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THE ROLE OF THE FLOCCULUS OF THE MONKEY IN SACCADIC EYE MOVEMENTS

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SUMMARY

1. Purkinje cell discharges were recorded from the flocculus of monkeys either spontaneously making saccadic eye movements (saccades) or trained to fixate a small visual target presented on a tangent screen. In the trained monkeys, saccades of known magnitude and direction were induced by changing the position of the fixation target.

2. Among 513 Purkinje cells, 343 units (66·9 %) paused during saccades in all directions (286 units) or in particular directions (57 units). In most units, there were intimate temporal relationships between the beginnings of pauses and saccades, and between the ends of pauses and saccades.

3. The pause in activity preceded saccades by an average of 9·6 msec, with a maximum lead time of 30 msec. In a fraction of the units (7·6 %), the pause started after the onset of saccades.

4. There were 104 units (20·3 %) which showed bursts during saccades in all directions (eighty-two units) or in particular directions (twenty-two units).

5. In sixty-six units (12·8 %) a burst was associated with saccades in one direction and a pause in the opposite direction.

6. The burst in the burst and burst-pause units preceded saccades by an average of 3·8 msec. There was no significant difference in the lead times between these two groups of units.

7. There was a linear relationship between the duration of the pause in Purkinje cell activity and that of the accompanying saccade. A linear relationship was also seen between the pause duration and the magnitude of saccade.

INTRODUCTION

It has been known for a long time that the vestibulo-cerebellum, especially the flocculus, is intimately related to the control of eye movements (see Precht, 1975 for a review). Remarkable progress has been made in recent years in the understanding of the anatomical substrate for interactions between the flocculus and brain stem oculomotor centres. The flocculus receives inputs through mossy fibres arising in numerous sources in the brain stem including vestibular, perihypoglossal, rapheal, and lateral reticular nuclei and through climbing fibres from the inferior olive (Alley, 1977). Fibres arising in the oculomotor complex and projecting to the flocculus have

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also been demonstrated recently by the horseradish peroxidase technique (Graybiel, 1977; Kotchabhakdi & Walberg, 1977). In return, the flocculus can influence the oculomotor complex disynaptically by way of the vestibular, prepositus hypoglossal, and dentate nuclei. As these nuclei are also reciprocally connected with the reticular formation, the flocculus can also influence the oculomotor complex through multisynaptic routes (references are in Discussion). In spite of a wealth of detailed anatomical information implicating the flocculus in gaze control, little is known of how the flocculus participates in supra-nuclear mechanisms of oculomotor control. In the present study, an attempt has been made to clarify the involvement of the flocculus in the control of saccadic eye movements. The role of the flocculus in stabilizing retinal images during (steady) fixation and smooth pursuit eye movements has been discussed elsewhere (Noda & Suzuki, 1979*a*).

METHODS

Identification of Purkinje cell activity

A total of 1488 units, showing phasic changes in activity associated with saccadic eye movements (saccades), were recorded from the flocculus of six monkeys (*Macaca nemestrina*). From the total, 513 units were identified as Purkinje cells by their characteristic discharges. Two types of spike potentials, namely simple and complex spikes (Thach, 1970), can be recorded from the Purkinje cell (Granit & Phillips, 1956). There is evidence that simple spikes are caused by input coming via mossy fibre granule cell channels, while complex spikes are caused by input from climbing fibres (Jansen & Fangel, 1961; Eccles, Llinás & Sasaki, 1966*a*, *b*). The existence of complex spikes interspersed within tonic spike discharges served to identify a Purkinje cell and the 513 units were chosen on this basis. Although the absence of complex spikes does not necessarily mean that the unit is not a Purkinje cell, units without any evidence of a complex spike were not selected for analysis. Discharge patterns of the majority of the remaining 975 units were similar to those of the identified Purkinje units. A further discussion concerning the identification of Purkinje cell activity has been made in a preceding report (Noda, Asoh & Shibagaki, 1977).

Surgical preparation

The method of single unit recording from alert monkeys through painless immobilization of the head was practically the same as for cats (Noda, 1975). In brief, following a 2–3 week initial training period, the moneky was anaesthetized with sodium thiopental supplemented with a tranquillizer (sernylan, phencyclidine hydrochloride). Electrooculogram (e.o.g.) electrodes were implanted in the zygomatic bones bi-temporally to record horizontal eye position, and above and below the left eye to record vertical eye position. For later insertion of micro-electrodes a stainless-steel recording chamber (bone adaptor, Trent-Wells Inc.) was stereotaxically implanted over the flocculus. Finally, for stabilizing the head, two transverse tubes were placed on the skull, in the horizontal stereotaxic plane, and embedded in dental acrylic cement.

Experimental conditions

After an additional training period of 4–6 weeks, the monkeys were ready to be used for recording. During an experiment a monkey was seated in a primate chair designed to offer a clear view of the central 30° of the visual field. By inserting two pair of bars into the two transverse tubes on the skull, the head of the monkey was affixed to the frame which provided support for the chair. This system resulted in complete immobilization of the head without the application of painful pressure and permitted micro-electrodes to be driven stereotaxically. The animal was placed in a small room facing a window furnished with a rear projection screen. When the animal was placed 55 cm from the screen, it subtended 60° of the visual field horizontally and 45° vertically. The behaviour of the animal was monitored through a closed circuit TV system employing an infra-red TV camera (Hitachi, model HV620U).

