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Presaccadic discrimination of receptive field stimuli by area V4 neurons

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ABSTRACT

Previous studies have shown that the visual responses of neurons in extrastriate area V4 are enhanced prior to saccadic eye movements that target receptive field (RF) stimuli. We used receiver-operator characteristic (ROC) analysis to quantify how well V4 neurons could discriminate stable RF stimuli targeted by visually-guided saccades or ignored during saccades elsewhere. We found that discrimination was transiently enhanced prior to saccades to RF stimuli whereas it was reduced prior to saccades elsewhere. Similar to what is observed during covert attention and after frontal eye field microstimulation, the changes in stimulus discrimination were due in part to changes in response magnitude. In addition, we found evidence of an increased reliability of responses when saccades were made to the RF stimulus. These results highlight the similarity of mechanisms driving covert spatial attention and the preparation of visually-guided saccades.

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1. Introduction

Many studies have examined the effects of covert visual attention on the responses of neurons within macaque area V4, where visual activity is biased in favor of attended stimuli (McAdams & Maunsell, 1999a; McAdams & Maunsell, 1999b; Moran & Desimone, 1985; Reynolds & Chelazzi, 2004). The attention-driven changes in visual activity in this area are paralleled by the modulation observed during the selection of receptive field (RF) stimuli as targets for saccadic eye movements (Fischer & Boch, 1981; Mazer & Gallant, 2003; Moore, 1999), suggesting a similarity of mechanisms underlying covert and overt spatial attention (Moore, Armstrong, & Fallah, 2003; Rizzolatti, Riggio, Dascola, & Umilta, 1987). More recent studies have addressed this apparent similarity by employing electrical microstimulation to perturb neural activity within saccade-related structures to alter the performance of monkeys on attention tasks (Cavanaugh, Alvarez, & Wurtz, 2006; Cavanaugh & Wurtz, 2004; Moore & Fallah, 2001, 2004; Muller, Philiastides, & Newsome, 2005) or the visual activity within V4 (Moore & Armstrong, 2003). The latter studies have shown that the changes in V4 responses following brief pulses of microstimulation delivered to spatially corresponding frontal eye field (FEF) representations are indistinguishable from the changes observed during covert attention (Armstrong, Fitzgerald, & Moore, 2006; Armstrong & Moore, 2007).

Among the similarities between the effects of covert attention and FEF microstimulation is that both alter the ability of V4 neurons to discriminate among RF stimuli. Although past studies of presaccadic modulation of V4 activity have argued that targeting of RF stimuli by saccades (i.e., during overt attention) also alters visual discriminability (Moore, Tolias, & Schiller, 1998), this has not been demonstrated. We therefore reexamined the visual activity of V4 neurons during a task in which monkeys made saccades to either the RF stimulus or to another location. We used receiver-operator characteristic (ROC) analysis to quantify how well V4 neurons could discriminate the orientation of stable RF stimuli during saccade preparation. We found that discrimination was transiently enhanced prior to saccades to RF stimuli whereas it was reduced prior to saccades elsewhere. These changes in stimulus discrimination are due in part to changes in response magnitude, similar to what is observed during covert attention and after FEF microstimulation, and may also be due to an increase in response reliability. These results suggest that the modulation of visual responses observed in V4 during the preparation of saccades is driven by mechanisms similar to those giving rise to covert attention effects, and similar to those perturbed during FEF microstimulation.

2. Methods

2.1. Subjects

Two male monkeys (*Macaca mulatta*, 8–12 kg) were used in these experiments. All experimental procedures were in accordance with National Institutes of Health Guide for the Care and Use of Laboratory Animals, the Society for Neuroscience Guidelines and Policies. General surgical procedures have been described previously (Zipser, Lamme, & Schiller, 1996).

2.2. Visual stimuli

Visual stimuli were displayed on a 34 × 27 cm Sony video monitor that was driven by a Number Nine graphics board (640 × 480) at a 60 Hz, non-interlaced, refresh rate. The video display was positioned 57 cm in front of the monkey. Visual

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stimuli consisted of light and dark bars with one of four orientations (0°, 45°, 90°, or 135° θ) presented at the center of a V4 neuron's RF. The fixation spot was a small (0.25° diameter) circle displayed at the center of the video display but was displaced (>5.0°) and used as a saccade target on some behavioral conditions.

