 1976).



This statistic, which is derived from Akaike's Information Criterion (Akaike 1973; Sakamoto et al. 1986), compares the quality of fit provided by two competing models for the same observed data by relating the coefficient of determination to the number of free parameters. The DOG equation, by virtue of having more free parameters, should be able to account for more of the variance of activity as a function of target direction than the single Gaussian function. The MSC statistic quantifies how much more of the total variance must be accounted for by the DOG model using seven parameters compared with the single Gaussian model with four parameters to select which provides a better overall fit. The model yielding a higher MSC statistic was judged to provide the better fit to the data.

RESULTS

The performance of monkeys with these displays has been reported previously (Bichot et al. 2001; Sato et al. 2001). The manipulation of the search display did have a significant impact on performance measured as reaction time or percent correct. A total of 142 neurons recorded in four macaque monkeys contributed to this report. Most neurons were also tested while monkeys performed memory-guided saccades to identify visual, visual-movement, and movement neurons.

The response of a representative FEF neuron during low similarity, efficient and high similarity, inefficient visual search for a singleton defined by color is shown in Fig. 2. Like every visually responsive neuron in FEF, this neuron had a spatially restricted receptive field and responded best to the target when it fell at one of the eight array positions. When the search target fell at the most sensitive position within the receptive field, the activity after the selection process was completed was maxi-

FIG. 2. Activity of a frontal eye field (FEF) neuron during color search. A: activity during interleaved efficient (top) and less efficient (bottom) search. In the raster displays, vertical tickmarks represent times of neuronal discharges. Rasters are aligned on target presentation and sorted according to interval between target presentation and saccade initiation. Superimposed on the raster is the average spike density function. Saccade initiation is indicated by the solid circle in each raster line. Inset: configuration of stimuli to which the monkey was responding. Shaded region indicates extent of receptive field. Activation was greatest when the target fell in the receptive field (left). Note the stronger, more rapid suppression of the response to the distractor when the target was beside the receptive field (middle) compared with when it was distant (right). B: selective response to stimulus in receptive field as a function of direction of the target during efficient (left) or inefficient (right) search. By convention, 0° corresponds to the center of the receptive field; positive angles progress counterclockwise, and negative angles, clockwise. Vertical lines indicate 1 SE. Parameters of the difference-of-Gaussian function for efficient search were $B = 31$ sp/s, $R_+ = 48$ sp/s, $\Phi_+ = -2^\circ$, and $T_+ = 26^\circ$, $R_- = 26$ sp/s, $\Phi_- = -6^\circ$, and $T_- = 52^\circ$ and for inefficient search were $B = 27$ sp/s, $R_+ = 66$ sp/s, $\Phi_+ = -1^\circ$, $T_+ = 23^\circ$, $R_- = 36$ sp/s, $\Phi_- = 0^\circ$, $T_- = 48^\circ$.

mal. When the target of the search array fell at locations on the edge of the neuron's receptive field, the level of the delayed activity evoked by the distractors in the receptive field was less than when the target fell at a more distant locations. To account for this pattern of variation, a DOG function was needed to provide an adequate fit of the data. Beyond the fact that the DOG equation has been used to model the facilitatory and suppressive zones of retinal ganglion neurons (Enroth-Cugell and Robson 1966; Rodieck 1965) and of neurons in the primary visual cortex (Hawken and Parker 1987), it provided a quantitative means of determining whether neural activity exhibited the specific pattern of variation with target direction during visual search characterized by a zone of higher activity flanked by zones of lower activity compared with more distant locations. For this neuron, the MSC of 0.177 for the best-fit DOG was greater than the MSC of 0.127 obtained for the best-fit single Gaussian curve for the efficient search. Likewise, the MSC for the DOG (0.305) was greater than that for the single Gaussian (0.247) for the less efficient search. Therefore the DOG provided a better fit of the data than did the single Gaussian.

The response of the same FEF neuron during efficient and inefficient visual search for a singleton defined by direction of motion is shown in Fig. 3. The variation of activity as a function of target direction relative to the receptive field for both efficient and inefficient search was fit better by a DOG than by a single Gaussian function [efficient search DOG (0.080), single Gaussian (0.048); less efficient search DOG (0.008), single Gaussian (0.004)].