Behavioural conditions and training

Four monkeys were trained to press a lever in response to a buzzer. When the animal pressed the lever the sound disappeared and a small spot of red light (0·3–1° in diameter) appeared on the tangent screen. After a pre-programmed interval the spot turned from red to green. The animal learned to fixate on the red light and to release the bar as soon as the red spot changed to green. If the animal succeeded in releasing the lever within a set time (0·3–0·5 sec) after the green light appeared, it was rewarded with a drop of water (or apple juice). The release of the lever before or after the onset of the green light was not accompanied by a reward. Using this procedure, the monkeys were trained to stabilize the image of the red spot on the fovea and to maintain fixation even if the position of the spot was changed. It was possible to induce saccades of known magnitude and direction merely by changing the position of the fixation target. The e.o.g. signals could be easily calibrated, in this manner. The behavioural task requires immense vigilance on the part of the animal and cannot be performed with peripheral vision, hence successful performance could only be achieved if the required eye movements were executed. The remaining two monkeys were not trained and the recordings were made during periods of spontaneous eye movements and fixation.

Recording procedures and data analysis

Tungsten (or steel) micro-electrodes insulated with Isonel 31 were introduced into the cerebellum through the bone-fixed adaptor implanted over the left or right flocculus. Electrodes were guided to 7–12 mm above the ventral surface of the flocculus through a cannula made from a 22-gauge spinal needle and were driven from the tip of the cannula into the flocculus by a hydraulic micro-drive.

Extracellular action potentials were led through an FET preamplifier to a conventional amplifier with a band pass of 35–10 kHz and displayed on an oscilloscope. After transformation by a Schmitt trigger which changed spikes into pulses of 0·5 msec in duration, the signals were fed into one channel of a polygraph. Simultaneously with the spike train, the following information was recorded on the other seven channels of the polygraph: (1) instantaneous discharge rate, (2) horizontal and (3) vertical e.o.g.s, (4) horizontal eye velocity signals, (5) target position signals, (6) background movement signals and (7) behavioural task information (periods of red and green and reward signals). The data were continuously monitored on the polygraph and when the unit activity was related either to saccades or to eye position all signals were recorded on magnetic tapes for later detailed analysis, using a 14-channel magnetic tape recorder (Ampex FR 1300). Unit activity and voice annotations were directly recorded on channels with bandpass of 50–10 kHz, while the other signals were recorded on separate FM channels (bandpass DC to 628 Hz) at a tape speed of $1\frac{7}{8}$ in./sec. The tape-recorded data were later photographed at a film speed of 5 or 10 cm/sec and latencies were measured with the aid of a photographic enlarger. Statistical computations were performed by utilizing the Campus Computing Network of the University of California, at Los Angeles.

Recording sites

Recording sites were anatomically reconstructed with reference to a micro-electrode track in the centre of an active zone where Purkinje cells exhibiting saccade related activity were located. The anatomical locations of a small number of units were determined directly. The central track was identified by the spot resulting from the Prussian blue reaction to deposited iron. By employing 'Starr' guides (Trent-Wells Inc.), which permitted sampling of cylindrical volumes at finite radii of 0·25, 0·5, 0·75, 1·0, 1·5, 2·0 and 2·5 mm, we were able to record from numerous tracks within a column of 5 mm in diameter. When the bone-fixed adapter was oriented correctly toward the flocculus we found the active zone in a discrete volume which was 2–3 mm in diameter and 1–3 mm in vertical depth. Even with the aid of a stereotaxic atlas (Winters, Kado & Adey, 1969), however, it was often difficult to place the adapter so that the central track was oriented correctly toward the flocculus. Pilot recordings were implemented in the search for the active zone and if the central track was found not to be directed toward the flocculus, we re-implanted the adapter, referring to the map of positive electrode tracks wherein saccade-related unit activity was observed. In the first two monkeys, histological confirmation of recording sites indicated that only the floccular units paused with saccades and changed tonic levels of activity

with shifts of gaze. We therefore did not try to identify all of the individual recording sites. Instead, by finding the central track, we could reconstruct the sites of recorded units with the help of the records of depth readings and of co-ordinate positions within the adapter. Nine locations where the central tracks were determined for five monkeys are shown in Fig. 1. We are still conducting experiments on the sixth monkey.

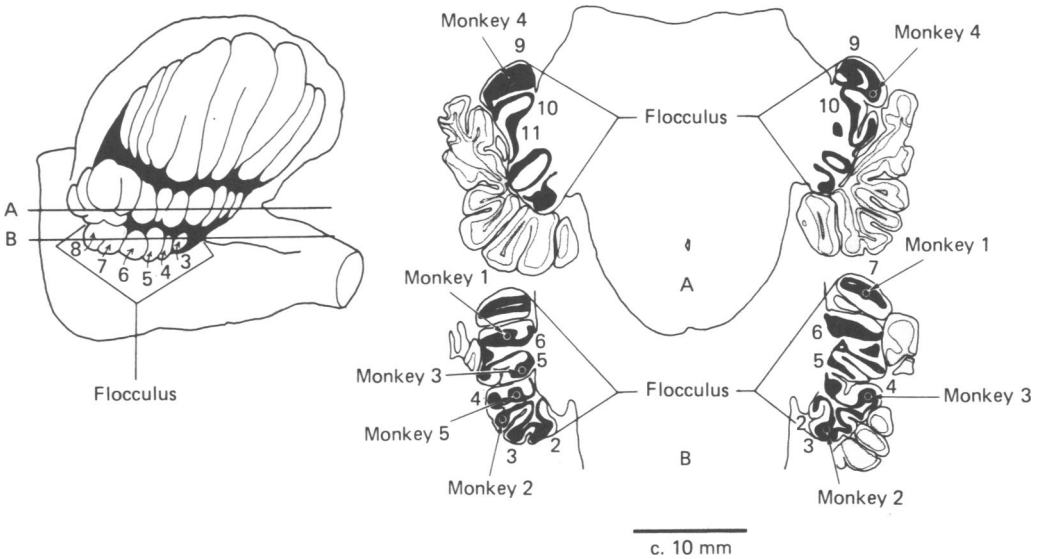

Fig. 1. Left: lateral aspect of the cerebellum, indicating the levels of the horizontal planes through the flocculus. Right: anatomical locations of the centre of recording sites verified in nine flocculi of five monkeys. Units were recorded in each preparation within 1·5 mm from the centre. Anatomical figures were constructed with reference to the atlas of the cerebellum of the rhesus monkey by Madigan & Carpenter (1971).

