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J Neurophysiol 97:3473-3483, 2007. First published Feb 28, 2007; doi:10.1152/jn.01054.2006

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MST Neurons Code for Visual Motion in Space Independent of Pursuit Eye Movements

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¹Department of Integrative Brain Science, Graduate School of Medicine and ⁴Department of Physics, Graduate School of Science, Kyoto University, Kyoto; ²Neuroscience Research Institute, National Institute of Advanced Industrial Science and Technology, Tsukuba; ³Graduate School of Comprehensive Human Sciences, University of Tsukuba, Tsukuba; and ⁵Maebashi Institute of Technology, Maebashi, Japan

Submitted 3 October 2006; accepted in final form 24 February 2007

Inaba N, Shinomoto S, Yamane S, Takemura A, Kawano K. MST neurons code for visual motion in space independent of pursuit eye movements. *J Neurophysiol* 97: 3473–3483, 2007. First published February 28, 2007; doi:10.1152/jn.01054.2006. When a person tracks a small moving object, the visual images in the background of the visual scene move across his/her retina. It, however, is possible to estimate the actual motion of the images despite the eye-movement-induced motion. To understand the neural mechanism that reconstructs a stable visual world independent of eye movements, we explored areas MT (middle temporal) and MST (medial superior temporal) in the monkey cortex, both of which are known to be essential for visual motion analysis. We recorded the responses of neurons to a moving textured image that appeared briefly on the screen while the monkeys were performing smooth pursuit or stationary fixation tasks. Although neurons in both areas exhibited significant responses to the motion of the textured image with directional selectivity, the responses of MST neurons were mostly correlated with the motion of the image on the screen independent of pursuit eye movement, whereas the responses of MT neurons were mostly correlated with the motion of the image on the retina. Thus these MST neurons were more likely than MT neurons to distinguish between external and self-induced motion. The results are consistent with the idea that MST neurons code for visual motion in the external world while compensating for the counter-rotation of retinal images due to pursuit eye movements.

INTRODUCTION

The world around us appears to remain stationary even when our eyes are in motion. Therefore the visual system possesses the ability to reconstruct a stable world in spite of the motion of the image on the retina resulting from eye movements. It has been postulated that to achieve this perceptual stability, internal eye-movement information is used (Sperry 1950; von Holst 1954). Two brain mechanisms that use eye-movement signals to achieve a stable visual world independent of eye movements have been proposed: suppression of the sensitivity to visual motion during eye movements or estimation of the physical motion of the visual image by compensating for the effects of the eye movements. The middle temporal (MT) and medial superior temporal (MST) areas of macaque monkeys are cortical structures in the dorsal superior temporal sulcus (STS) and are good candidate areas to test these hypotheses. Both areas are known to be rich in motion-sensitive neurons, and it has been proposed that area MST encodes extra-retinal signals relating to eye movements (Duffy and Wurtz 1991; Graziano et

al. 1994; Maunsell and Van Essen 1983; Newsome et al. 1988; Saito et al. 1986; Sakata et al. 1983). Additionally, neuronal activities related to perceptual stability have been reported in the human homologue of these areas (Haarmeier and Thier 1998; Thier et al. 2001).

Visual neurons that did not respond during saccades moving against a textured image, but did respond when the textured image shifted in a way that replicated the saccades across the retina, were identified in area MT and area MST of macaque monkeys (Thiele et al. 2002). In addition, a subpopulation of neurons that reversed their preferred direction of image motion during saccades was found, suggesting their activity could be used to annul signals for retinal motion during saccades. Although suppression may be employed during saccades, it is unlikely that it is employed during pursuit; psychophysical experiments have shown that when the eyes track a target moving against a textured image, any real motion of that textured image, as opposed to its motion on the retina, can be estimated fairly well (Mack and Herman 1973; Wertheim 1994; Wertheim and Van Gelder 1990).

It has been reported that some neurons in area MST, which do not respond to the retinal motion of a stationary object caused by pursuit, do respond to the retinal image motion induced by an object moving in space during stationary fixation (Erickson and Thier 1991; Sakata et al. 1985). Because the retinal signals are the same in these two situations and the only difference between the conditions is the movement of the eyes, these studies suggest that as a result of the extra-retinal information related to the eye movements, the neurons responded to afference but not to reafference. Inhibition (Sakata et al. 1985) and selective filtering (Erickson and Thier 1991) of the visual responses of these MST neurons by extra-retinal signals have been suggested as mechanisms to suppress responses to self-induced retinal slip. These studies, however, only attempted to account for the perception of a stationary object in space during smooth pursuit eye movements.

Neuronal activities in area MSTd (dorsal subdivision of the MST) that are less affected by pursuit eye movements have also been reported. Bradley et al. (1996) found that some MSTd neurons responded to a radial pattern of optic flow with selectivity for a focus of expansion in a specific part of the visual field, and this selective region shifted during pursuit eye movements in a way that compensated for the retinal focus shift. This suggested that eye-movement signals are used to

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compensate for the displacement of the focus of the optic flow caused by pursuit eye movements. This type of compensation is important when a subject moves forward while tracking a moving object and estimates their heading direction independent of eye movements, suggesting the MSTd neurons are important for estimating egomotion (Page and Duffy 1999; Shenoy et al. 2002). On the other hand, MST neurons have been suggested to be involved in perceiving the movement of a visual stimulus (Celebrini and Newsome 1994). When a stationary subject tracks an object moving against a textured image, the subject experiences the motion of the textured image in the front-parallel plane without the focus of optic flow expansion. Even under these circumstances, the subject is able to perceive whether the textured image is stationary or moving, suggesting an ability to compensate for the self-induced retinal slip velocity in addition to the compensation for the displacement of the focus of the optic flow.

In the present study, to explore the neuronal correlates that allow perceptual stabilization of visual image during eye movements, we studied MSTd and MT neuronal responses to a textured image that was moved briefly at various speeds during smooth pursuit or stationary fixation tasks. For every neuron in the area MSTd or area MT that responded to the motion of the textured image during fixation, it was always possible to find a motion of the textured image that could activate the neuron during pursuit, indicating that any suppression was certainly less than total. In addition, most MSTd neurons encoded the physical motion of the textured image, whereas most MT neurons encoded the retinal motion of the textured image. Therefore area MSTd is much more likely than area MT to be the site of perception of image motion in the visual world by compensating for the self-induced retinal image motion during pursuit eye movements.

METHODS

Animal preparation and visual stimuli

The data were collected from three macaque monkeys (*monkeys E and G: Macaca fuscata* and *monkey S: M. mulatta*) weighing 5–9 kg. All experimental protocols were approved by the Animal Care and Use Committee of the National Institute of Advanced Industrial Science and Technology and Kyoto University. The procedures used in the present study are similar to those previously described (Kawano

et al. 1992, 1994; Kodaka et al. 2004). Prior to the surgery, animals were trained to track a moving target spot, and anatomical pictures of their heads were obtained using MRI scans (Signa Horizon). A headpost, recording chambers, and scleral coils were surgically implanted under anesthesia, and the recording chambers were stereotactically placed to allow for a dorsal approach to the parietal cortex.

The animal was seated in a dark room with its head fixed in front of a screen at a viewing distance of 40 or 50 cm. During experiments, we turned off the room lighting and hang the shade curtains over light sources to black out the screen as much as possible. The peripheral visual field of the animal was restricted ($80 \times 80^\circ$) by the frame of the eye-coil system. A red spot (the fixation point or pursuit target, 0.3° diam) and a random-dot pattern (the visual stimulus), which were back-projected onto the screen by a light-emitting diode projector and a slide projector, respectively, were moved with mirror galvanometers in the light paths (Fig. 1). The random-dot pattern consisted of white dots on a black background image (white dots: 1° diam, luminance = 5.0 cd/m^2 ; black background: luminance = 0.06 cd/m^2). The white dots covered $\sim 50\%$ of the background except along the target spot trajectories (1- or 2° -wide radial bands extending in 8 directions from the center of background image with 45° intervals) that were used to facilitate the tracking performance of the monkeys during the pursuit trials (Fig. 1). An electromechanical shutter in the light path was used to turn the visual stimulus on and off (opening time = 5 ms).

