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Segregation of Object and Background Motion in Visual Area MT: Effects of Microstimulation on Eye Movements

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Summary

To track a moving object, its motion must first be distinguished from that of the background. The center–surround properties of neurons in the middle temporal visual area (MT) may be important for signaling the relative motion between object and background. To test this, we microstimulated within MT and measured the effects on monkeys' eye movements to moving targets. We found that stimulation at "local motion" sites, where receptive fields possessed antagonistic surrounds, shifted pursuit in the preferred direction of the neurons, whereas stimulation at "wide-field motion" sites shifted pursuit in the opposite, or null, direction. We propose that activating wide-field sites simulated background motion, thus inducing a target motion signal in the opposite direction. Our results support the hypothesis that neuronal center–surround mechanisms contribute to the behavioral segregation of objects from the background.

Introduction

We experience the visual world as containing many distinct objects. If one of these objects should move, we are capable of rapidly directing our gaze at the object and tracking its motion with our eyes. This ability requires that the visual system first distinguish the object from the background. The effortlessness of this discrimination is deceptive—for a century now, scientists have struggled to understand how the brain distinguishes individual figures from their surroundings based solely on a pattern of retinal illumination. Gestalt psychologists emphasized that we tend to perceive regions of a visual scene having similar color, texture, depth, and motion as belonging to a common object (Wertheimer, 1912; Rubin, 1915; Barlow, 1981). Motion cues can be particularly compelling: regions of the visual scene moving at the same velocity tend to be grouped together, and, conversely, regions of differential motion provide a strong percept of an object boundary (Braddick, 1993). These observations suggest that the visual system must compare the motion of adjacent regions of the visual scene. A hypothesized neural mechanism for this comparison is the center–surround opponency that is a prevalent feature of the receptive fields of cortical neurons involved in processing motion (Allman et al., 1985). We sought to provide a direct behavioral test of this hypothesis in the specific context of the visual motion processing used to guide pursuit eye movements.

For motion-based segregation of objects versus the background, direction-selective neurons with two different types of center–surround interaction have been proposed to play a role. Some motion-processing neurons possess antagonistic surrounds that render the neurons sensitive to local motion contrast and indifferent to wide-field motion (Allman et al., 1985). Other neurons have receptive fields that spatially sum similar motion cues over larger regions of the visual field and lack any such opponent surround; they thus respond best when the entire visual scene moves coherently. Such wide-field motion is generally an attribute of the background. Receptive fields of these types have been described in a wide variety of species, ranging from insects to birds to monkeys (Sterling and Wickelgren, 1969; Collett, 1971; Frost et al., 1981; Frost and Nakayama, 1983; von Grunau and Frost, 1983; Allman et al., 1985; Tanaka et al., 1986; Egelhaaf et al., 1988; Komatsu and Wurtz, 1988).

Neurons that are differentially sensitive to local or wide-field motion tend to be clustered anatomically. In the middle temporal visual area (MT) of the owl monkey, this organization is columnar (Born and Tootell, 1992). In the macaque, a laminar pattern of center–surround interactions has been reported (Lagae et al., 1989), and both physiological recordings (Raiguel et al., 1995) and 2-deoxyglucose (2dg) results (Tootell and Born, 1990) suggest that a columnar organization may also be present. Beyond MT, a grouping of neurons responding preferentially to local or wide-field motion has been reported in subdivisions of macaque area MST (medial superior temporal visual area; Tanaka et al., 1986; Komatsu and Wurtz, 1988).

The existence of clustering provided us the opportunity to address more directly the functional roles of neurons with specific types of receptive field structure by using microstimulation in the context of a behavioral task. Previous investigators have shown that chemical lesions (Newsome et al., 1985) or electrical stimulation with relatively large currents (≥100 μA) in areas MT and MST can disrupt smooth pursuit eye movements (Komatsu and Wurtz, 1989). We have demonstrated that smaller currents (20–80 μA) can produce direction-selective effects on pursuit eye movements and that the interaction between the target velocity and the signal introduced by microstimulation is well described by a vector averaging model (Groh et al., 1997). We were struck, however, by the fact that pursuit could be shifted

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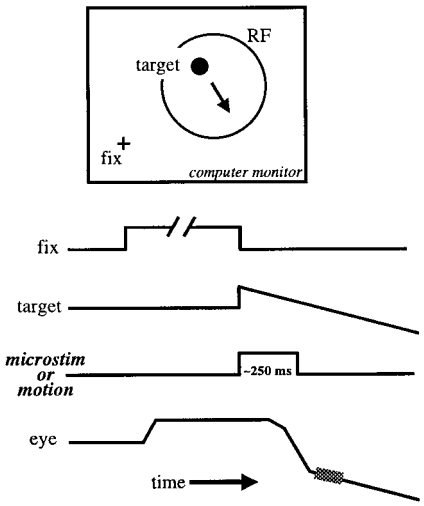

Figure 1. Schematic Diagram of the Main Events in the Step Ramp Tracking Task in Space and Time

The monkey first foveated a fixation point (fix) for a variable length of time, after which the fixation point was extinguished, and, simultaneously, a moving target appeared in the receptive field (RF) of the cells at the microstimulation site. The monkey made a saccade to the position of the target and used smooth pursuit to move his eyes at the same velocity as the target. On half of the trials, a train of microstimulation pulses was delivered from the time of target onset until the saccade to the target (mean stimulation time = 237 ms, SD = 55 ms). The velocity of pursuit was measured during the period from 20 to 60 ms after the saccade to the target (shaded region). For behavioral experiments, the procedure was the same, except for the substitution of 250 ms of background motion for the period of microstimulation.

either in the preferred direction of the stimulated neurons or in the opposite direction. These differences allowed us to test the hypothesis that stimulation at local motion sites causes a motion signal that is attributed to the object itself, while stimulation at wide-field sites is attributed to the background, thus causing pursuit of the object in the opposite direction due to induced motion (Duncker, 1929; Reinhardt-Rutland, 1988; Niemann and Hoffmann, 1997).

