THE ROLE OF THE FLOCCULUS OF THE MONKEY IN FIXATION AND SMOOTH PURSUIT EYE MOVEMENTS

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SUMMARY

1. Purkinje cell discharges were recorded from the flocculus of monkeys trained to fixate a small visual target and to track the target when moved slowly.

2. A striking feature of Purkinje cell activity during steady fixation was a high rate of tonic discharges with regular interspike intervals. The average discharge rate in the whole population of Purkinje cells ranged from 37 to 145 spikes/sec. The coefficient of variation of the interspike intervals was typically smaller than 0·5 in most units.

3. In 43·9 % of the Purkinje cells, tonic levels of activity changed by more than 20 % of the average background activity with shifts of gaze.

4. In some Purkinje cells, especially in most burst-pause units, discharge rates during steady fixation were proportional to eye positions in one plane, implicating these cells as sources of eye position information to their target cells.

5. When the monkey tracked a sinusoidally oscillating target, the activity of some Purkinje cells was clearly modulated in phase with the eye velocity.

6. In the other Purkinje cells exhibiting smooth pursuit modulation, the activity curve appeared with a phase shift. When these cells were tested with sinusoidal target movements at different frequencies, but with a constant magnitude, the peak firing rates were proportional to the frequencies of the excursions, i.e. the velocities.

7. The flocculus thus provides the oculomotor system with eye position information during fixation and with velocity information during smooth pursuit and participates in the control of oculomotor functions stabilizing retinal images.

INTRODUCTION

The cerebellum appears to be essential for steady fixation and smooth ocular pursuit, since impairments of gaze holding and abnormal pursuit eye movements are known to occur in patients with unilateral cerebellar lesions (Holmes, 1917; Meyers, 1931; Jung & Kornhuber, 1964; Dichgans & Jung, 1974). In hemi-cerebellectomized monkeys, Westheimer & Blair (1973) observed that ocular tracking was practically absent when the animal faced a sinusoidally moving target. These monkeys were also unable to maintain steady fixation of targets presented on the side of the lesion. Similar disturbances in smooth pursuit and the holding of eccentric gaze occurred after ablation of only the flocculus in the monkey (Takemori & Cohen, 1974; Zee,

Yamazaki & Gucer, 1978), although the symptoms were less complete than observed in the hemi-cerebellectomized monkeys.

These clinical and experimental observations would implicate the flocculus in a variety of oculomotor functions stabilizing retinal images. By studying Purkinje cell activity in monkeys trained to fixate a stationary visual target and to track a slowly moving target, the present study has provided a neurophysiological basis for the stabilizing functions of the flocculus. The data will show that the flocculus exerts tonic inhibitory influence on the oculomotor system during steady fixation. The degree of influence changes in relation to points of fixation, thereby providing eye position information to the oculomotor system. When tracking slowly moving targets, the output of the flocculus includes a component of velocity, providing the oculomotor system with the eye velocity information necessary for smooth pursuit eye movements.

METHODS

A total of 513 units, recorded from the flocculus of six monkeys, were identified as Purkinje cells by their characteristic discharge patterns. The basis for identifying Purkinje cell units, and the surgical preparations, experimental conditions, procedures for training monkeys, methods of recording neuronal activity and eye movements with electro-oculograms (e.o.g.s) and anatomical locations of the recording sites are described in the preceding paper (Noda & Suzuki, 1979). In brief, the monkeys were trained to fixate a small spot of red light and maintain fixation of the spot even if it was moved slowly. The dispensing of a juice reward was contingent upon the release of a bar during the brief presentation of a green spot following the red spot period. By presenting the red fixation target at a known position on the screen, it was possible to study discharges of neurones in relation to that particular eye position. By moving the fixation target, changes in neuronal activity could be correlated with smooth pursuit eye movements.

Visual target control unit

The target display unit consisted of an optical system, a set of home-made wave-form and step-function generators, and a programmable control system. The optical system included a light source, an iris, a pair of beam splitters, three pairs of focusing lenses, a pair of electric shutters (Vincent Ass. 26LOBOX5), red and green filters, four front surface mirrors, an optical scanner (MFE, 4-150B), and an image rotator. This iris opening in front of the light source determined the size of the spot on the screen. The beam from the iris was separated by the first beam splitter and each beam was passed through filters, resulting in a red and green beam. The red and green beams were independently interrupted by the electric shutters. The second beam splitter fused the red and green beams into one beam so that they appeared at the same position on the screen. The fused beam was reflected by the optical scanner, which was driven by the set of wave-form and step-function generators. The wave-form generator moved the scanner in a range from 0·1 to 10 Hz sinusoidally or in a zigzag fashion. The direction of the target movement was changed by an image rotator, consisting of a set of three reflecting prisms, whose rotation was controlled by a DC motor connected to a remote control system. The step function generator provided a potential which shifted the target position to one of ten positions arrange at 5 ° steps in a certain orientation which also could be changed by the image rotator. This was used to induce saccades to known positions and to calibrate e.o.g.s. The intervals of the fixation (red spot period) and the reward (green spot period) were controlled by the home-made programmable control system based on a microprocessor. This system not only controlled these intervals but also monitored the responses of the monkey as to correctness, and if a correct response had been made, the solenoid of the rewarding unit was opened. The system also evaluated the percentage of correct trials and correct performance on the part of the monkey resulted in simultaneous (or independent) increases in the fixation interval and decreases in the reward interval. The fixation intervals were randomized so that the monkey could not anticipate the appearance of the green spot. There was a rejection mode in the system that regarded any fast eye movements, detected

from the eye velocity signals resulting from the differentiation of the e.o.g.s, during fixation as a failure and discontinued the trial. This was very useful in training the monkey to maintain steady fixation. Because all the parameters were controlled, the task was always 'reasonably' difficult and required immense vigilance from the monkey.

