Dynamic sensitivity of area V4 neurons during saccade preparation

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During the preparation of saccadic eye movements, visual attention is confined to the target of intended fixation and there is a corresponding diminution of visual sensitivity at nontarget locations. Neurons within the macaque visual cortex exhibit correlates of these perceptual changes, such as in area V4, where neuronal responses are enhanced during the preparation of saccades to stimuli within the receptive field (RF), and responses are suppressed during the preparation of saccades to other locations. Both the perceptual and neurophysiological effects suggest that the sensitivity of visual cortical neurons to input is dynamic during saccade preparation. We probed the contrast sensitivity of area V4 neurons to nontarget stimuli at varying times during the preparation of saccades to locations outside of the neuron's receptive field. We found that the contrast sensitivity of many neurons is profoundly altered within 50 ms of saccade onset. The luminance or color contrast sensitivity of individual V4 neurons could increase, decrease, or remain unchanged before saccade onset. For luminance contrast sensitivity, decreases in sensitivity were more frequent and larger in magnitude, resulting in an overall decrement in sensitivity across the population. For color contrast, the effects were smaller and more heterogeneous, resulting in little or no overall change in sensitivity across the population. Our results demonstrate the dynamic influence that saccade preparation has on the sensitivity of visual cortical neurons and suggest a basis for the changes in perception known to occur during saccade preparation.

oculomotor | saccadic suppression | transaccadic integration | visuomotor integration | perceptual constancy

Visual spatial attention is typically time locked to the onset of saccades (1–2). Although attention is sometimes deployed to peripheral locations without concomitant saccades (covert attention), more often it is deployed along with them (overt attention). As a result of heightened attention at the saccade target, saccades are accompanied by diminished perception at nontarget locations (3). Neurophysiological studies have established that covert attention alters the responses of neurons in the visual cortex (4). For example, covert attention enhances the responses or contrast sensitivity of neurons in macaque area V4 to visual stimuli within their receptive fields (RFs) (5–9). The perceptual and neurophysiological effects of covert attention are thought to result at least in part from a direct influence of saccade-related signals on visual cortical representations (10). For example, the attentional modulation of visually driven responses of area V4 neurons can be recreated by electrical microstimulation within the frontal eye field (FEF) (11–13). Specifically, microstimulation of the FEF at sites that spatially overlap RFs of recorded V4 neurons transiently enhances the response to stable RF stimuli. In contrast, microstimulation of the FEF at sites that do not overlap with V4 RFs suppresses V4 responses. These results suggest that "top-down" signals corresponding to developing saccade plans alter the gain of visual cortical representations in favor of relevant targets, whether or not a saccade is actually executed.

Consistent with a possible role of saccade mechanisms in attention is the finding that V4 neurons exhibit enhanced visual responses when saccades are made to stimuli within their RFs (14–16). However, it is not yet known how saccade preparation dynamically affects the sensitivity of neurons in visual cortex. To address this question, we measured the dynamics of contrast sensitivity of area V4 neurons of monkeys during the preparation of saccades to non-RF targets. We found that the contrast sensitivity of many neurons is profoundly altered before saccade onset. For luminance contrast sensitivity, there was an overall decrement in sensitivity across the population of neurons that reduced sensitivity by about half. For color contrast, the effects were smaller and more heterogeneous and this resulted in little or no overall change in sensitivity across the population. Our results demonstrate the dynamic influence that saccade preparation has on the sensitivity of visual cortical neurons and suggest a basis for the changes in perception known to occur during saccade preparation.

Results

We measured the sensitivity of single V4 neurons to both luminance and color contrasts during the preparation of saccades to non-RF targets using an experimental paradigm in which thresholds could be measured at varying epochs relative to saccade onset (Fig. 1). For single V4 neurons we determined contrast thresholds for luminance and for equiluminant "red-green" (L/M-cone) and "blue-yellow" (S-cone) colors using optimally oriented bar stimuli briefly flashed (<2 ms) within each neuron's RF. Thresholds for luminance and for the 2 color contrasts were obtained via a "staircase" procedure adapted for single neuron responses. In this procedure, the contrast of the visual stimulus was adjusted on each trial according to the deviation of the neuron's visually driven response from its baseline activity (see *Methods*). Because the normal saccadic reaction time is ≈150 ms, the brief RF stimulus could be flashed during different time windows, thus allowing us to probe the dynamics of each neuron's contrast sensitivity during saccade preparation.

