Response Properties of Dorsolateral Pontine Units During Smooth Pursuit in the Rhesus Macaque

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SUMMARY AND CONCLUSIONS

1. The anatomical connections of the dorsolateral pontine nucleus (DLPN) implicate it in the production of smooth-pursuit eye movements. It receives inputs from cortical structures believed to be involved in visual motion processing (middle temporal cortex) or motion execution (posterior parietal cortex) and projects to the flocculus of the cerebellum, which is involved in smooth pursuit. To determine the role of the DLPN in smooth pursuit, we have studied the discharge patterns of 191 DLPN neurons in five monkeys trained to make smooth-pursuit eye movements of a spot moving either across a patterned background or in darkness.

2. Four unit types could be distinguished. Visual units (15%) discharged in response to movement of a large textured pattern, often in a direction-selective fashion but not during smooth pursuit of a spot in the dark. Eye movement neurons (31%) discharged during sinusoidal smooth pursuit in the dark with peak discharge rate either at peak eye position or peak eye velocity, but they showed no response during background movement or during other visual stimulation. These units continued to discharge when the target was extinguished (blanked) briefly, and the monkey continued to make smooth-pursuit eye movements of a spot moving either across a patterned background or in darkness.

3. Ninety-five percent of the units that discharged during smooth pursuit were direction selective. During sinusoidal movement of a large-field background, half of them also discharged in relation to stimulus velocity, whereas others did not. In contrast, when imperfect smooth pursuit in the dark produced slip of the small target spot on the retina, visual pursuit units discharged only weakly in relation to visual velocity, if at all. Therefore, while some units might respond to the velocity of large-field motion, few respond to the velocities of small spots. Visual receptive fields, which were tested while the monkey fixated a stationary target spot, ranged from $2 \times 2^\circ$ to over $70 \times 50^\circ$. All visual receptive fields included the fovea and, in the few cases tested, were binocular.

4. Most units that responded to large-field background movement were direction selective. During sinusoidal movement of a large-field background, half of them also discharged in relation to stimulus velocity, whereas others did not. In contrast, when imperfect smooth pursuit in the dark produced slip of the small target spot on the retina, visual pursuit units discharged only weakly in relation to visual velocity, if at all. Therefore, while some units might respond to the velocity of large-field motion, few respond to the velocities of small spots. Visual receptive fields, which were tested while the monkey fixated a stationary target spot, ranged from $2 \times 2^\circ$ to over $70 \times 50^\circ$. All visual receptive fields included the fovea and, in the few cases tested, were binocular.

5. Step-ramp tracking (38) was employed to determine whether DLPN units discharge before the initiation of smooth pursuit. The majority of eye movement units tested discharged at or after pursuit onset. As expected,
the discharge of all visual pursuit units leads
the initiation of smooth pursuit.

6. The direction selectivity for pursuit and
visual units was either the same or opposite
for smooth-pursuit and background move-
ment. During smooth pursuit over a fixed
background, the response of these units, how-
ever, was not usually a linear summation of
the smooth-pursuit and background re-
sponses.

7. The diversity of unit types found in the
DLPN demonstrates that it is more than a
simple visual relay nucleus signaling retinal
slip information to the cerebellum. Many
units do signal the direction of large-field
stimulus movement, and about half of these
also signal large-field slip velocity from 0 to
16°/s. Few, if any, signal the velocities of
small spots. Other DLPN units could be in-
volved in specifying the initial direction of
smooth pursuit. The remainder may play a
role in signaling selfinduced as opposed to
real visual motion.

INTRODUCTION

When humans want to observe a moving
object, they do so by following the object with
slow smooth eye movements that stabilize
the visual image of the object on the fovea.
In contrast to rapid saccadic eye movements,
which can be made in the dark, smooth-pur-
suit eye movements generally require the
presence of a moving visual target; if the tar-
get is extinguished, smooth pursuit can be
maintained for only a few hundred milli-
seconds (3, 6). In most natural situations, the
moving object being examined moves across
a stationary visual world. The eye move-
ments that track this object cause the image
of the stationary background to move in the
opposite direction. Such large-field visual
motion presented to a stationary subject elici-
ts an optokinetic response that drives the
eyes in the direction of the visual motion.
Therefore, in normal smooth-pursuit track-
ing, an optokinetic response might be ex-
pected to compete with the pursuit response
generated by target movement. The neural
mechanisms by which pursuit and optoki-
netic signals are combined to avoid this con-
flict are unknown.

One possible site where pursuit and optoki-
netic signals could interact is in the cerebellar
flocculus. Much evidence indicates that the
flocculus is required for normal smooth-pur-
suit eye movements. Large cerebellar lesions
that include the flocculus (55) or small lesions
restricted mainly to the flocculus (56) pro-
duce long-lasting deficits in smooth pursuit.
Furthermore, unilateral lesions of the floccu-
lus also cause decreased optokinetic nystag-
mus to stimuli moving in the direction ipsi-
lateral to the lesion (50). In accord with these
lesion effects, single-unit recording studies
(21, 28, 51) have demonstrated that simple
spike activity of floccular Purkinje cells is
modulated during smooth-pursuit and op-
tokinetic eye movements. It is unclear
whether this eye movement-related Purkinje
cell activity is delivered to the flocculus fully
developed or whether it is generated in the
cerebellar cortex by a combination of signals
arriving over several mossy fiber pathways.

Possible sources of eye movement, optoki-
netic, or visual inputs to the monkey floccu-
lus have been revealed by anatomical studies
(4, 19). Of the structures identified by retro-
grade labeling after injections of horseradish
peroxidase (HRP) into the flocculus, the dor-
solateral pons seems to be an attractive
source for one or more of these inputs for two
reasons. First, cells in this region show visual
responses in the cat and monkey (12, 30).
Second, the dorsolateral pontine nucleus
(DLPN) receives inputs from cortical areas
implicated in both visual motion processing
(e.g., middle temporal cortex) and smooth
pursuit (e.g., posterior parietal cortex) (3,
10, 36).

The goal of our study was to characterize
the unit activity in the DLPN during eye
movements and visual stimulation and to de-
termine whether the DLPN could be in-
volved with smooth pursuit. Preliminary re-
ports describing visual and eye movement-re-
lated activity in the dorsolateral pons of the
trained monkey have been reported else-
where (31, 32, 45).