Recording and histology

Initial mapping penetrations were made with hand-made glass-coated tungsten electrodes to determine the likely location of area MSTd within the STS, and MRI scans were used to confirm the location of the STS. Due to the vertical orientation of the recording chambers, the electrodes usually entered the parietal cortex, advanced through the anterior bank of the STS, and then penetrated the posterior bank or floor of the sulcus. After reconstructing the penetrations, we identified putative MSTd and MT neurons according to previously published reports regarding the characteristics of their receptive fields, speed-selectivity, and locations relative to the STS (Komatsu and Wurtz 1988). Visual receptive-field mapping was done while the animal looked at the central fixation spot. We restricted the projection of the random-dot pattern by putting cardboard in the light path or presented a moving visual stimulus (a spot or slit of light with variable sizes: 1×1 to $3 \times 10^\circ$) by hand. Because our main concern was the response properties of the neurons that discharge in relation to moving textured images in the areas MSTd and MT, we selected electrode tracks in which we identified such MSTd and MT neurons above and below the STS, respectively. We then put a grid system (Crist Instruments, Hagerstown, MD) in the recording chamber and im-

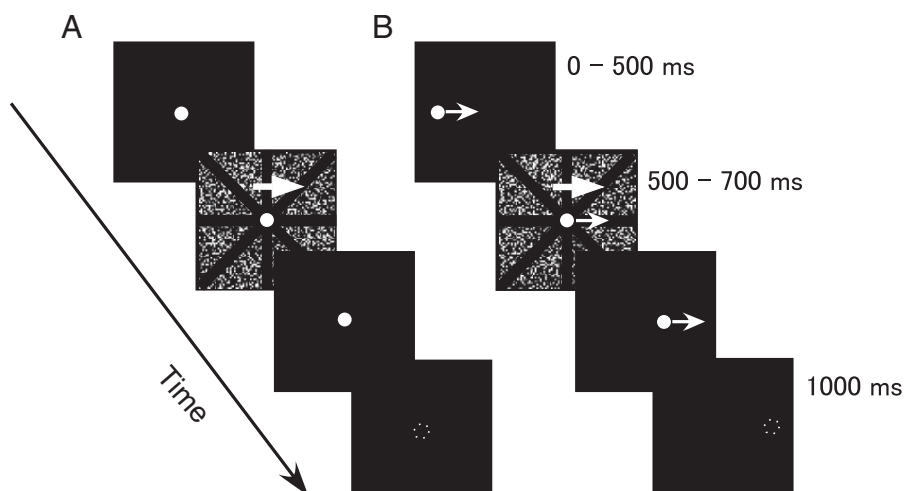


FIG. 1. Schematic diagrams of the sequence of the visual stimuli. *A*: fixation paradigm. The monkey was required to keep its eyes fixed on a target that was stationary at the center of the screen. *B*: pursuit paradigm. The target moved at a speed of $20^\circ/\text{s}$ in the direction parallel to the preferred direction of stimulus motion of the neuron. When the target reached the center of the screen, a textured image moving at a constant speed between -40 and $+60^\circ/\text{s}$ was turned on for 200 ms. The positive and negative angular velocity values indicate motion in the preferred and anti-preferred directions, respectively. The textured image consisted of random dots that filled the screen, except along the trajectories of the pursuit target.

planted guide tubes in the vicinity of the selected electrode tracks. The tips of the guide tubes were positioned 3–5 mm above the regions thought to be area MSTd. We recorded neuronal activity with a flexible tungsten electrode (Microprobe, Potomac, MD) introduced through the guide tube and applied the behavioral paradigms described in the following text. In two monkeys (*monkeys E and G*), histological sections through the STS were obtained at the end of the experiments as described previously (Kawano et al. 1994; Takemura et al. 2007). Histological verification of the recording sites indicated that these neurons were located either in area MSTd or in area MT (Kawano et al. 1994; Komatsu and Wurtz 1988; Maunsell and Van Essen 1983). In the other animal (*monkey S*), histological verification of the recording sites has not yet been obtained as recordings are still under way.

Behavioral paradigm

We attempted to characterize the properties of neurons that discharged in response to the motion of a large-field visual stimulus. To achieve this, we advanced the electrodes while exposing the monkey to a moving large-field textured image (the random-dot pattern) and selected neurons that were sensitive to this stimulus. After isolating a single unit and determining its receptive field, we observed responses to laminar motions of the textured image moving at 20 or 40°/s while the monkey fixated on a stationary target spot. This allowed us to determine the neuron's preferred direction of motion for the stimulus among the eight possible directions. Next, the monkey was required to pursue or fixate on the target spot (see Fig. 1). At the start of each trial, the stationary target spot appeared at the center of the dark screen. The monkey was required to keep its eyes fixed on the target spot, which either remained stationary (fixation paradigm, Fig. 1A) or moved at a constant speed of 20°/s in the preferred or anti-preferred direction (pursuit paradigm, Fig. 1B). For the pursuit paradigm, step-ramp target motions were used (Rashbass 1961). After the monkey fixated its eyes on the central position, the target spot was relocated to an eccentric position (8° from the center), thereby eliciting a saccadic eye movement. After a randomized period of 0.2–1.0 s during which the monkey kept its eyes fixed on the eccentric target, the target was moved further away from the center with a 2° step (a total of 10° from the center) and then moved back to the center at 20°/s (target ramp). The direction and size of the step (2°) were selected to minimize the likelihood of catch-up saccades. The target spot moved across the center position 500 ms after the onset of the ramp motion. When the target spot reached the center of the screen, the textured image was turned on for 200 ms and was either stationary or moving at a constant speed between –40 and +60°/s. The positive and negative values of the image speed indicate motion in the preferred and anti-preferred directions, respectively. Because the responses of most MST neurons saturate at high stimulus speeds, the range of the stimulus velocities was selected so that the MST neurons were able to encode the stimulus speeds (Churchland and Lisberger 2005; Kawano et al. 1994). The duration of each target ramp motion was 1,000 ms. The target spot was then turned off, which indicated the end of the trial, and the monkey was given a drop of fruit juice. To receive a fruit-juice reward, the monkey was required to keep its eyes within 2.5° of the target spot throughout the trial and to refrain from making any saccades during tracking (or fixation). Trials free of saccades for the first 800 ms following the onset of the target ramp motion were selected for averaging.

Data collection

The stimulus presentation and data collection were controlled by a personal computer (PC) using the REX system (Hays et al. 1982). Eye movements were measured with the electromagnetic search-coil technique (Fuchs and Robinson 1966). Voltage signals encoding the horizontal and vertical components of the eye position were low-pass

filtered with R-C circuitry (170 Hz, –3 dB) and digitized to a resolution of 12 bits with a 1-kHz sampling rate. All data were stored and transferred to a PC for analysis using an interactive computer program based on MATLAB (Mathworks, Natick, MA). Eye-position data were smoothed with a digital low-pass filter (33 points, 30 Hz, –3 dB), and eye velocity was obtained by two-point backward differentiation of the eye-position data to identify saccades using velocity criteria; eye movements were determined to be saccades if the eye velocity was more than $\pm 25^\circ/\text{s}$ from the target velocity (0°/s for fixation and 20°/s for pursuit). A time-amplitude window discriminator was used to measure spikes with a time resolution of 1 ms. Spike-density histograms were calculated by convolving the spike trains with a Gaussian curve ($\sigma = 10$ ms) (Richmond et al. 1987). Neuronal responses to the motion of the textured image were measured as the average of the spike density from 50 to 250 ms after the stimulus onset (i.e., from 550 to 750 ms after the onset of the target ramp motion).

Analysis

The neuronal responses to the visual stimulus were analyzed in relation to image motion on the screen and on the retina. Visual motion of the textured image on the retina was computed by subtracting the eye velocity (averaged over a period from 500 to 700 ms after the onset of the target ramp motion) from the angular velocity of the textured image on the screen.

Although responses were variable among individual neurons, they commonly exhibit sigmoidal speed dependence with a characteristic shift. We examined a Gabor function

$$f_a(\omega) = a_1 + a_2 \exp(-\omega^2/2a_3^2) \sin((\omega - a_4)/a_5)$$

and a sigmoidal logistic function in their ability to fit the data. These processing were performed using self-written scripts together with available package program in Mathematica (Wolfram Research, Champaign, IL). The Gabor function was better than the logistic function in fitting all the data (from 112 MST and 60 MT neurons for 3 tracking conditions), including some nonmonotonic responses. To select a fitting function for the analysis, we calculated deviations of individual data from the fitting functions: the Gabor function and the logistic function. Their SDs were 13.46 and 13.79 spikes/s for MST neurons and 19.97 and 20.23 spike/s for MT neurons, respectively. These differences in the SDs indicated the superiority of the Gabor fitting, significantly surmounting the penalty in the Akaike Information Criterion (AIC) for the higher complexity of the fitting function (Akaike 1974), and we report here the results obtained by the Gabor fitting.

