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

Jeffrey D. Schall*, Takashi R. Sato, Kirk G. Thompson, Amanda A. Vaughn, Chi-Hung Juan

Vanderbilt Vision Research Center
Center for Integrative & Cognitive Neuroscience
Department of Psychology
Wilson Hall
111 21st Avenue South
Vanderbilt University, Nashville, TN 37203

Running title Surround Suppression in FEF

*To whom correspondence should be addressed:
Jeffrey D. Schall
301 Wilson Hall
111 21st Avenue South
Vanderbilt University, Nashville, TN 37203
Email: jeffrey.d.schall@vanderbilt.edu
Tel: 615-322-0868 Fax: 615-343-8449

Number of text pages: 12 Number of figures: 4
Abstract word count: 156 Number of tables: 1

Copyright (c) 2004 by the American Physiological Society.
ABSTRACT

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 non-target 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 investigation 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 so 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 (Schall et al., 1995; Thompson et al., 1996; Sato et al. 2001, 2003). 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 (Schall et al., 1995; Sato et al. 2001). 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 (Figure 1). Low similarity (efficient) and high similarity (inefficient) search trials were randomly interleaved, and color and motion search 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 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.

Figure 1 here

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

$$ A(\phi) = B + R \cdot \exp\left(-\frac{1}{2}\left(\frac{\phi - \Phi}{T_\phi}\right)^2\right) $$

where activation (A) as a function of meridional direction (\(\phi\)) depends on the baseline discharge rate (B), maximum discharge rate (R), optimum direction (\(\Phi\)), and directional tuning (\(T_\phi\)). 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
SURROUND SUPPRESSION IN FRONTAL EYE FIELD – 4

\[
A(\phi) = B + R_+ \cdot \exp \left( -\frac{1}{2} \left[ (\phi - \Phi_i)/T_+ \right]^2 \right) - R_- \cdot \exp \left( -\frac{1}{2} \left[ (\phi - \Phi)/T_- \right]^2 \right)
\]

Positive subscripts denote the central facilitatory component, and negative subscripts, the broader antagonistic component. We compared the quality of fit of both functions using the Model Selection Criterion (MSC) statistic

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

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 difference of gaussian 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 difference-of-gaussian 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 difference-of-gaussian model using seven parameters as compared to 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 (Sato et al. 2001; Bichot 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 Figure 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 1 of the 8 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 maximal. 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 difference of gaussian function was needed to provide an adequate fit of the data. Beyond the fact that the difference-of-gaussian equation has been used to model the facilitatory and suppressive zones of retinal ganglion neurons (Rodieck, 1965; Enroth-Cugell and Robson, 1966) 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 as compared to more distant locations. For this neuron the MSC of 0.177 for the best-fit difference-of-gaussians 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 difference-of-gaussians (0.305) was greater than that for the single gaussian (0.247) for the less efficient search. Therefore, the difference-of-gaussians 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 Figure 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 difference-of-gaussian than by a single gaussian function (efficient search difference-of-gaussian (0.080), single gaussian (0.048); less efficient search difference-of-gaussian (0.008), single gaussian (0.004).

Figure 4 plots the difference between the MSC values for difference-of-gaussian 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 modulation 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 difference-of-gaussian 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 standard deviation ($T_N$) 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 ($\pm$ SEM) receptive field width was 6 ± 0.5° for visual neurons, 7 ± 0.3° for visuomovement neurons and 5 ± 0.8° for movement neurons. These values were somewhat less than those reported previously (12 ± 0.8°) using comparable methods (Bruce and Goldberg, 1985; Schall et al. 1995).

The extent of the suppressive surround was estimated from the standard deviation of the subtractive component of the difference-of-gaussian 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 ± 0.7° for visual neurons, 7 ± 0.4° for visuomovement neurons and 7 ± 2° for movement neurons. These values were also less than those of an earlier report (13 ± 2.0°) (Schall et al., 1995). This average value was just 1° larger than the width of the receptive field estimated from $T_N$. The estimate of the receptive field center width derived from the additive component of the difference-of-gaussian ($T_+$), was 6 ± 0.6° for visual neurons, 8 ± 0.5° for visuomovement neurons and 6 ± 2.7° for movement neurons, which were also somewhat less than reported previously (10 ± 1.5°). During efficient, pop-out search, the suppressive surround was larger than the receptive field center by on average 0.4 ± 0.6°. 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 ($\Phi_+$) and the center of the subtractive component ($\Phi_-$) averaged 4 ± 0.2°. 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\textsubscript{c}). For neurons best-fit by the difference-of-gaussian 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 ± 0.6° for visual neurons, 8 ± 0.8° for visuomovement neurons and 8 ± 1.3°. The estimate of the receptive field center width derived from the additive component of the difference-of-gaussian (T\textsubscript{+}), was 5 ± 0.5° for visual neurons, 7 ± 0.5° for visuomovement neurons and 8 ± 2° for movement neurons. During less efficient search the suppressive surround was larger than the facilitatory zone by on average 1.4 ± 0.4°. 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\textsubscript{+}) and the center of the subtractive component (Φ\textsubscript{-}) averaged 4 ± 0.2°. For neurons with the spatial pattern of activity best-fit by the difference-of-gaussian function during less efficient search, the average ratio of the strengths of the facilitatory and suppressive components (R/R\textsubscript{c}) 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 non-target 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 non-target 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 (Kuffler, 1953; Rodieck, 1965; Enroth-Cugell and Robson, 1966; Allman et al., 1985; Saito et al., 1986; Desimone and Schein, 1987; Hawken and Parker, 1987; Olavarria et al., 1992). 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 non-mono tonic variation of attention allocation with distance from a target (e.g., Kröse and Julesz 1989) which 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 pre-cued 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.