METHODS

Surgical preparation and behavioral training

Five juvenile rhesus macaques (Macaca mul-
latta) were used in this study. The surgical proce-
dures, performed under aseptic conditions and
deep anesthesia (halothane, 1–2%), have been de-
scribed in detail elsewhere (10). Briefly, three turns
of Teflon-insulated stainless steel wire were placed under the insertions of the four rectus muscles to form a search coil (11) that moved with the eye. When the monkey was placed within horizontal and vertical magnetic fields (kept in temporal and spatial quadrature), voltages were induced in the eye coil, which, when separated by phase detection electronics (C.N.C. Engineering), allowed measurement of the horizontal and vertical position of the eye in space. The sensitivity of this eye movement measurement technique is 15 min of arc. During the same surgery, a stainless steel recording chamber was stereotaxically aimed at the DLPN and fastened with dental acrylic over a hole trephined in the skull. Finally, three dental acrylic lugs for head stabilization were attached to the skull with stainless steel screws.

During the behavioral training and single-unit recording sessions, the monkeys sat in a restraining chair with their heads immobilized. The chair was placed in a sound- and light-proof booth with the animal facing a tangent screen 68 cm distant on which a target spot, as well as various background patterns, were rear projected. A booth light was kept on continually during all testing, except during smooth pursuit in the dark and during the target blanking described below. Therefore, the monkeys' visual system was in a light-adapted state during most testing. The eye with the implanted coil was centered within the field coils, and the eye coil first was calibrated grossly by having the monkey look at small pieces of food held at known eccentricities. The animal was then rewarded with applesauce, under electronic control, for looking to within 5° and eventually 1° of the target spot. Finally, the monkeys were trained to make smooth-pursuit eye movements either across a patterned large-field (70° x 50°) background or in the dark. The target, a red spot (0.25°) produced by a laser, was moved in two dimensions by mirror galvanometer systems. The stimuli included small (1-5°) spots, checkerboards, and large-field or full-screen random-dot patterns, which could be moved in a variety of amplitudes, directions, and velocities. The luminances of the target spot and the light and dark contours of the test stimuli were 30.0, 10.8, and 1.3 cd/m², respectively, measured with an SE1 photometer. The contrast of stimuli is defined by the relationship \((L_max - L_min)/(L_max + L_min)\), where \(L_max\) and \(L_min\) are the luminances of the light and dark contours, respectively. The contrast for the laser spot on the light contours of the random-dot pattern was 0.5, and the contrast of the random-dot pattern was 0.7. The shutter used to turn the visual stimuli on and off produced a click, providing an auditory stimulus to the animal. Therefore, any response linked with shutter operation was checked with the projector lamp off to test for the possibility of auditory responses. Although auditory units were never found in the DLPN, the clicks often elicited responses in adjacent structures such as the lateral lemniscus, and these responses often proved useful in localizing the DLPN.

**Single-unit recording and data analysis**

Single units were recorded extracellularly with tungsten microelectrodes by conventional methods (10). Eye and target-position signals, unit discharge, and signals related to the visual stimuli were saved on analog tape (Honeywell 5600) for off-line analysis. Eye and target-position signals were digitized by a computer (PDP 11/73) at 1 kHz, while unit sampling was interrupt driven, ensuring that no spikes were missed. Experiments in which either the target or background moved sinusoidally were analyzed by dividing each cycle (defined by the target- or background-position signal) into 64 equal time bins. The experimenter removed saccades and their associated neural activity from the eye position traces using an interactive program (21). The numbers of spikes in each of the 64 bins were accumulated until at least 10 samples occurred in each bin. To quantitatively describe unit response properties in relation to a given variable we plotted unit firing rate, averaged during the half cycle in which firing was raised above the resting rate (i.e., the on-half cycle).

Some units were tested while the monkey tracked a target moving in a step-ramp trajectory or when the target was extinguished unexpectedly during pursuit. For these special cases, unit data and accompanying target and eye movement signals were written out on paper by an oscillograph (Honeywell) and entered by hand into the computer via a digitizing tablet.
Histological preparation and electrode track reconstruction

To identify the location of the recorded cells, we placed electrolytic lesions (10–30 μA for 10 s) on representative electrode tracks at a depth where units that discharged during smooth-pursuit eye movements had been encountered. At the conclusion of the recording series, each animal was deeply anesthetized (lethal barbiturate dose) and perfused with saline followed by 10% Formalin. Frozen sections were cut at 40 μm, and every section was mounted on microscope slides and stained for histological reconstruction of electrode tracks. All of the units (n = 191) described in this study were histologically confirmed to be within the confines of the DLPN (37).

results

Classification of DLPN unit types

All DLPN units were tested under the following three search conditions: 1) smooth pursuit of a small (0.25") target spot against a dark background (hereafter called smooth pursuit in the dark); 2) smooth pursuit across a patterned visual background; and 3) visual stimulation alone during fixation (either background on/off, flash, or full-screen background movement). These conditions were continuously altered while we recorded, thus testing direction and visual preferences for each unit.

On the basis of their responses during smooth pursuit in the dark and during visual stimulation, units initially were separated into three general types (Table 1). Units that 1) responded during smooth pursuit in the dark, 2) exhibited the same firing pattern during smooth pursuit across a background, and 3) exhibited no response for a variety of visual stimuli when the eye was stationary were called tracking units. Units that responded to any of the visual stimuli but did not discharge during smooth pursuit in the dark were called visual units. Units that discharged during smooth pursuit in the dark and in response to visual stimulation (usually large field) during fixation were called tracking and visual. Both tracking and tracking and visual units (together 85% of all cells) discharged during smooth pursuit in the dark. Responses during smooth pursuit in the dark, however, can result from an eye movement sensitivity per se or a visual sensitivity (parafoveal) produced by retinal image slip during imperfect pursuit. To clarify the source of smooth-pursuit activity in 70 tracking and tracking and visual neurons, we turned off the moving target during tracking for periods so brief that the animal continued to make smooth eye movements in the dark. All of the tracking units so tested (n = 34) continued to fire with their usual pattern and therefore were designated as eye movement neurons. Of the 36 tracking and visual units tested, those that ceased to fire or returned to their low resting rates during the target blank (n = 15) were designated as visual pursuit units, whereas those that continued to fire during the target blank (n = 21) but also exhibited an overt visual sensitivity (e.g., a response to the moving background during fixation) were called pursuit and visual. No DLPN units had activity related to saccades.

