Electrical microstimulation of cortical area MST biases heading perception in monkeys

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As we move through the environment, the pattern of visual motion on the retina provides rich information about our movement through the scene. Human subjects can use this information, often termed "optic flow", to accurately estimate their direction of self movement (heading) from relatively sparse displays. Physiological observations on the motion-sensitive areas of monkey visual cortex suggest that the medial superior temporal area (MST) is well suited for the analysis of optic flow information. To test whether MST is involved in extracting heading from optic flow, we perturbed its activity in monkeys trained on a heading discrimination task. Electrical microstimulation of MST frequently biased the monkeys' decisions about their heading, and these induced biases were often quite large. This result suggests that MST has a direct role in the perception of heading from optic flow.

As recognized by Gibson[1], visual motion is important for the perception of our own movements through the environment. Self-motion produces complex patterns of motion on the retina, which can contain linear, radial and rotary components[2,3]. Many authors have suggested that area MST, a part of the so-called "motion system" of dorsal extrastriate cortex, is involved in the analysis of optic flow produced by self-motion through the environment. Neurons in MST possess very large receptive fields, and are selective for various optic flow components presented individually or in combination[4–11]. They are also selective for stimuli that simulate the visual effects of self-motion[12–14]. Although these observations suggest that signals in MST contain information sufficient for the perception of self motion, they do not demonstrate that the signals are actually used for this purpose.

We have tested the hypothesis that MST is involved in the analysis of self motion by electrically microstimulating MST while trained monkeys performed a visual heading discrimination task. This experimental approach, which is widely used in studies of premotor structures, has also been used successfully to document causal links between cortical activity and perception[15–18]. Signals representing heading direction are anatomically clustered within MST[19], so we can activate local clusters of similarly tuned neurons with low-amplitude, high-frequency currents. We presented blocks of trials in which half contained electrical microstimulation simultaneous with the visual heading stimulus upon which the monkey based its decision. In a majority of the experiments, microstimulation induced a significant bias in the monkey's decision. This result suggests that MST signals representing heading are used by the monkey in forming heading judgments.
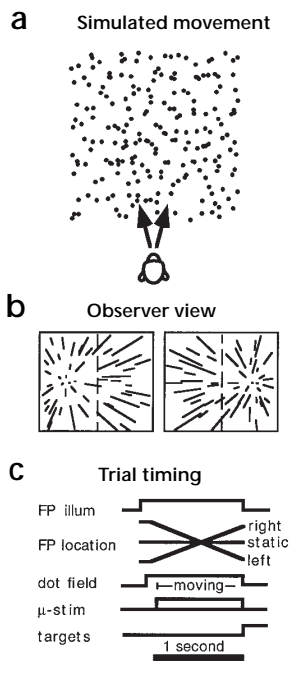
Results

Figure 1 illustrates the optic flow stimulus employed in the present experiments. While the monkey maintained fixation on a small red spot, randomly positioned dots moved to simulate a trajectory such as those illustrated by the arrows in Fig. 1a. The simulated motion display consisted of motion vectors pointing away from a "focus of expansion" which corresponds to the direction of heading, as shown in Fig. 1b. The range of headings was always centered on the screen, directly ahead of the monkey. By moving the fixation point to eccentric locations, we would endeavor to center the receptive field of the multi-unit site being recorded over the center of the screen. Following the stimulus, the dot field and fixation point disappeared, and two targets appeared on the screen, each 10 degrees away from the center of the screen. To receive reward, the monkey made an eye movement to the target on the side corresponding to the direction of heading on that trial. Thus, although actual headings could vary continuously, the monkeys had to make a simple left/right judgement. In cases where the heading was displaced by only a small angle from the center, the monkeys' performance fell to near chance.