We measured contrast thresholds in a total of 138 single V4 neurons in 2 monkeys. Fig. 2 depicts an example experiment in which visually evoked responses and thresholds were measured during the early and late presaccadic epochs for a neuron sensitive to luminance and equiluminant color probes. For probes presented long before saccade onset (−176 to −106 ms, median = −141.5 ms, n = 16 trials), the neuron responded reliably to low luminance contrast probes flashed in the RF, yielding a threshold of 11% in the staircase procedure (Fig. 2 *C*

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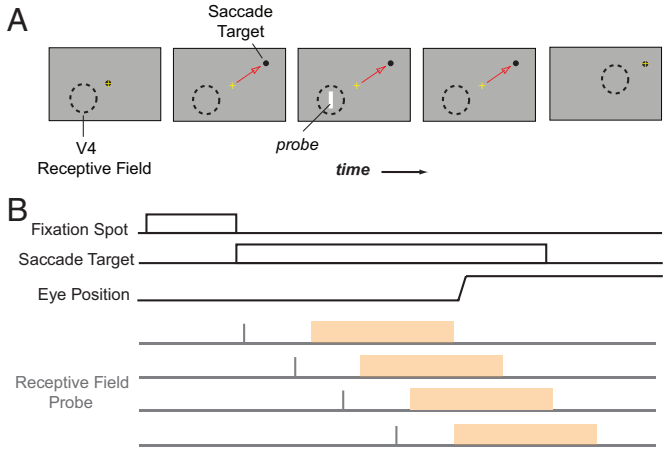

Fig. 1. Probing presaccadic sensitivity of V4 neurons. (*A*) Sequence of stimulus events. A visually guided saccade task was used to probe the sensitivity of V4 neurons during saccade preparation. In this task, monkeys initiated each trial by fixating a central spot (black dot in the first panel; cross illustrates monkey's gaze position). Dotted circle indicates the receptive field (RF) of a recorded V4 neuron. After a delay, the fixation spot was turned off and a saccade target appeared at an unpredictable location distant from the RF (second panel). While the monkey prepared a saccade (red arrow), an oriented bar (probe) stimulus was briefly flashed in the center of the RF (third panel), and removed before saccade onset (fourth panel). The fifth panel shows the relocated V4 neuron's RF following fixation of the saccade target. (*B*) Timing of stimulus events and measurement of V4 responses. Event plots show the timing of onset/offset of the fixation spot, saccade target, the saccade, and RF probe stimulus. The RF probe stimulus plots show the 4 presaccadic stimulus times (vertical lines) and the subsequent 120 ms window in which neuron responses were measured starting 50 ms after stimulus onset.