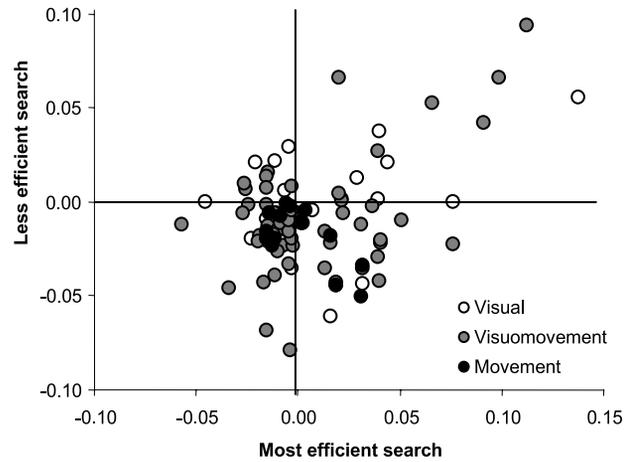


FIG. 4. Difference between the Model Selection Criterion (MSC) values for difference-of-Gaussian and single Gaussian fits for less efficient search plotted against the difference for efficient search for visual neurons (open symbols), visuomovement neurons (gray symbols), and movement neurons (closed symbols). Values > 0 were categorized as exhibiting significant suppressive surrounds.

Figure 4 plots the difference between the MSC values for DOG and single Gaussian fits for less efficient and more efficient search. Table 1 summarizes the incidence of distractor suppression dependent on target proximity for neurons of different types. The effect of target proximity on distractor suppression was observed most commonly in neurons with visual responses but no saccade-related modulation, less commonly in neurons with visual responses and saccade-related modula-

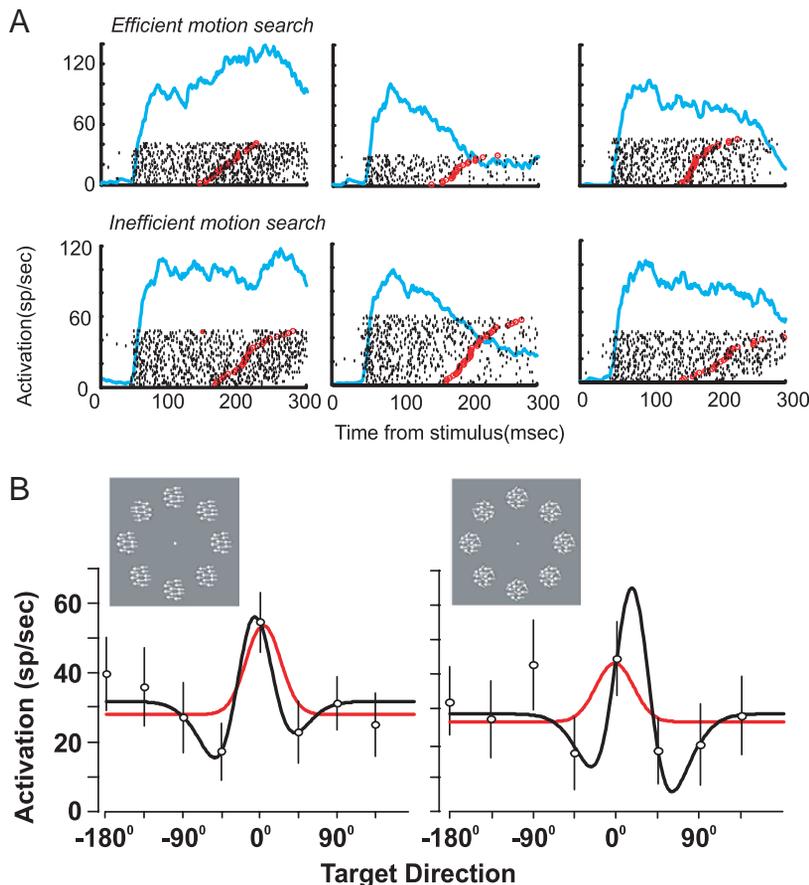


FIG. 3. Activity of the same neuron during motion search. Same conventions as Fig. 2. Parameters of the difference-of-Gaussian function for efficient search were $B = 81$ sp/s, $R_+ = 54$ sp/s, $\Phi_+ = -5^\circ$, and $T_+ = 2^\circ$, $R_- = 31$ sp/s, $\Phi_- = -11^\circ$, and $T_- = 39^\circ$. The parameters for less efficient search were $B = 77$ sp/s, $R_+ = 39$ sp/s, $\Phi_+ = 12^\circ$, $T_+ = 20^\circ$, $R_- = 22$ sp/s, $\Phi_- = -26^\circ$, $T_- = 44^\circ$.