Results

We conducted microstimulation experiments at 136 sites in MT in three monkeys who had been trained to perform a step ramp visual tracking task (Figure 1). The task required that the monkey first foveate a small square, after which a target spot appeared in the peripheral visual field and moved away in one of several possible directions and speeds. On half of the trials, randomly chosen, we applied biphasic current pulses through a metal microelectrode from the time of target onset to the time that the animal made a saccade to the target.

We obtained statistically significant effects (χ^2 analysis of regression parameters, $p < 0.01$) of microstimulation at 106 (78%) of the sites. Of the 106 effective sites, 49 yielded a slowing of pursuit regardless of the direction of target motion, similar to the effects seen with focal lesions in MT (Newsome et al., 1985). Wide-field and local sites were not significantly different with respect to the frequency of nonsignificant or nondirectional pursuit effects. We excluded sites yielding nonsignificant or nondirectional effects from subsequent analyses. The remaining 57 sites (42% of all sites) produced effects with a significant directional component, and these formed the basis for our comparisons of receptive field properties with microstimulation effects.

Effects on Speed

In our previous work (Groh et al., 1997), we found no significant correlations between the preferred speed at the stimulation site and the magnitude of the microstimulation effect vector. This remained the case when we analyzed wide-field and local sites independently (Figure 4b). The correlation coefficients for wide-field and local sites were 0.01 ($p = 0.55$, F test) and 0.0001 ($p = 0.99$), respectively, and in neither case was the slope of the regression line significantly different from zero. In most cases, the magnitude of the microstimulation effect vector was less than the preferred speed of the neurons stimulated—a difference that was highly statistically significant for the populations of both wide-field and local sites ($p < 0.00001$, one-tailed, paired t test). In the Discussion, we consider possible reasons for the lack of speed correlation and in the following sections, focus our analyses on the direction of the effects of microstimulation.

Effects on Direction

Figure 2 shows an example of a directionally selective microstimulation effect at a site that was physiologically characterized as preferring local motion. Neurons at this site met our qualitative criterion for the highest category of direction selectivity: the neurons were strongly activated by motion in the preferred direction—in this case, up and slightly to the left (112°)—and were suppressed below spontaneous levels of firing by a stimulus moving in the opposite, or null, direction. The neurons at the site were driven much better by a bar than by any patch of random dots and showed quantitative evidence of an antagonistic surround: the neurons responded moderately well to a small patch of random dots but responded poorly to a patch extending well beyond the classical receptive field (Figure 2a). Microstimulation at this site produced an effect on the postsaccadic pursuit that was evident even in the raw eye position traces (Figure 2b). The overall pattern, best appreciated in a velocity–space diagram (Figure 2c), is consistent with a vector averaging pattern in which the target velocity is weighted nearly equally (gain term = 0.49) with an "electrical velocity vector" pointing up and slightly to the left (108°)—very nearly matching the preferred direction of the neurons at the stimulation site. As was typical, however, the magnitude of this electrical vector was considerably less than the preferred speed of the neurons stimulated: 5.4°/s versus a preferred speed of 25°/s.

While this pattern was characteristic of many of the experimental sites, we also observed many cases in which the directional effect on pursuit was opposite to the preferred direction of the neurons stimulated (Figure 3). Here, the preferred direction was to the right and slightly upward ($\theta = 12°$), and, as for the site in the

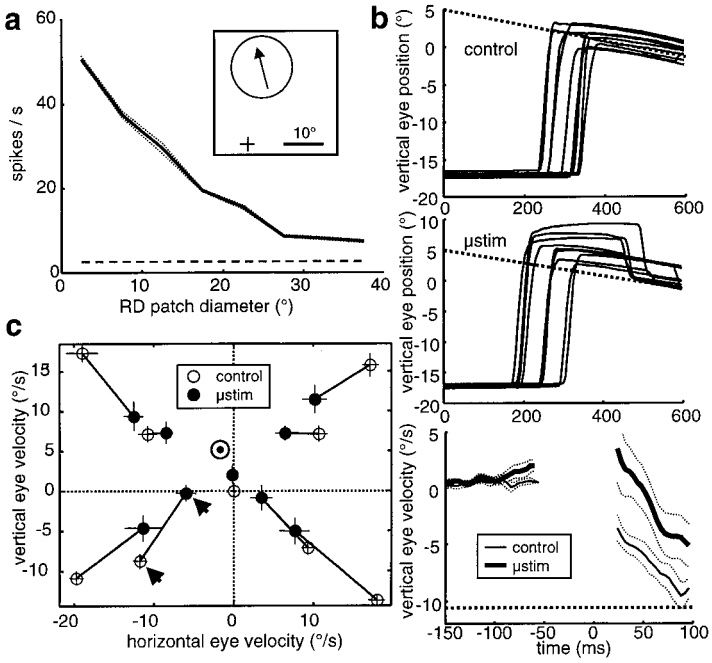

Figure 2. Preferred Direction Pursuit Effect at a Local Motion Site in MT

(a) Neurons at this site responded well to bars and to small, random dot patches but not to large fields of random dots. The solid line represents the multiunit average firing rate during the 2 s of stimulus presentation averaged over ten trials; the dotted line is the standard error of the mean; the dashed line indicates the spontaneous level of firing. For this site, the surround index was −0.84. As shown in the inset, the aggregate receptive field was located 3.5° to the right of and 20° above the fovea, its diameter was 15°, and the preferred direction was 112°.