2.3. Behavioral task

Monkeys performed a visually-guided, delayed saccade task which was initiated by fixation to within <1.0° of the central fixation spot. Immediately following fixation, an oriented bar stimulus appeared in the RF of the neuron under study and remained there until the end of the trial. Following the onset of the RF stimulus, the monkey was required to maintain fixation for a delay of 0.5–1 s, while it waited for the appearance of a saccade target (0.25° diameter) at one of two locations distant from the RF. In two-thirds of the trials (*away* conditions), the target appeared, simultaneously with the offset of the fixation spot, and the monkey was rewarded for making a saccade to the target. In the remaining one-third of trials (*toward* condition), the saccade target did not appear. Instead, when the fixation spot was extinguished, the monkey was rewarded for saccades to the RF stimulus. Both conditions were identical until the cue to saccade (disappearance of the fixation spot) and were randomly interleaved. During all behavioral trials, eye position was measured via the scleral search coil method, and digitized at 200 Hz for offline analysis.

2.4. Electrophysiology

The activity of single V4 neurons was recorded via glass-coated platinum–iridium electrodes lowered into the dorsal surface of the prelunate gyrus. Neural activity was sampled at 32 kHz, digitized and stored. The waveforms of single neurons were isolated by offline clustering (DataWave Technologies).

2.5. Data analysis

For each neuron, the preferred orientation was defined as that which evoked the maximum response, and the non-preferred orientation was defined as that which evoked the minimum response, out of four possible orientations (0°, 45°, 90°, and 135° θ). Neurons were considered orientation-selective if the preferred and non-preferred responses summed across the initial 600 ms of stimulus presentation (i.e., prior to saccade preparation) were significantly different using a *t*-test (significance level $P < .05$). Data from both the *toward* and *away* conditions were collapsed together to maximize the statistical power of the selectivity measurement. ROC analysis was carried out on the distributions of neuronal firing rates measured during the execution of the delayed saccade task. The areas under ROC curves were used as an index of stimulus discrimination and were calculated as in previous studies (Armstrong & Moore, 2007; Britten, Shadlen, Newsome, & Movshon, 1992). Specifically, we computed the average firing rate in a moving 50 ms window, from RF stimulus onset to saccade onset. We then computed the probability that the firing rate in each stimulus condition exceeded a criterion. The criterion was incremented from 0 to the maximum firing rate, and the probability of exceeding each criterion was computed. Thus, a single point on the ROC curve is produced for each increment in the criterion, and the entire ROC curve is generated from all of the criteria. The area under the ROC curve is a normalized measure of the separation between the two firing rate distributions obtained with the preferred and non-preferred RF stimuli, and provides a measure of how well the neuronal response discriminates the two stimuli. Differences in ROC areas, at the population level, were assessed by way of non-parametric tests on paired samples.

The analysis of presaccadic activity during abortive saccades consisted of extracting all trials in which the monkey broke fixation and made a saccade (>2°) either to a location within or near the RF stimulus (<5.0°), or to another location. Abortive saccades were only considered if they occurred after the onset of the RF stimulus and before the offset of the fixation spot.

3. Results

We studied the activity of 90 single neurons in area V4 of two monkeys performing a visually-guided, delayed saccade task in which the receptive field stimulus for a given neuron could be the target of a saccadic eye movement. On a given trial, the monkey made a saccade either to a stable stimulus in the RF of a V4 neuron (*toward*) or to a target outside the RF (*away*). Of the 90 neurons recorded, 63 were orientation-selective and were used for further analyses of the effect of saccade preparation on stimulus discrimination. Fig. 1 shows the average normalized response of orientation-selective neurons during both the stimulus onset and presaccadic phases of the saccade task. Following stimulus onset, there was a clear difference in response magnitude elicited by the preferred and non-preferred orientation. However, this response difference appeared to diminish later in the trial, even