For two reasons, we also included trials in which the fixation point was moving, causing the monkeys to make smooth pursuit eye movements during the visual stimulus period (indicated by the ramps in **Fig. 1c**). First, it is known that human observers are able to compensate for the distortions in the optic flow field produced by pursuit, and their judgments of heading remain accurate[3,20–22]. Although the mechanism of this compensation is unknown, there is reason to suspect the involvement of area MST; neurons in MST display explicit signals correlated with pursuit eye movements[23–25] and also seem to at least partially compensate their heading tuning for the distortions produced by smooth pursuit[14]. Second, the inclusion of pursuit renders local directional cues on the retina less useful for the task, because such local cues are distorted by eye movements. Because the trials with pursuit added considerably to the length of an experi-

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Fig. 1. Stimulus geometry and timing. **(a)** The simulated geometry of the "virtual" trajectory of the animal with respect to the stimulus, as seen from above. The arrows are approximately to scale, and illustrate large heading angles. Note that the cloud of points contains simulated depth. **(b)** Appearance of left and right heading stimuli, as seen from the observer's perspective. The length of each line shows the speed of each dot, which is inversely proportional to its simulated depth. The vertical dashed line corresponds to a heading of zero, directly ahead of the subject. The heading corresponds to the center of radial expansion, in the absence of pursuit eye movements. **(c)** The timing of events in a single trial.

a Simulated movement

b Observer view

c Trial timing

Data from a single microstimulation experiment are illustrated in Fig. 2. Each panel shows a pair of psychometric functions relating performance to the direction of the simulated heading. In all cases, we plot P(r), the fraction of choices made to the right-hand target, which increases monotonically as the heading moves further to the right. The vertical midpoints of these psychometric functions, corresponding to an even choice probability of 0.5, indicate the monkey's perceived "dead ahead", and thus provide information about choice bias, either native or experimentally induced. The steepness of these functions indicates the sensitivity of the monkey. In this case, 75% correct performance required a stimulus about 1-2 degrees away from the midpoint, which corresponds well to the performance of human observers under similar conditions.

In the experiment illustrated, the electrode was positioned in a region of MST containing neurons that consistently preferred leftward heading. The solid symbols depict the results from the stimulated trials, and the open symbols show the results of the unstimulated control trials. Consider the results for the static condition (**Fig. 2a**). At all points on the rising limb of the functions, the stimulated curve lies below the unstimulated curve, showing reduced proportions of right choices and thus increased choices in favor of the neurons' preference. This results in a horizontal shift of the function to the right (the function is shifted in a direction opposite the induced bias). The same shift can be seen in panels b and c, for left and right pursuit, respectively. We chose to quantify these effects by measuring the difference in horizontal position of the stimulated and unstimulated curves; this discounts baseline biases such as that seen in Fig. 2a (where the monkey's perceived dead-ahead is about 5 degrees to the left of the geometric center of the display). To do this, we fit each dataset with a curve corresponding to a cumulative Weibull distribution (or Quick function[28]; see Methods), which we use both to test the reliability of the difference between the stimulated and unstimulated curves and to extract the midpoints for population analysis.

We have performed this experiment 67 times in two monkeys, and in 46 of these (69%), microstimulation caused statistically significant effects. Figure 3 illustrates the effects of microstimulation for this sample. For these histograms, the shifts were respresented as positive if they were in the direction pre-
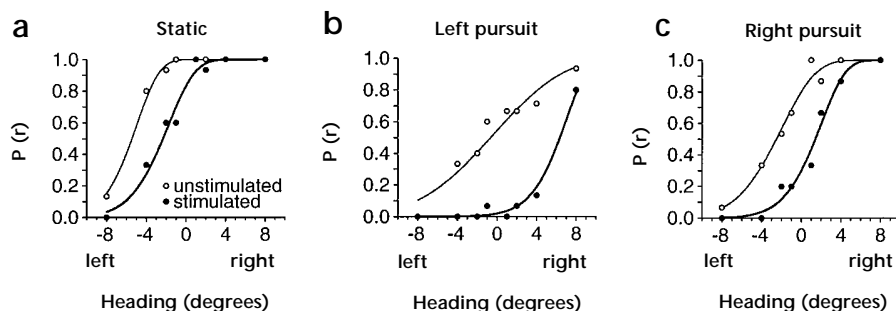
ment, we were only able to include them on a subset of the experiments reported in this paper.