(b) Effect of microstimulation on pursuit eye movements. The target motion on these trials was down and to the left at 15°/s. The top two panels show the vertical eye position on each of ten trials without (top) or with (middle) microstimulation (40 μA at 200 Hz) aligned on target onset. Stimulation caused a smooth eye movement upward just prior to and following the saccade. The bottom panel shows the mean vertical eye velocity for the same data after the individual traces were aligned on the endpoint of the saccade.

(c) Velocity–space diagram of the average eye velocity from 20 to 60 ms after the saccade for all trials. The target moved in one of four directions at one of two speeds (15° or 25°/s) or remained stationary. Each point is the average of ten trials (±SEM). Pairs of points connected by lines represent trials having identical target motion, but differing as to whether microstimulation was given (closed circles) or not (open circles). Arrowheads indicate the pair of data points from the trials shown in (b). These data were well fit by a vector-averaging model in which the velocity of the eye movement on stimulated trials is a weighted average of the target velocity due to the visual stimulus and of the electrical velocity induced by microstimulation. The bull's-eye corresponds to the regression estimate of the velocity induced by microstimulation. The direction of the microstimulation effect (108°) is close to the preferred direction of the neurons at the stimulation site (112°).

previous example, the neurons were inhibited by motion in the opposite direction. Microstimulation produced a strong, statistically significant effect on smooth pursuit whose direction was to the left and slightly downward ($\theta = 208°$), opposite to the preferred direction of the stimulated neurons. The major difference between this site and the one in the previous example (Figure 2) is that the neurons here responded extremely well to wide-field motion (Figure 3a), even to a stimulus that extended well beyond the boundaries of the classical receptive field.

These two examples were characteristic of the overall population of microstimulation effects obtained at the two different types of sites (Figure 4a). To demonstrate this, we first had to classify each site as "wide-field" or "local." This was done blindly (i.e., without knowledge of the effects of microstimulation), according to the physiological properties of the neurons recorded before the microstimulation experiment was performed. At 38 sites where we obtained quantitative area summation data, we used as the criterion for classification the "surround index," computed by dividing the difference of the neuron's response to wide-field (WF) and small-field (SF) motion by the sum (WF − SF)/(WF + SF). Sites having an index less than or equal to −0.5 (corresponding to a wide-field response less than or equal to one-third of the best small-field response) were classified as local, and all others as wide-field. At another 19 sites where no quantitative area summation data were obtained, we used the subjective criterion of the neurons' responses to a bar versus random dots: sites for which a bar was the most effective stimulus were classified as local; those that preferred large fields of random dots were classified as wide-field. This subjective classification was based on previous results from the owl monkey, in which it was found that many neurons in 2dg-labeled interbands (local motion regions) gave poor responses to random dot patches of any diameter but responded vigorously to single bars (see Figure 4 of Born and Tootell, 1992). When we plotted the direction of the microstimulation effects with respect to the preferred direction of the neurons at the stimulation site, we found that nearly all of the null direction pursuit effects occurred at sites more responsive to wide-field motion, and most of the preferred direction effects occurred at sites preferring local motion (Figure 4a). This difference between the two distributions of directions was highly significant ($p < 0.001$, Watson's U^2 test).

We also compared the surround indices of the sites showing preferred direction effects with those of the sites showing null directional effects. In this analysis, we used all sites for which microstimulation produced a statistically significant directional effect (at $p < 0.01$) and for which we had quantitative area summation data ($n = 38$). A one-way analysis of variance revealed a significant difference between the two populations (preferred direction sites, mean surround index = −0.46; null direction sites, mean surround index = −0.09; $p < 0.02$). Thus, the physiological distinction between wide-field and local motion sites was systematically related to null versus preferred direction microstimulation effects, respectively.

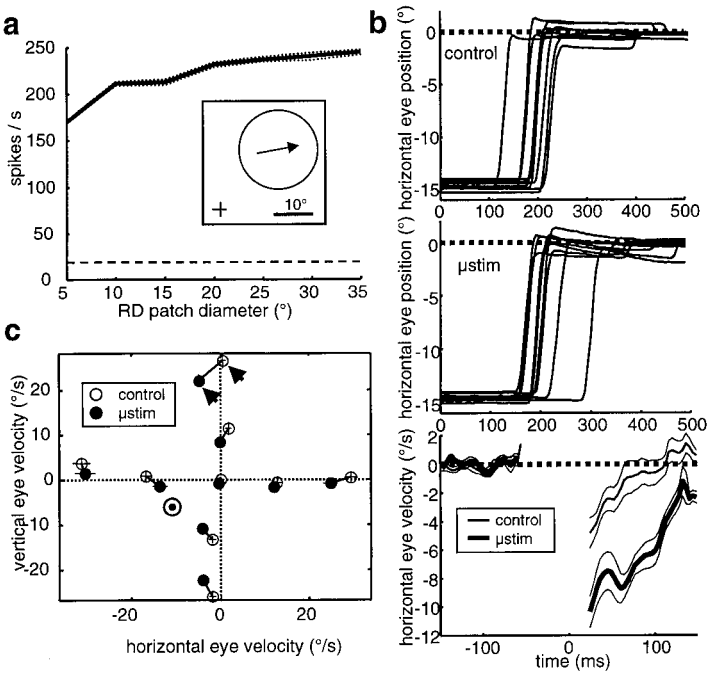

Figure 3. Null Direction Pursuit Effect at a Wide-Field Motion Site in MT

(a) The neurons at this site responded well to random dot patches of all sizes but responded better to large fields, even those extending well beyond the aggregate receptive field size, as mapped with a bar (20°). The firing rate is that of several units nearest the tip of the electrode.