RESULTS

(1) *Discharges of Purkinje cells in the flocculus*

In response to saccadic eye movements (saccades), most Purkinje cells in the flocculus, identified by their characteristic complex spikes, showed phasic changes in activity. Purkinje cells lacking responses to saccades were not recorded. Such cells might have been the ones responsive only to head movements, as observed by Miles & Fuller (1975) and Lisberger & Fuchs (1978). In our experiments, however, head movements had been completely eliminated in order to minimize the influence of vestibular inputs to the flocculus. Therefore cells which might have been exclusively related to vestibular inputs, and not to eye movement signals, could not be sampled.

Simple spike discharges. During periods of fixation, Purkinje cells discharged simple spikes at a relatively high rate, which in many cells changed with shifts of gaze. The level of tonic firing varied from unit to unit, and even in individual units it was different from one point of fixation to another. For different fixation points, the activity levels in some cells changed from 20 to 200 spikes/sec. Regradless of such variability, there were common features in the discharges of the Purkinje cells. For example, all the 513 Purkinje cells analysed were spontaneously active. No unit showed an average activity, evaulated from at least twenty periods of fixation, lower

than 15 spikes/sec. In the majority of the cells (451/513 units or 88 %), the over-all level of activity fell in a range between 30 and 150 spikes/sec. Furthermore, no cell became completely silent for any periods of fixation which were longer than one second. This was true even when the gaze was in the non-preferred direction.

Complex spike discharges. The frequency of complex spike discharges was invariably low in all Purkinje cells, ranging from 0·05 to 5 discharges/sec. The probability of their appearance was higher during saccades, although their temporal relationship with the onset or end of saccades was inconsistent. They appeared at any time during the pause of activity in the Purkinje cells. An account of the temporal relationship, together with a description of the behaviour of climbing fibre units, has been given elsewhere (Noda & Suzuki, 1979*b*). Under our experimental conditions, complex spike discharges occurred with greater probability during periods when simple spike activity decreased. This was in agreement with the observations made in the Purkinje cells of the monkey flocculus (Lisberger & Fuchs, 1978) and in other areas of the cerebellar cortex (Thach, 1967; Mano, 1970) of alert monkeys. Because of such low discharge frequencies we did not attempt a detailed quantitative analysis of complex spike discharges. The cellular activity in the following descriptions refers only to the simple spike discharges of the Purkinje cells.

(2) *Types of Purkinje cell responses to saccades*

Based on the phasic changes in activity during saccades, we distinguished three major classes of Purkinje cell units; pause, burst, and burst-pause units. These saccade related activity changes were not due to visual inputs, which might arise in the retina during transient excitations by saccades, as they persisted even in complete darkness. Typical examples of each class of cells are shown in Fig. 2.

Pause units. The example of a pause unit (Fig. 2*A*) shows steady activity during fixation but cessation of discharges slightly before and during saccades in all directions. The maintained firing during periods of fixation increased with downward shifts of gaze. This class of cells was the most frequently encountered in the flocculus. Of the 513 units identified as Purkinje cells, 343 units (66·9 %) were pause units. Most pause units (286/343 units or 83·4 %) ceased firing completely during saccades in all directions. While the remaining fifty-seven pause units (16·6 %) either partially decreased activity or ceased firing in association with saccades in particular directions.

Burst units. The discharge rate of burst units increased abruptly, starting slightly before saccades, as seen in the example of Fig. 2*C*. This class of cells was less frequently encountered in the flocculus than pause units. We recorded 104 burst units which comprised 20·3 % of the Purkinje cells. The majority of the burst units (eighty-two out of 104 units or 78·6 %) increased discharges with all saccades, while the remaining twenty-two burst units (21·4 %) showed a burst only with saccades in their preferred directions.

Burst-pause units. As the example of Fig. 2*E* shows, burst pause units were characterized by a maintained discharge related to static eye position and a phasic change in activity during saccades. They showed bursts during saccades in some directions and a higher tonic level of activity during the subsequent period of fixation. A linear relationship was found between firing rate and eye position in most burst-pause units (sixty out of sixty-six units or 91 %; Noda & Suzuki, 1979*a*). This class