Figure 1A shows an example of one of our electrode tracks with a marking lesion (arrow) at a location where units that discharged during smooth-pursuit eye movement were recorded. Figure 1B shows a reconstruction of the location of units recorded on this (thin line) and the other tracks of one animal; all tracks cross over from the left to the right side. The various unit types (indicated by different symbols) were not segregated to specific parts of the DLPN in this animal. We sampled the full extent of the DLPN (Fig. 1B, shading), using electrode approaches that were directed from either the ipsilateral or contralateral sides and found no anatomical segregation of unit types in any of the five animals.

<table>
<thead>
<tr>
<th>Initial Classification</th>
<th>Smooth Pursuit During Target Blank</th>
<th>Specific Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tracking, n = 59</td>
<td>Response continues</td>
<td>Eye movement, n = 34</td>
</tr>
<tr>
<td>(SPD/no visual)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tracking and visual, n = 104</td>
<td>Response continues</td>
<td>Pursuit and visual, n = 21</td>
</tr>
<tr>
<td>(SPD + visual)</td>
<td>Response drops out</td>
<td>Visual pursuit, n = 15</td>
</tr>
<tr>
<td>Visual, n = 28</td>
<td>Target blank not tested</td>
<td>Visual, n = 28</td>
</tr>
<tr>
<td>(no SPD)</td>
<td></td>
<td></td>
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</tbody>
</table>

SPD, response to smooth pursuit in the dark. DLPN, dorsolateral pontine nucleus.
Visual units

Visual units responded to the background being turned on and off and to strobecoscopic stimuli but showed no discharge during smooth pursuit in the dark. Such units were encountered infrequently and represented only 15% of our sample. They had large receptive fields that covered up to the entire tangent screen but had little or no movement response even to a large-field background. Because of their weak visual responses and lack of eye movement-related responses, we did not test these units extensively. Since our search stimuli emphasized parafoveal and large-field stimuli, we may have missed visual units with other stimulus preferences, thereby underestimating the actual percentage of visual units.

Eye movement units

Eye movement units could be divided roughly into two separate categories. During sinusoidal pursuit, one category discharged nearly in phase with eye position, like the cell shown in Fig. 2A. When the firing rates of such units were averaged for 4 s at fixed eye positions, a monotonic relation between discharge rate and eye position usually resulted. For the unit shown in Fig. 2A, this relation is illustrated by the curve identified by an asterisk in Fig. 3. We designated these eye movement neurons as eye position neurons. Neurons in the second category discharged as the eye was moving between its peak excursions, like the cell shown in Fig. 2B. When the eye

FIG. 1. Location of the dorsolateral pontine nucleus (DLPN) and placement of recording sites. A: photomicrograph of a Nissl-stained section, cut in the stereotaxic plane, showing an electrode track with a marking lesion (arrow) in the DLPN. B: electrode track reconstructions taken from the same case as in A are shown on the right. Locations were reconstructed according to their depth relative to lesions (e.g., large asterisk). •, eye movement; ◀, visual pursuit; ❅, pursuit and visual. Shading on left indicates the region sampled in all animals. DSCP, decussation of the superior cerebellar peduncle; SN, substantia nigra; RN, red nucleus; PN, pontine nucleus; NI, interstitial nucleus; NRTP, nucleus reticularis tegmenti pontis; III, oculomotor nucleus; IV, trochlear nucleus. Stereotaxic levels A6, A4, A2, equivalent to those illustrated in Snider and Lee, Stereotaxic Atlas of the Monkey Brain, Chicago, IL: Univ. of Chicago Press, 1961. Scale bar = 1 mm.
was stationary, the firing rate did not vary with eye position. Some of these units exhibited a clear relation of firing rate with eye velocity (Fig. 5; the unit shown in Fig. 2B is marked by an asterisk). We designated these units loosely as eye velocity units.

**Eye Position Units.** Nineteen percent (n = 36) of all of the DLPN units studied were eye position units. Figure 3 shows rate-position curves for 10 representative units. Data for these plots were obtained while the monkey fixated at different stationary target-spot locations (for at least 4 s). Horizontal, vertical, and oblique target positions were tested for each unit. Most rate-position relations are not linear. A variety of position sensitivities are evident in Fig. 3, ranging from 1 to 10 spikes·s⁻¹·deg⁻¹ (measured in the portion of the curve with steepest positive slope). Some eye position units are silent until they are recruited into steady firing. Other units fire at a low rate for some “off-direction” eye positions below a threshold; above this threshold, they exhibit a monotonic increase in firing rate with eye position. Since our search stimulus required the monkey to track target movements within ±10° of the fixation point, we may have overlooked units with position thresholds exceeding 10° in the “on-direction.” Nine of 36 eye position units also displayed visual sensitivity during background movement.

**Eye Velocity Units.** As the name implies, these units had a firing rate dependent on smooth-pursuit eye velocity (Fig. 4). From curves like Fig. 4, we constructed plots of average firing rate (for the on-half cycle) as a function of peak eye velocity (Fig. 5). Some units showed a monotonically increasing discharge rate with increasing eye velocity, whereas others showed only a weak relation between peak eye velocity and firing rate. The maximum slopes of different curves ranged from 0.2 to 2 spikes·s⁻¹·deg⁻¹·s⁻¹. Plotting peak rather than average firing rates produces curves with steeper slopes (i.e., up to 5 spikes·s⁻¹·deg⁻¹·s⁻¹) than those of Fig. 5. These higher velocity sensitivities occur because the firing rates immediately after the eye changes from the off- to the on-direction are higher than those throughout the remainder of the on-half cycle (Fig. 4).

Most eye velocity units and other DLPN types that discharge during smooth pursuit exhibit a nonsinusoidal modulation of firing rate. This point can be appreciated by considering Figs. 2B, 4, 7A, and 8A, where the discharge during smooth pursuit is silenced in the off-direction. Even when restricting consideration to the on-direction of pursuit, firing rate profiles are generally flat topped (Fig. 4). Only at lower frequencies, and hence lower velocities, do the smooth-pursuit discharge patterns of some units resemble sine waves (Fig. 4, top curve).