though the stimulus in the receptive field remained present. Furthermore, as previously reported (Moore, 1999; Moore et al., 1998), the response difference appeared to increase within 100 ms of saccades directed to the RF stimulus, as compared to saccades directed elsewhere. Prior to saccades to targets outside the RF, the preferred and non-preferred response difference was relatively unchanged or appeared to be slightly diminished. The previous accounts of presaccadic modulation of V4 responses have noted both the apparent reemergence of selectivity prior to saccades into the RF and the apparent decline prior to saccades elsewhere (Moore, 1999; Moore et al., 1998). However, the discriminability of visual responses was not explicitly quantified.

3.1. Changes in discriminability during saccade preparation

To better quantify the changes in stimulus discrimination during saccade preparation, an ROC analysis was performed on the responses of the 63 orientation-selective neurons during both the stimulus onset and the presaccadic phase of the trial (Fig. 2). The ROC curve, computed from each neuron's distribution of responses to the preferred and non-preferred orientations, quantifies the extent to which the responses discriminate between the two RF stimuli. The area under the ROC curve is equal to the performance expected of an ideal observer discriminating among stimuli based solely on the neuron's response (Green & Swets, 1966), and it is used here as an index of visual response discriminability. The mean ROC area of the orientation-selective neurons is shown for both the stimulus-aligned and the saccade-aligned data sets. Following stimulus onset, the mean ROC areas for both *toward* and *away* conditions rose to ~0.70 (~70% performance), where they remained stable for 100 ms. Subsequently, the mean ROC area of both conditions declined over the ensuing 300 ms to ~0.57. Thus, despite the continued presence of the oriented bar stimulus in each neuron's RF during the delay period, the ROC areas were reduced by more than half of that measured during the initial response. During the latter part of the delay period (−350 to −200 ms relative to saccade onset), the mean ROC areas for both conditions remained stable and indistinguishable from one another ($P > .3$, Wilcoxon signed rank test). However, within the last 100 ms prior to saccade initiation, the ROC areas of the two conditions diverged sharply. Saccades to the RF stimulus were preceded by an increase in ROC area ($P < .03$, Wilcoxon signed rank test, −50 ms versus delay period) while saccades to targets in the opposite hemifield were preceded by a decline in ROC area ($P < .03$, Wilcoxon signed rank test, −50 ms versus delay period). In both cases, the peak increment/decrement in ROC area occurred within ~50 ms of saccade onset, at which time the mean ROC area of the two conditions differed significantly ($P < 10^{-3}$, Wilcoxon signed rank test). Closer to, and following, saccade onset, the mean ROC areas of the two conditions converged again toward levels measured during the delay period. Thus, the dynamics in presaccadic stimulus discrimination depended on whether the RF stimulus was used as the target of the saccade. Importantly, the performance of the population at discriminating preferred from non-preferred stimuli was enhanced when those stimuli were targeted as compared to when they were non-targets.