The function was fit to the responses under the three different tracking conditions defined by $f_a(\omega - \omega_i)$, including target tracking in the preferred and anti-preferred directions, and fixation, by adopting independent shifts $\{\omega_1, \omega_{-1}, \omega_0\}$ using an identical set of shape parameters, $a = \{a_1, a_2, \dots, a_5\}$, so that a set of the parameters minimized the squared error

$$E = \sum_i \sum_j (r_j^i - f_a(\omega_j^i - \omega_i))^2$$

where r_j^i was the firing rate of the j th trial of the i th tracking condition, and ω_j^i was the angular velocity of the textured image.

In this matching function method (Gabor function analysis), the goodness of the fit was further quantified as the confidence intervals based on the likelihood ratio test (for an example, see Kass et al. 2005). Assuming a Gaussian distribution of the fitting errors

$$P(\omega) = \prod_j \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{(r_j^i - f_a(\omega_j^i - \omega_i))^2}{2\sigma^2}\right) \quad (3)$$

the optimal fitting parameters ω^*_i and $a^* = \{a^*_1, a^*_2, \dots, a^*_5\}$ and the SD σ^* were first determined by maximizing the likelihood

function. This can be performed by applying the least-square method to the fitting parameters and then computing the deviation of data from the fitted function. Then the 95% confidence interval of each response shift ω_i was obtained by numerically solving the equation

$$\sum_j (r_j^i - f_{a^*}(\omega_j^i - \omega_i))^2 / 2\sigma^{*2} - \sum_j (r_j^i - f_{a^*}(\omega_j^i - \omega_i^*))^2 / 2\sigma^{*2} = \chi_{0.05}^2(1) = 3.84 \quad (4)$$

We expressed the response shift and the confidence interval as $\omega_i^* \pm \delta\omega_i$. Our method is similar to the method for computing correlation coefficients proposed by Bradley et al. (1996) because both methods can determine shifts in neuronal responses $\{\omega_{-1}^*, \omega_0^*, \omega_1^*\}$. Our method is superior to the correlation method in its ability to estimate confidence intervals in the angular velocity coordinate. The narrower the confidence interval $\delta\omega$, the more reliably the stimulus velocity can be inferred from the neuronal spikes.

To quantify the spatial shifts of the neuronal tuning functions, a cross-covariance technique was used (Avillac et al. 2005; Duhamel et al. 1997; Fetsch et al. 2007). It is well-suited to determine the correlation between two response curves in which the data satisfy the periodic boundary condition ($0^\circ = 360^\circ$). On the other hand, it is not suitable for our data because the neuronal response in our study is a function of stimulus speed, which is not a periodic function. Furthermore our study focused on the neuronal responses to the visual stimulus moving at speeds in a limited range, between -20 and $+40^\circ/\text{s}$ (either on the screen or retina), which was not wide enough to calculate a cross-covariance index in relation to two tracking conditions in which eye velocities differed by $40^\circ/\text{s}$.

RESULTS

We recorded the activities of 559 neurons in the STS in three monkeys and examined the activities of neurons that discharged in response to movement of the large textured image (visual stimulus). The majority of the neurons (475/559, 85%) were determined to be direction selective because their average firing rates were ≥ 1.4 times higher for stimulus movement in the preferred direction than for stimulus movement in the anti-preferred direction. One hundred and seventy-two direction-selective neurons for which we were able to average the responses to the laminar motion of the large textured image over at least five trials [12 ± 5 (SD) trials] were examined further. After the preferred direction of the motion of the textured image was determined for each neuron, the monkey was required either to pursue a target spot that moved parallel to the preferred direction of the neuron or to fixate on a stationary target spot.

Responses of an MST neuron to image motion on the screen

The responses of 112 MST neurons to a brief presentation of the textured image moving at various speeds were recorded under the three tracking conditions. Figure 2A shows sample responses of an MST neuron (*top*) to motion of the textured image in the preferred direction ($+20^\circ/\text{s}$, leftward) while the gaze of the animal fixed on a target that was either stationary (blue traces) or moving at the same speed as the textured image in the same ($+20^\circ/\text{s}$, red traces) or opposite direction ($-20^\circ/\text{s}$, green traces). The presented data are from the time the target started to move (0 ms on the time axis) and the moving textured image was visible for 200 ms (from 500 to 700 ms). The movement of the textured image on the screen was always leftward, which was the neuron's preferred stimulus-move-

ment direction, at $20^\circ/\text{s}$ (see stimulus velocity traces on the screen of Fig. 2A). The firing rate increased in response to the motion of the textured image with a latency of ~ 50 ms, and the response patterns of this neuron were similar under the three tracking conditions in spite of the fact that the motion of the textured image on the retina was almost double ($+40^\circ/\text{s}$) the actual motion of the textured image when the animal tracked to the right (green traces, anti-preferred direction) and was almost zero when the animal tracked to the left (red traces, preferred direction) as shown by stimulus velocity traces on the retina of Fig. 2A. The response of this neuron appeared to be dependent on the stimulus motion defined by the speed of the image on the screen rather than the speed on the retina.

A similar pattern of neuronal behavior was observed for a wide range of image speeds by plotting the mean firing rate as a function of the velocity of the textured image on the screen (screen coordinates) under the three tracking conditions (Fig. 2B). We also found that the velocity dependence of this neuron was strongly asymmetric, i.e., the responses increased with an increase in the stimulus velocity in the preferred direction, but was almost unchanged for a velocity increase in the anti-preferred direction.

Figure 2C illustrates the results of the Gabor function analysis and indicates that the response curves for the three tracking conditions exhibited essentially the same stimulus-speed dependence but slightly shifted horizontally with respect to each other: $\{\omega_1, \omega_{-1}, \omega_0\} = \{26.6 \pm 2.6, 23.7 \pm 1.9, 19.2 \pm 2.6\}$. Therefore the response of this neuron depended on the stimulus velocity on the screen.

Responses of the MST neuron to retinal image motion

This observation that physical motion in the real world—rather than motion on the retina—was the key factor for activation of this MST neuron was further confirmed with the experiment in which the retinal image motion was roughly the same ($+20^\circ/\text{s}$, see stimulus velocity traces on the retina of Fig. 2D). Under these conditions, the activation associated with the image motion clearly showed substantial differences during the three tracking conditions, depending on the image motion on the screen (Fig. 2D). Thus the level of activation was very low when the textured image did not move on the screen (green traces), whereas it was higher when the textured image moved at $20^\circ/\text{s}$ on the screen (blue traces) and was the highest when the textured image moved at $40^\circ/\text{s}$ on the screen (red traces); due to saturation of the response, however, the response to the $40^\circ/\text{s}$ movement was only slightly larger than the response to the $20^\circ/\text{s}$ movement. Note that the same response curves for the firing rate and the ocular response are shown with the blue traces in Fig. 2, A and D.

A similar pattern of neuronal behavior was observed over a wide range of textured image speeds on the retina and this can be seen in Fig. 2E in which we re-plotted the data shown in Fig. 2B as a function of the speed of the textured image on the retina (retinal coordinates). Pursuit eye movements in the preferred or anti-preferred direction caused the response curve to shift along the axis representing the stimulus speed on the retina. This was confirmed in Fig. 2F where the data sets obtained in the three tracking conditions were fitted by Gabor functions. In contrast to the results from the Gabor function analysis of the stimulus motion on the screen (Fig. 2C), these three curves