**Temporal Relation of Firing Change to Eye Movement.** To determine whether the discharge of some eye movement units could provide a driving signal for smooth pursuit, we determined whether their discharge preceded or followed the initiation of smooth pursuit. To elicit smooth-pursuit eye movements without saccades, we used the step-ramp stimulus of Rashbass (38), in which an initial step movement of the target is followed by a ramp of constant velocity in the opposite direction. We adjusted the step size and ramp velocity to eliminate saccades and used constant-direction step ramps intermixed randomly with ordinary ramps of the same direction and velocity. Smooth-pursuit onset, estimated from eye velocity records (arrows in Fig. 6), occurred with a mean (n = 10) of 111 ms (SD ± 22 ms) after the onset of a target ramp. This rather short latency might be attributable to prediction, since the direction of the movement was always constant. Because eye position units generally had on-direction thresholds and were therefore activated only after smooth pursuit exceeded a certain eye position, we examined only eye velocity units. Nine of ten eye velocity units analyzed began discharging only at the onset of, or during, the smooth eye movement. One unit illustrated in Fig. 6A, however, led the onset of smooth pursuit (estimated by eye from eye velocity traces) by an average of 22 ms (SD ± 22). Note that the unit is silent until just before smooth-pursuit onset in all trials. Therefore, for the limited number of units tested, most eye velocity units alter their discharge too late to be responsible for the initiation of smooth pursuit.
Pursuit and visual units

The response of a pursuit and visual unit during the three search conditions is shown in Fig. 7. During smooth pursuit in the dark (Fig. 7A and first cycle of Fig. 7C), this unit shows a brisk response for upward eye movements and a complete cessation of discharge for downward eye movements. To determine whether the response during smooth pursuit in the dark was the result of visual activation by movement of the target’s image across the retina (i.e., retinal image slip) during imperfect pursuit, we also recorded the unit activity when the target was turned off (blanked) for brief periods (200–500 ms) so that smooth tracking continued without a target (Fig. 7C).
Although the eye velocity dropped toward the end of the target blank, the monkey continued to move its eyes smoothly and the unit exhibited a qualitatively similar discharge pattern with and without the blank. Because all visual input during the target blank had been completely eliminated, this result suggests that the continuing discharge of this unit reflects a motor component. Since the discharge of this and other similar units continued even when the target disappeared on the first cycle of pursuit after a period of steady fixation, the activity during the blank was not the result of discharging some type of visual storage mechanism.

Although the blanking experiment indicated that the discharge of this unit had a component related to eye movement, the results shown in Fig. 7B indicate the existence of another component related to vision. When a large-field visual background was moved vertically while the monkey fixated a stationary target spot, this unit exhibited a brisk response for upward background movement. The receptive field of this unit, tested with a 2°-diameter spot, was found to cover the entire 50° × 70° tangent screen. Taken together, these data suggest that this unit had both an eye movement-related and visual-related response. Of the 36 tracking and visual units tested, 21 had both eye movement and visual responses.

The "bursty" nature of the discharge of this unit was typical of most DLPN units. Although some bursts seemed to be associated with saccades as shown in Fig. 7, this was not an invariable occurrence. Careful examination of many cycles convinces us that bursts were related reliably neither to saccades nor to instants of increased retinal slip (see bursts indicated by arrows in Fig. 2B).

Visual pursuit units also discharge during smooth pursuit in the dark. Their discharge, however, reflects a visual response, since they respond to background movement during fixation and cease discharging or return to their low resting rate when the target is

**FIG. 3.** Ten representative rate-position tuning curves. Static eye position is plotted against the unit's firing rate averaged over 4 s of fixation on a dark background. Line with error bars (SDs) shows representative variability in response.

**FIG. 4.** Firing rate profiles averaged from at least 10 cycles of sinusoidal tracking. Each profile is plotted at the same vertical scale and is composed of 64 unequal time bins for the various frequencies indicated. Amplitude was ±10°. Bottom trace indicates the position of target turnaround.
blanked during smooth pursuit (Fig. 8). Like the unit of Fig. 7, the unit of Fig. 8 discharged for upward smooth pursuit in the dark and upward background movement with the eyes fixating. Unlike the unit of Fig. 7, however, it slowed essentially to its resting rate during a target blank (Fig. 8C), although the animal continued to pursue smoothly. The fall in discharge rate during the target blank is not due to a decrease in eye velocity. This is demonstrated in two ways. First, eye velocity does not show an appreciable decline until 120 ms after the target spot is extinguished, whereas the unit response decreases at 90 ms, which is the visual latency of the unit. Second, during shorter target blanks (e.g., 100 ms), when eye velocity shows no decline, the unit response still decreases at the visual latency of the unit. Finally, in the example shown here and in other visual pursuit units, the response at low pursuit velocities (i.e., just after the eye begins moving in the on-direction) immediately jumps to a high firing rate; therefore, even the modest decrease in velocity during the blank would not of itself cause a decrease in firing rate. Taken together, these data suggest that this unit had little, if any, firing-rate component related to eye movement. When the target was turned back on, the unit exhibited an on-response (arrows). Testing this unit with

\[ \text{FIG. 5. Eye velocity sensitivity of eye movement units tested during sinusoidal smooth pursuit. Average firing rate during pursuit is plotted against the associated peak eye velocity. Asterisk is unit shown in Fig. 2B.} \]

\[ \text{FIG. 6. Response of an eye movement unit (A) and a visual pursuit unit (B) during step-ramp tracking. A and B, top traces: horizontal target position (HE) and vertical target position (VT). Middle traces: horizontal eye position (HE) and vertical eye position (VE). Bottom trace: eye velocity obtained by electronic differentiation of eye position (E). Individual spikes during separate trials are shown as vertical dashes in A and B. The eye and target-motion traces were from one of the trials shown. Pursuit was horizontal in A and vertical in B. Step size was 3° in A and 4° in B. Horizontal scale bar = 100 ms; vertical scale bar = 10°/s.} \]
Visual receptive fields

The receptive fields of 48 visual pursuit and pursuit and visual units were plotted with a small (1–5°) moving test spot while the animal fixated a stationary target. The sizes of the receptive fields ranged from $2 \times 2^\circ$ to $70 \times 50^\circ$ (i.e., the entire tangent screen) (Fig. 9). The receptive-field size did not depend on unit type. All of the 11 representative receptive fields in Fig. 9 and those of all other DLPN units tested included the fovea. Most (81%) units were direction selective. Although not studied in detail, some of the very large receptive fields had local regions from which a particularly intense response was elicited. We often observed that the response, seen with large-field background movement during fixation, was comparable to that seen during smooth pursuit of a small target spot in the dark (e.g., see Fig. 14), suggesting that foveal and parafoveal regions provide the biggest contribution to the visual response. Of the seven units tested, all had binocular receptive fields.
FIG. 8. Response of a visual pursuit unit during 3 test conditions. A: smooth pursuit of a small target spot in the dark. B: large-field background movement during fixation of a stationary target spot. C: smooth pursuit in the dark when the target spot is blanked. Calibrations as in Fig. 7.