(b) Effect of microstimulation on pursuit eye movements. The target motion on these trials was straight up (90°) at 25°/s. The top two panels depict the horizontal eye position on each of ten trials without (top) or with (middle) microstimulation (40 μA at 200 Hz). On trials with stimulation, there is a smooth eye movement to the left (downward on the figure) following the endpoint of the saccade. The bottom panel shows the mean horizontal eye velocity for the same data after aligning the trials on the endpoint of the saccade. Microstimulation produced a significant leftward (and downward; data not shown) effect.

(c) Velocity–space diagram of the average eye velocity during the first 20–60 ms after the saccade for all trials. The target could move in one of four directions (up, down, right, or left) at one of two speeds (10 or 25°/s) or remain stationary (saccade only). Pairs of points connected by lines represent identical target motion but differ as to whether microstimulation was given (closed circles) or not (open circles). Arrowheads indicate the data points for the trials shown in (b). The black bull's-eye represents the velocity vector induced by microstimulation. The direction of the effect of microstimulation is opposite to the preferred direction of the neurons at the stimulation site.

Other Differences between Wide-Field and Local Motion Sites

A comparison of the width of the polar histograms in Figure 4a reveals that the directionality of the effects in local motion sites was more tightly correlated with the preferred direction of the neurons than was that of the wide-field motion sites with the null direction of the neurons. To quantitate this, we computed the angular–angular correlation coefficient, r_{aa}, as described by Fisher and Lee (1983) and tested its significance using a jackknife technique described by Upton and Fingleton (1989). For local motion sites, r_{aa} was 0.46 compared with a value of 0.086 at wide-field sites (both values significant at $p < 0.01$). Another difference between local and wide-field sites was the magnitude of the effects obtained, as measured by the gain term of the regression equation. The effects at local motion sites were stronger: the electrical velocity vector introduced by microstimulation was weighted significantly more heavily (mean gain term = 0.36) than it was at wide-field sites (mean gain term = 0.26, $p < 0.05$, one-way analysis of variance).

Behavioral Comparison

How well do these microstimulation effects at wide-field sites correlate with the behavioral effects of actual background motion? To test this, several of us conducted a behavioral simulation of the microstimulation signal at wide-field sites (R. Zhao et al., 1998, Soc. Neurosci., abstract). These experiments were formally identical to the microstimulation experiments, except that we substituted a brief period of real background motion for the period of microstimulation. The target eccentricities and velocities, as well as the velocity characteristics of the background, were matched to the properties of wide-field sites in our microstimulation data set. In one such experiment (Figure 5a), the monkey tracked a small spot that came on 10° to the right of the fixation point and that, on any given trial, could move away at one of nine different velocities across a sparse random dot background that was either stationary or moved downward for 250 ms, beginning at the onset of target motion. We compared the same period of pursuit initiation (20–60 ms after the saccade endpoint) on trials with and without background motion and fit the results with the same regression model used to characterize microstimulation effects. The pattern of the effects was clearly to shift pursuit in the direction opposite to that of the background motion. This type of effect was seen for most of the background motion experiments we conducted, and the overall distribution of effects was similar to that seen for microstimulation at wide-field sites in MT (Figure 5b). The distribution of constant terms for the behavioral data was not statistically different from that of the microstimulation experiments ($p = 0.17$, two-dimensional Kolmogarov-Smirnov test). Thus, when both target and background moved independently, smooth pursuit of the target was shifted away from the velocity of the background, closely resembling the effects of microstimulation at wide-field sites in MT.

In the series of experiments shown in Figure 5b, the moving background covered the entire computer screen, which subtended a 55° × 40° region of the visual field. However, how large the background stimulus should be in order to be more nearly comparable to a given microstimulation experiment would depend on both the size of the population activated by microstimulation and the size of the receptive fields of the activated neurons. The size of the activated population is uncertain, but the receptive fields of individual neurons have been well

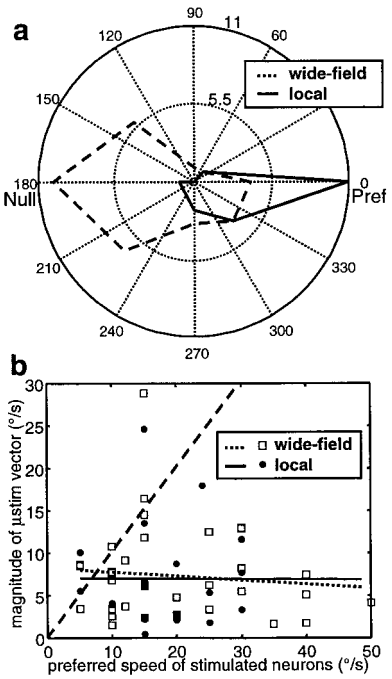

Figure 4. Population Data for Direction and Speed Effects of Microstimulation in MT on Pursuit

(a) Polar histograms of the direction of the microstimulation effect at each of 57 different sites. All directions are specified relative to the preferred–null axis of neurons at the stimulation site, such that points lying to the right correspond to the preferred direction, and points lying to the left correspond to the null direction. The dashed and solid lines represent sites characterized as wide-field or local, respectively. Both populations differ significantly from circular uniformity (wide-field, $p = 0.0058$; local, $p = 0.000036$, Rayleigh's test; see page 616 of Zar, 1996). The mean angle of the wide-field distribution is 190° ± 40°, and that of the local distribution is 340° ± 25° (95% confidence interval). The probability that the samples of directions from the different types of sites are from the same underlying distribution is small ($p < 0.001$, Watson's U^2 test; see pages 629–632 of Zar, 1996).