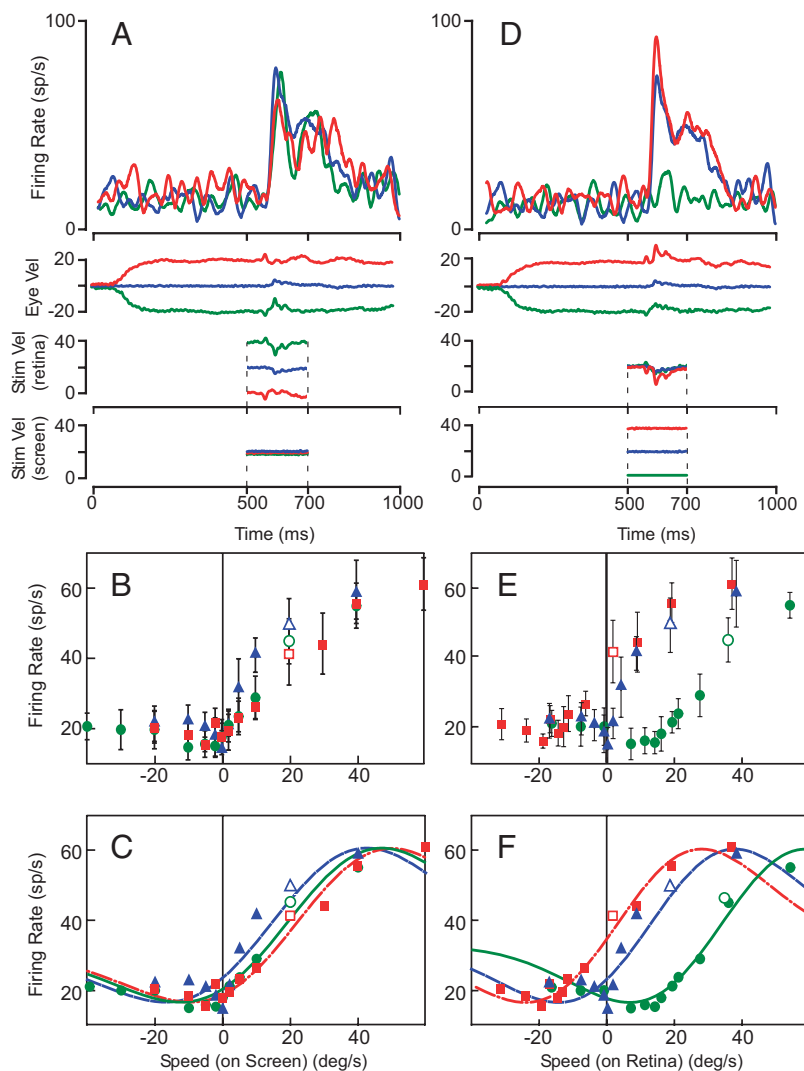


FIG. 2. *A*: effects of smooth pursuit eye movements on the responses of a medial superior temporal (MST) neuron to a moving textured image. When the animal fixated on a stationary target at the center of the screen (blue), the firing rate of the neuron increased when the textured image moved to the left (the preferred direction). The textured image was presented for 200 ms starting 500 ms after the onset of the motion of the pursuit target, and moved at $20^\circ/\text{s}$ in the preferred direction of the neuron. The pursuit target moved at $20^\circ/\text{s}$ in preferred direction (red) or in the anti-preferred direction (green). From top to bottom, the records indicate the spike density function of the neuronal responses, the mean horizontal eye velocity profiles, and the stimulus velocity profiles on the retina and on the screen. *B*: responses of this neuron to the textured image moving at various angular velocities on the screen. The positive and negative values indicate the angular velocity of the motion in the preferred and anti-preferred directions, respectively. The red, green, and blue dots represent the responses when the monkey was pursuing the target moving in the preferred direction at $20^\circ/\text{s}$, pursuing the target moving in the anti-preferred direction at $20^\circ/\text{s}$, and fixating on a stationary target, respectively. Each point is the average firing rate (\pm SD) of the neuron during the time period from 550 to 750 ms after the start of the target ramp. The 3 responses shown in *A* are represented by the 3 open symbols at the speed of $20^\circ/\text{s}$. *C*: data obtained under the 3 tracking conditions were simultaneously fitted by single Gabor functions by adopting 3 independent shifts along the angular-velocity axis using the screen coordinates. The shifts in the response curves $\{\omega_1, \omega_{-1}, \omega_0\}$ for the 3 tracking conditions in the preferred (red) and anti-preferred directions (green) and fixation (blue) were estimated to be $\{26.6 \pm 2.6, 23.7 \pm 1.9, 19.2 \pm 2.6\}$ along the axis for the stimulus speed on the screen. *D*: responses to retinal image motion of the textured image that was selected to be $\sim 20^\circ/\text{s}$ in the preferred direction. The conditions are the same as in *A* except that the textured image moved at $40^\circ/\text{s}$ in the preferred direction during pursuit in preferred direction (red), $20^\circ/\text{s}$ in the preferred direction during stationary fixation (blue), or remained stationary during pursuit in the anti-preferred direction (green). *E* and *F*: same as *B* and *C* except that the data points were plotted against the image speed on the retina. Open symbols in *E* are the re-plotted data corresponding to the open symbols in *B*. The shifts in the response curves $\{\omega_1, \omega_{-1}, \omega_0\}$ were estimated to be $\{6.5 \pm 2.2, 37.3 \pm 1.7, 16.3 \pm 2.3\}$ along the axis for the stimulus speed on the retina.

were widely separated with large horizontal shifts ($\{\omega_1, \omega_{-1}, \omega_0\} = \{6.5 \pm 2.2, 37.3 \pm 1.7, 16.3 \pm 2.3\}$), the pursuit in the preferred direction (red line) shifted to the negative and that in the anti-preferred direction (green line) to the positive away from the response-curve for the fixation task (blue line). All of these findings are consistent with the observation that the response of the MST neuron was closely correlated with the physical motion of the textured image on the screen rather than with the motion of its retinal image.

Response characteristics of an MT neuron

Similar analysis revealed that the responsiveness of MT neurons to the image motions defined by the screen and retinal coordinates was opposite of that of the MST neuron. Figure 3 illustrates responses of an MT neuron under the same experimental conditions used for the MST neuron shown in Fig. 2. The responses were almost the same for the condition with three different stimulus velocities on the screen but with the same velocities on the retina (Fig. 3*D*). On the other hand, the responses were different for the condition with the same screen but different retinal velocities (Fig. 3*A*); accordingly, the velocity-response relationship shifted for the screen coordinates

(Fig. 3, *B* and *C*) but was consistent for the retinal coordinates (Fig. 3, *E* and *F*). These findings contrasted with the results obtained for the MST neuron, which indicate that the response curves for the speed of the image on the screen (Fig. 3*C*) were clearly separated with large horizontal shifts $\{\omega_1, \omega_{-1}, \omega_0\} = \{31.1 \pm 1.9, -1.3 \pm 2.0, 13.6 \pm 1.8\}$, whereas the response curves for the speed of the image on the retina (Fig. 3*F*) were similar with small horizontal shifts $\{\omega_1, \omega_{-1}, \omega_0\} = \{7.5 \pm 1.7, 15.4 \pm 1.9, 10.8 \pm 1.6\}$. These findings suggest that the responses of the MT neuron were sensitive to the retinal motion of the textured image rather than the motion of the image on the screen.

Comparison of ensembles of MST and MT neurons

The analysis conducted for 112 MST neurons and 60 MT neurons revealed a systematic difference between the responses of the MST and MT neurons to the image motion defined by the screen and retinal coordinates.

Figure 4, *A* and *B*, illustrates the velocity-response relationship expressed according to the screen and retinal coordinates, respectively, and fitted by Gabor functions for the nine MST neurons with the narrowest confidence intervals