Latency of visual response

Figure 6B illustrates the response of a visual pursuit unit during step-ramp tracking. Note that the unit is relatively silent until after ramp onset in all trials. The unit discharged 100 ms (SD ± 20) after a ramp in the unit’s on-direction and ~40 ms (SD ± 15) before the onset of pursuit. This timing was typical for the 20 visual pursuit DLPN units tested, suggesting that the visual signal carried by these units could provide a driving signal for pursuit.

Direction selectivity of DLPN units

The majority of DLPN units discharged for eye movements and/or visual stimuli that moved in a particular direction. The on-direction was tested by having the animal track horizontal, vertical, and oblique (±45° from horizontal) target movements and/or by...
moving a large-field background in the same directions during fixation. Directional tuning curves were produced by using an fast Fourier transform algorithm (52) that fitted a curve to averaged unit data like that of Fig. 4. The parameter fitted was the average firing rate during one direction of smooth pursuit or background movement (see Fig. 14, C and D).

Examples of averaged firing rates during smooth pursuit and the curves fit through them are shown in Fig. 10 (see also Fig. 14, A and B) for representative units. The arrows indicate the best directions of the units, determined by the computer on the basis of the maximum change in firing rate relative to resting rate. The maximum of the fitted curve was considered the on-direction (arrows) for the unit. A unit was considered direction selective if the firing rate in the on-direction was at least twice that in the off-direction. Consequently, units A and B in Fig. 10 were directionally selective, with nearly down and up selectivities, respectively. In contrast, unit C had an approximately equal change in firing rate in all directions tested and was, therefore, directionally nonselective. Most (95%) of the units that discharged during smooth pursuit in the dark were direction selective. They were generally, however, broadly tuned. For example, the widths at half-maximum amplitude for the curves in Fig. 10, A and B are 90 and 120°, respectively. The average for all 46 units tested is 129 ± 42°.

Although the on-directions for these units (Fig. 10D) were distributed over a wide range of angles, vertical and near-vertical directions were most common. There was no evidence of segregation in the DLPN according to directional preference. Indeed, two simultaneously recorded or neighboring units often had opposite on-directions.

**Response to background movement**

To determine how the visual response of pursuit and visual and visual pursuit units is related to movement across the retina, we tested their velocity sensitivities by moving a large-field background sinusoidally at different frequencies (0.25–1.0 Hz) with a constant amplitude (±10°) while the monkey fixated a stationary target spot. The peak image veloci-

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**FIG. 9.** Receptive-field plots for 11 representative units. Receptive fields were plotted with a small test spot while the monkey fixated the stationary target spot. All receptive fields (n = 48) plotted included the fixation point (●). Although receptive fields are plotted here as rectangles with small circles marking top right border of each receptive field, their precise shapes were not determined.
FIG. 10. Directional tuning curves fit to data points (●) for 2 direction-selective units (A and B) and 1 nonselective unit (C) during smooth pursuit in the dark. The calculated best directions (arrows) for all tested units (n = 46) are shown in D. Tick marks = 10 spikes/s.

Firing rates at these frequencies ranged from 16 to 60°/s. Figure 11 shows the relation of average (on-half cycle) firing rate to peak stimulus velocity for 15 representative units that exhibited the full range of slopes. Some units (lower curves) showed modest, if any, changes in firing rates over the range of velocities tested. A few units exhibited a convincing monotonically increasing discharge rate with increasing stimulus velocity. Like the discharge patterns described for eye velocity units during sinusoidal smooth pursuit, the firing rate profiles for visual pursuit and pursuit and visual units during sinusoidal background movement (on-direction) typically were flat topped, making it problematic to determine whether the units were firing in phase with the velocity of the background movement.

Although we typically did not use large-field visual stimuli with peak velocities less than 16°/s, our lowest frequency sinusoidal stimuli do produce a variety of velocities (i.e., from 0 to 16°/s) at different parts of a single cycle. To determine whether the discharge of DLPN units could encode lower visual velocities during sinusoidal background movement, we divided each cycle into 64 equal time bins and averaged the firing rate across 10 cycles to obtain an average firing rate for each bin. Average firing rates were then plotted against the average visual velocity that had occurred in an earlier time bin appropriate for the unit’s visual latency. Thirty units were so tested, and data from four representative units are shown in Fig. 12, where firing rate is plotted against visual velocity in both the on- and off-directions. For these units and the other 26, the discharge during off-direction stimulation is independent of stimulus velocity. For half of the units, on-direction discharge increased monotonically with velocity over part of the stimulus-velocity range.
DORSOLATERAL PONS AND SMOOTH PURSUIT

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ity (e.g., Fig. 12D). The apparent monotonic relation between firing rate and velocity over the \(-10 \text{ to } 10^\circ/\text{s}\) range for the unit shown in Figure 12D is due, at least in part, to the time it takes the unit to turn on and off during changes in stimulus direction.

Response to small spot movement

As mentioned in the section on receptive fields, most DLPN units also responded to small-spot stimuli; however, we did not perform a parametric study of the small-spot response. A previous report (44) suggested that the discharge of cells in DLPN encode retinal slip velocity of a small spot during pursuit. Although we did not produce them explicitly, very slow movements of the visual target spot resulted when eye velocity lagged slightly behind target velocity during smooth pursuit in the dark. To assess the possible relation of firing rate with the slip velocity of the spot on the retina, we displayed single-unit activity and retinal slip velocity obtained by differentiation of the retinal error signal (target position minus eye position) on a high-speed recorder. When this subtraction was performed, essentially constant slip velocities occurred for epochs of 100 ms. The velocities in these epochs were plotted against the averaged (>100 ms) firing rates that occurred after a delay corresponding to the unit’s visual latency to flashed stimuli. In the 15 units tested, the mean latency was 100 ± 20 ms.