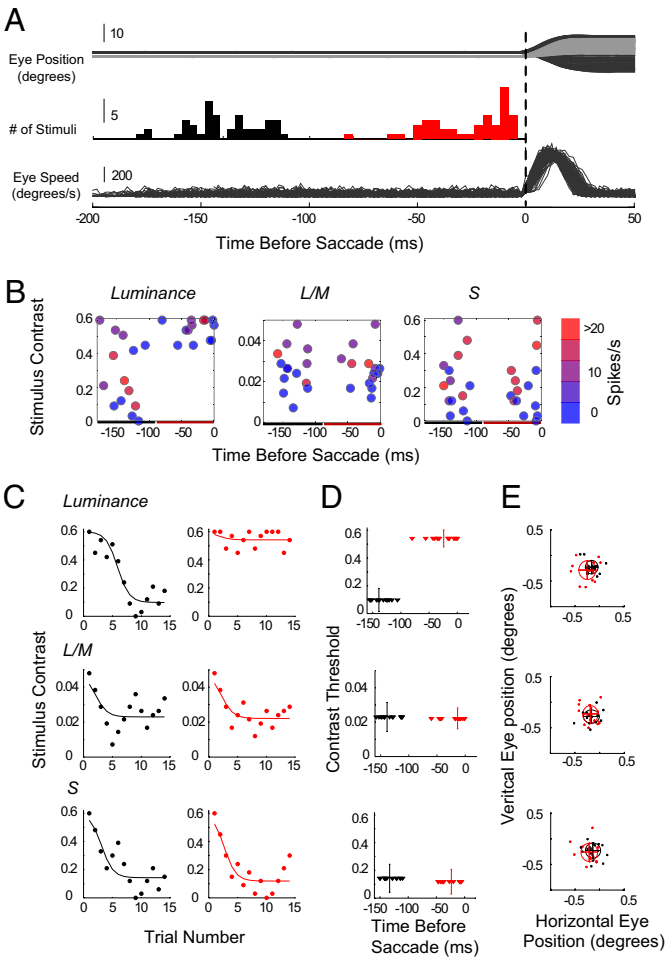

Fig. 2. Measurement of presaccadic contrast thresholds in a single V4 neuron. (*A*) *Top* and *Bottom* plots show the eye position (horizontal in gray, vertical in black) and eye speed for saccades made to targets distant from the V4 neuron's RF. *Middle* plot shows the distribution of RF probe times relative to saccade onset for 2 presaccadic epochs, *early* (< −106 ms, black) and *late* presaccadic epochs (> −83 ms, red). (*B*) Visual responses of a V4 neuron to luminance and color (L/M, S) contrast during the early and late presaccadic times (indicated by the black and red bars at the *Bottom*). (*C*) Threshold estimates for luminance and color contrast obtained from the staircase procedure during the early (black) and late (red) presaccadic epochs. Each dot indicates the contrast of the probe stimulus on a given trial, and the solid line shows the asymptotic fit used to obtain the neuron's threshold. (*D*) Contrast thresholds shown with the distribution of RF probe presentation times (black and red arrow heads). Vertical lines denote the threshold ± standard error of mean. (*E*) Plot of the monkey's eye position at the time of visual stimulus presentation for the 2 presaccadic epochs. Crosses and circles indicate the mean and standard deviation, respectively.

and *D*). However, for probes appearing immediately before saccade onset (−83 to −3 ms, median = −23 ms), the neuron failed to respond to the lower or medium luminance contrast probes and only responded to the highest contrast probes (Fig. 2*B*). During the late presaccadic period, the neuron's contrast threshold to luminance was elevated to 53% (Fig. 2 *C* and *D*). Thus, the contrast threshold of this neuron increased by ≈5-fold in less than 100 ms. This effect was not the result of differences in RF stimulation between the 2 epochs because in both cases the presentation of the RF stimulus occurred during fixation and was completed before saccade onset. The position of the monkey's gaze at the time of stimulus presentation (Fig. 2*E*) confirmed that the retinotopic location of the probe did not differ between the early and late presaccadic epochs ($P > 0.11$, ANOVA).

Unlike what we observed for luminance contrast, the neuron's color contrast thresholds were not affected by saccade preparation (Fig. 2 *B–D*). Because this neuron responded both to "red-green" (L/M) and "blue-yellow" (S) color contrast, we also measured its sensitivity to equiluminant color probes across the presaccadic period. As in the luminance contrast trials, gaze position was unchanged before saccade onset ($P > 0.18$, ANOVA) (Fig. 2*E*). Yet unlike luminance contrast, responses of this neuron to color and the corresponding color contrast thresholds were also unchanged during the early and late presaccadic epochs. Thus, for this V4 neuron there was a dramatic increase in contrast threshold during saccade preparation that was confined to luminance.

Increases in luminance contrast thresholds (decreases in sensitivity) during the presaccadic period were readily observed in V4 neurons in the 2 monkeys studied. Fig. 3 shows 4 more example neurons, each of which responded to all 3 contrasts, and displays the thresholds obtained at 4 different presaccadic epochs. In 3 of the examples (Fig. 3 *A–C*), contrast threshold to luminance rose by varying amounts within the last 100 ms before saccade onset. However, the results were more variable for color contrast. In only 1 of the 4 cases shown was the color contrast threshold significantly increased presaccadically (Fig. 3*A*, $L/M_{-123\ ms} = 0.12\%$ vs. $L/M_{-30\ ms} = 3.5\%$, $P < 0.003$, ANOVA). In many cases, color contrast thresholds remained stable. In other cases, the color contrast threshold decreased significantly just before saccade onset (Fig. 3*C*, $L/M_{-108\ ms} = 4\%$ vs. $L/M_{-23\ ms} = 1\%$, $P < 0.003$, ANOVA; Fig. 3*D*, $S_{-118\ ms} = 40\%$ vs. $S_{-24\ ms} = 12\%$; $P < 0.007$, ANOVA). As in the first example, for these 4 neurons presaccadic eye position was constant during each of the 4 epochs and across contrast types ($P > 0.22$, ANOVA), and thus the location of probe stimuli within the RF was held constant.

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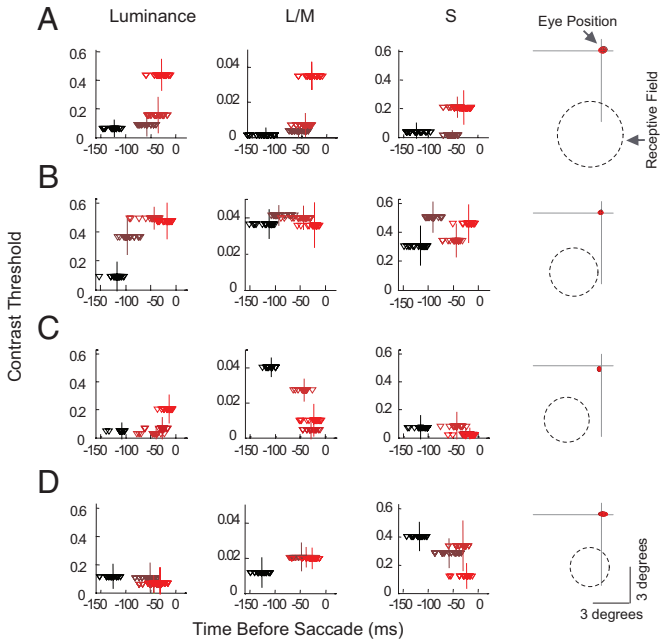