(b) Lack of correlation between the magnitude of the electrical velocity vector and the preferred speed of the neurons stimulated. For neither wide-field nor local sites was the slope of the regression line significantly different from zero. The dashed line is a line of slope 1. Note that the majority of data points fall below this line, indicating that the magnitude of the microstimulation-induced vector was generally less than the preferred speed of the neurons stimulated.

characterized. For many of the more peripheral microstimulation sites, the nonclassical surrounds extend far beyond the region responsive to a single bar and include a large part of the ipsilateral hemifield (Allman et al., 1985). For these sites, the size of the monitor was probably a reasonable approximation. For less eccentric sites, however, it is possible that using the entire screen overestimated the region of background motion attributable to microstimulation. We thus conducted another series of experiments in which the area of the background that moved was matched to the classical receptive field size measured at the corresponding microstimulation site. For all trials, the entire screen was covered with the same random dot pattern used above, the only difference being that on the trials containing background motion, only a small window of dots, centered around the location of target onset, actually moved. All other parameters were also matched as described above. The overall pattern of results was the same as for the full-screen experiments, with the majority showing a significant effect on pursuit in the direction opposite to that of the background (Figures 5c and 5d).

Effects of Microstimulation on Saccades

As we reported previously (Groh et al., 1997), microstimulation can also affect the saccade to a moving target. We measured this "saccadic velocity compensation" (SVC) as the target velocity for which the saccade would have been appropriate (Ron et al., 1989; Keller and Steen Johnsen, 1990; Gellman and Carl, 1991; Keller et al., 1996). Directional effects of microstimulation on SVC were found for 70 of 136 sites (51%). Interestingly, microstimulation shifted SVC in the null direction much less often than it did for pursuit—most sites shifted the SVC in the preferred direction, though the distribution was much broader than it was for pursuit (see Figure 11 of Groh et al., 1997). However, both the reduced number of null direction effects and the greater scatter of the effects with respect to the preferred direction appeared to be due to two things: (1) a greater tendency of saccades to be hypometric on microstimulation trials and (2) a correlation between the receptive field direction, relative to the fovea, and the preferred direction at the microstimulation sites for which we obtained statistically significant directional effects, the preferred direction being much more likely to point back toward the fovea. (This "foveopetal" bias was quantified by computing the preferred direction with respect to a line drawn between the receptive field center and the fovea, after Albright [1989].) Because of these factors, the direction of the microstimulation-induced SVC effect was correlated with both the preferred direction ($r_{aa} = 0.122$) and the receptive field direction or foveopetal bias ($r_{aa} = 0.173$).

To determine if the center–surround properties of the microstimulation site were related to the direction of the microstimulation-induced effects on saccades, we first controlled for the foveopetal bias. We selected the sites at which the preferred direction differed from the foveopetal axis by at least 45° (39 sites) and examined the component of the microstimulation-induced SVC effect that lay along the preferred–null axis for this subset. This analysis confirmed that the preferred direction did influence the direction of the microstimulation effect in a fashion related to the center–surround properties of the microstimulation site (Figure 6), with stimulation at local sites being substantially more likely to shift SVC in the preferred direction, and stimulation at wide-field sites shifting SVC more often in the null direction. Thus, the relationship between the center–surround properties and the direction of the effects of microstimulation on SVC was similar to that found for pursuit, though somewhat obscured by the tendency toward microstimulation-induced hypometric saccades.

Discussion

Center–Surround Opponency, Figure–Ground Segregation, and Eye Movements

Discrimination of objects from the background is a very general problem, not only for vision, but for other sensory modalities as well. The hypothesis that center–

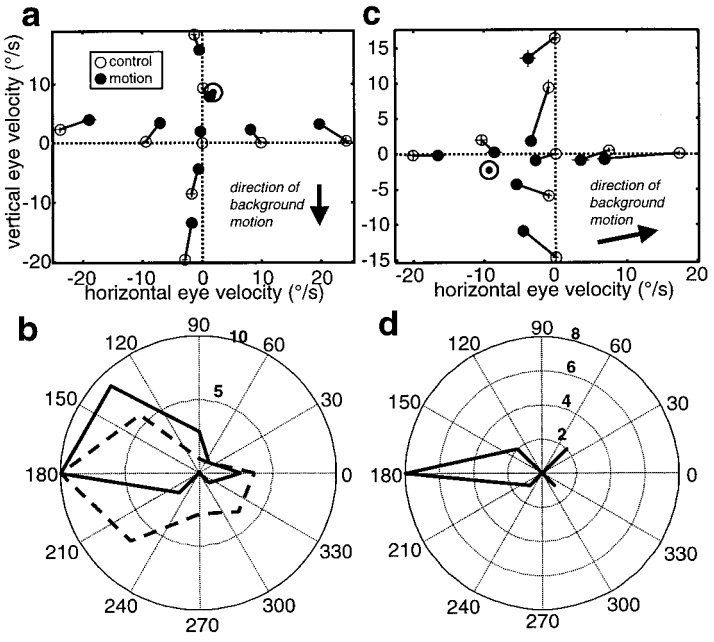

Figure 5. Effect of Background Motion of Pursuit Initiation

(a) Velocity–space diagram similar to those shown in Figures 1c and 2c. In this experiment, however, the microstimulation condition was replaced by downward motion (270° at 10°/s) of a large-field (55° × 40°) random dot background for 250 ms, beginning at target onset. Closed circles represent the monkey's average eye velocity from 20 to 60 ms after the saccade to the target with background motion, and open circles represent the eye velocity on trials during which the background was visible but remained stationary. The black bull's-eye represents the velocity vector induced by background motion. The direction of this effect (76°) is nearly opposite to that of the background motion.

(b) Population histogram of the direction of the effects of background motion (solid line) on pursuit initiation for two monkeys. The regression vector for each experiment has been rotated to lie along the axis of background motion, such that 0° indicates an effect in the same direction as the background, and 180° indicates an effect in the opposite direction. This distribution differs significantly from circular uniformity ($p = 0.00010$, Rayleigh's test), with a mean angle of 150° ± 30° (95% confidence interval). For comparison, the effects of microstimulation at wide-field sites in MT are also plotted (dashed line; same data as represented by the dashed line in Figure 3b). The two populations of angles do not differ significantly from one another ($p > 0.05$, Wheeler-Watson two-sample test for circular data).