TABLE 1. *Percentage of cells exhibiting flanking suppression*

Cell Type	Efficient Search	Inefficient Search	Both	Number
Visual	35%	28%	17%	40
Visuomovement	22%	16%	7%	85
Movement	0%	18%	0%	17

tion, and least commonly in neurons with only movement-related activity. The incidence of neurons exhibiting the target proximity effect was slightly higher during efficient search, but nearly one-fourth of all neurons sampled exhibited the target proximity effect regardless of the visual similarity of the target and distractors.

Receptive field center and surround size

The parameters from the best-fit Gaussian and DOG curves provide quantitative measures of the receptive field organization of FEF neurons. The following values were derived from both color and motion search because no clear differences were observed. The width of the receptive field was estimated by the SD (T_{ϕ}) of the Gaussian curve best-fit to the variation of activity when the target was presented alone. The value, which was calculated in polar angle, was converted to visual field angle according to the eccentricity of the stimuli using the law of cosines. All receptive fields in this sample were responsive to and tested with stimuli at 10° eccentricity. Based on the Gaussian curves fit to the response to the target presented alone for all of the cells, the average \pm SE receptive field width was $6 \pm 0.5^{\circ}$ for visual neurons, $7 \pm 0.3^{\circ}$ for visuomovement neurons, and $5 \pm 0.8^{\circ}$ for movement neurons. These values were somewhat less than those reported previously ($12 \pm 0.8^{\circ}$) using comparable methods (Bruce and Goldberg 1985; Schall et al. 1995).

The extent of the suppressive surround was estimated from the SD of the subtractive component of the DOG equation (T_{-}). We will report data from efficient and less efficient search trials separately. From data collected during efficient search, the mean value for the width in the visual field of the suppressive zones was $8 \pm 0.7^{\circ}$ for visual neurons, $7 \pm 0.4^{\circ}$ for visuomovement neurons, and $7 \pm 2^{\circ}$ for movement neurons. These values were also less than those of an earlier report ($13 \pm 2.0^{\circ}$) (Schall et al. 1995). This average value was just 1° larger than the width of the receptive field estimated from T_{ϕ} . The estimate of the receptive field center width derived from the additive component of the DOG (T_{+}) was $6 \pm 0.6^{\circ}$ for visual neurons, $8 \pm 0.5^{\circ}$ for visuomovement neurons, and $6 \pm 2.7^{\circ}$ for movement neurons, which were also somewhat less than reported previously ($10 \pm 1.5^{\circ}$). During efficient, pop-out search, the suppressive surround was larger than the receptive field center by an average of $0.4 \pm 0.6^{\circ}$. The suppression was commonly asymmetric about the center of the receptive fields. The absolute value of the separation in the visual field between the center of the facilitatory component (Φ_{+}) and the center of the subtractive component (Φ) averaged $4 \pm 0.2^{\circ}$. The strength of the suppression of the distractor-elicited response by the target when it fell in the flanking regions was quantified by the ratio of the magnitudes of the suppressive and facilitatory components (R_{-}/R_{+}). For neurons best fit by the DOG function, the average ratio was 0.54 ± 0.045 for visual neurons, 0.58 ± 0.056 for visuomovement neurons, and 0.61 ± 0.084

for movement neurons. These values were somewhat less than the previous report (0.85 ± 0.11).

