

Posterior Parietal Cortex Neurons Encode Target Motion in World-Centered Coordinates

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Summary

The motion areas of posterior parietal cortex extract information on visual motion for perception as well as for the guidance of movement. It is usually assumed that neurons in posterior parietal cortex represent visual motion relative to the retina. Current models describing action guided by moving objects work successfully based on this assumption. However, here we show that the pursuit-related responses of a distinct group of neurons in area MST of monkeys are at odds with this view. Rather than signaling object image motion on the retina, they represent object motion in world-centered coordinates. This representation may simplify the coordination of object-directed action and ego motion-invariant visual perception.

Introduction

In order to exploit the advantages of foveal vision, we shift the image of an object of interest into the fovea by making a saccadic eye movement, followed by smooth pursuit eye movements (SPEM) in the case of object motion that would otherwise tend to move the object image again away from the fovea. SPEM have been successfully conceptualized as an automatic feedback behavior, converting retinal error signals such as target image velocity or acceleration into eye movements that reduce these error signals (Krauzlis and Lisberger, 1989; Lisberger et al., 1987). It is well established that neurons in visual area MT, located on the posterior bank of the superior temporal sulcus (STS) of monkeys (Allman and Kaas, 1971; Dubner and Zeki, 1971), contribute to the extraction of these retinal error signals (Maunsell and van Essen, 1983a; Mikami et al., 1986). Neurons in area MT encode target image velocity on the retina during SPEM (Komatsu and Wurtz, 1988), and correspondingly, lesions of selected parts of area MT render monkeys unable to pursue targets moving toward the lesioned hemisphere (Dursteler and Wurtz, 1988).

Directionally selective neurons in the STS are not confined to area MT but also dominate neighboring area MST, located on the floor and the anterior bank of the sulcus (Maunsell and van Essen, 1983b; Ungerleider and Desimone, 1986). Although neurons in area MST are also sensitive to retinal image slip, they show a number of features that distinguish them from the kind of pure elementary motion detector neurons that characterize

area MT. For instance, unlike neurons in area MT, many neurons in area MST and neighboring parts of the posterior parietal cortex will maintain their response to object motion when the object is moving invisibly behind an occluder along an inferred trajectory (Assad and Maunsell, 1995). Moreover, many neurons in area MST, usually referred to as visual tracking (VT) neurons (Sakata et al., 1983), will discharge during steady-state SPEM, even in the absence of any retinal image slip, for example, if the pursued target disappears briefly (Kawano and Sasaki, 1984; Newsome et al., 1988; Thier and Erickson, 1992). Although this has not been tested directly, it seems likely that these VT neurons may actually correspond to the ones responding to inferred object motion while the eyes are stationary (Assad and Maunsell, 1995). The discharge during the disappearance of the target while the eyes are either stationary or moving could simply be a reverberation of retinal image slip information that was collected and stored while the moving target was visible. However, this explanation is not able to account for the observation that the VT neurons will discharge if high-performance SPEM are elicited by *imaginary* targets on the fovea, implied by cues confined to the visual field periphery outside the receptive field (Ilg and Thier, 2003). Hence, a more appropriate view seems to be the assumption that these neurons respond to the *percept* of object motion, independent of whether or not object image slip is actually available on the retina. What is the coordinate system to which this neuronal representation in area MST references the object motion percept? Is it the retina? This might be suggested by the fact that this representation most probably builds on *real* object image slip on the retina provided by area MT. However, if this were so, these neurons should stop discharging when, during high-performance SPEM, the retinal image of the object does not move relative to the eyes. However, as already mentioned, this is not the case, indicating that an eye movement-related signal takes over determining the neuronal response. Similar responses to target movement with the eyes fixed and with the eyes moving, as typically found in area MST VT neurons, suggest that these neurons reference target movement to the head or, alternatively, relative to the external world. Experiments in which the head is fixed relative to the world cannot distinguish between these alternatives. Actually, previous work applying rotation of the head has shown that at least VT neurons in the lateral subdivision of area MST (MSTl) have access to information on head movements (Thier and Erickson, 1992). If this head movement-related signal were accessible during active head movements, contributing to target pursuit, it might allow these neurons to reconstruct target motion in world-centered coordinates. In order to test if this is the case, we trained monkeys to pursue dot targets using only their eyes (SPEM) or, alternatively, to match target movement by an accurate gaze movement based on a combination of smooth pursuit eye and head movements (SPEHM). This pattern allows one to readily disen-