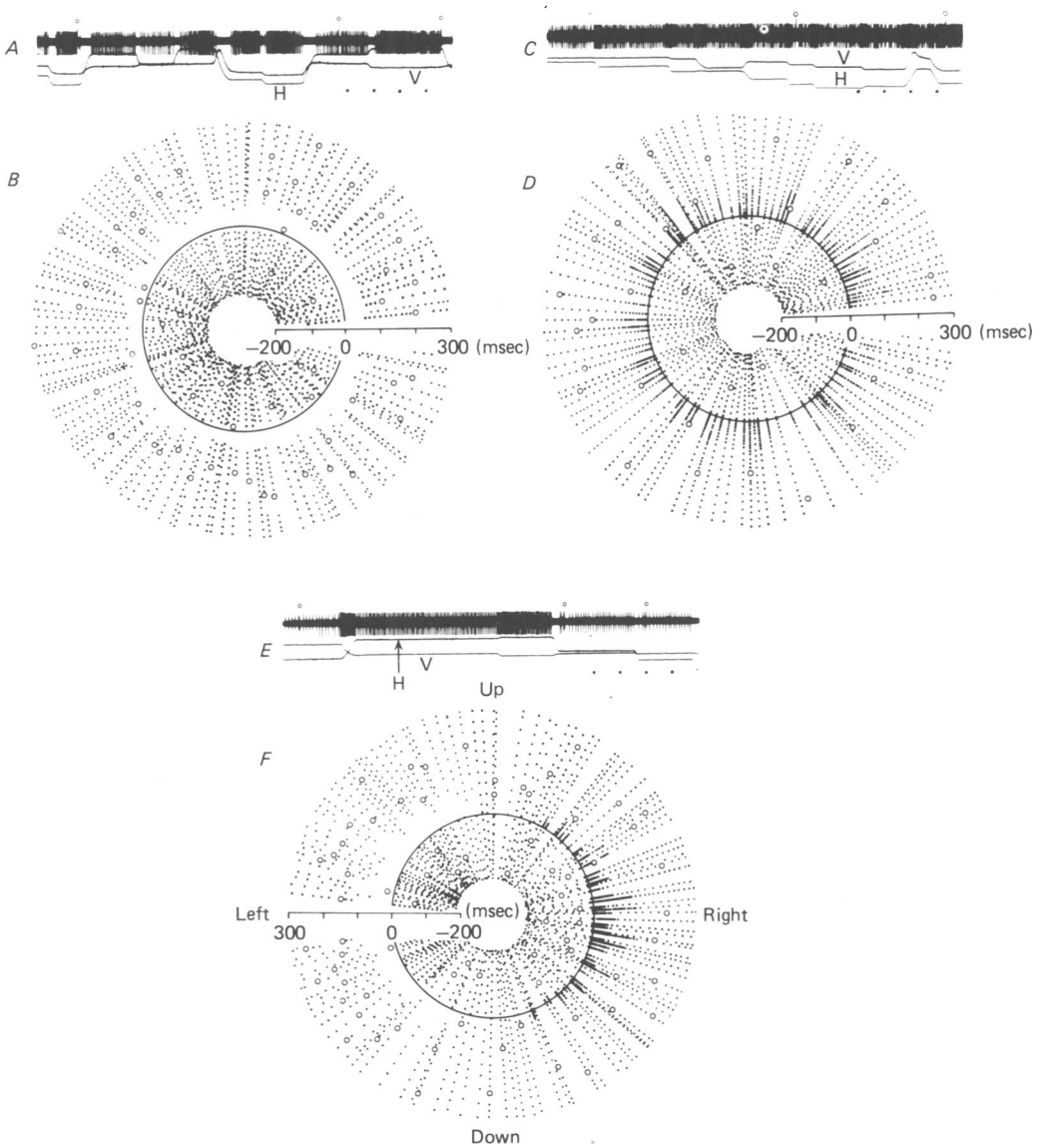

Fig. 2. Discharge patterns of Purkinje cells of the monkey flocculus during spontaneous eye movements. Purkinje cell discharges are characterized by complex spikes interspersed within tonic simple spike discharges. *A*, discharge pattern of an omni-pause Purkinje cell. *B*, polar raster for the unit in *A*, illustrating pauses in unit activity with saccades in all directions. Simple spikes (dots) and complex spikes (open circles) are displayed on the corresponding radii, which represent the directions of eye movements. The spike trains were sampled for periods from 200 msec before to 300 msec after the onset of saccades (from the centre to the circumference) and aligned on the circle at time 0. *C*, discharge pattern of a burst cell. *D*, polar raster for the unit in *C*, showing the bursts associated with saccades in every direction. *E*, discharge pattern of a burst-pause cell. *F*, polar raster for the unit in *E*. Note that the cell showed a burst with a saccade to the right (preferred direction) and a pause to the left. The changes in activity were not prominent with up or down eye movements. H and V, horizontal and vertical electro-oculograms (e.o.g.s). Time marks in *A*, *C*, and *E* denote 10 Hz. ●, simple spike; ○, complex spike.

of cells comprised the smallest portion of the Purkinje cell population. We recorded sixty-six burst-pause units which constituted 12·8 % of the Purkinje cells.

Except for the burst-pause units, which showed directional selectivity but comprised only 12·8 % of the Purkinje cells, the majority of the Purkinje cells in the flocculus did not show directional selectivity. Among the pause units (66·9 % of the