3.2. Magnitude and reliability of the presaccadic response

The ability of the population of V4 neurons to discriminate between the preferred and non-preferred RF stimuli depends both on the mean response elicited by the two stimuli and on the response reliability. Presaccadic changes in stimulus discrimination could either be due to changes in response magnitude or changes in response reliability or both. To determine which is the case, we first examined the difference between the mean presaccadic responses
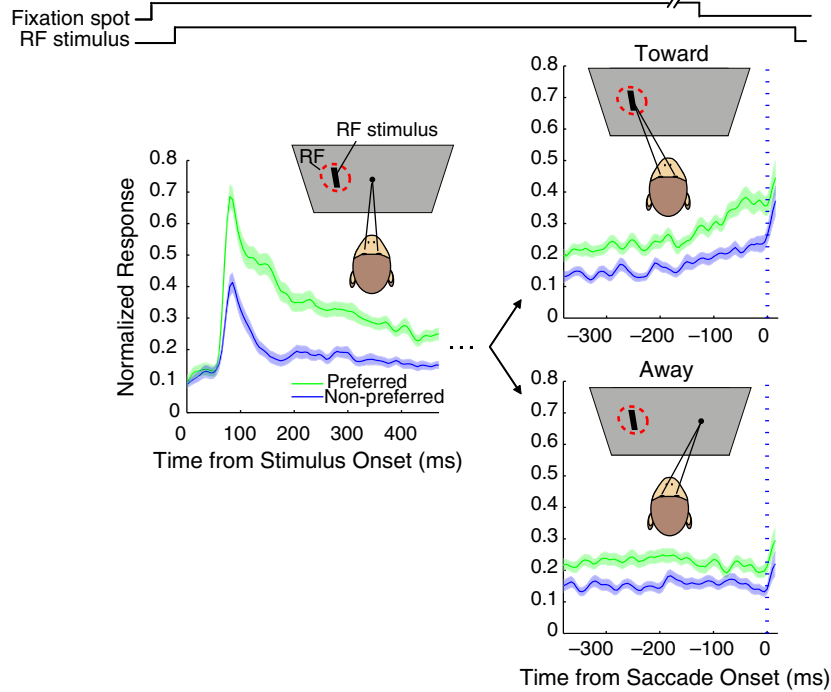
Fig. 1. Normalized responses of V4 neurons during the visually-guided, delayed saccade task. The task was separated into two phases: first, the monkey fixated a central spot while an oriented bar stimulus was presented within the neuron's RF; second, the monkey was either cued to saccade to the RF stimulus (*toward*) or to a saccade target in the opposite direction (*away*) when the fixation spot was extinguished. The saccade target only appeared on *away* trials and thus distinguished the two conditions. Cartoon diagrams of the task illustrate an example of a bar stimulus within a single neuron's receptive field (red dotted circle) and the monkey's gaze for both phases of the task. Each plot shows the mean response of 63 orientation-selective neurons to their preferred (green) and non-preferred (blue) orientations over time, centered on a 50 ms sliding window. The plot on the left shows the combined response of all trials, aligned to stimulus onset, while the plots on the right separate responses in the *toward* and *away* cases, aligned to saccade onset. Shading indicates standard error of the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)
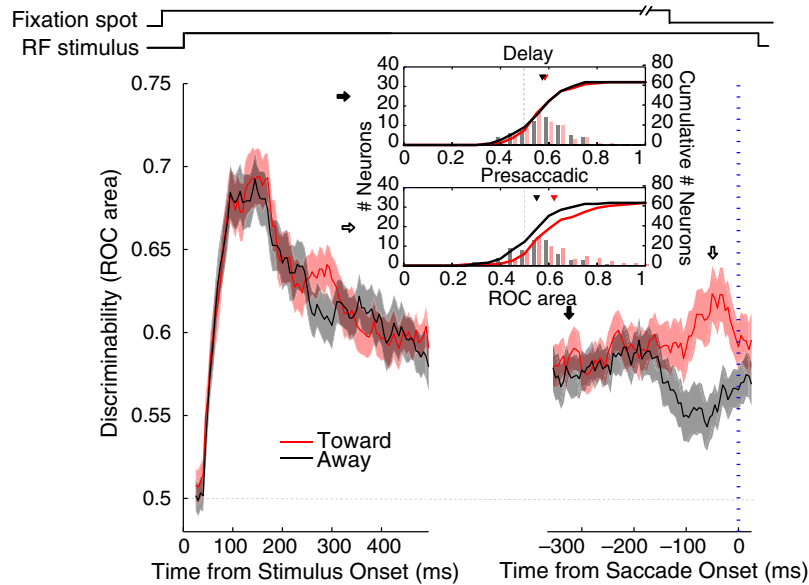

Fig. 2. Discriminability of V4 neurons measured by ROC area during the delayed saccade task. For each neuron, ROC curves were computed for preferred and non-preferred orientations in a sliding 50 ms analysis window. The main axes show the mean ROC area of 63 orientation-selective cells across time, aligned to stimulus and saccade onsets, for saccades *toward* (red) and *away* (black) from the RF. Shading indicates standard error of the mean. The inset histograms show the distribution of ROC areas across neurons for a 50 ms segment during the delay period (top, filled arrow; 325 ms before the saccade) and presaccadically (bottom, open arrow; 50 ms before saccade onset) with the corresponding cumulative distribution functions (right ordinate). Triangles indicate the mean ROC areas in each time period. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

to preferred and non-preferred stimuli and compared the difference in the *toward* condition to that of the *away* condition. As previously reported (Moore et al., 1998), saccades *toward* the RF stimulus were preceded by a significantly greater difference in preferred and non-preferred responses than saccades away (*P* < .04, Wilcoxon signed rank test). Thus, the improvement in presaccadic

stimulus discrimination was at least partly due to an increased difference in the response magnitude of visual responses.