Fig. 3. Heterogeneity of presaccadic changes in sensitivity. Each set of plots (*A–D*) shows contrast threshold estimates of a single V4 neuron measured at 4 presaccadic epochs with respect to saccade onset (black to red) for luminance, L/M and S contrast. For each neuron, the corresponding mean (crosses) and standard deviation (circles) of the monkey's eye position during probe presentation is shown with the neuron's RF on the *Right*.

We categorized V4 neurons according to the overall change in contrast sensitivity during the last 40 ms (late presaccadic) of saccade preparation. Of the 138 neurons recorded in 2 monkeys, we obtained late presaccadic luminance contrast sensitivities for 68 (Table 1). Of these, 29 neurons (43%) exhibited a significant suppression of contrast sensitivity in the late presaccadic epoch (compared with the early presaccadic period, >97 ms before saccade onset), while 32 neurons (47%) were not significantly modulated (Fig. 4*A*). For the 29 "suppressed" neurons, sensitivity was reduced to a median 29% of the early presaccadic value, a >3-fold reduction. A remaining 7 neurons (10%) showed significant decreases in luminance contrast thresholds and thus had heightened presaccadic sensitivity. For these "enhanced" neurons, sensitivity was increased to a median 174% of the early presaccadic value, a roughly 2-fold enhancement. Thus not only were luminance-suppressed neurons twice as frequent as luminance-enhanced neurons ($\chi^2 = 13.4, P < 0.001$), but the suppression was of greater magnitude. In addition, the median sensitivity of the 32 nonmodulated neurons approached significant suppression (median = 82%, $P = 0.1$, Wilcoxon sign rank).

Across the population of neurons, the pattern of results for color contrast sensitivity differed from that of luminance contrast sensitivity in that an overall trend toward suppression or enhancement was not apparent. Of the 58 neurons sensitive to L/M contrast, 21 neurons (36%) were suppressed, 23 (40%) were unaffected, and 14 (24%) were enhanced. Of the 67 neurons sensitive to S contrast, 26 neurons (39%) were suppressed, 23 (34%) were unaffected, and 18 (27%) were enhanced. Significant changes in color contrast sensitivity (suppression or enhancement) were therefore about as frequent as that of luminance contrast sensitivity (L/M = 60%; S = 66%; luminance = 53%). However, the balance of suppression and enhancement for color contrast was roughly equal across the population of neurons. Not only was the frequency of suppression and enhancement statistically equal across the population of neurons (L/M: $\chi^2 = 1.4$, $P > 0.23$; S: $\chi^2 = 1.5$, $P > 0.22$), but the magnitude of suppression and enhancement was generally smaller for color contrast (L/M: median suppression = 51%; median enhancement = 141%; S: median suppression = 60%; median enhancement = 147%). Moreover, unlike luminance, there was no apparent change in sensitivity to either color contrast for the combined subpopulation of "nonmodulated" neurons (L/M, median = 93%, $P > 0.8$; S, median = 101%, $P > 0.9$, Wilcoxon sign rank). Consequently, there was no significant change in L/M or S contrast sensitivity across the population overall from the early to late presaccadic epoch (L/M, $P > 0.17$; S, $P > 0.11$ Wilcoxon sign rank). By comparison, there was a highly significant decrease in luminance contrast sensitivity for the overall population ($P < 10^{-4}$, Wilcoxon sign rank). Suppression of luminance contrast was also consistent across neurons recorded from the 2 different monkeys, while changes in color contrast were variable (Table 1). Importantly, presaccadic eye position during the last 40 ms of saccade preparation was identical to that of the early presaccadic epoch in both monkeys (monkey 1: $\text{horizontal}_{\text{early}}$ vs. $\text{horizontal}_{\text{late}}$, $P > 0.65$; $\text{vertical}_{\text{early}}$ vs. $\text{vertical}_{\text{late}}$, $P > 0.53$; monkey 2: $\text{horizontal}_{\text{early}}$ vs. $\text{horizontal}_{\text{late}}$, $P > 0.48$; $\text{vertical}_{\text{early}}$ vs. $\text{vertical}_{\text{late}}$, $P > 0.36$, ANOVA), and thus the location of probe stimuli within the RF remained stable across time and contrast types (Fig. 4*B*).