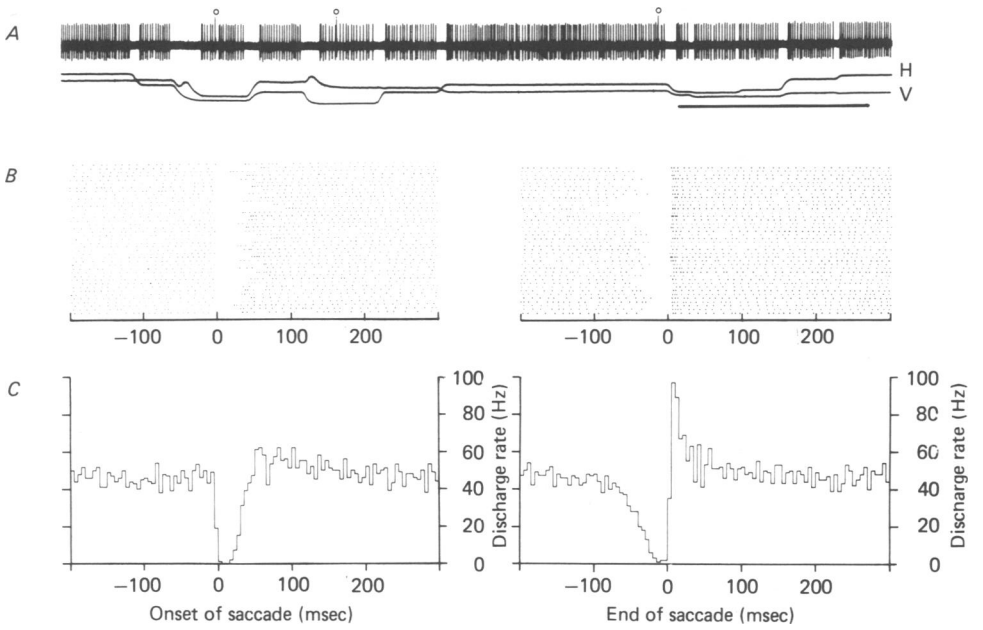

Fig. 3. Time relationship between the onsets of saccade and pause, and between the ends of saccade and pause in a typical pause unit. *A*, original spike train. Time mark: 1 sec. *B*, rasters. The raster on the left was made by sampling spike trains from 200 msec before to 300 msec after the onset of saccades. That on the right covers the same length of time before and after the ends of approximately the same set of saccades. *C*, perisaccadic time histograms showing changes in discharge rate before and after saccades. The left histogram shows the activity changes with respect to the onset of saccade and the right histogram shows them with respect to the end of saccade. Note an increase in activity immediately following the end of saccades.

Purkinje cells), 83·4 % ceased firing for saccades in all directions. Among the burst units (20·3 % of the Purkinje cells), 78·6 % increased activity for saccade in all directions. As a whole, 82·5 % of the Purkinje cells recorded from the flocculus did not show directional selectivity. Fig. 2*B* and *D* illustrate the lack of directional selectivity in pause and burst units, respectively. In contrast, the directional selectivity of a burst pause unit is apparent in the polar raster of Fig. 2*F*. Simple spikes (dots) and complex spikes (open circles) found in spike trains associated with saccades are displayed on a circular plot where the radii represent directions of the eye movements. The spikes were sampled from the records 200 msec before to 300 msec after the onset of saccade and aligned on the circle indicating time zero.

The complete cessation of firing or phasic increases in activity, or both, were characteristic of Purkinje cell responses to saccades. Based on combinations of these responses, all Purkinje cells were categorized into one of the three cell classes. Beyond

these major categories, further variations in cell types became apparent when the cells were analysed in more detail according to the temporal relationships existing between the responses and the saccades.

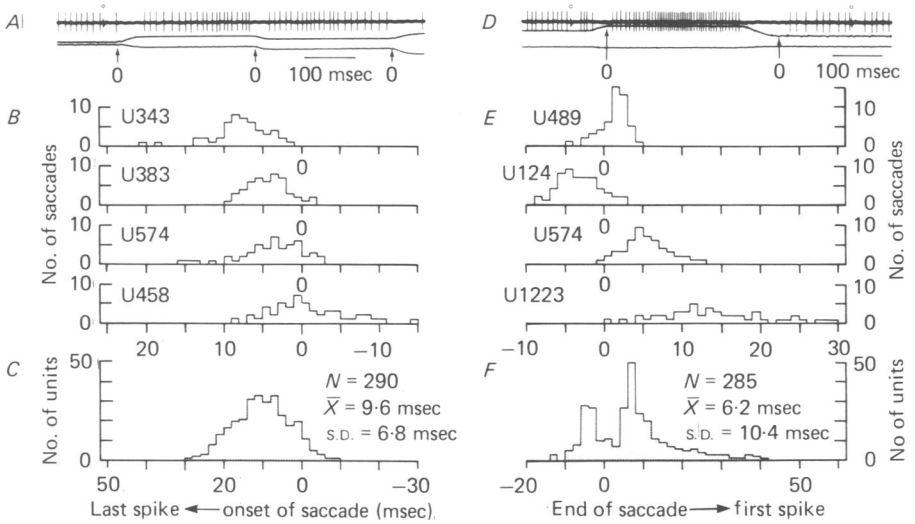

Fig. 4. Time relationships between the onsets of saccade and pause, and between the ends of saccade and pause in the whole population of pause units. *A*, spike train indicating the onset of saccade with an arrow. *B*, examples of units showing saccade-to-saccade variation in the latencies measured from the last spike before the pause to the onset of saccade (onset latency). The histogram for each unit is based on measurements from fifty saccades. *C*, distribution of the onset latencies for a total of 290 pause units. The value for each unit is represented by the mean latency derived from distribution histograms exemplified by the four units in *B*. *D*, spike train indicating the end of saccade. *E*, saccade-to-saccade variation in the latencies measured from the end of saccade to the first spike following the pause (end latency). *F*, distribution of the end latencies for a total of 285 cells. In forty-eight cells, the first spikes did not appear within 50 msec following the end of saccades.

(3) *Activity changes at the ends of saccades*

The tight relationship between the end of a saccade and the resumption of tonic activity was one of the most prominent features of the pause units. The unit shown in Fig. 3 is an example of the units in which the activity changes associated with the ends of saccades were analysed statistically. The raster and the peri-saccadic time histograms on the left of Fig. 3*B* and *C* were constructed after alignment with the onset of saccade. Those on the right were constructed after re-aligning the spike trains of approximately the same set of saccades with respect to the end of saccade. This unit showed a fairly constant level of tonic firing regardless of the eye position. This is apparent in the spike train (Fig. 3*A*), which exhibited a flat level of activity at about 50 spikes/sec up to 2 bins before (1 bin = 5 msec) the onset of saccade (Fig. 3*C*, left). Following the end of saccade (right) the level of activity almost doubled for about 10 msec; otherwise, the level of activity was fairly constant. The transient increase in firing may be important for the initial stage of steady eye position.