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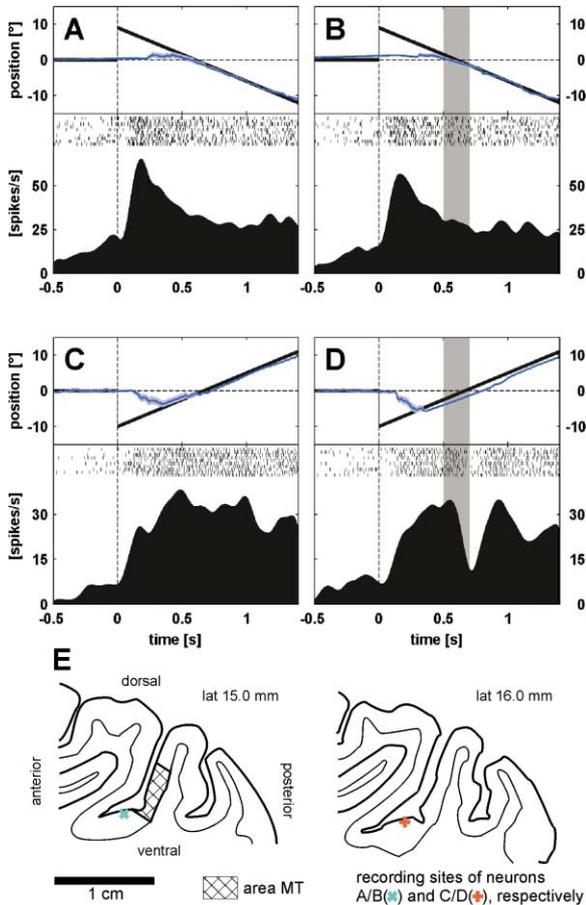


Figure 1. Existence of Extraretinal Signals in the Neuronal Activity
Discharge of two representative neurons that were recorded from area MST, during smooth pursuit eye movements (head fixed) guided by a continuously visible target (A and C) or, alternatively, a target (B and D) that was turned off for 200 ms (gray background) during maintained pursuit. Target position (black) and mean eye position (blue) plus standard error (the latter shown as blue envelopes) are shown together, with the neuronal discharge depicted as raster plots and spike density functions ($\sigma = 40$ ms). The onset of target movement at time 0 is marked by a vertical dashed line. Both neurons displayed a significant directional selectivity (two-way ANOVA factor *pursuit direction*; $p = 0.0002$ for the neuron shown in [A] and [B], $p < 0.0001$ for the neuron in [C] and [D]). Whereas the neuron shown in (A) and (B) was uninfluenced by the temporary disappearance of the pursuit target (factor *trial type*; $p = 0.51$), the neuron depicted in (C) and (D) displayed a significant drop in its discharge rate ($p < 0.0001$; see text for detailed description of statistics). (E) shows the reconstructed localization of these two neurons in parasagittal sections.

tangle neuronal preferences for the movement of the eyes, the head, and finally, the gaze.

Results

Neurons were recorded mostly from area MST during eyes-only pursuit of a dot target moving at constant speed ($10^\circ/\text{s}$) along the horizontal axis in the frontoparallel plane starting from straight ahead. Out of 116 neurons that were recorded from three male rhesus monkeys, most of which were located in the MSTI, 86 showed