To examine the dynamics of presaccadic contrast sensitivity more closely, we combined the sensitivities across the population of neurons and sorted them into 8 presaccadic epochs (Fig. 5). For each neuron, the sensitivity at each epoch was normalized to that of the earliest presaccadic epoch to obtain a relative sensitivity measure throughout saccade preparation. This analysis revealed a systematic decline in luminance contrast sensitivity before saccade onset. For the entire population of neurons, luminance contrast sensitivity began to decline at ≈50 ms of the saccade onset and was reduced to nearly half of the early presaccadic value within 20 ms of saccade onset (28 neurons,

Table 1. Presaccadic contrast sensitivity changes for neurons recorded in the 2 monkeys

	Luminance		L/M		S	
	Number of neurons	Median relative sensitivity	Number of neurons	Median relative sensitivity	Number of neurons	Median relative sensitivity
Monkey 1						
Suppressed	11	0.26	9	0.41	13	0.46
Enhanced	4	2.65	2	1.46	7	1.42
Nonmodulated	11	0.99	8	0.92	8	1.05
Monkey 2						
Suppressed	18	0.55	12	0.74	13	0.67
Enhanced	3	1.63	12	1.41	11	1.51
Nonmodulated	21	0.77	15	1.02	15	0.97

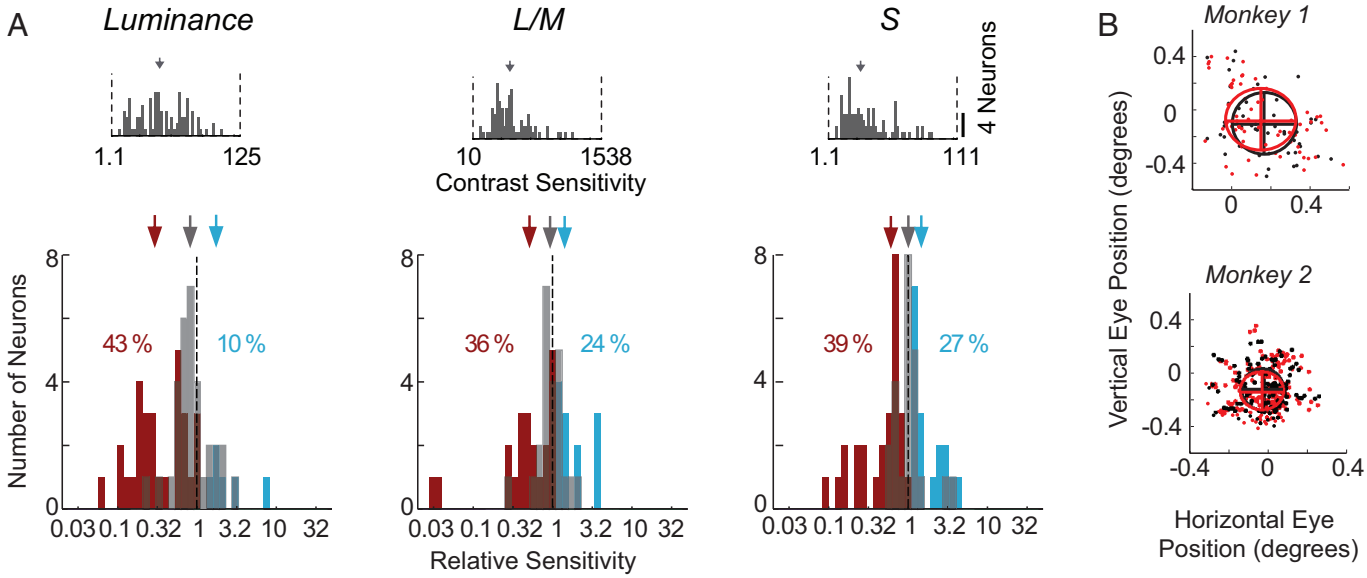

Fig. 4. Presaccadic changes in contrast sensitivity for the population of V4 neurons. (*A*) *Top* gray histograms show the distributions of luminance and color contrast sensitivities measured during the early presaccadic epoch (< −97 ms before onset; mean = −121 ms) for the population of neurons. Dotted lines on *Left* and *Right* indicate the lowest or the highest measurable contrast sensitivity. Arrows show the median values. *Bottom* histograms show the distribution of V4 neurons with significantly suppressed (red), enhanced (blue), or unaffected (gray) sensitivity to luminance and color contrast during the late presaccadic epoch (within 40 ms of saccade onset). Relative sensitivity values (log scale) compare the late presaccadic sensitivity relative to that measured during the early presaccadic epoch. Arrows show the median values for enhanced, suppressed, and unaffected neurons. The dotted vertical lines at 1 (relative sensitivity) show where unchanged sensitivities should fall. (*B*) Plot of mean eye positions at the time of probe presentation for each neuron and at both early (black) and late (red) presaccadic epochs. Data from the 2 monkeys are shown separately.

mean relative sensitivity = 0.57, $P < 0.007$, Wilcoxon sign rank). Yet, although there were clear examples of both suppression and enhancement of color contrast sensitivity for individual neurons, there was no overall suppression across the population. For neither L/M nor S was the presaccadic sensitivity measured just before saccade onset (20 ms) significantly different from that measured long before the saccade (L/M, 26 neurons, mean relative sensitivity = 0.87, $P > 0.73$; S, 30 neurons, mean relative sensitivity = 0.81, $P > 0.23$, Wilcoxon sign rank). Thus for the combined population of V4 neurons, presaccadic changes in visual sensitivity were only reliable for luminance contrast.