<div align="center">RESULTS</div>

Discharges of Purkinje cells during fixation

Purkinje cells were identified by the characteristic complex spikes interspersed within tonic discharges of simple spikes. The frequency of complex spike discharges was invariably low in all Purkinje cells in the flocculus, appearing on average once every second. Because of such a low frequency, complex spikes did not contribute significantly to quantitative analyses and, therefore, were not included in the statistical analyses. In the following description, Purkinje cell activity refers exclusively to simple spike discharges.

When the monkey looked spontaneously about the random-dot background or fixated a stationary red spot target displayed on the tangent screen, Purkinje cells exhibited high levels of tonic discharges which, in many cases, changed with shifts of gaze. The range of the changes varied from unit to unit. In some units, the level of tonic activity was a linear function of eye position in one plane. These units changed discharge levels markedly with shifts of gaze, covering a range from 20 to 200 spikes/sec. In 43·9 % of the Purkinje cells, tonic level of activity changed more than 20 % of the average background activity. We defined these as position-related units.

Position-related activity changes in three classes of Purkinje cells

The tonic firing level shifted with eye position in all three classes of units: pause, burst-pause, and burst units. Fig. 1 illustrates these shifts in the examples of pause (A), burst-pause (B), and burst (C) units. The behaviours of these classes of units during saccadic eye movements (saccades) have been analysed and described in detail elsewhere (Noda & Suzuki, 1979). In brief, pause units discharged steadily at high tonic rates, but stopped firing abruptly and completely during saccades typically in all directions, as seen in Fig. 1 A. They formed the majority (66·9 %) of the Purknjie cells. Burst-pause units increased firing with saccades in the preferred directions and paused during saccades in the opposite directions (Fig. 1 B). They comprised 12·8 % of the Purkinje cells. Burst units showed bursts with saccades and were found in 20·3 % of the Purkinje cells. Of these 78·6 % showed burst in all directions (Fig. 1 C) and 21·4 % showed burst in only the preferred directions.

Fig. 1 shows examples of the changes in tonic discharges associated with shifts of gaze. The points of gaze during periods of steady fixation are illustrated in the circles at the bottom of the records. The circles repsent the central 30° visual field and have been divided into quadrants by the vertical and horizontal meridians as seen by the monkey. The pause unit (A), while discharging with regular interspike intervals, showed a higher level of tonic discharges with downward shifts of gaze. The burst-pause unit (B) increased tonic activity with changes in eye position to the right. The burst unit (C), on the other hand, increased firing with shifts of gaze to the left.

Position-related Purkinje cells were found in slightly over one third of the pause

units (118/343 units or 34·5%) and in less than half of the burst units (forty-seven out of 104 units or 45·5%). The other pause units (225/343 units or 65·5%) and burst units (sixty-seven out of 104 units or 54·5%) were classed as non-position-related Purkinje cells. In comparison with burst-pause units, it was relatively difficult to establish a simple relationship between firing rates and eye positions for both pause and burst units. In the pause and burst units the relationship was not always linear but higher levels of tonic activity were consistently associated with shifts of gaze in one direction.
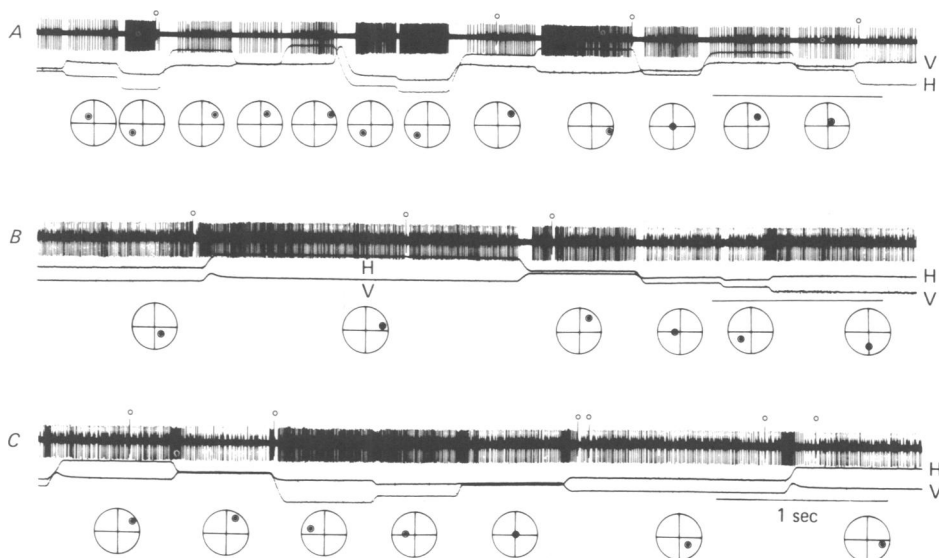