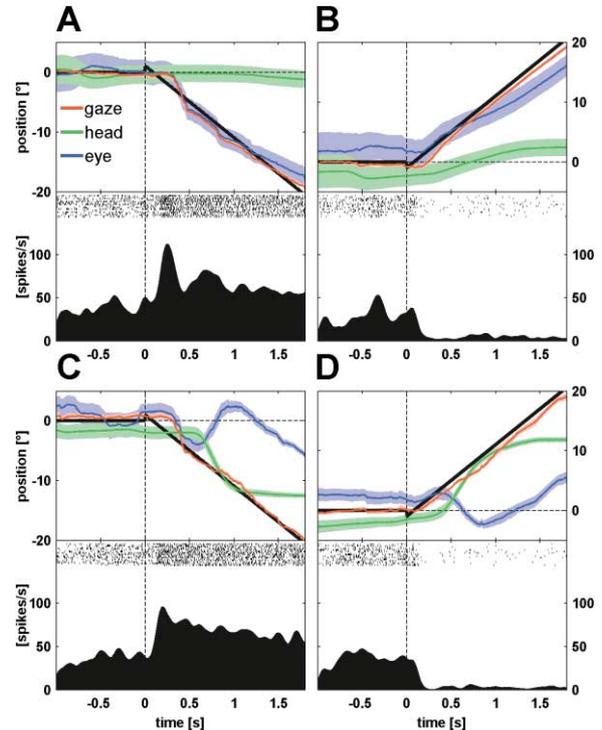


Figure 2. Similar Neuronal Responses during SPEM and SPEHM
Discharge of VT neuron recorded from area MST during pursuit with only the eyes moving (SPEM) (A and B) and with both the head and eyes moving (SPEHM) (C and D). In (A) and (C), target movement was in the preferred direction of the neuron; in (B) and (D), the movement occurred in the nonpreferred direction. Target position is shown in black, mean eye position in blue, mean head position in green, and mean gaze position in red. The colored envelopes accompanying the mean position curves reflect the standard errors. The discharge is characterized by raster plots and spike density functions ($\sigma = 40$ ms). Note that during SPEHM (C and D), the head movements were characterized by an overshoot in velocity, prompting a compensatory eye-in-head movement in the opposite direction. However, the discharge rate in the preferred as well as in the nonpreferred direction did not change as a consequence of these eye movements. Moreover, the discharge rate depended significantly on the *direction of target movement* (two-way ANOVA; $p < 0.0001$). On the other hand, the influence of the *type of tracking* was not significant ($p = 0.182$).

pursuit-related activity in conjunction with horizontal SPEM, which did not change significantly when the target was turned off for 200 ms during steady-state pursuit while the monkey continued to pursue the invisible target. Figures 1A and 1B show a representative example from this group of VT neurons, insensitive to the temporal disappearance of the pursuit target. Figures 1C and 1D depict the counterexample of a purely visual neuron recorded from area MST whose discharge drops as soon as the target image is no longer available on the retina.

All of the 86 VT neurons that maintained their activity despite the brief removal of the pursuit target displayed a clear response to SPEM along the horizontal axis that was significantly higher either for pursuit to the right or for pursuit to the left, although in many cases this direction was not the best direction. All 116 neurons that were examined were subjected to a comparison of horizontal pursuit with only the eyes moving (SPEM) or, alterna-