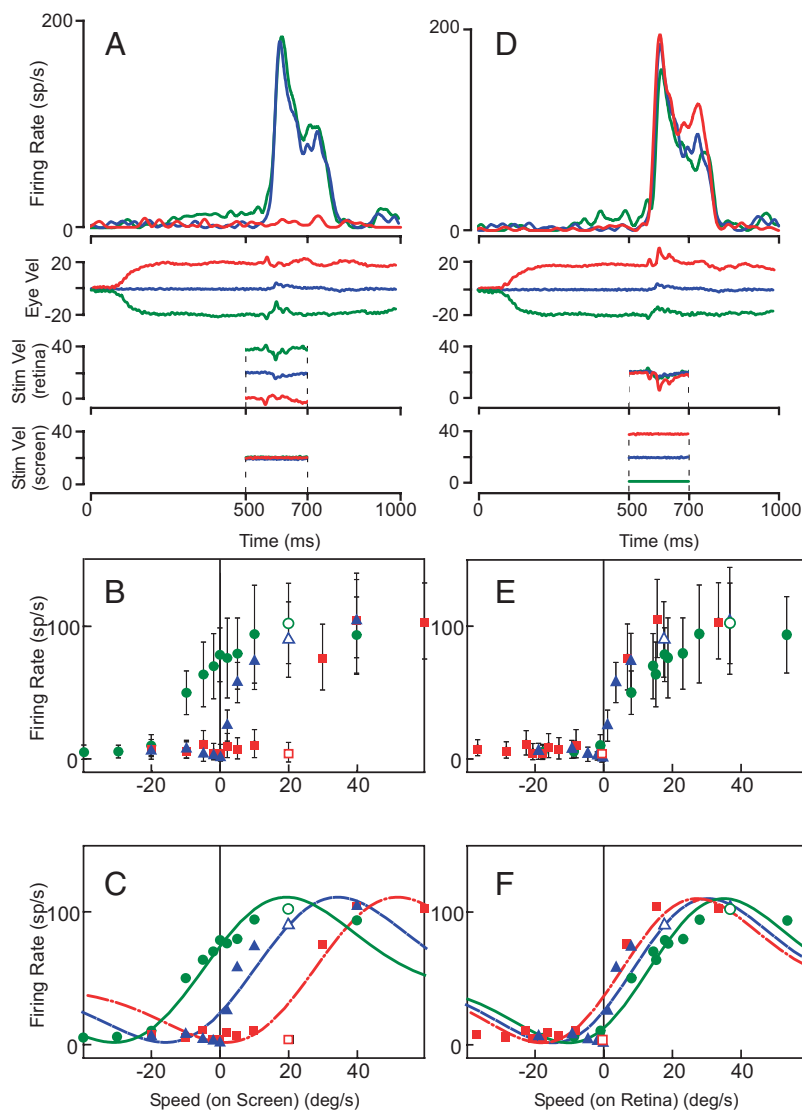


FIG. 3. Effects of smooth pursuit eye movements on the responses of a middle temporal (MT) neuron. Details of A–F are the same as in Fig. 2. The shifts in the response curves $\{\omega_1, \omega_{-1}, \omega_0\}$ were estimated to be $\{31.1 \pm 1.9, -1.3 \pm 2.0, 13.6 \pm 1.8\}$ along the axis for the stimulus speed on the screen, whereas the shifts $\{\omega_1, \omega_{-1}, \omega_0\}$ were estimated to be $\{7.5 \pm 1.7, 15.4 \pm 1.9, 10.8 \pm 1.6\}$ along the axis for the stimulus speed on the retina.

($\delta\omega_i$ values from 1.7 to 3.0). The neuron shown in Fig. 2 also had a narrow confidence interval (originally the 8th position in the list) but was omitted from this figure. For the nine neurons, the velocity-response relationship was consistent for the screen coordinates but shifted for the retinal coordinates. Conversely, the velocity-response plots for the nine MT neurons with the narrowest confidence intervals ($\delta\omega_i$ values from 1.4 to 2.0) showed shifted and consistent relationships for the screen and retinal coordinates, respectively (Fig. 4, C and D). The neuron shown in Fig. 3 was originally the eighth position in the list but was omitted from this figure.

To quantify the relationship between the neuronal responses and the stimulus speed, whether it is on the retina or on the screen, we calculated the shift of the response curve of each neuron for the pursuit conditions with the target moving in the preferred or anti-preferred direction relative to the response curve obtained for the fixation condition. These results are summarized in Fig. 5A as scatter diagrams for the 104 MST neurons (104/112, \circ) and the 57 MT neurons (57/60, \bullet); the responses of eight MST neurons (8/112) and three MT neurons (3/60) were omitted because

they were poorly fitted by Gabor functions ($\delta\omega_i > 60$). If a neuron responds purely in relation to the motion on the screen, the relative response shifts for the pursuit conditions with the target moving in the preferred (x axis) and anti-preferred directions (y axis) based on retinal coordinates (Fig. 5B) should be -20 and $+20^\circ/s$, respectively, whereas the shifts based on screen coordinates (Fig. 5A) should be zero for both pursuit conditions. Alternatively, if a neuron responds purely in relation to the retinal motion, the shifts for the pursuit conditions with the target moving in the preferred and anti-preferred directions in speeds on the screen (Fig. 5A) should be $+20$ and $-20^\circ/s$, respectively, whereas the shifts in speeds on the retina (Fig. 5B) should be zero for both conditions. For example, the relative response shifts of the MST neuron shown in Fig. 2 for the pursuit conditions with the target moving in the preferred and anti-preferred directions on the basis of the speed of the image on the screen were 7.4 and $4.5^\circ/s$, respectively (Fig. 5A, ∇), whereas on the basis of the speed of the image on the retina, they were -9.8 and $21.0^\circ/s$, respectively (Fig. 5B, ∇). On the other hand, the shifts in the response curves of the MT neuron shown in Fig. 3 with the target moving in the

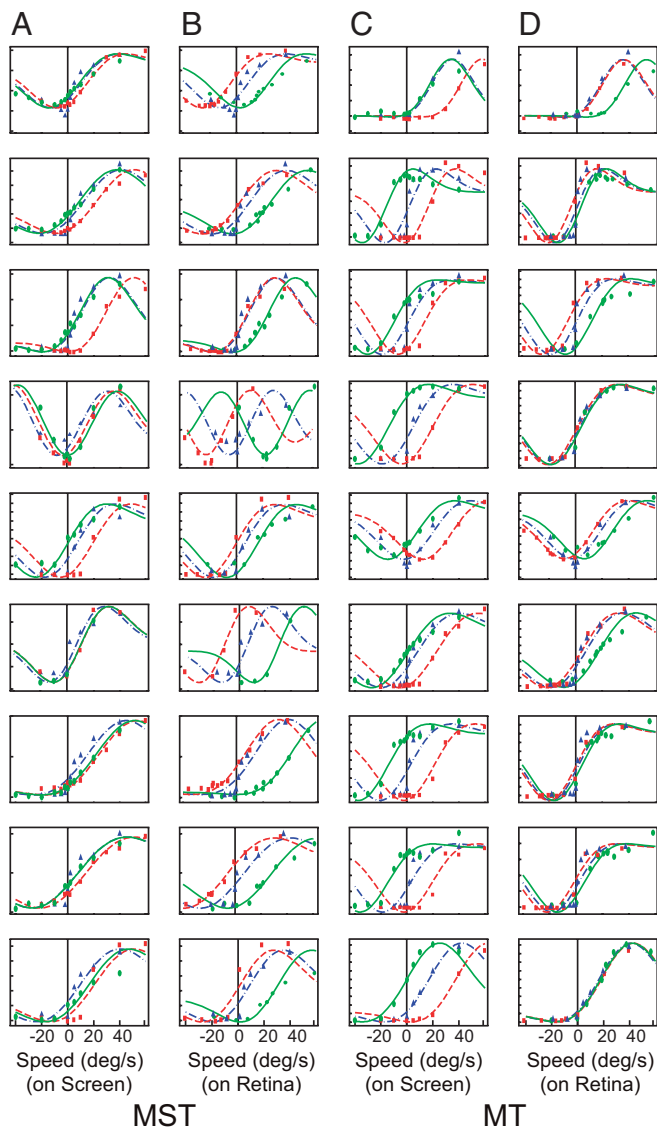


FIG. 4. *A*: responses and fitted Gabor functions of nine sample MST neurons plotted as functions of the stimulus speed on the screen. The neurons were selected for their narrow confidence intervals derived from simultaneously fitting the same Gabor function to the 3 sets of response data. *x* axis: the speed of the motion of the textured image on the screen (deg/s). *y* axis: the mean firing rate of each neuron averaged over the time period from 550 to 750 ms after the start of the target ramp. Small ticks indicate 20 spikes/s. The color scheme is the same as in Fig. 2. *B*: responses and fitted Gabor functions of the same MST neurons in *A* plotted as functions of the stimulus speed on the retina. *C*: responses and fitted Gabor functions of nine sample MT neurons plotted as functions of the stimulus speed on the screen. *D*: responses and fitted Gabor functions of the same MT neurons in *C* plotted as functions of the stimulus speed on the retina.

preferred and anti-preferred directions were 19.5 and $-14.9^\circ/\text{s}$ based on screen coordinates, whereas based on the retinal coordinates, they were -3.3 and $4.6^\circ/\text{s}$, respectively (Fig. 5, \blacktriangledown).

The means of the response shifts of the 104 MST neurons for the pursuit conditions in the preferred (*x* axis) and anti-preferred directions relative to the fixation condition (*y* axis) on the basis of the stimulus speed on the screen (Fig. 5*A*; \circ) were $+4.3 \pm 15.1$ and $+7.6 \pm 16.8^\circ/\text{s}$ (means \pm SD), respectively (Table 1; MST screen). On the other hand, the means of the

relative response shifts of 57 MT neurons based on the screen coordinates (Fig. 5*A*; \bullet) were $+20.6 \pm 9.0$ and $-16.0 \pm 8.9^\circ/\text{s}$, respectively (Table 1; MT screen).

The mean of the relative response shifts of the 94 MST neurons (94/112, $\delta\omega_i \leq 60$) for the pursuit conditions in the preferred and anti-preferred directions on the basis of the stimulus speed on the retina (Fig. 5*B*; \circ) were -14.2 ± 12.6 and $+22.5 \pm 17.3^\circ/\text{s}$, respectively (Table 1; MST retina). On the other hand, the mean of the relative response shifts of the 59 MT neurons (59/60, $\delta\omega_i \leq 60$) on the basis of the stimulus speed on the retina (Fig. 5*B*; \bullet) were 0.2 ± 7.7 and $+2.3 \pm 10.1^\circ/\text{s}$, respectively (Table 1; MT retina).