(4) *Temporal relationship between the pause and saccade*

Fig. 4 summarizes the temporal relationships between saccade and response for the whole population of pause units. The histograms in *B* show the distributions of the onset-latencies (the time from the last spike before the pause to saccade onset) for four arbitrarily chosen pause units, illustrating the considerable saccade-to-saccade variation in latencies. This variation did not exhibit any relation to either the direction or the magnitude of saccade. The histogram for each unit was derived from measurements for fifty saccades. The means ($\pm$ standard deviations) were 8·4 ($\pm$ 3·5), 3·8 ($\pm$ 2·6), 3·4 ($\pm$ 4·0), and $-1{\cdot}1$ ($\pm$ 4·6) msec for units U343, U383, U574, and U458, respectively; negative latencies indicate that saccade onsets preceded the onsets of pauses. From the onset-latency distribution, a mean latency was calculated for each unit. The means for all 290 units are compiled in the histogram (Fig. 4*C*). In most units (268/290 units or 92·4 %), the onset of pause preceded the onset of saccade. The maximum onset latency was 30 msec and the group mean was 9·6 msec. In a fraction of the units (twenty-two out of 290 units or 7·6 %), the pause started after the onset of saccade.

In a small sub-population of pause units (fifty-three out of 343 units or 15·5 %), the relationship between the onsets of pause and saccade was extremely variable, showing a wide onset-latency distribution (S.D. > 10 msec). These units are not included in the histogram.

The histograms in Fig. 4*E* show the distributions of the end-latencies (measured from the end of saccade to the first spike after the pause) for four units. Similar saccade-to-saccade variations were also observed here. The means were 1·8 ($\pm$ 1·8), $-2{\cdot}7$ ($\pm$ 2·6), 5·0 ($\pm$ 2·5) and 14·5 ($\pm$ 6·7) msec for units U489, U124, U574 and U1223, respectively; negative latencies indicate that pauses ended before saccades. The distribution of mean end-latencies for 285 pause units (Fig. 4) was found to be bimodal with peaks of -5 and 7 msec despite the considerable overlap seen among end-latency distributions for individual units (Fig. 4*E*). In about one-third of the units (ninety-three out of 285 units or 32·6 %), tonic firing resumed before the end of saccade, while in the remaining units (192/285 units or 67·4 %) tonic acitivity resumed sometime after the end of saccade. The fact that the tonic activity in the first group of cells preceded the onset of fixation by an average of 4·3 msec would implicate some physiological significance for these Purkinje cells in the initiation of fixation.

(5) *Temporal relationship between the burst and saccade*

Fig. 5 shows the temporal relationship between the burst and saccade, studied in ninety-eight units, including seventy-two burst units and twenty-six burst-pause units. The histogram shows the distribution of the mean latencies, measured in individual units from the first spike of the burst to the onset of saccade for fifty eye movements. At a preliminary stage of analysis we constructed two histograms, one for burst units and the other for burst-pause units. There was no significant difference between the two sets of histograms. Furthermore, we carefully checked individual units for any eye movement direction consistently associated with longer latencies.

This check was undertaken because the recording of some floccular mossy fibre units showed that bursts appeared earlier when the eyes moved in a particular direction (Noda & Suzuki, 1979*b*). However, no similar response was observed in the Purkinje cells.

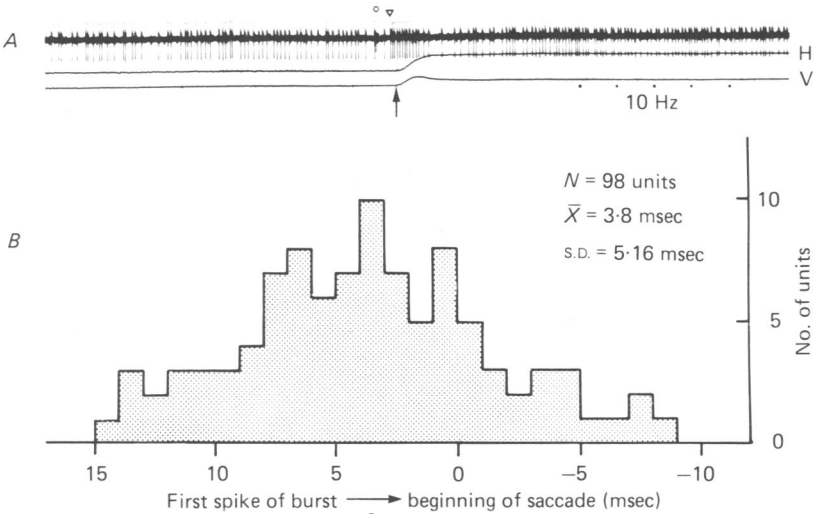

Fig. 5. Time relationships between the onsets of saccade and burst. *A*, spike train indicating the onset of saccade with an arrow. *B*, distribution of the latencies for a total of ninety-eight units. The latency was measured from the first spike of the burst to the onset of saccade for fifty eye movements with accompanying bursts. Mean latencies derived from seventy-two burst units and twenty-six burst-pause units are compiled in the histogram. There was no significant difference between the distributions of the two groups of units.