Fig. 1. Examples of discharge patterns of Purkinje cells in the flocculus during saccadic eye movements. The top trace in each record is unit discharge. Complex spikes are marked with circles. The middle two traces are horizontal (H) and vertical (V) electro-oculograms (e.o.g.s). Upward deflexions in the horizontal and vertical e.o.g.s represent eye movements to the right and up, respectively. Circles at the bottom represent central 30° visual field, indicating the eye position in each fixation. *A*, pause unit. Note that the pause appeared with saccades in all directions. The cell showed different levels of tonic activity during fixation, showing a higher level with downward shift of gaze. *B*, burst-pause unit. The cell showed a burst with a saccade to the right and a pause with a saccade to the left. The level of tonic activity increased with a shift of gaze to the right. *C*, burst unit. The cell showed burst with saccades in all directions. The level of tonic activity was higher with gaze shifts to the left. All three units were recorded from the right fluocclus. Time mark: 1 sec.

Discharge rate–eye position relationship

Fig. 2 shows a typical example of a burst-pause unit. As seen in the spike train, the unit showed a burst of spikes with a saccade to the right (contralateral) and a pause in activity with a saccade to the left (ipsilateral). During the periods of fixation the unit discharged with regular interspike intervals. Discharge frequency was linearly related to horizontal eye position in the preferred direction (preferred fixation) to the right. Such a relationship is illustrated in the scattergram where the discharge rate is
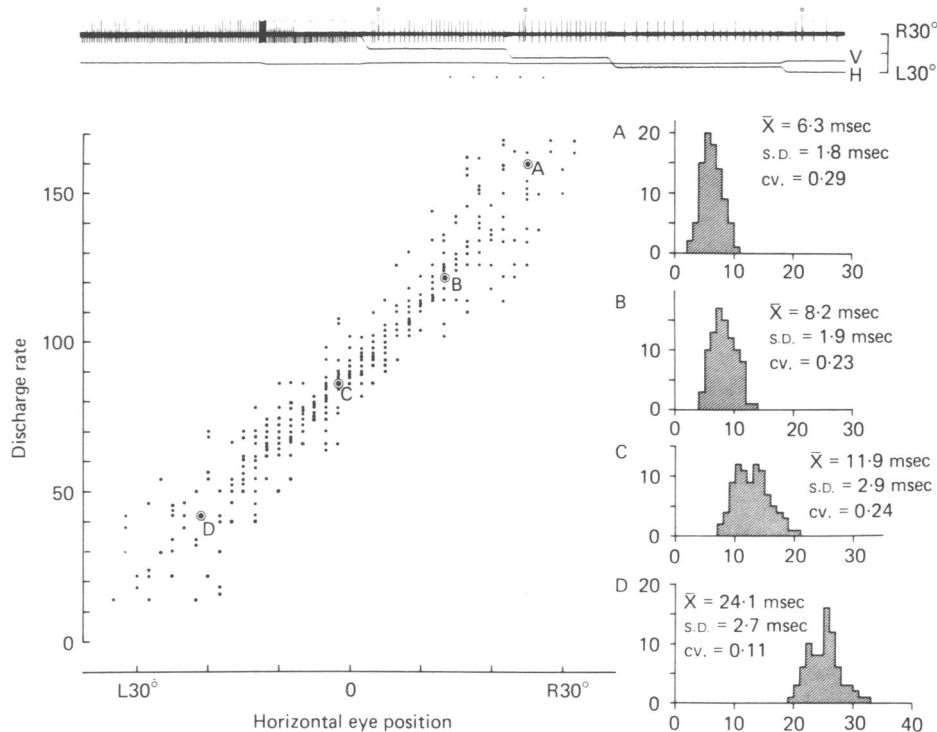
Fig. 2. An example of Purkinje cells changing the level of tonic activity with static eye position in the horizontal plane. The top record shows a spike train with horizontal (H) and vertical (V) e.o.g.s. Complex spikes are marked with circles. Calibration for the horizontal e.o.g. is shown at the right. Time mark dots are at 10 Hz. The scattergram shows the relationship between discharge rate and horizontal eye position. Discharge rates were evaluated by counting simple spikes in consecutive 100 msec periods. When a fixation was discontinued in less than 1 sec, discharge rate was evaluated from the average of available periods. Histograms on the right show distributions of interspike intervals constructed from the data points shown in the scattergram. Note small values of coefficient of variation. $\bar{X}$, mean interspike interval; s.d., standard deviation around the mean; c.v., coefficient of variation (standard deviation/mean).

shown as a function of eye position in the horizontal plane. The regularity of the interspike intervals of the unit during steady fixation can be appreciated by inspection of the spike train. To obtain some quantitative measure of this variability and to determine whether the degree of regularity could be related to either activity level or eye position, standard deviations of the interspike intervals at various activity levels were determined. The four interspike interval histograms on the right show the results of the analyses, representing the four points shown in the scattergram. As seen by the values of the coefficient of variation (standard deviation/mean), the standard deviations were less than 30 % of the average interspike intervals at these activity levels. The coefficient of variation at the point D was as small as 0·11, indicating that the intervals became more regular when discharges slowed down.