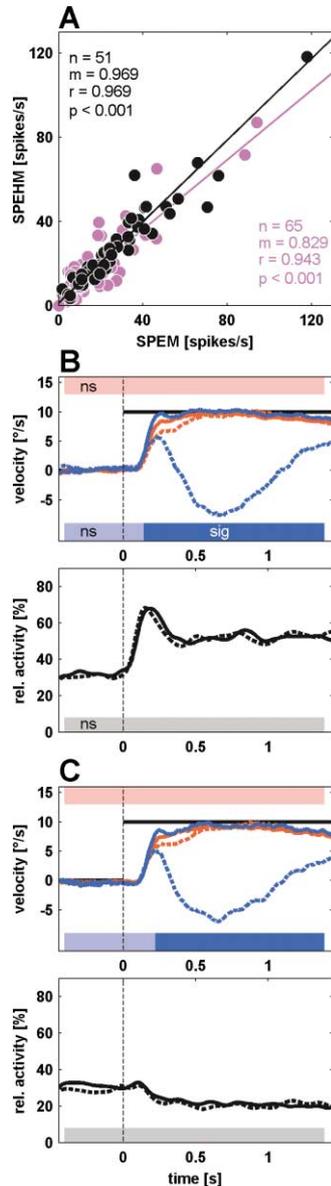


Figure 3. Population Responses during SPEM and SPEHM
 (A) Plot of average discharge rate during SPEHM as function of SPEM for the 51 VT neurons recorded from area MST that were directional and exhibited no statistical difference in their mean responses in the two tracking conditions (black circles) and the remaining 65 neurons (magenta circles) from MST, for which the statistical analysis revealed significant differences in the discharge exhibited in the two tracking conditions. In addition, the linear regression lines are shown for both groups of neurons together with the slopes (m) and the coefficients of correlation (r). Note that, despite the substantially larger scatter, the linear regression analysis of the second group of neurons was also significant. The regression lines for the two groups of MST neurons were statistically different from each other ($p = 0.0038$). (B and C) The lower parts of these panels depict the average responses (black curves) of the same neurons as a function of time for pursuit in the preferred horizontal direction (B) and the opposite horizontal direction, respectively (C). The curves in the upper parts of these panels show associated average target (black), gaze (red), and eye-in-head (blue) velocities. Continuous curves reflect the SPEM condition, and dashed curves reflect the SPEHM condition. Note that the comparison of gaze and mean discharge as a function of time was based on running Student's t tests applied to a sliding 200 ms window. The intensity

tively, both the head and the eye being allowed to move, with the relative weights of the two pursuit effectors left to the choice of the monkey (SPEHM). The color of the target (red, SPEM; green, SPEHM) instructed the monkey on the type of pursuit behavior that was required. Head movements were unrestrained about the yaw axis during both types of trials, and the active suppression of head movements in the eyes-only trials was the consequence of the learned reward contingencies. SPEM and SPEHM trials were presented in the horizontal projection of the preferred and the nonpreferred direction randomly interleaved, having average shares of 25% each.

As exemplified in Figure 2 and represented in Figures 3B and 3C by average records, the quality of pursuit, as determined by how well the gaze velocity matched that of the target, was in general very good and, moreover, did not depend on the choice of the effectors. Average gaze gain was determined as the ratio of mean gaze velocity for a period from 300 ms to 1300 ms after target onset divided by target velocity. For the three monkeys used, the average gain was 0.984 for SPEM and 0.988 for SPEHM, the two values not being statistically different (Student's t test; $p = 0.72$; $n = 116$). As shown in Figures 3B and 3C, the pursuit velocity of the population response in the SPEM and the SPEHM conditions did not differ significantly at any point in time. This is surprising, since in the case of eye-plus-head (i.e., SPEHM) pursuit, the component trajectories were usually quite complex, with the head typically overshooting the target, requiring the eyes to move in the opposite direction.

The VT neuron whose discharge is reproduced in Figure 2 preferred leftward pursuit. This neuron belongs to the group of neurons that are insensitive to the temporal disappearance of the pursuit target. Independent of whether the gaze movement was based on just the eyes or a combined eye-head movement, this neuron started to discharge approximately 100 ms before the onset of the gaze shift to the left. In both conditions, the discharge rates showed the same early transient response, peaking about 250 ms after target movement onset and then passing into a stable plateau response.

That the response reflected the gaze shift rather than the eye movement is clearly indicated by the fact that the change in eye movement direction in SPEHM trials did not influence this response. Actually, independent of the point in time, during maintained pursuit of the target, the responses that were recorded during SPEM and SPEHM were very similar, although the contributions of the two pursuit effectors changed continuously during SPEHM. Out of the 116 neurons recorded from area MST and tested in this task, 51 neurons were directional, preferring one of the two pursuit directions, and showed statistically not different average responses

of the horizontal bands reflects the outcome of the uncorrected Student's t tests: low for nonsignificant outcome (ns), high for significant outcome (sig); the level of significance was 0.01. If a correction for multiple comparisons according to Bonferroni was applied, the first significantly different bin of eye velocity in the two tracking conditions turned nonsignificant.