We measured the reliability of visuals responses in two ways. First, we examined the relationship between the mean presaccadic responses and the variance in response across trials for the population of selective neurons (Fig. 3A). Mean response and variance data were taken from a 50 ms window centered at −50 ms (−75 to −25 ms) relative to saccade onset for both *toward* and *away* conditions. The data from the two conditions were then fit with power functions and compared as in previous studies (Armstrong & Moore, 2007; Bichot, Thompson, Rao, & Schall, 2001; McAdams & Maunsell, 1999b). The relationship between mean response and variance did not differ between the two saccade conditions. Both the power terms (power$_{toward}$ = 1.3, power$_{away}$ = 1.3; $P > .7$, Wilcoxon signed rank test) and the coefficients (coeff$_{toward}$ = 0.87, coeff$_{away}$ = 0.94; $P > .4$) were statistically indistinguishable for saccades made *toward* or *away* from the RF. Thus, by this metric, it appeared that the improvement in stimulus discrimination prior to saccades to the RF stimulus was not due to an increase in response reliability, suggesting that it was due only to changes in the response magnitude.

However, a recent study reported evidence of an increased reliability of V4 responses during covert attention as measured by the Fano factor (Mitchell, Sundberg, & Reynolds, 2007). The Fano factor is simply the ratio of spike count variance to the mean spike count, and because it can be computed on an individual neuron basis, it may be a more sensitive measure of response variability. Thus, we also computed the Fano factor for responses in the *toward* and *away* case for the same 50 ms time window used to measure ROC areas (Fig. 3B). Consistent with the findings of Mitchell et al. (2007), we found a difference between the two behavioral conditions. The Fano factor was significantly reduced prior to saccades *toward* the RF, as compared to the *away* condition (toward = 1.08; away = 1.23, $P < .02$, Wilcoxon signed rank test). Moreover, the magnitude of the decrease (median = 15.7%) was comparable in size to that reported during covert attention in the above study (~10%). Thus, the presaccadic changes in stimulus discrimination appeared to be due to changes in both the magnitude and the reliability of the visual response.

3.3. Is presaccadic enhancement stimulus-driven?

Although the cue to saccade in both *toward* and *away* trials included the offset of the fixation spot, only the latter condition included the onset of a visual target on the display. Thus, there remains the possibility that the changes in presaccadic activity, and stimulus discrimination, were primarily visually-driven, rather than due to differing saccade plans. While one may not expect a small (0.5°) target flashed in the hemifield opposite of the RF to elicit the modulation observed, and indeed it is has been shown that surround effects in area V4 require sufficient size and contrast beyond that of the targets used here (Desimone, Moran, Schein, & Mishkin, 1993), the dependence of the presaccadic modulation on stimulus events remains an open question. To address this question, we examined neuronal activity during trials in which the fixation offset (cue to move) had not yet occurred but the monkey initiated a saccade and aborted the trial. Data from the entire population of visually responsive neurons ($n = 90$) were used to extract trials on which the monkey aborted the trial and made a saccade to the RF stimulus ($n = 239$ trials) or to a location outside of the RF ($n = 471$ trials). These abortive saccade trials were used to test the effect of saccade direction (*toward* versus *away*) on presaccadic activity in the absence of any differences in the visual display (Fig. 4). Similar to what is observed during correct *toward* and *away* trials in which the direction of the saccade is cued, the uncued, abortive saccades to the RF stimulus are preceded by a significant enhancement in visual activity, compared to when they are made to locations outside of the RF ($P < .01$, one-sided Kolmogorov–Smirnov test). Thus, the preparation of a saccade appeared to be sufficient to drive the enhancement of V4 responses when RF stimuli were targeted.