As exemplified by the unit in Fig. 2, all burst-pause units recorded in the flocculus exhibited changes in their tonic level of activity in relation to eye position. The

positions associated with higher tonic discharge levels (preferred fixation) were found
to be in the same direction associated with the burst responses to saccades. Examples
of preferred fixations were found for practically all saccade directions. Among the
sixty-six units, they were ipsilateral to the recording side for twenty-five units,
contralateral for twenty-four units, upward for eight units, downward for five units
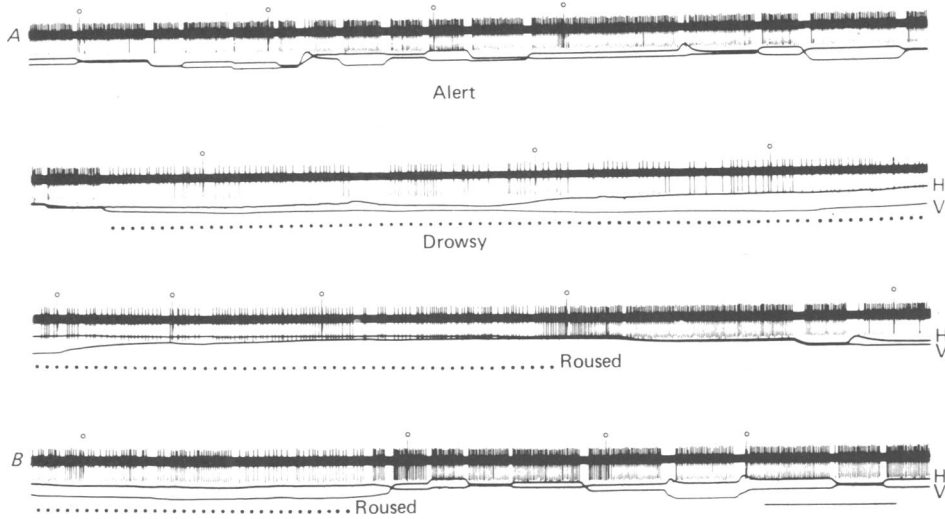and diagonal for the remaining four units.

Fig. 3. Changes in discharges of a Purkinje cell during static and drifting eye position.
The upper three records (*A*) are continuous and the bottom record (*B*) shows another
period of drowsiness found in the same unit. Spike trains are recorded with horizontal
(H) and vertical (V) e.o.g.s. Complex spikes are marked with circles. When the monkey
was alert and making frequent eye movements the cell showed a considerably high level
of regular firing during static eye position and ceased firing during saccades. With a
behavioural shift of the animal into a drowsy state, as indicated by slow drifts in eye
position, the firing of the cell decreased and became irregular. As soon as the animal
was roused, the regular firing resumed and the pause during saccades became evident.

The regularity in Purkinje cell discharges during fixation

The striking feature of Purkinje cell activity during steady fixation was the high
rate of tonic discharges with regular interspike intervals. This was consistently
observed in both position-related and non-related units. In 100 position-related
units, arbitrarily chosen, the average discharge rate ranged from 67 to 136 spikes/sec
with a group mean of 104 spikes/sec, evaluated in the primary position of the gaze
(a central fixation point in the horizontal plane through the eyes). In 100 non-position-
related units, the frequencies ranged from 37 to 145 spikes/sec, with a group mean of
86 spikes/sec. Regardless of the level of the activity, all Purkinje cells showed
regular discharges during steady fixation. The coefficient of variation of the inter-
spike intervals was typically smaller than 0·5 in most Purkinje cells.

The degree of regularity in the intervals appeared to reflect the degree of stability
in eye position during fixation. This is indicated by the observation that the regular
tonic discharges were no longer maintained when the eyes began to drift aimlessly in

association with lowered alertness. Fig. 3 shows the behaviour of a non-position-rerelated Purkinje cell, when the monkey went through periods of lowered alterness. When the monkey looked spontaneously about the random-dot background, the cell discharged tonically during the periods of fixation.

The cell paused during saccades in all directions. The discharge rate during fixation was fairly constant, ranging from 104 to 128 spikes/sec with a mean of 115 spikes/sec. The interspike intervals during the same period were also very regular, showing small coefficients of variation in the intervals (0·13–0·25). When the behavioural state shifted into the drowsy state, as indicated by the aimless slow drift in the e.o.g.s. the firing rate of the cell markedly decreased and the interspike intervals became irregular. The discharge rate during this period was variable, ranging from 19 to 51 spikes/sec with a mean of 34 spikes/sec. The interspike intervals were also irregular, with large coefficients of variation, ranging from 1·11 to 1·90. When the monkey was roused, the tonic high rate of discharges with regular interspike intervals resumed.