Prior to commencing a microstimulation experiment, we mapped multi-unit responses to heading stimuli along electrode penetrations through MST. Although MST contains weak or negligible retinotopy, it does contain clustered or columnar organization for components of optic flow and for heading[8,11,19,26]. We were thus able to position the electrode in the center of a region containing neurons with consistent preferences for either left or right heading. Then, while behavioral data were collected, we electrically stimulated the region using 200 Hz low-amplitude pulse trains simultaneous with the visual motion stimulus. These pulse trains were designed to approximate the maximum sustained firing frequency of MST cells to normal visual stimuli, and to only activate neurons in the same cortical column whose properties we had recorded. In related experiments in the middle temporal area (MT, also called V5)[27], increasing current amplitude eventually degraded the specificity of the behavioral effects (presumably from invasion of nearby columns), but this did not occur until currents two to four times as large as those in the present study were used. A recent imaging study[26] indicates that columns in MT and MST are of similar dimensions; it is therefore likely that the effects of our stimuli are largely confined to a single column within MST. Stimulated and unstimulated trials were equally probable and randomly interleaved within a block of trials.

Fig. 2. Example data from a single MST microstimulation experiment. We plot the proportion of rightward choices, P(r), as a function of the horizontal heading, measured in degrees with respect to directly ahead, or head-centered zero. The multi-unit receptive field at the stimulation site was very large, covering the entire superior contralateral quadrant, and extending at least 20° ipsilaterally and 10° below the horizontal meridian. The neurons were selective for rightward optic flow and for left headings. The fixation point was positioned on the midline, 20° below the plane containing the centers of heading. **(a)** Static fixation. **(b)** 10 °/sec left pursuit. **(c)** 10 °/sec right pursuit.

ferred by the nearby neurons, and negative if opposite. Solid bars indicate experiments in which the two functions were significantly different (nested log likelihood test, *p*<0.05; see Methods), whereas open bars indicate effects that were not significant under our test conditions. From these histograms, we can see that microstimulation produced frequent and often substantial effects on behavior. Of the 169 individual conditions tested, 83 (49%) were statistically significant. Of these 83, 56 (67%) showed shifts in the direction predicted by the preferences of the neurons at the stimulation site, whereas the rest showed significant effects in the opposite direction. Despite its heterogeneity, the mean effect was statistically significant as well (two-way ANOVA, main effect of site preference, $F_{1,163} = 11.51$, $p< .001$). From this we conclude that the direction of the effect is significantly correlated with the preference of the neurons being activated. This frequent induction of biases, many of which were large in comparison with behavioral thresholds, provides direct and convincing evidence for a causal role of MST neuronal activity in the perception of heading.

The distributions of microstimulation effects plotted in Fig. 3 are clearly different for the different eye movement conditions. Both pursuit conditions had more and larger effects compared with the static condition, and effects under left pursuit were somewhat larger than those under right pursuit. In the same two-way ANOVA described above, the main effect of pursuit condition on
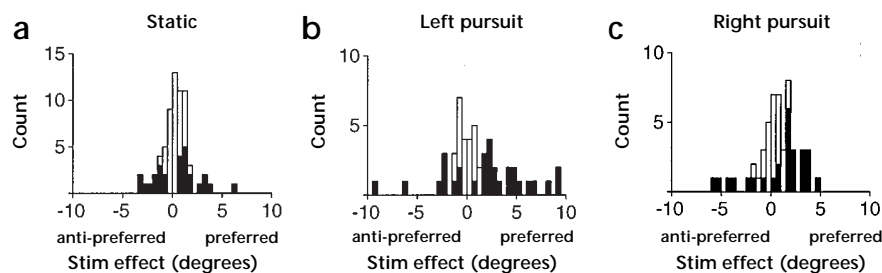