(c) Example of an effect of background motion on pursuit initiation for an experiment in which only a small portion of the background (10° × 10°) immediately surrounding the target moved on half of the trials. The direction of background motion was to the right and slightly upward ($\theta = 12°$).

(d) Population histogram for 14 experiments consisting of partial background motion.

surround interactions are a prominent neural mechanism for this discrimination is appealing both because of its mechanistic simplicity and because of the ubiquity of such interactions in sensory systems throughout the animal kingdom. This hypothesis has received support from a number of recent studies demonstrating neural correlates of stimulus manipulations that affect figure-ground perception (Lamme et al., 1998) but has thus far received no direct behavioral test. We have provided such a test in the specific context of motion processing necessary for the successful visual tracking of a moving target. Our microstimulation results are consistent with the predictions of the center–surround hypothesis and thus provide evidence for a link between the spatial properties of direction-selective neurons and the discrimination of a pursuit target from the visual background.

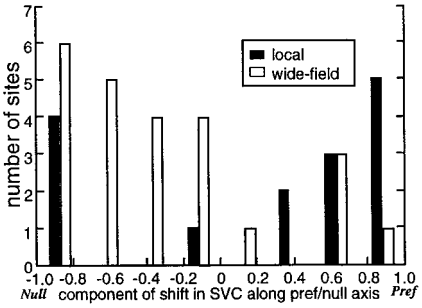

Figure 6. Population Data for Effects of Microstimulation in MT on Saccades

Frequency histogram of the relationship between the direction of the stimulation-induced shift in SVC and the preferred–null axis of the microstimulation site. Only sites in which the preferred direction differs from the foveopetal axis by at least 45° are included. The component of the shift was calculated as the cosine of the difference in angle between the direction of the constant term of the regression model and the preferred direction of the microstimulation site. Positive values indicate the preferred direction, and negative values indicate the null direction. For local sites, the mean component of the shift in SVC was 0.2352 (preferred direction), while for wide-field sites, the mean component of the shift was −0.3335 (null direction). This difference between the wide-field and local sites for SVC was statistically significant ($p = 0.028$, Wilcoxon rank sum test).

Distinguishing the target from the background is particularly important for tracking eye movements. When a target moves with respect to the background, two competing systems vie for oculomotor control. The pursuit system attempts to follow the motion of the target, while the optokinetic system, designed to stabilize gaze as we move through the world, attempts to track the motion of the visual background caused by the pursuit eye movement itself (Miles et al., 1991). Indeed, previous reports in human subjects suggest that the pursuit system may not always succeed at segregating the target from the background. Different labs studying pursuit initiation across moving backgrounds have obtained different results (Masson et al., 1995; Niemann and Hoffmann, 1997; Schwarz and Ilg, 1999). Masson et al. (1995) reported increased pursuit gain when the target and background moved in the same direction and a decrease for the opposite condition. Schwarz and Ilg (1999) also found a "same direction" effect, but the asymmetry they report was only manifest when the background

motion began well after (200 ms) pursuit was initiated. In contrast, Niemann and Hoffmann (1997) reported an increase in the initial eye acceleration when the target and background moved in opposite directions, compared with the effect when target and background moved synergistically.

A variety of methodological differences could account for these different findings and for differences with our own results. The three earlier studies (Masson et al., 1995; Niemann and Hoffmann, 1997; Schwarz and Ilg, 1999) were all performed in humans, considered only horizontal eye movements, and used targets of different sizes and contrasts. They also analyzed different epochs of the eye movement data in different ways (see page 538 of the Discussion of Niemann and Hoffmann, 1997). One consistent difference between those studies finding same direction effects (Masson et al., 1995; Schwarz and Ilg, 1999) and those reporting "opposite direction" effects (Niemann and Hoffmann, 1997; present study) is that the former two used a ramp motion paradigm in which each trial began with the subject foveating the pursuit target, whereas the latter two used step ramp motion in which the target appeared eccentrically. This is potentially a very important difference given that the gain of pursuit initiation is extremely sensitive to the eccentricity of the target's starting position (Lisberger and Westbrook, 1985).

Because the differences among studies suggest that results can vary depending on exactly how the experiment is done, we felt it important to test the effects of moving backgrounds on pursuit initiation in monkeys under conditions precisely matched to those used in our microstimulation experiments. When we did this, we found that both moving backgrounds and microstimulation of wide-field sites affected pursuit initiation similarly and that the direction of the effects was consistent with the motion contrast effect previously reported by Niemann and Hoffmann (1997). Because we have tested a limited range of target and background conditions, it remains to be determined exactly which features of the target and background determine the outcome. The most important attribute of our behavioral experiments is that they were directly comparable to our microstimulation experiments and, as such, support our interpretation that wide-field motion-processing neurons are likely to represent motion of the visual background.