The regularity in the interspike intervals was an indication of active maintenance of fixation. This is apparent when the behaviour of the unit in Fig. 3 is compared with that of the position-related Purkinje cell in Fig. 2. In the interspike interval histograms on the right of Fig. 2, the coefficients of variation (the reciprocals of the means) at discharge rates of 159, 122, 84, and 42 spikes/sec were 0·29, 0·23, 0·24, and 0·11, respectively. On the other hand, the coefficients of variation of the unit activity in Fig. 3, discharging at 115 spikes/sec (alert) and 34 spikes/sec (drowsy) were 0·19 and 1·5, respectively. In the alert state, although the discharge rate decreased with shifts of gaze, the regularity of firing was maintained. This is because the eyes were actively held, even for fixation points in non-preferred directions. When the monkey was drowsy, however, the reduced activity would simply reflect the lowered activity due to the relief from the active process involved in maintaining steady eye position.

Velocity component in Purkinje cell activity

Fig. 4 shows the firing pattern of a typical Purkinje cell during sinusoidal smooth pursuit, elicited by the tracking of a visual target moving slowly in the horizontal plane. The discharge displayed a consistent periodic modulation which reached peak firing rates during ipsilateral smooth pursuit (toward the recording side) and minimum firing rates during contralateral smooth pursuit. Fig. 4*B* shows the changes in the instantaneous discharge rates for 30 cycles of smooth eye movements.

The Purkinje cell activity showed relatively smooth sinusoidal modulations in phase with the eye velocity curve (with $\frac{1}{2}\pi$ radian shifts from the eye position curve, horizontal e.o.g.). Analogous discharge patterns observed during sinusoidal smooth pursuit eye movements were analysed in a total of 162 Purkinje cells which showed phasic responses to saccades. The peak firing rate appeared during ipsilateral smooth eye movement in sixty-nine units (42·6 %) and during contralateral smooth pursuit in fifty-nine units (36·4 %). In fourteen units (8·6 %) the Purkinje cell activity curve was in phase with the eye position curve. In the remaining twenty units (12·3 %) no modulation was observed.

In Purkinje cells wherein the activity modulation did not appear in phase with the

eye velocity curve, a non-velocity component may be reflected in the modulation of the activity. Regardless of the origin or the proportion of such a non-velocity component, a component related to eye velocity could be demonstrated in most Purkinje cells whose activity was modulated sinusoidally during tracking. Fig. 5 shows such an example. The original record in *A* shows the discharge pattern of a Purkinje cell which paused during saccades. It is interesting to note that firing stopped with a saccade even in the same direction (ipsilateral) as the increased activity during smooth pursuit, as indicated with an arrow. This would indicate that the neuronal mechanism producing the sinusoidal modulation in the activity of the Purkinje cell must be independent of that producing the complete silence in the same cell during saccades.
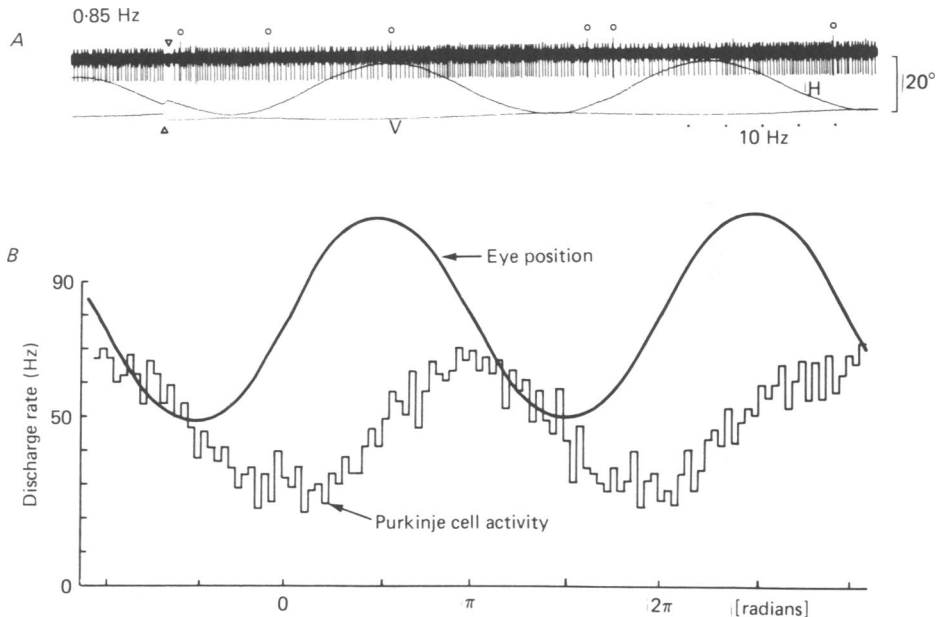

Fig. 4. Changes in Purkinje cell activity during smooth pursuit eye movements tracking a visual target moving sinusoidally in the horizontal plane. The sinusoidal excursion covered $\pm 10°$ of visual field at 0·85 Hz. *A*, original recordings of spike train, horizontal (H) and vertical (V) e.o.g.s. Complex spikes are indicated by circles. The cell ceased firing during a saccade, as indicated by triangles. Time mark dots are at 10 Hz. *B*, instantaneous discharge rate evaluated from 30 cycles of smooth eye movements in the same cell. The sinusoidal modulations of cellular activity, tested at different frequencies from 0·1 to 1·0 Hz, have been normalized in radians. Eye position represents the changes in the horizontal plane and corresponds to the horizontal e.o.g.