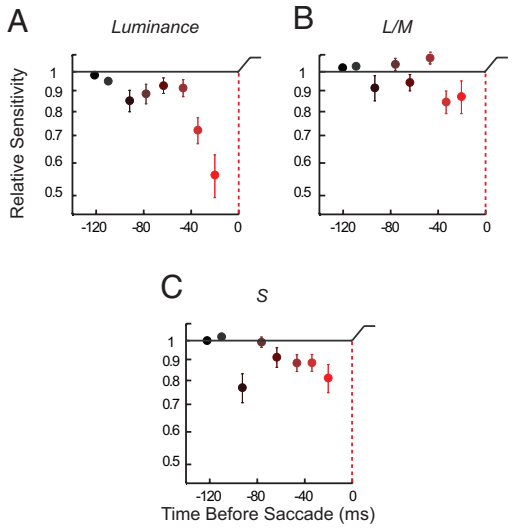

Fig. 5. Fine temporal dynamics of presaccadic sensitivity to luminance (*A*) and color contrast (*B*, *C*) for the population of V4 neurons. Suppressed, enhanced, and unaffected neurons are combined, but relative sensitivity values from each neuron are binned into 15-ms intervals relative to saccade onset (dotted red line). From long before saccade onset (black) to immediately before (red), the number of neurons contributing to each mean is: $N_{Luminance}$ = [54, 54, 31, 51, 38, 65, 56, 28], $N_{L/M}$ = [44, 52, 20, 40, 47, 75, 46, 26], and N_S = [46, 60, 16, 48, 47, 60, 52, 30].

Discussion

Our results demonstrate that the contrast sensitivity of area V4 neurons is highly dynamic during saccade preparation. Saccades that target stimuli outside of a neuron's RF are preceded by large changes in luminance and color contrast sensitivity, often many-fold, including both increases and decreases. Both types of changes are extremely rapid and occur within 50 ms before saccade onset. Although there is clear heterogeneity across the population, the net effect of saccade preparation on V4 neurons is a marked decrease in luminance contrast sensitivity, which is largely the result of a greater magnitude and frequency of suppression of luminance contrast sensitivity among individual neurons. Below we discuss some possible explanations for our observations and their relevance to known changes in visual perception during saccades.

Although comparisons of neuronal sensitivity were made across presaccadic epochs with the same visual stimuli, and at the same retinotopic locations, it is nonetheless important to consider the extent to which RF stimulation was held constant during saccade preparation. For example, it is known that the RFs of V4 neurons can be altered during saccade preparation (17). Specifically, V4 RFs can shift in the direction of the saccade within 50 ms of saccade onset. This observation raises the possibility that the diminished luminance contrast sensitivity before saccade onset exhibited by many V4 neurons in our study was the result of RFs shifting beyond the location of our probe stimuli. However, if the primary effect of saccade preparation were a shift in RF position, this would not explain the lack of overall changes in color contrast sensitivity across the population of neurons, or the contrast-selective suppression observed in individual neurons (Fig. 3). Indeed, any form of divergent effect

of saccades on contrast sensitivity in single neurons (e.g., enhancement for L/M contrast sensitivity, but suppression for luminance contrast sensitivity) seems to rule out any wholesale shifts in RF position, but would instead require more complex changes in RF structure. Moreover, in the previous study, the occurrence of RF shifts tended to coincide with saccades made to locations near the RF, whereas saccades made to more distant target locations did not typically produce measurable shifts (17). In our task, saccade targets always appeared in a different visual field quadrant than the RF and the distance between target and RF was on average >12°. Lastly, we also observed that all of the neurons tested responded to the highest contrasts during the presaccadic period. Therefore, it is unlikely that presaccadic changes in contrast sensitivity are the result of RF shifts.