Speed Tuning and Microstimulation Effects

In both this study and in our previous work (Groh et al., 1997), we failed to find significant correlations between the magnitude of the velocity vector imparted by microstimulation and the preferred speed of the neurons stimulated. Most likely this is because our stimulating electrode activated a heterogeneous population of neurons with a range of different speed tuning preferences. Although speed tuning preferences in MT do show some clustering (Maunsell and Van Essen, 1983; DeAngelis and Newsome, 1999), the tuning of single units is quite broad, and the overall clustering appears weak. Perhaps more importantly, we did not optimize our experiments to capitalize on what organization may exist—we did not seek out portions of the electrode track that were homogeneous for preferred speed, as we did for preferred direction and center–surround properties. Furthermore, we have previously shown that the readout of MT for eye movements most closely resembles the computation of a vector average (Groh et al., 1997), and this has profound consequences for the interpretation of microstimulation effects on speed. If the population of neurons activated by microstimulation all have different preferred directions, then, even if they all have identical preferred speeds, the speed of the average vector will tend to be lower than the preferred speed of the individual cells. Thus, any spread of current to adjacent direction columns will reduce the net speed without necessarily affecting direction, provided the spread is reasonably balanced across different directions. This would predict that the speed component of the microstimulation effect should, in general, be smaller than the preferred speed of the neurons, and this was indeed the case (Figure 4b). In sum, the lack of a correlation between the preferred speed of the neurons stimulated and the effect of microstimulation at a given site might be explained by any or all of these factors. It should not be construed as evidence against a role for speed tuning in guiding eye movements in the absence of microstimulation.

Microstimulation Effects on Saccades

We observed that microstimulation could affect pursuit and saccades differently but that this difference was largely explained by a foveopetal bias in the effects of microstimulation on SVC and that both pursuit and saccade effects were correlated with the center–surround properties of the stimulation site. This suggests to us that, with respect to the saccade system's calculation, microstimulation introduced both a directional velocity signal related to the preferred direction of the neurons stimulated and a retinotopic position signal related to the receptive field location of the neurons stimulated. This is perhaps not so surprising given that MT is retinotopically organized (Gattass and Gross, 1981) and that position is a critical cue for saccade generation (Rashbass, 1961). It might also account for the foveopetal bias in the preferred directions of stimulation sites at which we obtained significant microstimulation effects on SVC: at these sites, the directional effect and the positional effect were in roughly the same direction, hence more likely to produce an overall effect in this direction, whereas at sites where the preferred and foveopetal directions differed considerably, the two types of effects would be more likely to cancel and result in no net effect. We are currently performing experiments that will allow us to address this issue more directly.

Experimental Procedures

Surgical Preparation

Four rhesus monkeys (*Macaca mulatta*, three male, one female) were surgically prepared for chronic physiological recording and then trained to perform a fixation task and a visual tracking task. The experimental protocols were approved by the Stanford University Animal Care and Use Committee and the Harvard Medical Area Standing Committee on Animals. In a sterile surgical procedure under isoflurane anesthesia, a coil of fine wire was implanted between the conjunctiva and the sclera for the measurement of eye

position (Robinson, 1963; Judge et al., 1980). During the same surgical procedure, stainless steel or titanium bone screws were implanted in the skull, and a fixture for immobilizing the head was attached using dental acrylic. When behavioral training was complete (see below), the animals underwent a second surgery for implantation of a cylinder for chronic electrophysiological experiments in MT. Three of the animals (monkeys P, D, and B) were used for microstimulation experiments, and two (monkeys B and C) served as subjects in the experiments with moving backgrounds.

Behavioral Training

The animals were placed on a controlled fluid intake schedule and received water or juice as reinforcement during training and experimental sessions. Visual stimuli were presented on a Mitsubishi monitor (70 × 52 cm, 57 cm away). Monkeys were trained to perform two types of behavioral tasks: (1) fixation trials and (2) visual tracking trials (Figure 1). On fixation trials, monkeys maintained gaze within ±1.5° of a fixation point for several seconds to allow receptive field properties of neurons to be mapped. On visual tracking trials, the animal first foveated the fixation point (a small red square, 0.17° on a side, luminance 20.6 cd/m^2) for a randomly varied period of 500–1300 ms, at the end of which the fixation point disappeared, and, simultaneously, a dim red target (circular disk, 0.6° diameter, luminance = 2.19 cd/m^2) appeared elsewhere in the visual field. The target either could remain stationary or could move with a constant velocity. The animal made a saccade to this second target within 400 ms and either fixated or pursued the target for 1.3–8 s, depending on the speed of the target. The target location and ramp velocity were tailored in each experiment to the receptive field location and velocity selectivity of the MT site to be stimulated.

For all microstimulation experiments, the background of the monitor was dim (6.58 × 10^{-2} cd/m^2) but plainly visible. We know that such a visual stimulus is sufficient to cause wide-field MT neurons with extrafoveal receptive fields to fire vigorously during pursuit eye movements (C. C. Pack and R. T. B., unpublished data).

Physiological Recording

While the animal performed the fixation task, we mapped the receptive fields of MT neurons (recorded extracellularly with metal microelectrodes). We used standard electrophysiological recording techniques (for details, see Britten et al., 1992). MT was identified based on its depth, prevalence of directionally selective visual responses, receptive field size, and visual topography. MT was easily distinguished from MST based on the ratio of receptive field size to eccentricity, which is much lower in MT than in MST (Van Essen et al., 1981; Desimone and Ungerleider, 1986). In one animal, the approximate location of MT was first determined using magnetic resonance imaging. Once the electrode entered MT, we explored the receptive field properties of single units and multiunit clusters. While the animal maintained fixation, the borders of the receptive field were qualitatively mapped using computer-generated stimuli, such as moving bars or patches of moving dots. We then qualitatively assessed the direction tuning at the site using either moving bars or dots, or both. Finally, we quantified center–surround interactions with an area summation test. While the monkey performed a fixation task, we presented a window of moving random dots centered on the multiunit receptive field for 2 s. On all trials, the direction, speed, and density of the dots were held constant, and the diameter of the random dot patch was randomly varied from trial to trial. Patch diameters were selected so that the smallest would be well within the neurons' classical receptive field (as mapped qualitatively), and the largest would cover an area several times that of the classical receptive field. While this test tells us little about the precise nature of the spatial interactions within a receptive field—such as, for example, whether the surround is annular or irregular (Xiao et al., 1995)—it gives a good indication of the neuron's response to background versus target motion, and this is the most important kind of information for our experiments.