Table 1. Latencies of Neuronal Activities, Gaze, and Head Movements

	activity [ms]	gaze [ms]	head [ms]
SPEM	96±29	115±27	/
SPEHM	88±23	117±23	275 ± 80

$P_{t\text{-test}}=0.0006$
 $P_{t\text{-test}}=0.129$ $P_{t\text{-test}}=0.649$
 $P_{t\text{-test}}<0.0001$

Mean and standard deviations of latencies relative to target movement onset of neuronal activity as well as gaze and head movement in the two tracking conditions (n = 51).

during maintained SPEM and SPEHM from 80 ms after target onset until the end of the trial (two-way ANOVA, nonsignificant main effect of *type of pursuit*, significant main effect of *pursuit direction*, and nonsignificant interaction between both factors). The independence of the pursuit-related discharge from the type of pursuit effector in this group of neurons is also reflected by the highly significant linear correlation ($p < 0.001$) between the mean discharge rate observed during maintained SPEM and SPEHM. The resulting regression line did not deviate significantly from the bisector ($p = 0.230$), indicating that the responses during SPEM and SPEHM did not differ (see Figure 3A). The lack of discrimination of the responses between the two tracking conditions holds not only for the average discharge rates but also for the response profiles. This is indicated by a comparison of the population average responses for this group of neurons as well as a comparison of the associated gaze, head, and eye velocity records for the two tracking conditions (Figures 3B and 3C). Neither the population discharge nor the population-based mean gaze velocity differed between the two tracking conditions at any point in time (running Student's *t* test; $p > 0.01$, uncorrected). In the 51 neurons whose maintained pursuit discharge was the same for SPEM and for SPEHM, the latency of the discharge led gaze movement onset on average by 26 ms (± 33 ms) independent of the movement condition. Neither the latency of the neural activity nor the latency of the gaze movement differed significantly in the two tracking conditions (see Table 1).

In 45 out of these 51 neurons (88%), the existence of an influence of an extraretinal signal could be demonstrated by the persistence of the response when turning the target off during maintained SPEM. Most of these VT neurons that were not activated differently by SPEM and SPEHM also exhibited a clear sensitivity to retinal image slip. First, 49 of them showed transient bursts early after pursuit onset, most probably reflecting the processing of retinal image slip before eye movement onset. Moreover, 50 out of 51 neurons responded to the movement of irrelevant visual stimuli, such as a cloud of moving dots within a stationary aperture or a moving bar, with the eyes and the head stationary, mostly (34/50 neurons) in directions corresponding to the preferred

pursuit direction and less frequently (16/50 neurons) in directions opposite to it. The size of their visual receptive fields was on average 15° , the fovea was included in 68% of the neurons, and the preferred speed was on the order of $40^\circ/\text{s}$. The relatively small size of the receptive fields suggests that these neurons were recorded from MSTl rather than from MSTd, which contains neurons with much larger receptive fields.

Do these visual responses indicate that these neurons indeed incorporate information on object motion on the retina into a representation of object motion in world-centered coordinates as proposed above? Alternatively, these neurons might already be on the motor side of the visuomotor chain, in charge of controlling gaze shifts, possibly using the early, visually driven response transients in order to help accelerate the gaze movements but ignoring residual retinal errors during later phases of maintained pursuit.

To decide between these two possibilities, we correlated the discharge rate of 39 out of the 51 neurons that gave nondifferent SPEM and SPEHM responses with target velocity and gaze velocity, respectively. In order to generate the wide range of target, gaze, and eye velocities needed for a regression of discharge as function of velocity, and in order to emphasize differences between target and gaze velocity, we subjected these neurons to a second experiment, in which we asked the monkeys to pursue a target moving sinusoidally along the horizontal at 0.33 Hz, 10° amplitude, while the monkey was rotated sinusoidally passively about his yaw axis. The frequency of this vestibular stimulation was 0.2 Hz, and its amplitude was 10° . Although the head movement contribution in this second experiment was passive and not active as in the first one, the neuronal response profile of the example VT neuron shown in Figure 4 nicely reflected the gaze and target velocity trajectories, rather than those of eye or head velocity (see Figure 4C). The correlation of its discharge rate with target velocity (Figure 4D) resulted in a larger coefficient ($r = 0.808$) than the correlation of the discharge rate with gaze velocity ($r = 0.721$; see Figure 4E).

Figure 5 plots the correlation coefficients for discharge rate as a function of target velocity versus the correlation coefficients for discharge as a function of gaze velocity for the 39 VT neurons recorded from area MST whose responses were subjected to this test. In most neurons, the correlation coefficients lay on the left of the bisector line, indicating equal coefficients, and this deviation from a distribution centered on the bisector was statistically highly significant ($p = 0.0007$). In other words, target velocity is a significantly better predictor of the discharge of this specific group of VT neurons than gaze velocity.