The dramatic changes in V4 sensitivity observed during saccade preparation suggest a correlate of known changes in visual perception at the time of saccades. Because spatial attention is often time locked to the onset of saccades (2–3), our results are consistent with the effects of covert attention on the luminance contrast sensitivity of V4 neurons (8). Withdrawing attention from RF stimuli, without a concomitant saccade, reduces the luminance contrast sensitivity of V4 neurons to ≈66% of the sensitivity measured during attention. Thus, although the change in sensitivity caused by varying covert attention appears to be smaller than the change with saccades (overt attention), the effects of both types of attention on V4 neurons are consistent with evidence that they are both driven by oculomotor mechanisms (11–13). The effects of overt and covert attention on luminance contrast also supports the view that neuronal sensitivity is related to the probability that a saccade will be made to a neuron's RF (18), reaching the lowest probability when targeting stimuli outside of the RF just before saccade onset. This view predicts that visual events occurring at nontarget locations during saccades are less likely to interfere with an accurate and robust representation of the saccade target (3, 14), and thus it begins to suggest a causal basis for perceptual stability during visual scanning.

On the other hand, the effects of saccade preparation on color contrast sensitivity paint a more complicated picture. Psychophysical studies have found that covert attention alters color contrast sensitivity (19), as it does for luminance contrast sensitivity (20). Yet, color contrast sensitivity is largely unaltered during saccades, at least at nontarget locations (21). Thus, the simple view that sensitivity in general is primarily determined by saccade probability seems flawed. Our finding of less reliable changes in color contrast sensitivity in V4 during saccade preparation, although consistent with the psychophysical results, indicates that the dynamics of visual sensitivity are not solely accounted for by the coupling of visual attention with saccades. Instead, the findings suggest that when actually carried out, saccades exert an additional influence on visual cortical signals than when they are merely planned, but withheld. The additional influence of triggered saccades, although continuous with the effects of planned saccades in the luminance domain, may be divergent in the color domain. In fact, 3 important points suggest that while saccade preparation may be sufficient to alter visual signals, the influence of the saccade trigger is unique. First, it has long been argued that to achieve perceptual stability across saccades, particular visual features, such as luminance contrast and motion, are most important to suppress when a movement is made. Therefore, one would expect triggered saccades to selectively suppress those features (21–22). Second, a recent neurophysiological study found that "movement" neurons within the FEF are not enhanced during covert attention, in contrast to their "visual" and "visuomovement" counterparts, but are instead suppressed (23). Thus, it is argued that neurons triggering a saccade are not the ones driving stimulus selection in the visual cortex, but rather the neurons involved in converting visual input into an appropriate saccade plan (18, 24). Third, a series of elegant studies by Sommer and Wurtz (25–26) has identified a specific pathway from the superior colliculus through the thalamus and into cortex in which copies of movement commands, so-called "corollary discharge" signals (27), appear to alter visual representations. The results of these studies provide evidence of a unique mechanism by which triggered saccades may exert systemwide influences on visually responsive neurons. Moreover, the fact that the putative corollary discharge signals impact heavily on thalamic nuclei is consistent with evidence that psychophysically measured saccadic suppression originates at the thalamic level (21).

Methods

Electrophysiology and Behavior. We recorded single neurons in area V4 of 2 macaque monkeys using standard neurophysiological techniques. General experimental and surgical procedures were in accordance with National Institutes of Health Guide for the Care and Use of Laboratory Animals and Stanford University Animal Care and Use Committee. Each animal was surgically implanted with a head post, a scleral eye coil, and a recording chamber. Craniotomies were performed on the prelunate gyrus for access to dorsal V4 (12). Eye position was monitored with a scleral search coil and digitized at 500 Hz (CNC Engineering). The spatial resolution of eye position measurements was ≪0.1° in both monkeys and our system allowed us to easily detect displacements of that size on individual trials (28). Stimulus presentation, data acquisition, and behavioral monitoring were controlled by CORTEX system. Data analysis was with Matlab.

We used a visually guided saccade task to probe the sensitivity of V4 neurons at varying times before saccade onset. In this task, monkeys initiated the trial by fixating a central spot (0.1–0.15°) within a 2 × 2° error window. After 300–900 ms, the fixation spot was turned off and a saccade target appeared at an unpredictable location (10–20° from the fixation spot) in a non-RF quadrant. To receive a reward, monkeys made a saccade to the target within 300 ms of fixation spot disappearance, and fixated it for at least 100 ms. The location of the saccade target varied randomly from trial to trial and was thus unpredictable to the monkey. However, the target always appeared in 1 of the non-RF quadrants and was on average >12° from the RF. During the presaccadic interval, a small bar stimulus (1.7°–1.75° × 0.75°–0.9°) was flashed for 1 frame on a CRT monitor (75 Hz) in the center of the RF, and at the neuron's preferred orientation. The bar stimulus was turned off before saccade onset. We used bar stimuli instead of gabor gratings because our initial experiments revealed that bars were more effective at evoking responses of V4 neurons when briefly presented, consistent with previous studies (29). However, we used relatively large bar widths to maximize power at "low" spatial frequencies (21). V4 neurons' RFs were mapped with moving oriented bars during fixation in a separate behavioral paradigm. V4 neurons recorded had RFs located between 2°–9° eccentricity (mean = 5.7°, standard deviation = 1.2°) and in the lower contralateral visual field.