4. Discussion

We found that the discrimination of RF stimuli by V4 neurons, as measured by ROC analysis, is significantly altered prior to saccadic eye movements. The discriminability of orientation-selective neurons was transiently increased within 50 ms of saccades directed to the RF stimulus. In contrast, stimulus discrimination was
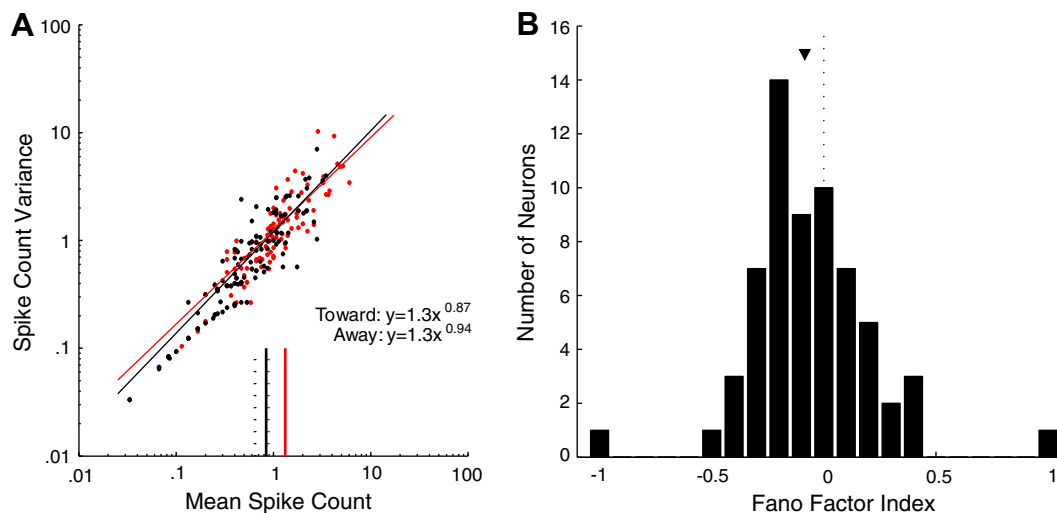

Fig. 3. Effect of saccade direction on presaccadic response magnitude and reliability. (A) Response variance and mean response (total spike count) within a 50 ms presaccadic analysis window (50 ms before saccade onset) are plotted for the preferred and non-preferred orientations of each cell for the *toward* (red) and *away* (black) cases. Power functions were fit to the data for both saccade conditions with the best-fit equations shown. The mean response of the preferred orientation is indicated by a solid vertical line, while the mean response of the non-preferred orientation is indicated by a dotted vertical line. (B) Distribution of Fano factor indices during the same 50 ms presaccadic analysis window. Fano factor (FF) index was computed as (FF$_{toward}$ − FF$_{away}$)/(FF$_{toward}$ + FF$_{away}$). The arrowhead at the top of the distribution indicates the median index (−0.084). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)
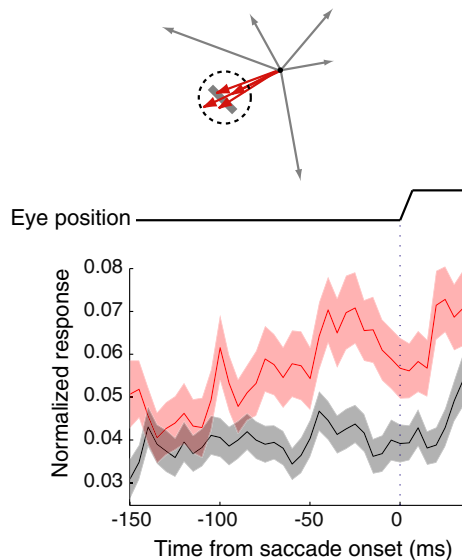
Fig. 4. Responses of V4 neurons during aborted trials. Trials in which the monkey broke fixation before the cue to saccade are grouped by the endpoint of the un-cued saccade. The diagram at the top depicts the two classes of abortive saccades, with red arrows indicating saccades into the RF and gray arrows indicating saccades elsewhere. The plot below shows the average normalized response of neurons aligned to the onset of the saccades with endpoints inside (red) and outside (gray) the RF. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