Microstimulation

After characterizing a site, we carried out a microstimulation experiment while the monkey performed a visual tracking task (Figure 1) in which a target appeared in the multiunit receptive field of the recording site and either moved across it at a constant direction and speed or remained stationary. The monkey had to wait until the fixation point disappeared, then make a saccade to the target and follow it using pursuit eye movements in order to receive a liquid reward. On half of the trials, randomly chosen, we stimulated through the microelectrode from target onset until the monkey made the initial saccade. Trials with microstimulation were randomly interleaved with an equal proportion of nonstimulated trials and were identical to nonstimulated trials in all other respects. We used biphasic stimulating pulses (cathodal phase leading; phase length, 0.2 ms; interphase interval, 0.1 ms; pulse amplitude, 40 μA) at a frequency of 200 Hz (Bak Electronics pulse generator and stimulus isolation unit). To ensure that visually evoked and electrically induced activity in MT coincided in time, the train of pulses was turned on 40 ms after the onset of the visual tracking target in order to approximate typical latencies of visual responses in MT (Maunsell and Van Essen, 1983; Maunsell, 1986; Mikami et al., 1986). The stimulation train was terminated at the time of the saccade to the target, because the saccade removed the visual target from the receptive field of the stimulation site. The average duration of microstimulation was 237 ms (SD = 55 ms) for all experimental sites and 233 ms (SD = 48 ms) for the subset of sites at which statistically significant effects were obtained. Eye position was measured using the scleral search coil technique, digitized at 1 kHz, and stored to disk at 250 Hz for offline analysis.

Data Analysis

Saccades were identified in the eye position records using an automated acceleration-based algorithm with an accuracy of ~99% (for details, see Groh et al., 1997). Individual eye movement traces were aligned on the endpoint of the saccade to the target and the average eye velocity over the first 20–60 ms after the saccade was determined. This epoch of pursuit was chosen as the most reliable metric of the effects of combined visual target motion and the microstimulation-induced velocity signal (see Lisberger et al., 1987; Groh et al., 1997).

We fit these data with a multivariate linear regression model in which the velocity of the eye movement on stimulated trials was taken to be a weighted average of the target velocity due to the visual stimulus and of the "electrical velocity" induced by microstimulation. We have previously shown this to be a good model of the effects of microstimulation on pursuit and on SVC (the compensation of saccadic eye movements for target velocity; Groh et al., 1997). We used the model to obtain an objective measurement of the directional effect of microstimulation.

The regression equation was derived as follows. If a weighted vector average determined the animal's behavior on stimulated trials, then

$$\vec{V}_s = g\vec{V}_e + (1 - g)\vec{V}_{ns}, \quad (1)$$

where V_{ns} is the pursuit velocity on nonstimulated trials, V_s equals the pursuit velocity on stimulated trials, V_e equals the value of the electrically induced velocity signal (an unknown), and g is a scalar weighting factor between 0 and 1 that indicates the relative contributions of the electrical and visual velocity signals. For convenience, this equation can be solved for ΔV, where

$$\Delta\vec{V} = \vec{V}_s - \vec{V}_{ns}, \quad (2)$$

yielding

$$\Delta\vec{V} = g\vec{V}_e - g\vec{V}_{ns}. \quad (3)$$

Since g and V_e are both unknowns, we can replace them with a single constant vector, C, or

$$\Delta\vec{V} = \vec{C} - g\vec{V}_{ns}, \quad (4)$$

yielding the regression equation that we fit to the data for each stimulation site. The constant, C, corresponds to the regression estimate for the velocity on stimulated trials with a stationary visual target (step trials, V_{ns} equal to zero). The electrically induced velocity signal, V_e, is

$$\vec{V}_{ns} = \frac{\vec{C}}{g} = \vec{V}_e \quad (5)$$

or the pursuit velocity (V_{ns}), for which stimulation should have no effect ($\cdot V = 0$).

For each experimental site, we tested whether the constant, C, and/or gain, g, were significantly different from zero using maximum likelihood estimation (for details, see Groh et al., 1997). The same analysis was performed for SVC.

Experiments Using Moving Backgrounds

These experiments were formally identical to the microstimulation experiments described above, except that we substituted background motion for microstimulation. The background consisted of a sparse field (0.3% density) of random white dots (each dot subtended 0.1° of visual angle and had a luminance of 4.56 cd/m^2) on a dark background (6.58×10^{-2} cd/m^2) covering an area $55° \times 40°$ of the visual field. On half of the trials, randomly chosen, the field of dots moved coherently at a constant velocity for 250 ms, beginning at the time of target onset; on the other half of the trials, the random dot background was visible but did not move. Note that there was no 40 ms delay between target onset and background motion (as there was between target onset and microstimulation). The characteristics of the fixation point and target were identical to those described above for microstimulation experiments.

Each background motion experiment was designed to match a particular microstimulation experiment for which we obtained a significant result at a wide-field motion site in MT. Thus, the location of target onset matched the coordinates of the corresponding MT receptive field, and the direction and speed of background motion matched the preferred direction and speed of the neurons at the same site. In the first series of experiments (Figures 5a and 5b), we did not attempt to match the size of the background to the size of the neuronal receptive fields and instead moved the entire screen ($55° \times 40°$) of random dots on motion trials. In the second series of experiments (Figures 5c and 5d), the region of background motion was matched in size to that of the multiunit classical receptive field, measured at the corresponding microstimulation site. In the latter experiments, the entire screen was covered with random dots. On motion trials, however, only a square window of these dots, centered around the location of target onset, was actually moved.

For all behavioral experiments, the data collection and analysis were exactly as described above for microstimulation experiments.

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