Fig. 3. Histograms showing the shifts of the psychometric functions for all of the 67 experiments in the sample, signed according to the preference of the neurons at the stimulation site. Positive values correspond to shifts in favor of the preferred heading for the site. Means of each were 0.33°, 1.15°, and 0.51° from left to right. The distributions in **(b)** and **(c)** were significantly shifted to the right of zero (t test, $p < 0.05$), while the shift in **(a)** did not quite reach significance. Filled bars indicate individually significant effects; open bars were those that did not differ statistically. The numbers of significant cases (preferred shifts in parentheses) were 27/67 (16) static; 30/51 (21) left pursuit; and 26/51 (19) right pursuit. The static condition has more total cases because pursuit was only included in 51 experiments due to time constraints.

stimulation-induced shift was also highly significant ($F_{2,163} = 6.45$, $p = 0.002$), showing that the average effect of microstimulation depended upon pursuit. To explore this further, we compared the effects of microstimulation with and without pursuit, and illustrate the results in Fig. 4. For each pursuit direction, we plot the shifts of the psychometric functions, measured in terms of actual heading direction (rather than signed by neuronal preference, as in Fig. 3). With left pursuit, note that the cloud of points is shifted above the diagonal, indicating more left choices under pursuit, whereas the opposite holds for right pursuit. Thus, pursuit appears to quantitatively influence the magnitude of the microstimulation effect, such that pursuit enables the microstimulation to produce more choices in the direction of the pursuit itself.

Discussion

With these experiments, we have demonstrated that locally perturbing the activity of clusters of neurons in area MST can have reliable and substantial effects on heading judgments in our two-alternative task. We take this as evidence that MST is involved in heading perception, but some of the complexities in the data require further consideration. Specifically, we will address the heterogeneity of behavioral effects and the pattern of interaction with pursuit eye movements.

HETEROGENEITY OF EFFECTS

The presence of reliable effects on behavior in a direction opposite to the preference of the neurons at the electrode tip is puzzling. This pattern of results is different from those of Celebrini and Newsome, who stimulated MST in the context of a linear direction discrimination task[18], and found 30/31 (97%) significant effects in the predicted direction. We have considered several possibilities to explain this difference. First, the tasks are rather different; in their experiment the monkey was required to discriminate stimuli that were in one of two opposite directions, while in ours the angle of heading could vary continuously, requiring finer discrimination. Because of this, the behavioral effects of stimulating nearby neurons with unknown preferences might be larger in our case. Second, it is possible that the within-column heterogeneity of heading signals in MST is greater than for signals of linear direction, which would be difficult to determine using multi-unit mapping techniques. Third, in our exper-
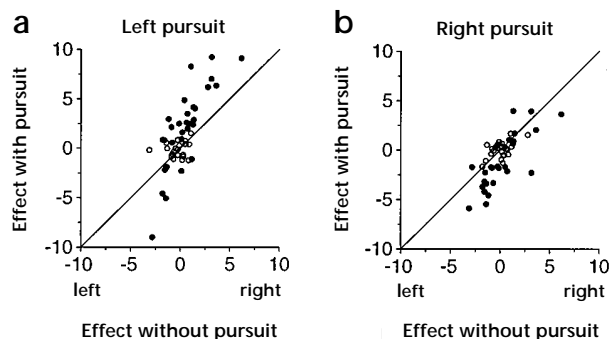

Fig. 4. Interaction between pursuit and microstimulation effect. For each of the 51 cases including pursuit, and for each pursuit direction, we plot the midpoint of the psychometric function for heading, with and without pursuit. Offsets from the unity diagonal (indicated by the line) show systematic changes in bias conditional upon the presence of pursuit. Offsets for both pursuit conditions were statistically significant (paired *t*-test, $p < 0.05$). Solid symbols indicate cases in which the effects of microstimulation were significant for either of the eye movement conditions. Note that positive shifts of the psychometric functions indicate more left choices, and negative shifts indicate more rightward choices. **(a)** Effects under left pursuit compared with static fixation. **(b)** Effects under right pursuit compared with static fixation.

iments, the stimuli always filled the screen, and often exceeded the dimensions of the receptive fields of the neurons. The monkeys could be using cues throughout the stimulus, not necessarily within the receptive field of the neurons being activated, so that lateral interactions in MST could produce the reverse effects. Lastly, it is possible that this heterogeneity reflects the greater complexity of heading computations. If local circuitry in MST is performing more complex computations, which might involve other dimensions such as the depth structure of the scene[29–31], then we might not expect completely predictable results, mapped onto the single dimension of horizontal heading. The heterogeneity of the effects does not weaken the conclusion that MST is involved in heading perception, but it forms a clear challenge for the simplest models of how it is involved.