Discussion

VT neurons in area MST represent a distinct class of neurons with properties that are qualitatively different from those of the purely visual neurons with which they intermingle (Kawano and Sasaki, 1984; Newsome et al., 1988; Thier and Erickson, 1992). Like other motion-sensitive neurons in area MST and in neighboring area MT, they respond to object image slip. However, unlike those

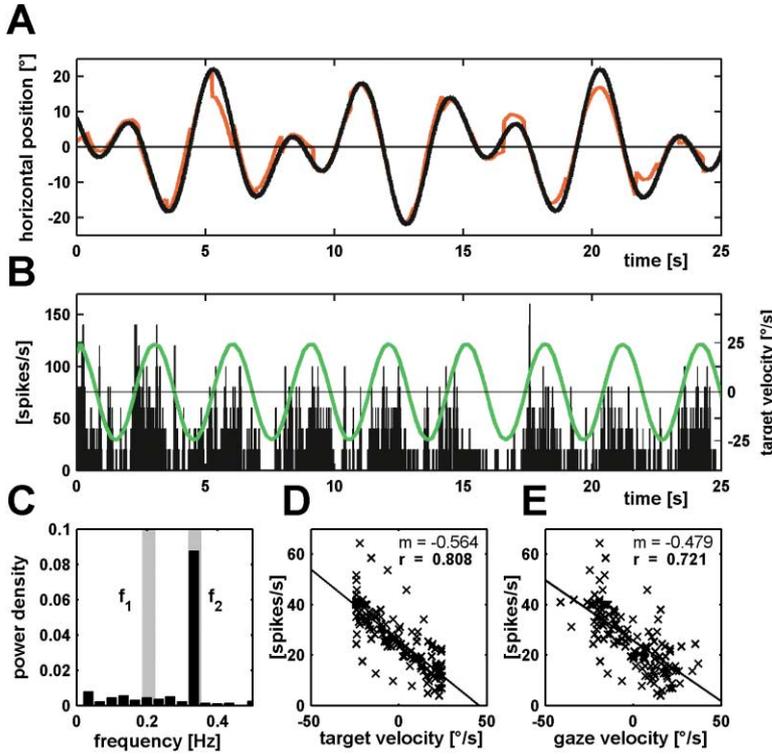


Figure 4. Combination of Pursuit Task and Vestibular Stimulation

Recordings from a VT neuron of a monkey pursuing a horizontally moving target, while being rotated sinusoidally en bloque about the yaw axis. (A) depicts the target (black) and gaze (red) trajectories in a head-centered coordinate system, while (B) shows target velocity in space (green) as well as the discharge rate as raster plot and spike density function ($\sigma = 40$ ms) for the same period of time. (C) gives the power spectrum of the neuronal activity, exhibiting a clear peak at the frequency of target movement (i.e., $f_2 = 0.33$ Hz) and not at the frequency of body oscillation ($f_1 = 0.2$ Hz). (D) and (E) are plots of discharge rate as function of target velocity (D) and gaze velocity (E), respectively, fitted by a linear regression (m , slope; r , coefficient of correlation). The corresponding coefficients of correlation were 0.088 (ns) for eye position and 0.026 (ns) for head velocity (data not shown).

of simple image slip detectors, their responses persist when direct vision of the object is masked and its motion has to be inferred by extrapolating the past object trajectory (Assad and Maunsell, 1995). By the same token, these neurons do not distinguish between motion of a fully visible object and the motion of a partly occluded object whose image has to be completed perceptually (Ilg and Thier, 2003). Finally, as shown by the present study, their discharge persists when movement of the object is compensated by eye and/or head movements, reducing the amount of image motion on the retina to