Acknowledgements
We thank E. Kim for assistance with data analysis and G. Fox and J. Jewett for manuscript preparation. Supported by R01-EY08890 and P30-EY08126.
References

Akaike H. Information theory and an extension of the maximum likelihood principle. In: 2nd
International Symposium of Information Theory, edited by Petrov BN and Csazi F. Akademiai


Allman JM, Miezin F and McGuinness E. Stimulus specific responses from beyond the classical
receptive field: Neurophysiological mechanisms for local-global comparisons of visual motion.

Bahcall D, Kowler E. Attentional interference at small spatial separations. Vision Research 39: 71-86,
1999.

Basso MA, Wurtz RH. Modulation of neuronal activity in superior colliculus by changes in target

Basso MA, Wurtz RH. Neuronal activity in substantia nigra pars reticulata during target selection. J

Bichot NP, Schall JD. Effects of similarity and history on neural mechanisms of visual selection. Nature
Neurosci 2: 549-554, 1999.

Bruce CJ and Goldberg ME. Primate frontal eye fields I Single neurons discharging before saccades. J


Cave KR, Zimmerman JM. Flexibility in spatial attention before and after practice. Psychological Sci 8:
399-403, 1997.

Cutzu F, Tsotsos JK. The selective tuning model of attention: psychophysical evidence for a suppressive

Desimone R and Schein SJ. Visual properties of neurons in area V4 of the macaque: Sensitivity to

Enroth-Cugell C and Robson JG. The contrast sensitivity of retinal ganglion cells of the cat. J Physiol


Hawken MJ and Parker AJ. Spatial properties of neurons in the monkey striate cortex. Proc R Soc Lond

Kim J-N, Shadlen MN. Neural correlates of a decision in the dorsolateral prefrontal cortex of the
Figure Legends

Figure 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.

Figure 2. Activity of an 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. The rasters are aligned on target presentation and sorted according to the 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. The inset cartoon indicates the configuration of the stimuli to which the monkey was responding. The shaded region indicates the extent of the receptive field. The 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) as compared to when it was distant (right). Selective response to stimulus in receptive field as a function of the 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 one standard error of the mean. The 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/sec, $R_+ = 66$ sp/s, $\Phi_+ = -1^\circ$, $T_+ = 23^\circ$, $R_- = 36$ sp/s, $\Phi_- = 0^\circ$, $T_- = 48^\circ$.

Figure 3. Activity of the same neuron during motion search. Same conventions as figure 2. The 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, $\Phi_- = -26^\circ$, $T_- = 44^\circ$.

Figure 4. Difference between the MSC values for difference-of-gaussian and single gaussian fits for less efficient search plotted against the different for efficient search for visual neurons (open symbols), visuomovement neurons (gray) and movement neurons (black). Values greater than 0 were categorized as exhibiting significant suppressive surrounds.
Tables

Table 1.
Percentage of cells exhibiting flanking suppression

<table>
<thead>
<tr>
<th>Cell Type</th>
<th>Efficient search</th>
<th>Inefficient search</th>
<th>Both</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Visual</td>
<td>35%</td>
<td>28%</td>
<td>17%</td>
<td>40</td>
</tr>
<tr>
<td>Visuomovement</td>
<td>22%</td>
<td>16%</td>
<td>7%</td>
<td>85</td>
</tr>
<tr>
<td>Movement</td>
<td>0%</td>
<td>18%</td>
<td>0%</td>
<td>17</td>
</tr>
</tbody>
</table>
Figure 1

A  Low Similarity  High Similarity

B

Figure 1
Figure 2
Figure 3

A

Efficient motion search

Inefficient motion search

Activation (sp/sec)

Time from stimulus (msec)

B

Target Direction

Activation (sp/sec)

Target Direction

Figure 3
Figure 4