The onset time of the RF stimulus was systematically varied with respect to the disappearance of the fixation spot (cue to move) up to 4 fixed times to experimentally control the time of presaccadic stimulus presentation. Because of the inherent variability in saccadic reaction time, the exact timing of the RF stimulus appearance varied within each of those fixed times. Nevertheless, because the variability of saccadic reaction time tended to be fairly small (standard deviation = 20 ms), probe appearance was largely controlled by the fixed times from fixation spot disappearance (Fig. S1). The exact timing of RF stimulus appearance with respect to saccade onset was determined for each trial offline using a saccade velocity and displacement trigger (28). Thus the set of fixed times could yield up to 4 largely discrete presaccadic time windows in which the RF stimulus appeared. For all measurements of sensitivity, only trials in which stimulus presentation was completed before saccade onset were used. The timing of stimulus offset was based on the direct measurement of phosphor excitation and decay at the RF location during separate experiments. These measurements confirmed the short decay of the CRT's (medium short persistence) phosphor to be <1 ms. Thus, even for a vertically elongated (1.75°) bar stimulus, the total presentation time was completed in <2 ms.

Equiluminant Color Stimuli. All stimuli were presented on a colorimetrically calibrated CRT monitor (Mitsubishi Diamond Pro 2070sb). Judd chromaticities of the phosphors were measured with a Spectra Colorimeter (PR-650, Photo Research Inc.) and the output of each phosphor was linearized using an International Light IL1700 Radiometer. The values were red (0.628, 0.342), green (0.294, 0.612), and blue (0.152, 0.081). The display background was

neutral gray, equal energy spectrum (EES) reference color (Judd (x, y) = (0.333, 0.333), 10cd/m^2). Color contrast was varied independently along the 2 principal color axes (''red/green'' and ''blue/yellow'') in Macleod and Boynton color space (30), specifically L/(L+M) or S/(L+M), abbreviated as L/M and S, respectively. All color stimuli were equiluminant with the background based on the equiluminance values obtained from each monkey in a ''minimum motion'' procedure (31), but varied in L/M or S contrast relative to EES. Color contrast was specified using Michelson contrast, computed as $(L/M_{\text{stimulus}} - L/M_{\text{EES}})/(L/M_{\text{stimulus}} + L/M_{\text{EES}})$ for L/M stimuli and $(S_{\text{stimulus}} - S_{\text{EES}})/(S_{\text{stimulus}} + S_{\text{EES}})$ for S stimuli.

Measurement of Contrast Threshold/Sensitivity. Within each of the presaccadic epochs, we were able to probe the luminance and color sensitivity by measuring contrast thresholds using a ''simultaneous staircase'' procedure, adapted from psychophysics (e.g., ref. 32) for single neuron responses. In this procedure, the luminance or color contrast of the RF stimulus was increased or decreased on each trial according to whether the neuron responded above baseline to the contrast presented on the previous trial (see Fig. 1*C*). The baseline activity was measured online in separate trials in which no stimulus appeared in the RF. In all conditions, the response of the neuron was measured between 50 ms and 170 ms from stimulus onset. Thresholds for each of the 3 contrast types were obtained with this method during randomly interleaved trials. Each trial lasted ≈2 s, and thus for each contrast type the interstimulus interval was >6 s. Comparison of the stimulus evoked response (R_{stim}) and baseline response (R_{baseline}) was accomplished by computing the Poisson ''surprise'' index (S), where:

$$S = -\ln(P)$$

and

$$P = R_{\text{baseline}}^{R\text{stim}} * e^{-R\text{baseline}}/R_{\text{stim}}!$$

according to a Poisson distribution (33–34). The staircase procedure always started with the highest contrast, and the contrast step size (increase or decrease) was scaled according to the surprise index (S) to reach asymptote in the fewest possible trials. Each neuron's contrast threshold was then estimated by fitting the staircase results with the asymptotic function:

$$(\text{contrast}_{\max} - \text{contrast}_{\text{threshold}})(1 + e^{t-m}) + \text{contrast}_{\text{threshold}}$$

where $\text{contrast}_{\max}$ is the initial (highest) contrast, t is the trial number, and m is the slope of the curve. For convenience, negative color thresholds (i.e., −L/M or −S) were converted to their absolute values. Luminance, L/M and S contrast sensitivity was computed from the reciprocal of each of the resulting threshold values. For the population analysis, only thresholds that differed significantly from the minimum and maximum contrast values were used.

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