Figure 13 shows such an instantaneous retinal slip analysis for 2 of 15 units tested that had direction-selective visual responses during smooth pursuit. Although retinal slip was usually <5°/s, larger slips often occurred when the monkey tracked higher frequencies (0.75–1.0 Hz), especially in the vertical direction. The plots in Fig. 13 represent a typical relation (unit A) and the best relation (unit B) between firing rate and retinal slip. The correlation coefficients for A and B were 0.14 and 0.5, respectively. The unit data illustrated in Figure 13A is from the same unit illustrated in Fig. 12A during large-field testing. From these data, we conclude that low retinal slip velocities produced by imperfect tracking of a small spot do not seem to be encoded in the discharge of the 15 individual visual pursuit units tested here.
FIG. 12. The response of 4 different visual pursuit units during sinusoidal stimulation with a large-field visual stimulus. Units A, B, and C have responses that are monotonically related to stimulus velocity over part of the stimulus velocity range. Asterisks in A, B, and D are actual firing-rate values for each of the 64 bins (see text); the squares (averaged from 3 neighboring bins) are connected by a least-squares regression (—) of the firing rate data for each unit. In C, the response in the on-direction while the stimulus is accelerating (○) or decelerating (▲) is plotted against stimulus velocity. The firing rate value given on the ordinate in each plot is in spikes/s. Tic marks on abscissa are at 10°/s intervals.

**Interaction between smooth pursuit and visual responses**

Many DLPN units (n = 104) responded both during smooth pursuit in the dark and during large-field background movement during fixation. The smooth-pursuit-related and the background-related responses of these units were either in the same (49%) or opposite (51%) directions. Figure 14 illustrates directional tuning curves for two units, one with opposite (A and C) and the other with the same (B and D) pursuit and background directional preferences. For such units, it might be expected that the discharge due to the background and pursuit components would be combined (e.g., simple linear addition) during smooth pursuit over a fixed background.

This suggestion is examined in Fig. 15, which summarizes the relative contributions to unit discharge of background movement and smooth pursuit at the same frequency of movement (i.e., 0.5 Hz). Figure 15A shows that the firing rate modulation during smooth pursuit and that during background movement are usually dissimilar. The discharge
FIG. 13. Responses of 2 visual pursuit units during smooth pursuit in the dark. Unit firing rate (ordinate) is plotted against retinal slip velocity in both the on- (positive) and off-directions (negative).

FIG. 14. Directional tuning curves for 2 pursuit and visual units during smooth in the dark (A and B) and during fixation with large-field background movement (C and D). Tic mark = 10 spikes/s.
during either pursuit or background movement could be the greater, with the correlation coefficient relating the two variables being only 0.41. As seen in Fig. 15B, DLPN units usually were less responsive during smooth pursuit in the dark than during pursuit over an illuminated background ($r = 0.76$), indicating that in the latter condition the unit's visual sensitivity affects its smooth pursuit response. During smooth pursuit over a stationary background, units with opposed direction selectivities (antiphase units; □) would be expected to add background and pursuit response components, whereas units with the same background and pursuit direction preferences (inphase units; □) would be expected to have components that subtract. Figure 15C compares the discharge predicted for smooth pursuit over a background based on the algebraic sum of individual background and pursuit sensitivities (spontaneous activity subtracted out) with that actually measured. Points falling on or near (within ±20 spikes/s) the dashed line, which would apply if there were a linear interaction between smooth-pursuit and background responses, describe more than 50% of the units. Typically, for those units whose responses should add (●), the actual response was less than that predicted. On the other hand, for those units whose responses should subtract (□), the actual response was greater than predicted. As can be seen in Fig. 15A, these differences in the behavior of the in- and antiphase units cannot be accounted for by a difference in their relative smooth-pursuit and background sensitivities. The possible reason for the nonlinear interaction between the smooth-pursuit and background-related discharges is considered in the DISCUSSION.

**DISCUSSION**

One of our unexpected discoveries was the rich variety of DLPN neurons that discharge during smooth pursuit of a small moving spot. The firing patterns of various neurons have different combinations of visual and eye movement sensitivities. The existence of units with visual sensitivity is no surprise, because studies of this area in the anesthetized cat and monkey (12, 30) have reported DLPN cells with visual responses. The discovery of eye movement cells and the finding that many visual cells also have eye movement sensitivities suggests that this area may be more than simply a passive relay for visual information and implicates it, more directly, in smooth pursuit.

In the most simple terms, if the DLPN is part of a smooth-pursuit pathway, it might be expected to have cells that either carry some parameter of an already constructed motor smooth-pursuit signal (e.g., direction or velocity), or discharge with the visual stimulus that elicits smooth pursuit (e.g., retinal slip velocity). Also, the DLPN could be part of the
interface between the sensory stimulus and the smooth-pursuit response, in which case it might contain units with combined visual and oculomotor responses. We will, therefore, consider the behavior of each of the DLPN cell types and speculate about its possible role in smooth pursuit.

*Are there true eye movement cells in the DLPN?*

The large majority of cells in the DLPN discharge with smooth pursuit of a small target spot in otherwise complete darkness. By extinguishing the target spot briefly, we ascertained that, for some units, the smooth-pursuit response was independent of visual stimulation. Two types of true eye movement neurons have been identified.

Eye position neurons, in addition to responding to smooth pursuit in the dark, also exhibit a steady discharge proportional to eye position. Usually these units are inactive or have a low discharge rate in the primary direction of gaze and show a marked increase only for more eccentric eye positions. These cells usually begin to change their firing frequency during a saccade to an appropriate eccentric location, implying that they are not involved in initiating the movement. Because of their preference for eccentric gaze, such neurons may be involved with head movements, perhaps especially those outside the oculomotor range. Neurons with similar characteristics have been reported in the mesencephalon (17).

Eye velocity neurons, on the other hand, discharge mostly when the eye is changing position. However, unlike putative smooth-pursuit units in the flocculus of the cerebellum (21, 28) and in the vicinity of the abducens nucleus (7), the discharge rate of most DLPN neurons during sinusoidal pursuit does not accurately follow the position or velocity of the stimulus, nor does it accurately predict the waveform of the resulting eye movements. Furthermore, the cells often have an irregular “bursty” discharge that varies considerably from trial to trial. Finally, the step-ramp paradigm indicates that for the limited samples of neurons tested, eye velocity neurons begin discharging simultaneously with, or during, the smooth-pursuit movement. The single neuron (Fig. 6A) whose discharge did precede the movement exhibited changes of firing that led by different amounts from trial to trial. Taken together, these data indicate that eye velocity cells provide signals that are unsuitable for eye movement initiating commands, although they could participate in the maintenance of pursuit.