To quantify the distribution of the relative response shifts obtained in the MST and MT neurons, the relative response shifts were summarized as frequency histograms for the MST neurons and MT neurons (Fig. 6). The relative response shifts of the MST neurons for the pursuits in preferred (red) and anti-preferred directions (green) basis of the stimulus speed on the screen were distributed around the means $+4.3 \pm 15.1$ and $+7.6 \pm 16.8^\circ/\text{s}$, respectively (Fig. 6*A*; the SEs were 1.5 and 1.6, respectively; paired *t*-test: $P > 0.01$; $n = 104$). On the other hand, their relative response shifts on the basis of the stimulus speed on the retina were -14.2 ± 12.6 and $+22.5 \pm 17.3^\circ/\text{s}$, respectively (Fig. 6*B*; the SEs were 1.3 and 1.8, respectively; paired *t*-test: $P < 0.001$; $n = 94$).

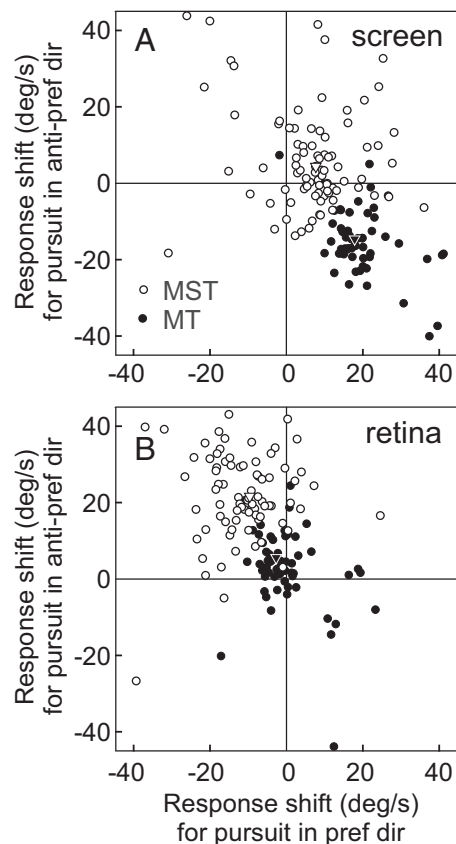


FIG. 5. *A*: scatter diagram of the relative response shifts on the basis of the stimulus speed on the screen for pursuit in the preferred direction (*x* axis) and in the anti-preferred direction (*y* axis). \circ , MST neurons; \bullet , MT neurons. ∇ , MST neuron in Fig. 2; \blacktriangledown , MT neuron in Fig. 3. *B*: scatter diagram of the relative response shifts on the basis of the stimulus speed on the retina for pursuit in the preferred direction and in the anti-preferred direction. Symbols are the same as in *A*.

TABLE 1. *Relative response shifts of neurons for pursuits in preferred and anti-preferred directions*

Monkey	Area	Speed On	Relative Response Shift for Pursuit		N ($\delta\omega_j \leq 60$)
			Preferred direction	Anti-preferred direction	
All	MST	Screen	4.3 ± 15.1	7.6 ± 16.8	104/112
		Retina	-14.2 ± 12.6	22.5 ± 17.3	94/112
	MT	Screen	20.6 ± 9.0	-16.0 ± 8.9	57/60
		Retina	0.2 ± 7.7	2.3 ± 10.1	59/60
Monkey E	MST	Screen	4.0 ± 13.3	9.2 ± 15.8	57/57
		Retina	-13.6 ± 11.0	25.2 ± 12.5	52/57
	MT	Screen	17.1 ± 5.4	-12.5 ± 8.2	29/29
		Retina	-3.0 ± 3.6	6.2 ± 7.5	29/29
Monkey G	MST	Screen	5.5 ± 7.7	-9.1 ± 0.6	2/5
		Retina	-16.0 ± 10.5	11.1 ± 0.9	2/5
	MT	Screen	30.6 ± 13.3	-25.6 ± 11.8	7/8
		Retina	3.4 ± 13.1	-4.8 ± 11.3	8/8
Monkey S	MST	Screen	4.6 ± 17.5	6.3 ± 18.1	45/50
		Retina	-14.8 ± 14.7	19.5 ± 22.0	40/50
	MT	Screen	22.0 ± 8.7	-17.5 ± 5.6	21/23
		Retina	3.2 ± 7.7	-0.1 ± 11.0	22/23

Values are means \pm SD in degrees. MST, medial superior temporal; MT, middle temporal. in degrees.

The relative response shifts of the MT neurons for the pursuit conditions in the preferred and anti-preferred directions on the basis of the stimulus speed on the screen were $+20.6 \pm 9.0$ and $-16.0 \pm 8.9^\circ/s$, respectively (Fig. 6C; the SEs were 1.2 and 1.2, respectively; paired t -test: $P < 0.001$; $n = 57$). On the other hand, the relative response shifts on the basis of the stimulus speed on the retina were 0.2 ± 7.7 and $+2.3 \pm 10.1^\circ/s$, respectively (Fig. 6D; the SEs were 1.0 and 1.3, respectively; paired t -test: $P > 0.01$; $n = 59$).

Table 1 shows the overall statistics results for each monkey. It confirms that the MST neuronal population consistently encoded the image motion on the screen rather than that on the retina, whereas the MT neuronal population encoded the retinal image motion rather than image motion on the screen.

Neuronal activity in absence of textured image motion during pursuit

Our original analysis presumed that we would only observe changes in the dependence of the neuronal responses on the stimulus speed either on the screen or on the retina. Therefore we conducted one-way Gabor function analysis of the neuronal responses to the image motion during the three tracking conditions while assuming only a shift along the x axis. However, there might be other changes such as changes in the magnitude of the responses depending on the tracking condition. If pursuit eye movements per se modulated the neuronal activities as reported previously (Erickson and Thier 1991; Kawano et al. 1984; Komatsu and Wurtz 1988; Sakata et al. 1983), the assumption of the shift only along the x axis may result in errors. In the present study, the activities in the absence of textured image motion were found for 27 MST and 27 MT neurons during pursuit. In the present study, such modulations of the firing rate were measured as the average of the spike density from 300 to 500 ms after the onset of the target ramp motion (during 200 ms before the onset of the visual stimulus) and were compared with that during stationary fixation. For instance, in Fig. 3, the baseline activity increased slightly (16 spikes/s) when the animal tracked a target moving in the anti-preferred direction in the absence of image motion (the green traces in the top panels). In the majority of neurons, however, these modulations were weak compared with the responses to the motion of the textured image. There may be a shift in the response curves along the y axis for each neuron (for example, see Fig. 4C). These shifts, however, were much weaker than those for the image motion. To check for possible errors introduced by the one-way Gabor function analysis, we fitted the data in a way that allowed another parameter to simultaneously vary and then analyzed the shifts in the presence of the varying parameters. In other words, we conducted

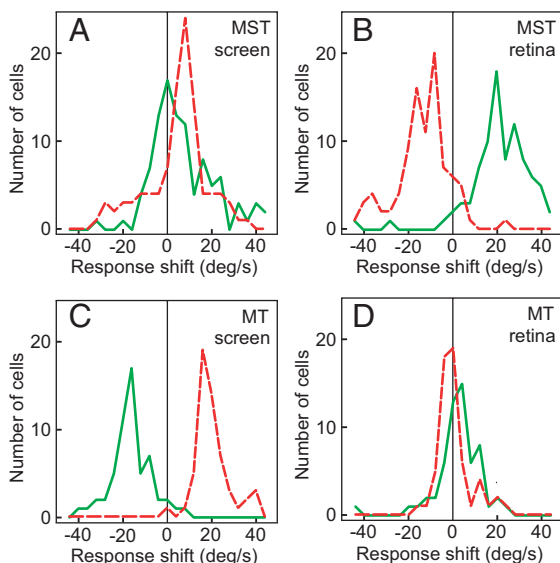


FIG. 6. A: distributions of the relative response shifts of 104 MST neurons for pursuit in the preferred (red) and anti-preferred (green) directions on the basis of the stimulus speed on the screen ($+4.3 \pm 15.1$ and $+7.6 \pm 16.8^\circ/s$, respectively). B: distributions of relative response shifts of the 94 MST neurons on the basis of the stimulus speed on the retina (-14.2 ± 12.6 and $+22.5 \pm 17.3^\circ/s$ for pursuit in the preferred and anti-preferred directions, respectively). C: distributions of the relative response shifts of 57 MT neurons for the pursuit on the basis of the stimulus speed on the screen ($+20.6 \pm 9.0$ and $-16.0 \pm 8.9^\circ/s$ for pursuit in the preferred and anti-preferred directions, respectively). D: distributions of the relative response shifts of the 59 MT neurons on the basis of the stimulus speed on the retina ($+0.2 \pm 7.7$ and $+2.3 \pm 10.1^\circ/s$ for pursuit in the preferred and anti-preferred directions, respectively). The red and green lines indicate the response shifts during pursuit in the preferred and anti-preferred directions, respectively. All data are the means \pm SD.

two-way Gabor function analysis assuming shifts along both the x and y axes. As a result, the distributions of the response shifts in the x direction were not significantly different from the original distributions shown in Fig. 6 (data not shown). The relative shifts in the y direction (firing rate) determined by two-way Gabor function analysis were distributed around zero with a relatively small SD, ranging from 2.9 to 10.4 spike/s (data not shown). Each panel in Fig. 4 also indicates that the response shifts in the y direction were negligible for most neurons. These results confirmed the validity of the one-way Gabor function analysis.