transiently decreased prior to saccades made to other locations. The opposing changes in presaccadic stimulus discrimination resulted in a substantial difference in the ability of V4 neurons to discriminate the RF stimulus depending on the direction of the imminent saccade. The changes in stimulus discrimination resulted in part from significant changes in the difference in response magnitude between preferred and non-preferred RF stimuli. This observation is consistent with those of previous studies of the effects of covert attention on V4 responses (McAdams & Maunsell, 1999a; McAdams & Maunsell, 1999b; Spitzer, Desimone, & Moran, 1988), as well as in studies that have evoked changes in visual responses of V4 neurons with FEF microstimulation (Armstrong & Moore, 2007). Both experimental manipulations improve V4 response discriminability, and do so at least in part via changes in response magnitude.

A recent study found that the effects of covert attention differ between regular-spiking and fast-spiking neurons in V4 (Mitchell et al., 2007). Fast-spiking neurons, which correspond to presumed locally-projecting interneurons, exhibit more dramatic effects of attention than regular-spiking neurons which should largely consist of distally projecting cells. Moreover, the effects of attention on the responses of both regular-spiking neurons and fast-spiking responses included an increase in response reliability, particularly in the latter class of neurons. This result differs from the report of McAdams and Maunsell (1999b) in which no changes in response reliability were observed using the population-level relationship between mean spike count and spike count variance as a measure. We also found no evidence of a difference in response reliability between the *toward* and *away* conditions using the population-level measure (Fig. 3A), similar to our observed effects of FEF microstimulation (Armstrong & Moore, 2007). However, using the Fano factor as the measure of reliability, we found evidence of increased reliability of visual responses in the *toward* condition. Thus, evidence of changes in response reliability appears to depend on the way in which it is measured. This dependence may be due to a greater sensitivity of the Fano factor analysis, which allows for

a *within* comparison for each neuron, in contrast to the population-level analysis used in the other method. Thus, it appears that for both covert attention and saccade preparation, the increased discriminability of V4 visual responses occurs as a result of increased reliability as well as increased response magnitude.

The similarities between the effects of covert attention, saccade preparation (overt attention), and FEF microstimulation are consistent with the hypothesis that the filtering of visual signals within cortex is due at least in part to an interaction of visual and saccade-related signals during the preparation of saccades (Moore et al., 2003). This interaction could involve the direct feedback projections from the FEF to areas within extrastriate cortex (including V4) (Stanton, Bruce, & Goldberg, 1995), an influence of projections from the superior colliculus via the pulvinar nuclei (Wurtz, Sommer, & Cavanaugh, 2005), an influence of the lateral intraparietal area (LIP) (Goldberg, Bisley, Powell, & Gottlieb, 2006), or all of the above. Nevertheless, the interaction appears to be sufficient to bring about perceptual benefits of the type observed during covert attention when saccades are withheld (Cavanaugh & Wurtz, 2004; Cavanaugh et al., 2006; Moore & Fallah, 2001, 2004; Muller et al., 2005). This interaction also appears to facilitate the influence of visual target features, such as orientation (Moore, 1999) or direction of motion (Schafer & Moore, 2007), on the metrics of saccades when they are actually made. Furthermore, the timing of presaccadic increases in discriminability is consistent with the presumed synaptic delays of signals sent from extrastriate cortex to the FEF and the SC, which mediate the triggering of the saccade during overt attention. The enhancement of visual responses during overt and covert attention, and the increase in the discriminability of RF targets suggest that the interaction of visual and saccade-related signals is reciprocal and that it results in the simultaneous selection of target features and the appropriate/optimal saccade metrics with which to direct gaze. A challenge of future studies will be to identify the specific neurons that contribute the cross-areal interactions that give rise to the combined visual and oculomotor benefits of attentional selection.

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