The burst onset latencies ranged widely from −9 to 15 msec, with a group mean of 3·8 msec and a standard deviation of 5·16 msec. In 70·4% of the units (sixty-nine out of ninety-eight units) the burst preceded the onset of saccade, while it followed the onset in the remaining twenty-nine units (29·6%). The onset of the burst was abrupt and easily identified in spike trains, as indicated in Fig. 5 with a triangle. In general, intraburst discharge frequency reached a peak at burst onset and tended to diminish thereafter. It was, therefore, difficult to distinguish the last spike of the burst from the first spike of the subsequent tonic activity. For this reason the end-latencies were not analysed for the burst responses.

(6) *Pause–saccade duration relationship*

The most prominent feature in the responses of pause units to saccades was the linear relationship between the duration of the pause and that of the accompanying saccade. Fig. 6 shows such relationships where the durations of saccades (*b*) are shown as a function of the durations of pauses (*a*) for six Purkinje cells. Open circles represent the durations measured in 108 saccades for one unit with the distribution fitted by the solid line ($y = 0{\cdot}94x - 9{\cdot}5$). The two sets of durations showed a high correlation ($r = 0{\cdot}94$). Regression lines found in five other Purkinje cells are displayed on the same figure with dashed lines. For this analysis, we chose twenty units with apparently high saccade and pause duration correlations; from among these, the six units with the best correlation coefficients were selected for presentation.

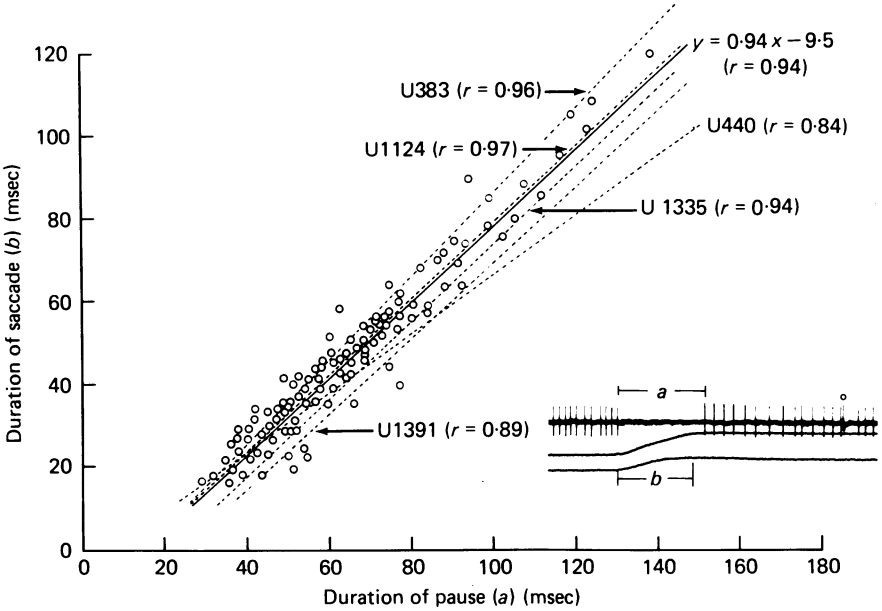

Fig. 6. Saccade duration (*b*) as a function of pause duration (*a*) for typical pause units. Open circles represent the values in a total of 108 saccades from one unit, and were fitted by the continuous line. Their correlation coefficient was 0·94. Linear regression lines for five other Purkinje cells are shown as dashed lines, with correlation coefficients 0·97, 0·96, 0·94, 0·89 and 0·84. The inset shows the durations *a* and *b*. The open circle at the top of the spike record denotes a complex spike.

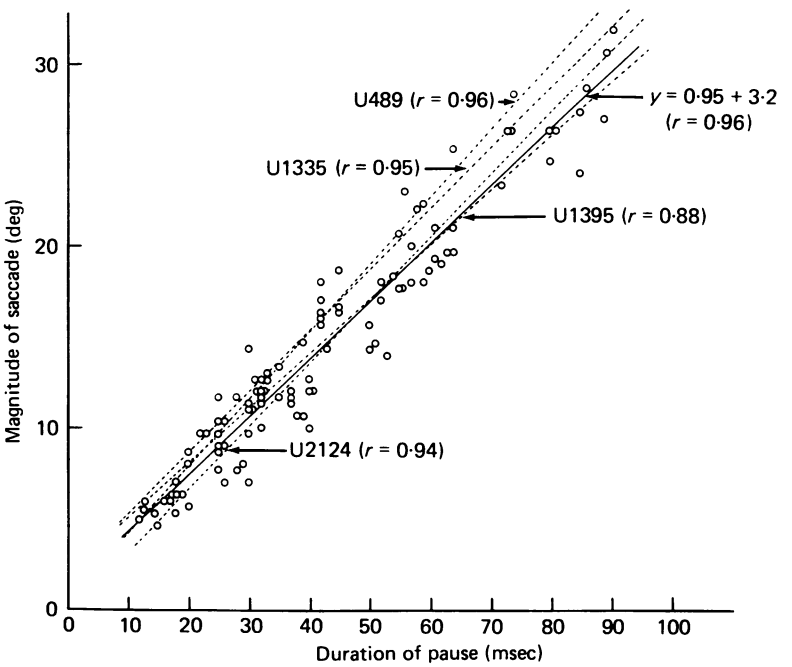

Fig. 7. Relation between magnitude of saccade and duration of accompanying pause in Purkinje cell activity. The magnitude represents a linear distance between pre- and post-saccadic fixation points and data from non-linear saccades, such as blinks, were eliminated. Open circles represent the data from 103 saccades in one unit and were fitted by the continuous line. Correlation coefficient was 0·96. Linear regression lines for four other Purkinje cells are shown as dashed lines, with correlation coefficients 0·96, 0·95, 0·94 and 0·88.