a large extent. The only common denominator able to account for these characteristic features is the representation of the motion of objects of interest in a world-centered frame of reference. Up to the level of area MT, object motion is represented relative to the retina. Given the well-established projection from area MT to area MST (Maunsell and van Essen, 1983b; Ungerleider and Desimone, 1986), it seems likely that the world-centered representation offered by VT neurons in area MST builds on this earlier retinal representation of object motion, possibly using the visual-only neurons in area MST as interfacing elements. In order to reconstruct a world-centered representation, VT neurons need to have access to both information on the eye movement relative to the head and information on the head movement relative to the external world. While the latter must reflect signals ultimately originating from the vestibular apparatus, given the fact that these neurons can be driven by passive head movement (Thier and Erickson, 1992), the former must be based on an efference copy of the eye movement motor command (Holst and Mittelstaedt, 1950; Sperry, 1950) rather than proprioceptive feedback from the eye muscles. This conclusion is prompted by the fact that the discharge of these neurons leads eye movement onset. Unlike the source of the visual signal impinging on VT neurons, the sources of the eye and head movement signals remain elusive. Moreover, unimodal eye or head movement-only neurons, the formal equivalents of the visual-only neurons, have as yet not been described in area MST. Irrespective of these uncertainties, the clear evidence for an integration of eye and head movement-related signals, as well as the distinct frame of reference for the representation of object motion, sets area MST qualitatively apart from neighboring area MT.

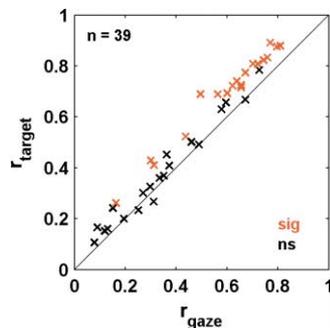


Figure 5. Neuronal Activity Reflects Target Velocity

Plot of coefficients of correlation between neuronal activity and target velocity (r_{target}) as function of coefficients of correlation between neuronal activity and gaze velocity (r_{gaze}). Each of the 39 symbols marks an individual neuron recorded from area MST. Shown in red are the symbols representing 19 out of 39 neurons in which both coefficients were significantly different ($p < 0.05$). On average, the coefficients for target velocity were significantly larger than those for gaze velocity (paired Student's t test; $p < 0.001$), reflected by the fact that all but a few of the symbols lie above the bisector.

The notion of a world-centered neuronal representation of object motion has the advantage of being able to accommodate the allocentric nature of our everyday perceptual experiences (Andersen et al., 1993). SPEM and SPEHM, the model behavior exploited in our experiments, are a case in point: the object of interest is perceived as moving, although its image is stable on the retina. The background, on the other hand, is perceived as being stationary, although its image moves on the retina at the speed of the eye movement. Given the fact that the responses of area MST VT neurons are concordant with our perception of object motion during pursuit, these neurons must be considered prime candidates for mediating the approximately eye movement-invariant perception of object motion during SPEM and possibly other forms of ego motion (Bradley et al., 1996; Duffy and Wurtz, 1995; Lappe et al., 1996). While the need for a world-centered representation in perception is hard to dispute, its necessity is less clear when it comes to visuomotor behavior. As pointed out earlier, most current models of SPEM, a form of visually guided behavior in which area MST is clearly involved, foresee a direct conversion of target-related retinal signals into eye movement motor commands without any intermediate nonsensory and nonmotor representation (Krauzlis and Lisberger, 1989; Lisberger et al., 1987). Hence, although not necessary for the guidance of behavior, a world-centered representation of target motion may nevertheless be part of the visuomotor transformations for pursuit, because it might help simplify the coordination of object-directed action and ego motion-invariant visual perception.

Experimental Procedures

Experimental Setup

Three male rhesus monkeys (F, B, and G) were prepared for chronic recordings of single units as well as eye and head position. In brief, under intubation anesthesia, a search coil for gaze recording, a head post, and recording chambers were implanted as described in detail elsewhere (Ilg and Thier, 2003). All animal procedures were carried out in accordance with national law as well as the guidelines laid down by the NIH and were approved by the local committee overseeing animal experiments. Head position was measured using a search coil attached to the head post, and gaze position was recorded by means of the implanted search coil underneath the conjunctiva. The position of the eye relative to the head was computed as the difference between gaze and head position. The head holder allowed free head movements about the yaw axis within a range of $\pm 30^\circ$. The color of the small target indicated whether pursuit should be carried out by isolated eye movements (SPEM, target red) or by combined eye and head movements (SPEHM, target green). During training of SPEM, head movements were prevented by locking the head holder using an electromagnetic brake. Although the brake was not used in the later recording experiments in order to avoid artifacts and the head therefore was in principle free to move in any condition, no appreciable amounts of head movements were observed when the red cue signaled that eye pursuit only would be required.