The graphs in Fig. 5*B* show the changes in the Purkinje cell activity during smooth pursuit, at frequencies from 0·3 to 0·9 Hz. The Purkinje cell activity at each frequency was evaluated from 30 cycles of smooth pursuit eye movements. The activity at all seven frequencies underwent roughly sinusoidal modulation and reached a peak which lagged the peak of eye position by approximately $\frac{1}{4}\pi$ radians. The phase lag, in terms of radians, increased slightly with lower frequency sinusoidal excursions. For example, the phase lag increased from $\frac{1}{4}$ to $\frac{3}{10}\pi$ radians as the frequency was
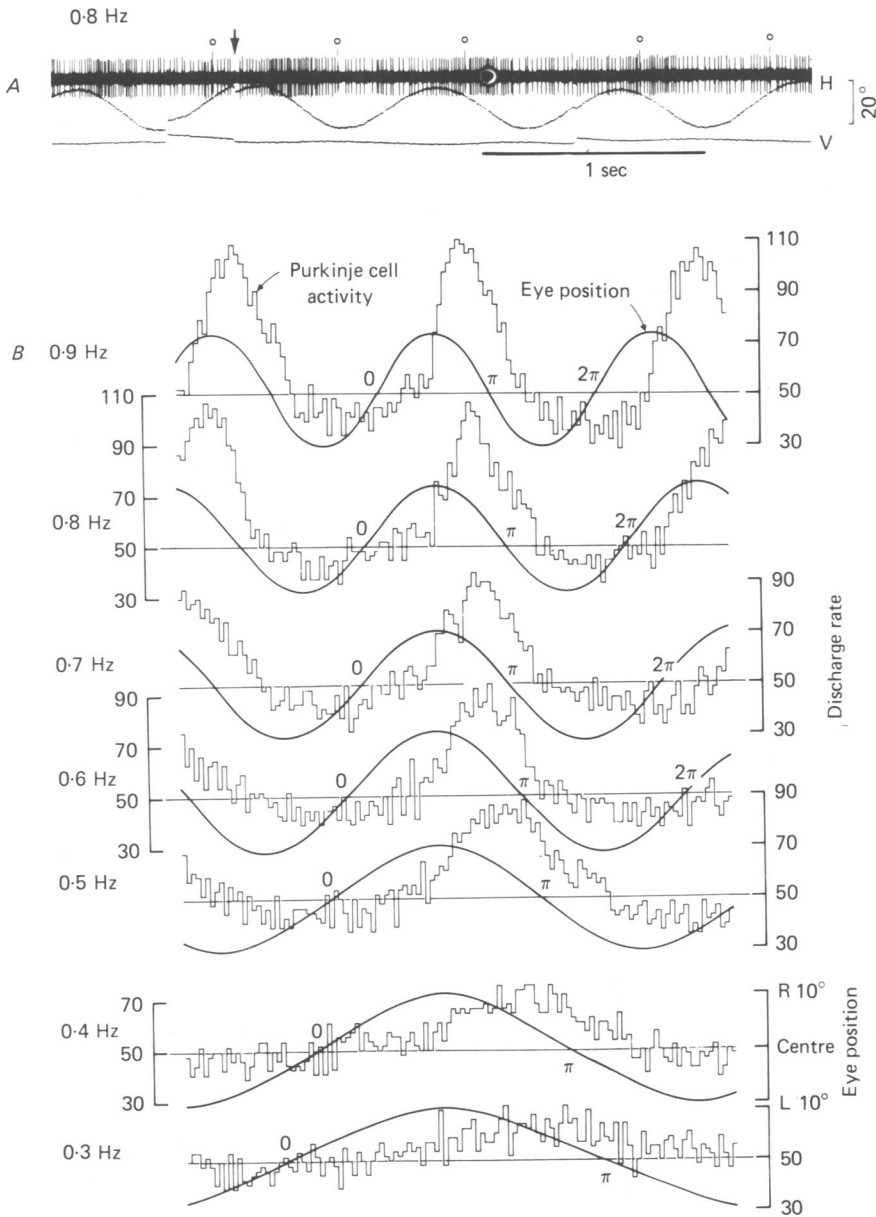
Fig. 5. Changes in Purkinje cell activity during smooth pursuit at frequencies from 0·3 to 0·9 Hz. The peak-to-peak eye position was kept constant (±10°). *A*, original records of spike train, horizontal (H) and vertical (V) e.o.g.s. Complex spikes are indicated by circles. Note that firing stopped with a saccade even in the same direction (ipsilateral) as the increased activity during smooth pursuit, as indicated with an arrow. *B*, instantaneous discharge rate of the same Purkinje cell evaluated at each frequency from 30 cycles of smooth pursuit eye movements.