There were some neurons (22/172) in both areas MST and MT that responded when the textured image was turned on irrespective of the textured image motion, the "on-responses." Because these "on-responses" were observed under all three tracking conditions, one-way Gabor function analysis could also be applied for these neurons.

DISCUSSION

The present study demonstrated the differential responsiveness of MST and MT neurons; the MST neurons were sensitive to the motion of the image on the screen, whereas the MT neurons were sensitive to the retinal image motion. This finding indicates that area MST but not area MT is involved in the perceptual stability of visual scene during pursuit eye movements.

Previous studies have shown that there are neurons in area MST that do respond to the retinal image motion induced by an object moving in space during stationary fixation but do not respond to the retinal image motion of a stationary object caused by smooth pursuit eye movements (Erickson and Thier 1991; Sakata et al. 1985). On the other hand, V4 and MT neurons were found to respond indiscriminately to retinal image motion arising from any source (Erickson and Thier 1991). These studies were only concerned with the perception of a stationary object in space during smooth pursuit and concluded that the visual inputs to MST neurons were subject to inhibition or selective filtering by extra-retinal signals to eliminate the input from self-induced retinal slip. Consistent with these studies, we found that the responses of MST neurons were not modulated when the textured image was stationary on the screen during smooth pursuit eye movements (green traces in Fig. 2D). We, however, found that all of the MST and MT neurons responded vigorously to image motion in the presence of pursuit eye movements. This argues against the view that eye-movement-related signals are used to suppress input signals for retinal slip directed to area MST and supports the idea that these signals are used to compensate for the retinal slip caused by the eye movements.

It should be noted that the confidence intervals for the Gabor functions fit to the responses to the moving image were generally smaller for MT neurons than for MST neurons, which implies that the image motion was more precisely encoded by the MT neurons. There are several possible reasons to explain the wider confidence intervals obtained for the MST neurons. It has been reported that a substantial number of MST neurons code for other types of motion, such as radial, rotational, and spiral optic flow patterns (Duffy and Wurtz 1991; Graziano et al. 1994; Orban et al. 1992; Saito et al. 1986). The MST neurons that code for laminar motion as well as other

types of motion might have wider confidence intervals. Another possible reason for the wide confidence intervals is that neural noise in the sensory signal could be larger at higher levels of sensory information processing, i.e., in area MST as compared with area MT. In addition, the internal signal that codes for the eye velocity might not be sufficiently precise.

In area MST, it has been reported that some of the visual-tracking neurons (or pursuit cells) continue to respond during pursuit even in the brief absence of the pursuit target (Newsome et al. 1988; Sakata et al. 1983). This indicates that MST neurons may receive extra-retinal signals coding for eye movements. In the present study, we found that some MT and MST neurons exhibited small responses when the animal pursued a target moving against a dark background prior to the presentation of the large-field visual stimulus. The possible sources of the pursuit modulation could be the extra-retinal signals related to eye movements, the retinal slips of the tracking target, or the image of the frame of the coil-system in the peripheral field, which might have been visible even in the dark room. However, the primary interest of the present study was to characterize the properties of the neuronal responses to the moving textured image, and therefore we did not attempt to further characterize the origin of this modulation when the animals pursued a target in the dark. The pursuit modulation might affect the Gabor function analysis of the image motion that assumed there were response curve shifts only along the x axis by causing a shift along the y axis. The two-way Gabor function analysis assuming shifts along both the x and y axes tested this possibility and revealed no significant difference in the estimates of the shifts in the x direction from those obtained with one-way Gabor function analysis.

Although our study was concerned only with neural responses to linear planar motion on the screen, it is known that in area MST, there are neurons sensitive to other types of motion, such as expansion, contraction, and rotation of large-field visual stimuli (Duffy and Wurtz 1991; Graziano et al. 1994; Orban et al. 1992; Saito et al. 1986). Page and Duffy (1999) demonstrated a possible contribution from population encoding by MST neurons to pursuit-tolerant heading perception. Bradley et al. (1996) reported that MSTd neurons compute the position of the focus of expansion, which indicates the direction of self-motion (heading), during pursuit in a way that compensates for the retinal focus shift induced by pursuit eye movements through the use of both retinal and extra-retinal signals. The results of our study are consistent with this view in that the MST neurons use retinal and extra-retinal signals to perceive the visual world. More than one mechanism, however, may contribute to compensate for laminar eye movement and the shift of optic flow.

It is important to note that the compensation for the shift of retinal signals due to the eye movement reported by Bradley et al. (1996) is significantly weaker (~50%) than that observed in this study. It is possible that the two types of compensation are performed by different neuronal populations. They sampled neurons responsive to expansive optic flow, whereas we sampled those responsive to linear planar motion. Moreover, they reported strong modulation of the neuronal responses by pursuit eye movement, whereas we found only a slight modulation in a small percentage of the examined neurons. It has been reported by Komatsu and Wurtz (1988) that pursuit cells were encountered only in localized regions within the areas MT and

MST (see their Fig. 4). Because our primary interest was to characterize the response properties of the neurons that discharge in relation to moving textured images, we implanted guide tubes directed at specific areas rich in these neurons but not toward the areas where pursuit cells were recorded (see METHODS). This most likely explains why we did not encounter neurons that strongly modulated during pursuit in the present study.

It is also known that a considerable number of MT neurons have an inhibitory annulus surrounding their receptive field and do not respond to a large-field visual stimulus (Allman et al. 1985; Tanaka et al. 1986). In this study, the selective sampling of MT neurons that were sensitive to a large-field visual stimulus might have excluded neurons associated with strong inhibitory annuluses. To ascertain the question whether the surround effects were the same during fixation and pursuit, we need further experiments. However, the similar response properties of the MT neurons to the stimulus motion on the retina suggest that the effects of the surround are similar during fixation and pursuit.

Because monkeys were able to see the frame of the eye coil system that restricted their visual field in the peripheral field ($80 \times 80^\circ$), motion of the textured image relative to the stationary frame might have some influence on the responses of the MST neurons and cause different responses between real and self-induced motion. However, we think the influence would be small because of the following reasons. First, we found that some of the MST neurons (11/112) including the neuron shown in the Fig. 2, the receptive fields of which fell far short of the frame ($<30 \times 30^\circ$), were also modulated in relation to stimulus speed on the screen, irrespective of the eye movements. Second, as we have already described, MST neurons did not respond to a visual stimulus stationary on the screen even when pursuit eye movements induced its retinal motion, which had elicited substantial responses during fixation. Sakata et al. (1985) reported similar results by a distinctive method. They used an electrooculogram to record eye movements (no stationary frame in the peripheral visual field) and used a light-emitting diode (LED) spot as a tracking target and an acrylic rod illuminated with LEDs as a visual stimulus. Either one of them was mounted on a bench that could be moved along a straight rail. By adopting this method, they executed the experiment in complete darkness except for the target and visual stimulus. Their result supports the idea that the MST neurons distinguish between the real and self-induced visual motion by using extra-retinal information. A further study is needed to evaluate the contribution of peripheral visual stimuli in distinguishing the motions.

A person looking at a visual scene moves both his/her eyes and head. Therefore monitoring the eye-head coordination is important to allow proper perception of the real world during motion. Because the animals' heads were fixed in space in our experiments, it is not clear whether the MST neurons could be influenced by head movements as well as eye movements. Ilg et al. (2004) designed experiments in which monkeys were trained to track a moving target either by an isolated eye movement or by combined eye-head movements. The gaze movements (i.e., position of the eye in space) were identical in both tracking conditions, whereas the eye-head movements differed. The activities of the MST neurons were found to persist when movement of the pursuit target was compensated

for by eye and/or head movements, which reduced the movement of the image on the retina. These results suggest that MST neurons encode the movement of the pursuit target relative to the body (in space) independent of eye and/or head movements and that extra-retinal signals in area MST represent gaze movements but not genuine eye movements. If this is the case in our study, then the internal estimation of the stimulus speed by the MST neurons would be independent of both eye movements and head movements.