Area MST was approached with standard tungsten-in-glass microelectrodes penetrating the brain at an angle of 30° with respect to the horizontal in the parasagittal plane. Using this approach, the electrode tip crossed white matter before it reached the fundus of the STS, known as MSTl. The first penetrations were directed toward a region that was centered on stereotaxic coordinates posterior 3.5, lateral 19, and dorsal 16 mm, known to approximate the location of area MST. Well-established physiological criteria were used to further refine the location of area MST and its two major subdivi-

sions, the dorsal one (MSTd) and the lateral one (MSTl), in the individual monkeys as well as the boundary with neighboring area MT (Komatsu and Wurtz, 1988). The identification of 116 recording sites based on these physiological criteria was supported by processing the brains histologically and reconstructing electrode tracks and recording sites relative to small focal marks made on selected tracks.

All visual stimuli were back projected at a temporal resolution of 60 Hz and a spatial resolution of 1280×1024 pixels onto a tangent screen at a viewing distance of 85 cm, using a CRT projector. The visual field area that was covered comprised $86^\circ \times 66^\circ$. The room was totally dark, and the borders of the screen were invisible. In order to prevent dark adaptation, a bright homogeneous background was turned on for 100 ms during the reward period of every trial. The visual stimuli that were presented were dot targets (red, SPEM; green, SPEHM, diameter, 0.5° ; luminance, 0.5 cd/m^2) for fixation and pursuit as well as random dot kinematograms moving within a stationary aperture adjusted to the size and position of the receptive field. Receptive field boundaries were determined by the investigator using a mouse-driven bar. Monkeys were trained to keep their gaze within a fixation window of 2° during visual fixation with both the eyes and the head stationary, of 6° during SPEM with the head fixed, and 8° during combined smooth eye and head movements. Compliance with the task requirements was rewarded by the delivery of juice at the end of a trial.

Data Analysis

Brief Removal of Pursuit Target

To capture the effect of blanking the pursuit target for 200 ms, as shown in Figure 1, we measured the average discharge rate within a period of 200 ms, shifted by 100 ms relative to the target blank in order to account for the expected delay of a possible visual response. The target blank occurred within 500 to 700 ms after target movement onset on half of the trials. The average discharge rate for trials without target blanks was determined for corresponding periods. The discharge rates were subjected to a two-way ANOVA with the two factors *pursuit direction* (left versus right) and *trial type* (target turned off versus target continuously on). Here and for all other statistical comparisons, a significance level of $p < 0.01$ was chosen.

Pursuit-Related Activity

The mean discharge rate was determined for an interval starting 80 ms after the onset of target motion and lasting until the end of the trial. A two-way ANOVA with the factors *direction of target movement* (left versus right) and *type of pursuit* (SPEM versus SPEHM) was calculated in order to assess the impact of pursuit direction and pursuit type, respectively.

The population for the group of 51 VT neurons whose mean average discharge rate was the same for SPEM and SPEHM was obtained by first normalizing the discharge rate of an individual neuron to its maximum. Subsequently, the discharge rates of all 51 neurons were averaged for preferred and nonpreferred direction, respectively. The resulting population responses during SPEM and SPEHM were compared by a running Student's *t* test (significance level, $p < 0.01$; running Student's *t* test of sliding 200 ms window). The associated eye and gaze velocity records were likewise compared bin by bin by a running Student's *t* test.

The spectral composition of the spike density function for the experiment, in which the monkeys pursued smoothly while being turned passively, was obtained by subjecting this function to a Fast-Fourier transform after low-pass filtering with a Hamming window of 500 ms.

Correlation with Gaze and Target Velocity

To correlate the discharge rate of an individual neuron with either gaze or target velocity, we cut each data set into 205 ms bins and calculated a linear regression between gaze velocity and discharge rate as well as between target velocity and discharge rate. Beforehand, saccades were removed from the gaze velocity records. The corresponding segments of these records were linearly interpolated as described in detail earlier (Ilg and Thier, 1999). To compensate for the latency of the discharge rate, we shifted the neuronal activity for 100 ms relative to target or gaze velocity.

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