lowered from 0·9 to 0·5 Hz. On the other hand, the peak activity increased mono-
tonically with higher frequency excursions of the eyes. As the peak-to-peak eye
position remained constant ($\pm 10°$), an increase in the frequency of sinusoidal smooth
pursuit was associated with a larger value of the maximum eye velocity. The peak
firing rates at eye movement frequencies 0·3, 0·5, 0·7, and 0·9 Hz were 65, 80, 90, and
110 spikes/sec, respectively. Whereas, the maximum eye velocities at these fre-
quencies were 19, 31, 44, and 57 deg/sec, respectively. Thus, the modulation of the
Purkinje cell activity involved a component of firing rate that was related to eye
velocity. In summary: the flocculus of the monkey contains Purkinje cells responsive
to eye position during steady fixation and those responsive to eye velocity during
smooth pursuit eye movements.

DISCUSSION

(1) *Tonic influence of the flocculus on the oculomotor system*

A striking feature of Purkinje cell activity of the flocculus was the high rate of dis-
charges with regular interspike intervals during steady fixation. This would imply
that the flocculus exerts a continuous inhibitory effect upon supranuclear oculomotor
centres during fixation. Oculomotor symptoms in patients with an acute lesion of a
cerebellar hemisphere include conjugate ocular deviation towards the opposite side
and gaze nystagmus towards the side of the lesion (Meyers, 1931; Fisher, Picard,
Polak, Dalal & Ojeman, 1965; Nashold & Slaughter, 1969; Dichgans & Jung, 1974).
Although involvement of brain-stem lesions cannot be excluded in these clinical
cases, the assumption of a cerebellar origin of the oculomotor symptoms has been
supported by leasion experiments in animals. Contralateral gaze deviation and ipsi-
lateral gaze nystagmus were observed in hemi-cerebellectomized monkeys (Botterell
& Fulton, 1938; Westheimer & Blair, 1973; Zee et al. 1978). The contralateral gaze
deviation may be explained as the result of removal of the floccular inhibitory control
and the consequent imbalance occurring between the steady-state outputs of the
vestibular nuclei on both sides (Cogan, 1956; Westheimer & Blair, 1974). It has been
shown that the fluoccular Purkinje cells inhibit neurones in the medial vestibular
nucleus, which in turn inhibit ipsilateral abducens neurones and excite ipsilateral
oculomotor neurones innervating the medial rectus muscles (Ito, 1977). The removal
of floccular inhibition on one side would result in stronger inhibition of lateral rectus
and increased excitation of medial rectus motoneurones due to disinhibition of the
medial vesticular nucleus of the same side and, consequently, contralateral gaze
deviation occurs.

An analogous interpretation may be given for the gaze nystagmus beating towards
the side of the lesion. The continuous inhibition, originating in the flocculus, of
supranuclear oculomotor centres prevents them from initiating uncontrolled eye
movements. A sufficient condition for the occurrence of gaze nystagmus is a de-
ficiency in the stable positioning of the eyes. The eyes will tend to slip back towards a
neutral position each time a gaze directed away from this position is attempted.
Small saccades will be executed in an attempt to refixate on the target. An important
function of the flocculus, therefore, is to maintain steady fixation on a target.
Floccular dysfunction may also contribute to oculomotor symptoms of cerebellar

disorders other than gaze nystagmus, such as opsoclonus in myoclonic encephalo-pathy, pendular mystagmus in multiple sclerosis and ocular flutter, all of which are considered to be manifestations of fixation disturbances.

It was shown in the present study that the regularity in the tonic Purkinje cell discharges is an indication of the degree of stability of eye position. An aimless slow drifting of eye position was characterized by an irregularity of discharges of Purkinje cells. It was shown statistically that unstable fixation is always associated with a larger coefficient of variation in the interspike intervals. This observation provides a piece of neurophysiological evidence for Robinson's suggestion (1970) that the holding of the eyes in a certain position is just as much of an active process as movement and, in fact, displays a greater degree of fine motor control than do the eye movements.

(2) Eye position information in the flocculus

For holding the eyes in a certain position, the oculomotor neurones need tonic inputs from a structure whose activity is, in turn, controlled by visual, vestibular and efference-copy information concerning eye position. The possibility of cerebellar involvement in stabilizing eye positions has been implicated by ablation studies in the cat (Carpenter, 1972; Robinson, 1974) and in the monkey (Westheimer & Blair, 1973; Ritchie, 1976). The precise locus of this function, however, has not yet been determined. Kornhuber (1971) proposed the deep cerebellar nuclei as a probable site of position control. The observation of Ritchie (1976) that the removal of lobuli V, VI and VII of the vermis resulted in saccadic dysmetria strongly suggests the involve-ment of the vermal aresa in the holding function.

The present study has shown that the output of the flocculus is related to informa-tion concerning eye position. In some Purkinje cells, the tonic levels of discharges during intersaccadic periods were proportional to eye positions in a certain plane. Such position-related tonic discharges of the Purkinje cells indicate a role of the flocculus in maintaining eye position, especially in eccentric gaze. Since the tonic changes occur in complete darkness, without changes in head position, the position information must arise in some structure which produces eye movements. There is no evidence to eliminate an input from extraocular muscle proprioceptors. This possi-bility, however, seems unlikely because the bursts or pauses preceded eye movements and there is no known anatomical substrate for such an input to the flocculus.