In data collected when the target and distractors were more similar, the mean value for the width in the visual field of the suppressive zones was $9 \pm 0.6^{\circ}$ for visual neurons, $8 \pm 0.8^{\circ}$ for visuomovement neurons, and $8 \pm 1.3^{\circ}$. The estimate of the receptive field center width derived from the additive component of the DOG (T_{+}) was $5 \pm 0.5^{\circ}$ for visual neurons, $7 \pm 0.5^{\circ}$ for visuomovement neurons, and $8 \pm 2^{\circ}$ for movement neurons. During less efficient search, the suppressive surround was larger than the facilitatory zone by an average of $1.4 \pm 0.4^{\circ}$. The suppression was commonly asymmetric about the center of the receptive fields. The absolute value of the separation in the visual field between the center of the facilitatory component (Φ_{+}) and the center of the subtractive component (Φ) averaged $4 \pm 0.2^{\circ}$. For neurons with the spatial pattern of activity best fit by the DOG function during less efficient search, the average ratio of the strengths of the facilitatory and suppressive components (R_{-}/R_{+}) was 0.55 ± 0.083 for visual neurons, 0.47 ± 0.034 for visuomovement neurons, and 0.49 ± 0.153 for movement neurons. Overall, the center-surround organization of FEF neuron receptive fields was quantitatively similar whether the target was dissimilar or similar to the distractors.

DISCUSSION

Center-surround suppression is a common property in the visual pathway (reviewed by Allman et al. 1985). In a previous description of the activity of neurons in FEF of monkeys performing efficient pop-out visual search, we reported that some neurons in FEF exhibit greater suppression of nontarget responses when the target was near the receptive field (Schall et al. 1995). We now show that this spatial characteristic of the target selection process in FEF occurs to the same degree when the target and distractor are more similar yielding less efficient search.

Relation to previous neurophysiology studies

The incidence of neurons with distractor suppression that varied with target proximity was not much different from what was observed in a previous study (Schall et al. 1995) that found the target proximity effect for 21% of the visually responsive neurons. The present experiment demonstrated that a fraction of FEF neurons exhibit greater suppression of nontarget responses when the target was nearby in both efficient and inefficient search. This observation indicates that the surround suppression is not stimulus dependent and may therefore be an endogenous property of the neural target selection process.

The variation of presaccadic discharge as a function of search target direction that we observed can be described as a central excitatory zone flanked by suppressive regions, a pattern resembling that observed in other cortical areas and subcortical structures (Allman et al. 1985; Desimone and Schein 1987; Enroth-Cugell and Robson 1966; Hawken and Parker 1987; Kuffler 1953; Olavarria et al. 1992; Rodieck 1965; Saito et al. 1986). Thus a basic mechanism of sensory coding seems also to operate to guide eye movements. In fact, other studies of neural correlates of saccade target selection have reported variation of distractor suppression with target proximity in the

superior colliculus (Basso and Wurtz 1998) and substantia nigra (Basso and Wurtz 2002).

Relation to previous behavior studies

Several studies have investigated the allocation of attention in space as a function of proximity to the selected target and have provided evidence for a nonmonotonic variation of attention allocation with distance from a target (e.g., Kröse and Julesz 1989) that is a central feature of certain models of attention (Tsotsos et al. 2001). For example, when subjects perform a same-different judgment on two precued letters in a circular ring, response times were fastest for adjacent and diametrically opposite pairs of cued targets and slowest when one letter intervened between the two cued letters (Skelton and Eriksen 1976). Likewise, probing the allocation of attention reveals an inhibitory field centered on the selected target when attention is directed to a pair of targets with an irrelevant, competing letter probe (Pan and Eriksen 1993) or a spatial probe is presented in an circular array of letters among which a target must be located (Cave and Zimmerman 1997). The allocation of attention directed by a visual cue measured by a motion illusion exhibits a center-surround organization (Steinman et al. 1995). The influence of a competing singleton on discrimination of the properties of a singleton target increased with proximity to the target (Caputo and Guerra 1998; Mounts 2000). Also, the accuracy of identifying two target letters at precued locations in an array of letters increased with the separation of the two targets, indicating that processing one target impaired processing of the other if it was too close (Bahcall and Kowler 1999; see also Cutzu and Tsotsos 2003).

The temptation to regard the pattern of modulation observed in this study as the basis for these observations in studies of attention must be tempered by the realization that the behavior and stimulus conditions used for this report (response terminated presentation of stimuli distinguished by color or motion) are markedly different from those employed in the aforementioned studies (e.g., brief presentation of more complex stimuli). It should also be noted that in singleton search with saccades errors to distractors neighboring the target are more, not less, common than errors in other directions (Findlay 1997). Nevertheless, reasoning by analogy, we suggest that the spatial variation of target selection by certain neurons in the FEF may contribute to the corresponding variation in the allocation of attention.

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