Our diagnosis that a cell discharges only in relation to eye movements depends on the fact that it continues to discharge during smooth pursuit without a visual target. Can the continuing neuronal discharge during the blank have other explanations? One possibility is that the residual discharge reflects the activity of a visual velocity storage circuit that continues the preceding discharge during the blank. This seems unlikely, since the discharge during target blanking is present even to the first presentation of a target movement, presumably before a hypothetical storage circuit has had time to charge up. Another possibility is that the discharge occurring during the blank is part of the signal that allows the smooth-pursuit system to bridge the target gap. In humans, the target spot can be blanked for periods of up to 2 s, and the eyes will continue to move smoothly but at a reduced velocity (2). This residual velocity could be controlled, in part, by the discharge that continues during the blank.

*Visual signals in DLPN*

Moving visual stimuli elicit brisk responses in many cells of the DLPN. The discharge patterns of either visual pursuit cells or pursuit and visual cells are strongly directional. In addition, about half of the neurons discharge in relation to the velocity of movement of a large-field background, but the relation is often weak at best (Fig. 11). Some of these same units tested with sinusoidally moving large-field stimuli encoded visual velocity on a moment-by-moment basis over part of the velocity range. In contrast, the firing rate of most of our cells was only weakly correlated, if at all (Fig. 13), to the velocity difference between the target and eye movement (i.e., retinal slip) during imperfect smooth pursuit in the dark. The velocity of this parafoveal retinal slip would seem to be an important parameter for smooth-pursuit control. In our slip-velocity analysis, we selected units (e.g., visual pursuit) with strong visual responses during smooth pursuit, so it
seems unlikely that we would have missed a strong correlation between firing rate and velocity if one existed.

Taken together, these data suggest that there may be a difference in the way visual velocity is encoded for large-field as opposed to parafoveal stimuli. However, this difference must be tested explicitly by using identical conditions for small-spot and background stimuli. For example, at the level of the DLPN, the "active" visual stimulation occurring during smooth pursuit may not be entirely comparable to the "passive" visual stimulation employed while the monkey fixates. It is possible that the balance of DLPN input from different cortical areas (see below) during smooth pursuit may be different from that occurring during large-field visual stimulation while the monkey fixates.

Our findings regarding visual velocity sensitivity are in partial agreement with those of Suzuki and Keller (44), who reported that some of their DLPN cells encoded retinal slip velocity for large-field visual motion. However, they emphasized the visual velocity encoding capability of DLPN units for small-spot slip during smooth pursuit, whereas we feel this property is not reliably reported by the DLPN. Unfortunately, Suzuki and Keller (44) provided only one raw data record regarding foveal slip during smooth pursuit, making a comparison with our data impossible. Using quantitative measures (see Fig. 13), we have found only weak relationships between unit firing rate and foveal retinal slip during pursuit. In addition, their search conditions differed from ours in that they required the animal to fixate while the visual sensitivity of units was tested with a moving test spot or background. Furthermore, most of their units were recorded in the rostral DLPN (D. Suzuki, personal communication). In contrast, we sampled the entire DLPN using search stimuli that were best suited to reveal eye movement sensitivity and parafoveal visual sensitivity. As a result, some of our visual units may not have been tested adequately. Owing to limited time in the recording session, we chose to look for and test units that were responsive during large-field background movement and/or smooth pursuit. Such selection criteria may have caused us to miss units that had a strong relation to visual stimulus velocity. Nevertheless, our data suggest that DLPN units with vigorous responses during smooth pursuit and/or background movement do not have a robust discharge to retinal slip velocity produced during inadequate smooth pursuit of a small spot.

We did not systematically examine DLPN cells for other sensory inputs. However, click stimuli, which were effective in eliciting responses in surrounding structures, elicited no responses in the DLPN, suggesting that unlike in the cat (14), the DLPN of the monkey probably receives no auditory information.

What sort of smooth-pursuit signal could the DLPN provide?

The most consistent and striking feature in the discharge of all cell types in the DLPN is their direction selectivity. Ninety-five percent of the units that discharged during smooth pursuit of a spot in the dark responded to movement in a particular direction; these direction-selective units included eye movement, visual pursuit, and pursuit and visual units. Since, in the step-ramp paradigm, all visual pursuit units and probably some eye movement units begin discharging before the onset of pursuit eye movements, such units could provide direction information for smooth pursuit. Indeed, behavioral studies (23) suggest that direction is the first parameter specified in the initiation of smooth pursuit. It is only 60–80 ms later that other factors, such as target velocity, begin to influence smooth pursuit. Therefore the visual pursuit units, in particular, could be involved in the early directional component of smooth-pursuit initiation, while units with eye velocity or visual sensitivity could participate in the later parts of smooth-pursuit initiation or the maintenance of smooth-pursuit tracking.

A role for the DLPN in the initiation of smooth-pursuit seems generally consistent with the results of some stimulation and lesion studies of the DLPN. Small ibotenic acid lesions near regions containing visual motion or smooth-pursuit-related units cause the initial eye acceleration of smooth-pursuit movements in certain directions to be reduced by more than one-half of normal values (45). Also, electrical stimulation during the initial phase of smooth pursuit in a specific direction produces an eye acceleration (27). The deficit produced by lesions and the effects of electrical stimulation both appear to be directional. Since the effects of focal lesions also
are short lasting and the effects of electrical stimulation appear to be weak (27), the DLPN may not be crucial for smooth-pursuit initiation, although complete lesions of the DLPN would be required to unequivocally evaluate this point.

**Pursuit and visual units in the DLPN**

A significant percentage of our units discharged both in response to visual stimuli and during smooth pursuit of a small spot in the dark. Such "hybrid" DLPN units were also reported in earlier studies (32, 44). The preferred directions for the visual and pursuit responses of our hybrid units were in either the same (inphase) or opposite (antiphase) directions. Curiously, when both responses were elicited together by requiring the animal to track a small spot over a fixed patterned background, the response was not always the algebraic sum of the two (Fig. 15, A-C).