In human subjects, cortical potentials, which are evoked by pursuit-induced retinal slips, have been recorded from the parieto-occipital area, the human homologue of area MT/MST in monkeys, and were found to be closely correlated with the subjective perception of motion (Haarmeier and Thier 1998; Thier et al. 2001). It has also been reported that a human subject with bilateral lesions involving large parts of the dorsal extrastriate and posterior parietal cortex had difficulty in perceiving the stability of a visual scene during pursuit eye movements (Haarmeier et al. 1997). Our finding that MST neurons sense the velocity of the motion of the visual image largely independently of pursuit is consistent with these studies and further suggests a role for MST neurons in perceiving motion in the visual world, independent of eye movements.

ACKNOWLEDGMENTS

We are deeply grateful to Drs. F. A. Miles, K. Toyama, and T. Ogawa for their valuable suggestions about the manuscript. We thank Drs. K. Hashimoto and H. Tabata for advice on data analysis, and Drs. M. Yamamoto, K. Yoshida, Y. Iwamoto, and H. Sakata for continuous encouragement. We also thank A. Muramatsu, T. Takasu, and M. Okui-Uchiyama for technical assistance.

GRANTS

This work was supported by Japan Society for the Promotion of Science.KAKENHI (16GS0312), Ministry of Education, Culture, Sports, Science and Technology.KAKENHI (17022019), JSPS Research Fellowships for Young Scientists (16-12044), Special Coordination Funds for Promoting Science and Technology, and the National Institute of Advanced Industrial Science and Technology.

REFERENCES

- Akaike H.** A new look at the statistical model identification. *IEEE Trans Automat Control* 19: 716-723, 1974.
- Allman J, Miezin F, McGuinness E.** Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons. *Annu Rev Neurosci* 8: 407-430, 1985.
- Avillac M, Deneve S, Olivier E, Pouget A, Duhamel JR.** Reference frames for representing visual and tactile locations in parietal cortex. *Nat Neurosci* 8: 941-949, 2005.
- Bradley DC, Maxwell M, Andersen RA, Banks MS, Shenoy KV.** Mechanisms of heading perception in primate visual cortex. *Science* 273: 1544-1547, 1996.
- Celebrini S, Newsome WT.** Neuronal and psychophysical sensitivity to motion signals in extrastriate area MST of the macaque monkey. *J Neurosci* 14: 4109-4124, 1994.
- Churchland AK, Lisberger SG.** Discharge properties of MST neurons that project to the frontal pursuit area in macaque monkeys. *J Neurophysiol* 94: 1084-1090, 2005.
- Duffy CJ, Wurtz RH.** Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *J Neurophysiol* 65: 1329-1345, 1991.
- Duhamel JR, Bremmer F, BenHamed S, Graf W.** Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389: 845-848, 1997.
- Erickson RG, Thier P.** A neuronal correlate of spatial stability during periods of self-induced visual motion. *Exp Brain Res* 86: 608-616, 1991.

- Fetsch CR, Wang S, Gu Y, Deangelis GC, Angelaki DE.** Spatial reference frames of visual, vestibular, and multimodal heading signals in the dorsal subdivision of the medial superior temporal area. *J Neurosci* 27: 700–712, 2007.
- Fuchs AF, Robinson DA.** A method for measuring horizontal and vertical eye movement chronically in the monkey. *J Appl Physiol* 21: 1068–1070, 1966.
- Graziano MS, Andersen RA, Snowden RJ.** Tuning of MST neurons to spiral motions. *J Neurosci* 14: 54–67, 1994.
- Haarmeier T, Thier P.** An electrophysiological correlate of visual motion awareness in man. *J Cogn Neurosci* 10: 464–471, 1998.
- Haarmeier T, Thier P, Repnow M, Petersen D.** False perception of motion in a patient who cannot compensate for eye movements. *Nature* 389: 849–852, 1997.
- Hays AV, Richmond BJ, Optican LM.** A UNIX-based multiple process system for real-time data acquisition and control. *WESCON Conf Proc* 2: 1–10, 1982.
- Ilg UJ, Schumann S, Thier P.** Posterior parietal cortex neurons encode target motion in world-centered coordinates. *Neuron* 43: 145–151, 2004.
- Kass RE, Ventura V, Brown EN.** Statistical issues in the analysis of neuronal data. *J Neurophysiol* 94: 8–25, 2005.
- Kawano K, Sasaki M, Yamashita M.** Response properties of neurons in posterior parietal cortex of monkey during visual-vestibular stimulation. I. Visual tracking neurons. *J Neurophysiol* 51: 340–351, 1984.
- Kawano K, Shidara M, Watanabe Y, Yamane S.** Neural activity in cortical area MST of alert monkey during ocular following responses. *J Neurophysiol* 71: 2305–2324, 1994.
- Kawano K, Shidara M, Yamane S.** Neural activity in dorsolateral pontine nucleus of alert monkey during ocular following responses. *J Neurophysiol* 67: 680–703, 1992.
- Kodaka Y, Miura K, Suehiro K, Takemura A, Kawano K.** Ocular tracking of moving targets: effects of perturbing the background. *J Neurophysiol* 91: 2474–2483, 2004.
- Komatsu H, Wurtz RH.** Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *J Neurophysiol* 60: 580–603, 1988.
- Mack A, Herman E.** Position constancy during pursuit eye movement: an investigation of the Filehne illusion. *Q J Exp Psychol* 25: 71–84, 1973.
- Maunsell JH, Van Essen DC.** Functional properties of neurons in middle temporal visual area of the macaque monkey. II. Binocular interactions and sensitivity to binocular disparity. *J Neurophysiol* 49: 1148–1167, 1983.
- Newsome WT, Wurtz RH, Komatsu H.** Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. *J Neurophysiol* 60: 604–620, 1988.
- Orban GA, Lagae L, Verri A, Raiguel S, Xiao D, Maes H, Torre V.** First-order analysis of optical flow in monkey brain. *Proc Natl Acad Sci USA* 89: 2595–2599, 1992.
- Page WK, Duffy CJ.** MST neuronal responses to heading direction during pursuit eye movements. *J Neurophysiol* 81: 596–610, 1999.
- Rashbass C.** The relationship between saccadic and smooth tracking eye movements. *J Physiol* 159: 326–338, 1961.
- Richmond BJ, Optican LM, Podell M, Spitzer H.** Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex. I. Response characteristics. *J Neurophysiol* 57: 132–146, 1987.
- Saito H, Yukie M, Tanaka K, Hikosaka K, Fukada Y, Iwai E.** Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *J Neurosci* 6: 145–157, 1986.
- Sakata H, Shibutani H, Kawano K.** Functional properties of visual tracking neurons in posterior parietal association cortex of the monkey. *J Neurophysiol* 49: 1364–1380, 1983.
- Sakata H, Shibutani H, Kawano K, Harrington TL.** Neural mechanisms of space vision in the parietal association cortex of the monkey. *Vision Res* 25: 453–463, 1985.
- Shenoy KV, Crowell JA, Andersen RA.** Pursuit speed compensation in cortical area MSTd. *J Neurophysiol* 88: 2630–2647, 2002.
- Sperry RW.** Neural basis of the spontaneous optokinetic response produced by visual inversion. *J Comp Physiol Psychol* 43: 482–489, 1950.
- Takemura A, Murata Y, Kawano K, Miles FA.** Deficits in short-latency tracking eye movements after chemical lesions in monkey cortical areas MT and MST. *J Neurosci* 27: 529–541, 2007.
- Tanaka K, Hikosaka K, Saito H, Yukie M, Fukada Y, Iwai E.** Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *J Neurosci* 6: 134–144, 1986.
- Thiele A, Henning P, Kubischik M, Hoffmann KP.** Neural mechanisms of saccadic suppression. *Science* 295: 2460–2462, 2002.
- Thier P, Haarmeier T, Chakraborty S, Lindner A, Tikhonov A.** Cortical substrates of perceptual stability during eye movements. *Neuroimage* 14: S33–39, 2001.
- von Holst E.** Relations between the central nervous system and the peripheral organs. *Br J Anim Behav* 2: 89–94, 1954.
- Wertheim AH.** Motion perception during self-motion: The direct versus inferential controversy revisited. *Behav Brain Sci* 17: 293–355, 1994.
- Wertheim AH, Van Gelder P.** An acceleration illusion caused by underestimation of stimulus velocity during pursuit eye movements: Aubert-Fleischl revisited. *Perception* 19: 471–482, 1990.