The position information becomes crucial when fixation has to be maintained in the absence of visual cues. In darkness, animals without the flocculus have difficulty in maintaining eccentric gaze, because position information is no longer available to the oculomotor system. Westheimer & Blair (1974) observed in hemi-cerebellectomized monkeys, with or without removal of the vermis, that there was a constant smooth conjugate drift of the eyes away from the side of the lesion when tested in the absence of a patterned visual stimulus. The significant role of the flocculus in maintaining steady eye position has been also shown in the rabbit. Barmack (1977) states that climbing fibre inputs through the olivo-cerebellar pathway provide visual cues which are useful for preventing aimless drifting of gaze. The visual inputs through the climbing fibre system, however, appear to be less prominent in the monkey. From our studies, it appears that the flocculus is involved in maintaining eye positions not only in the horizontal plane but also in the vertical plane. The observations support-

ing this notion were twofold. First, almost equal numbers of units were found in two groups exhibiting position-related tonic activity in relation to either horizontal or vertical planes. Secondly, in two monkeys in which a small discrete lesion was accidentally made in the left flocculus by recording micro-electrodes, we transiently observed a smooth conjugate drift, upward in both cases, followed by a quick return to the primary gaze position. The amplitude of the drift varied from time to time and seemed to depend on the level of alterness. The drift was dominant only when tested in darkness and was suppressed by a visual pattern.

Saccadic dysmetria is also a common oculomotor symptom of cerebellar system disorders. The position information of floccular Purkinje cells appears to contribute to the proper adjustment of saccade magnitudes with reference to the starting eye position. Evidence is growing for the notion that a correct saccade must depend upon a combination of visual information concerning the retinal error (the distance between the image of an object and the fovea) and an efference copy (corollary discharge) of eye position derived from internally monitored commands to the oculomotor nuclei (Ritchie, 1976; Zee, Optican, Cook & Robinson, 1976). For example, in the dark one can make accurate saccades to either a remembered visual target or to a sound source, where there is no retinal error information. In such cases, the efference copy is used to compute the location of object in space. One such source of eye position information for the saccadic system may be the burst-pause Purkinje cells of the flocculus that discharge in proportion to eye position. Defects of this function of the flocculus may result in saccadic dysmetria.

(3) The role of the flocculus in smooth pursuit

It has been shown that a primary role of the flocculus is to sustain the holding (fixation) function of the oculomotor system. Selected images are thereby maintained on the fovea and stabilized for detailed visual processing. In this case, the tonic activity of position related Purkinje cells furnishes the oculomotor system with eye position information required for stable fixation. On the other hand, when fixating a slowly moving target, the oculomotor system needs to move the eyes at a rate which will nearly match the velocity of the moving target.

In the present study, in accord with previous studies (Miles & Fuller, 1975; Lisberger & Fuchs, 1978), it has been demonstrated that Purkinje cell discharges include an eye velocity component. This velocity component of the Purkinje cell activity was clarified in two ways. First, while the monkey tracked a sinusoidally oscillating target, we observed that the activity was clearly modulated in phase with eye velocity (the derivative of eye position, namely, a $\frac{1}{2}\pi$ radians phase shift from the e.o.g.) (Fig. 4). Secondly, when the monkey tracked the target oscillating sinusoidally at different frequencies, but with a constant magnitude, the peak firing rates were proportional to the frequencies of the excursions, i.e. the velocities (Fig. 5).

When the monkey makes a smooth pursuit eye movement at a peak velocity less than 50 deg/sec, the eye movement signal (horizontal e.o.g.) matches almost perfectly the target movement signal. A question now arises as to whether the modulation in the Purkinje cell activity (the velocity information) reflected the eye movement itself (eye velocity) or the movement of the target (target velocity). Miles & Fuller (1975) are of the opinion that target velocity is the primary determinant of the

modulation. They observed similarly prominent modulation even when the target and the head were oscillated together, hence in the absence of eye movement. When the fixation target was stationary, merely oscillating the monkey failed to produce the modulation, albeit clear oscillation of the eyes due to the vestibulo-ocular reflex occurred. Lisberger & Fuchs (1978), on the other hand, are of the opinion that the modulation reflects eye velocity and is due to a corollary discharge.

In accordance with the observation of Lisberger & Fuchs (1978), in the majority of Purkinje cells the cyclic modulation of activity appeared only in association with eye movements and merely oscillating the visual background failed to produce any consistent modulation. The degree of the modulation observed in these cells during tracking of the red spot in darkness was almost identical with that observed during tracking in the presence of the visual background. In a small population of Purkinje cells, however, similar cyclic changes in activity were observed during fixation of a stationary target while the background was moved sinusoidally (H. Noda & D. A. Suzuki, unpublished data). Since there were no measurable eye movements, the primary determinant of the changes in activity of these Purkinje cells was the velocity of the retinal image slip. To different degrees, therefore, both sensory and oculomotor information aid the flocculus in the control of eye movements.

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