What role might such hybrid units serve during smooth pursuit? When smooth-pursuit eye movements are made in a natural visual environment, the image of the stationary background moves in a direction opposite to target movement. Slip of the large-field visual background image might be expected to interfere with smooth-pursuit performance by inducing an optokinetic eye movement that would drive the eyes in the direction opposite to pursuit. Indeed, smooth-pursuit gain is lower during smooth pursuit over a fixed background than during smooth pursuit in the dark (personal observation), although there is some controversy on this issue (16). The pursuit system might use the activity of hybrid units to minimize the detrimental effects of the visual background. For example, during smooth pursuit over a stationary background, antiphase units generally exhibit a greater response than during smooth pursuit in the dark (personal observation), although there is some controversy on this issue (16). The pursuit system might use the activity of hybrid units to minimize the detrimental effects of the visual background. For example, during smooth pursuit over a stationary background, antiphase units generally exhibit a greater response than during smooth pursuit in the dark (personal observation), although there is some controversy on this issue (16). The pursuit system might use the activity of hybrid units to minimize the detrimental effects of the visual background. For example, during smooth pursuit over a stationary background, antiphase units generally exhibit a greater response than during smooth pursuit in the dark (Fig. 15B). This greater smooth pursuit drive might partially overcome an oppositely directed optokinetic drive. Inphase units, on the other hand, seem little affected by the presence of the background, showing approximately equal modulation during smooth pursuit over a dark or over an illuminated background (Fig. 15B). Therefore, inphase units appear to be equally active during smooth pursuit in any circumstance, although their behavior during smooth pursuit and vestibular stimulation remains to be tested. Perhaps inphase and antiphase units serve a sensory rather than motor role.

The smooth-pursuit system must be able to separate real image motion from self-generated image motion. Units with both pursuit and visual sensitivity might play such a role. For example, units in the flocculus could compare activity in the inphase and antiphase hybrid units to determine whether there is motion confined to the visual world or whether the eye is moving. We have not looked at DLPN units during head movement, but if these units were playing a role in the signaling of selfmovement, they might be expected to carry a head movement signal. Indeed, others have reported vestibular sensitivity in the DLPN (42). Of course, the flocculus also could construct a signal that encodes self-generated or real visual motion from the strong visual eye movement and vestibular input it receives from other sources.

**Where do DLPN cells project?**

As indicated in the introduction, we initiated our exploration of the DLPN to find signals that could be involved in producing the well-known (21, 28, 36) response of floccular Purkinje cells during smooth pursuit. As suggested above, the visual pursuit and some eye movement cells could provide inputs related to pursuit direction. A small percentage (<20%) of input elements to the flocculus, either neural elements in the granule cell layer (28), putative mossy fibers (34), or "non-Purkinje cells" in the flocculus (50) respond to visual stimuli. Using visual stimuli comparable to ours, Noda (34-36) found that about one-third of his visual mossy fibers conveyed information about the direction, but not velocity, of the motion of a random-dot background; the firing patterns of his representative unit look similar to some of ours. The remainder of his visual units, like some of the visual units depicted in Fig. 11, were sensitive not only to direction but also to velocity. Such visual information also reaches floccular Purkinje cells, since a small percentage are sensitive to direction, velocity, or both. Also, although it appears that no mossy fibers have both visual and eye movement responses, some Purkinje cells do and may have vestibular sensitivity as well. Like our "hybrid" units, such Purkinje cells did not add the various response components lin-
early (36). Finally, floccular mossy fibers with eye velocity and eye position discharge patterns similar to those shown in Fig. 2, A and B are encountered infrequently. The relative paucity of floccular input elements with discharge patterns characteristic of DLPN cells is consistent with the relatively weak projection of the pontine nuclei to the flocculus (19).

Projections from the DLPN also reach the cerebellar vermis, where cells have discharge properties similar to those we have reported. For example, some Purkinje cells in lobules VI and VII also respond only to the direction and not to the velocity of a moving background (46). Other vermal Purkinje cells not only respond to background movement but also fire during smooth pursuit of a small moving target in the dark.

In summary, all the information present in the discharge of our various DLPN neurons can be identified in the discharge of either mossy fibers or Purkinje cells in the cerebellum. Furthermore, although injections of HRP into the flocculus also label other pontine areas (e.g., the ventrolateral pontine nuclei), our cursory exploration of these other areas reveals few, if any, cells with discharge properties like those of DLPN cells. We conclude, therefore, that the pontine input to the cerebellum conveys a variety of visual and oculomotor information. How important this pathway is for the putative roles of the flocculus and other cerebellar structures in smooth pursuit and the optokinetic response is unclear, however, since it must be remembered that the bulk of the mossy fibers to the flocculus originate in the vestibular nuclei and surrounding brain stem (19).

Sources of DLPN inputs

The rather wide variety of cell types in the DLPN may reflect a diverse set of input sources. The DLPN of the monkey receives inputs from essentially all of the extrastriate cortex except the frontal pole (3, 12). Three cortical visual association areas, the middle temporal (MT), the middle superior temporal (MST), and the posterior parietal, appear to be particularly attractive sources because the firing patterns of their units and the deficits produced by lesions implicate them in smooth pursuit.

Many features of the discharge patterns of MT and MST neurons are similar to those of visual pursuit DLPN units. MT and MST units often respond to large-field stimuli moving in a particular direction (5, 26, 44, 57); MT and MST direction tuning curves are similar in width to those of DLPN units (1, 8). Also, the receptive fields of MT units range in size from relatively small to the entire tangent screen. When the target is blanked during smooth pursuit, MT units cease firing (18). Unlike DLPN neurons, however, MT units prefer movements of certain velocities, with preferred velocities ranging from 2 to 256°/s (26). Finally, ibotenic acid lesions of small regions of MT (33) affect a monkey's ability to initiate smooth pursuit at normal velocities.

In contrast to the purely visual units in MT, some units in both MST (18) and the posterior parietal cortex appear to have eye movement as well as visual sensitivity (25, 29, 39, 42). Like our pursuit and visual units, one type of unit in MST and posterior parietal cortex discharges in response to large-field background movement and also during smooth pursuit, even when the target is extinguished briefly. Also, the smooth-pursuit and background sensitivities can be in the same or opposite directions. Like our eye position units, another type of parietal unit has a steady firing rate in the dark that increases in an on-direction that can be either horizontal, vertical, or oblique. Finally, lesions of the parietal cortex produce a decrease in smooth-pursuit gain, especially when the lesions are combined with lesions of the frontal eye field (24).

Conclusion

The DLPN contains a variety of different cell types that are active during and before smooth pursuit of a small target. The discharge properties of most of the DLPN unit types could be provided by inputs from the posterior parietal, MT, or MST cortex. Current neuroanatomy suggests that the DLPN projects to the flocculus and the vermis. On the basis of our data, we conclude that the information disseminated to the cerebellum concerns the direction, and, to a lesser extent, the velocity of the impending or ongoing smooth pursuit movement. The diversity of unit types encountered in the DLPN and the complexity of their response component interactions suggest that this nucleus provides more than just visual slip direction and veloc-
ity information to the cerebellum and possibly to other, as yet unidentified, destinations.

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