INTERACTION WITH PURSUIT

We believe the interaction with pursuit (**Figs. 3** and **4**) reflects a disturbance in the compensation process by which observers (and our monkeys; see **Fig. 2**) can accurately judge heading in the presence of pursuit eye movements. In heading tasks where the eyes are stationary, but where the visual effects of pursuit are simulated, large errors in heading judgment ensue, especially with medium to high pursuit velocities, as we use[3,20–22,32]. This suggests that extraretinal signals (derived from efference copy of motor signals or proprioceptive feedback) of eye velocity are combined with visual signals of optic flow to produce a more accurate percept of heading. The biases in these psychophysical experiments are in the direction of the simulated pursuit, as are the added biases in our microstimulation experiments with pursuit. Therefore, the interaction we observe might reflect a shift in the balance of the retinal and extraretinal signals, such that retinal signals are emphasized under microstimulation of MST relative to extraretinal signals of ongoing pursuit.

Extraretinal signals influencing the representation of heading are also consistent with the results of Bradley et al., 1996[14]. They report two main findings: single neurons in MST are frequently tuned for heading stimuli, and this tuning appears to interact with ongoing pursuit eye movements. The compensation for pursuit is not seen for stimuli that simulate the visual effects of pursuit, so is probably based upon extraretinal signals. However, their summary histogram (their figure 3c) shows many neurons compensating in the counterintuitive direction as well. In these cells, there is an interaction with eye movements, but the sign is not consistent with the requirements of behavioral compensation. In both experiments, then, the mean effect is consistent with theory, and in both the effects are heterogeneous. The two results thus mesh well: the physiology shows sufficiency of the representation, and the microstimulation results suggest the signals are actually employed in perceiving heading direction.

Of course, the interaction with the pursuit might be a result of MST microstimulation affecting the pursuit movements themselves. We think this unlikely, because in our experiments we targeted the dorsal subdivision of MST (MSTd), where effects of microstimulation on pursuit are relatively rare[33]. In addition, we used much weaker currents than did Komatsu and Wurtz[33]. The strongest argument comes from direct measurement of pursuit in our experiments. In a subset of our experiments we measured eye position during the experiment. In three such experiments, significant effects on choice behavior were found, and in two of these, there were interactions with pursuit. In none did we find a significant effect of microstimulation of MST on the velocity of the ongoing pursuit eye movements. Thus, we feel confident that the interactions with pursuit reflect a direct effect on the per-

ception of heading, and are not indirectly mediated through an effect on the pursuit itself.

Overall, the results from this experiment lead us to conclude that MST is involved in the process by which heading is perceived from optic flow information. The effects are particularly striking when one considers the restricted area of visual cortex likely to be activated by these small currents. However, these experiments do not specify the nature of the involvement, because many cues are available for performing the task. For example, one of the most informative cues in such displays is the horizontal component of the flow vectors, especially near the specified heading[22]. Left-right direction selectivity is common in MST, and is a good predictor of horizontal heading selectivity. Therefore, the stimulation effects we observe might be heavily mediated by manipulation of signals of linear horizontal flow. Under this simple model, one might expect to find similar results wherever linear direction selectivity is found, such as the area MT. Preliminary results from our laboratory (Nace, K.L. & Britten, K.H. *Soc. Neurosci. Abstr.* **23**, 458: 1997) suggest that indeed this is the case, and that MT microstimulation can cause substantial effects on heading perception as well.

Methods

SUBJECTS AND TASK. Two adult female rhesus macaques (*Macaca mulatta*) were employed in these experiments. Each was equipped with a head post for stabilizing head position, a scleral search coil for monitoring eye position[34], and a recording cylinder over occipital cortex providing access to area MST. Prior to recording, the animals received extensive training on the heading task and had achieved stable thresholds over all the conditions used (heading eccentricities ± 30°, pursuit velocities 5-10 °/sec). MST was localized by physiological and anatomical criteria according to the methods of Celebrini and Newsome[35]. Mapping experiments revealed that MST contained regions of consistent heading tuning spanning as much as 500 μm. In each microstimulation experiment, we would localize such a region using conventional extracellular multi-unit recording methods. We included a site if it demonstrated clear and consistent preference for either left or right heading for an electrode track distance of at least 250 μm.

The electrode was positioned in the center of the site and the parameters of the heading display were adjusted to jointly maximize directionality and minimize monkey biases resulting from eccentric headings. The response targets lay in the horizontal line containing the possible headings, and the vertical coordinate of the fixation point was always at least 5° above or below this line. A warm-up block of trials was given using the chosen parameters. Headings used in each experiment were spaced by approximate $\log_2$ intervals, and were chosen to span psychophysical threshold for the eccentricity in use; typically they ranged from 0.5° to 4° or 8°. A block of trials consisted of 15 trials in each condition (usually 700 to 900 successfully completed trials in total) and lasted approximately an hour and a half. On half the trials, electrical microstimulation was applied (20 μA amplitude, biphasic at 200 Hz; each phase lasted 200 μsec with 100 μsec between phases). Trials where the monkey broke fixation (window dimensions were typically 2° vertically by 4° horizontally) were discarded from subsequent analysis. Correction trials were employed in both training and experimental blocks to minimize bias; these were also discarded from analysis.

STIMULI. Stimuli consisted of clouds of 400 or 2000 black dots (<0.5 cd/m², 15 minutes of arc wide) randomly positioned on a uniform light (30 cd/m²) background, which were moved to simulate a range of trajectories differing in their azimuth (horizontal angular coordinate). These were generated on a CRT display (1280 X 1024 pixels, 72 Hz frame rate) by custom software. The stimulus display was located 23 cm in front of the monkey, and subtended 80° horizontally by 60° vertically. The dots simulated a uniform cloud of points in 3-dimensional space, and were moved according to a linear observer trajectory of 2 m/sec towards a cloud of points 10 m in depth, whose near boundary is 1 m from the eye

at the start of the movement. Non-motion cues to depth such as disparity, size, and blur were not present.

DATA ANALYSIS. For each pursuit and microstimulation combination, the proportion of rightward choices was fit by a Quick function of the form

$$P(r) = 1 - \exp{-(h/\alpha)^{\beta}}$$

where h corresponds to heading (offset to positive values for fitting), α specifies the heading where P(r) = 0.63, and β specifies the slope of the function. All functions were fit using maximum likelihood estimation. The midpoints (P(r) = 0.5) of the best-fit functions were used to evaluate the shifts resulting from microstimulation (**Figs. 3** and **4**). To evaluate the significance of the shift for a single experiment and pursuit condition (e.g., any single panel in **Fig. 2**), likelihood ratio testing was used. Log likelihoods were calculated under two models, one in which a single function was fit to the stimulated and unstimulated functions, and another in which two separate functions were jointly fit to the two data sets. The difference in log likelihoods from the two fits is approximately chi-square distributed under the null hypothesis of no difference between the two data sets[36], with an associated df = 2 (the number of free parameters added to the relaxed model), and we tested against a critical value corresponding to $p = 0.05$. For calculating the shifts of these functions with microstimulation, only the horizontal position parameter was allowed to vary, and the corresponding df for the test statistic was 1.

For eye movement analysis, eye position data were sampled at 1 kHz, differentiated, and the resulting velocity records were smoothed with a 21 msec triangle function to reduce the high-frequency noise present in our apparatus. 'Catch-up saccades' were clearly visible in these records, and were removed using a velocity Z-score criterion of 2.5. In each experiment, between 30 and 100 trials were measured in each pursuit and stimulation condition. The distributions of single-trial velocities with and without microstimulation were compared using unpaired sample t-tests.

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