(7) *Pause duration–saccade magnitude relationship*

For eye movements between 3 and 25°, a linear relationship is known to exist between the amplitude and the duration of saccade in the horizontal plane in both humans and monkeys (Robinson, 1964; Fuchs, 1967; Yarbus, 1967; Henn & Cohen, 1973). From these results, a linear relationship would be expected to exist between the magnitude of saccade and the duration of pause in the Purkinje cell activity. The relationship was analysed in the twenty selected units by computing the vector magnitude of saccades from their horizontal and vertical components, measured in the e.o.g.s. Fig. 7 shows the relationships found in the five pause units having the best correlation coefficients. Here again, open circles are the values for one cell, with a continuous regression line having a correlation coefficient of 0·96. The relationships for the other four units are represented by their dashed regression lines. It can be concluded that the length of the pause in these Purkinje cells was a linear function of the magnitude of the saccade.

DISCUSSION

The significance of Purkinje pause units in the control of saccades

The present study in the monkey has shown that the majority of Purkinje cells in the flocculus stop firing completely during saccadic eye movements. While showing high levels of tonic discharges during steady fixation, the Purkinje cells ceased firing slightly before the onset and continuing throughout the period of a saccade. This was characteristic of the pause units which comprised 66·9 % of the Purkinje cells identified in the present study. In addition, the burst-pause units, which constituted 12·8 % of the Purkinje cells, also paused when a saccade occurred in non-preferred directions. Altogether, about 80 % of the Purkinje cells in the flocculus paused during at least some saccades.

It is known that Punrkije cell axons constitute the only output from the flocculus and through this channel Purkinje cells exert inhibitory synaptic action upon their direct target cells (see Eccles, Ito, & Szentágothai, 1967 for a review). The high rates of discharges of Purkinje cells during intersaccadic periods imply that the flocculus sends tonic inhibitory impulses to the target cells during steady fixation, the disruption of which may result in a disinhibitory action upon the target cells during saccades.

It is now widely accepted that the discharge of a class of neurones (burst units) located in the mid-brain and pontine reticular formation provides the necessary control signal for the generation of saccades of proper direction and size. These neurones show a high frequency burst of activity which slightly precedes saccade onset and lasts for a duration equal to that of the saccade (Luschei & Fuchs, 1972; Keller, 1974; Robinson, 1975; Henn & Cohen, 1976; Büttner, Hepp & Henn, 1977; King & Fuchs, 1977). It has been suggested that the duration of the burst discharge is controlled by an inhibitory input from another class of neurones (pause units), which abruptly interrupt their high frequency tonic activity during saccades in all directions for an interval also equal to saccade duration (Keller, 1974). Such pause units have been found in neurones located on the mid line in the raphe nucleus com-

plex of the pons (Keller, 1974, 1977). Their inhibitory influence on target cells has been suggested by the observation that high frequency micro-stimulations applied to the pause area produced complete inhibition of spontaneous saccades (Keller, 1977).

The remarkable similarity in the behaviours of the floccular pause units and of the pontine pause units recorded by Keller (1974, 1977), together with the fact that Purkinje cells are inhibitory, suggests that the flocculus may constitute another locus of pause units which exerts a gating influence on target cell activity. Anatomical evidence has not yet been accumulated sufficiently to conclude whether or not Purkinje cell axons reach the brain stem reticular core directly from the flocculus. It is not certain, therefore, whether floccular pause units directly influence the reticular burst units or constitute part of another 'pause and burst' complementary set which influences neurones of the oculomotor complex in a way similar to that of brain stem pause and burst units.

Possible pathways for floccular control of eye movements

Three major pathways through which the flocculus disynaptically influences neurones of the oculomotor complex, have been postulated. In the first pathway, the target cells of floccular Purkinje cells are in the vestibular nuclei and correspond to the relay neurones of the vestibulo-ocular reflex. The projections of the floccular Purkinje cells onto the vestibular nuclei (Dow, 1938; Angaut & Brodal, 1967) and those from the vestibular nuclei to the oculomotor complex have been anatomically established (Carpenter & McMasters, 1963; Carpenter & Strominger, 1965; McMasters, Weiss & Carpenter, 1966; Tarlov, 1970). In alert monkeys, neurones showing bursts during saccades have been recorded from the vestibular nuclei (Luschei & Fuchs, 1972; Miles, 1974; Fuchs & Kimm, 1975; Keller & Kamath, 1975). According to Miles (1974), the burst appeared in most of these neurones associated with saccades toward the side of recording. On the other hand, most pause units in the flocculus (83·4 %) stopped firing with saccades in all directions, suggesting that either the flocculus is not the sole source of afferents to these vestibular burst units or that these burst units are not target cells. If they were related to the flocculus they might constitute the origin of mossy fibres (Noda & Suzuki, 1979*b*).

The second pathway involves the nucleus prepositus hypoglossi. Several lines of new evidence have indicated that this nucleus is involved in the control of eye movements in conjunction with the cerebellum. It receives direct afferent projections from the flocculus (Angaut & Brodal, 1967; Alley, 1977) and projects to the oculomotor (Graybiel & Hartwieg, 1974), the abducens (Maciewicz, Eagen, Kaneko & Highstein, 1977) and the trochlear nuclei (Baker, Berthoz & Delgado-Garcia, 1977). Neurones showing bursts with saccades have been recorded from the prepositus hypoglossal nucleus in alert cats, with the burst usually preceding the onset of saccade by 6–10 msec and appearing with eye movements in all directions (Baker, 1977). These neurones seem to be good candidates for the target cells of the floccular pause units. However, a definitive conclusion will have to await further detailed investigations, preferably on alert monkeys.

In the third pathway, the target cells are in the dentate nucleus. A projection from the flocculus to ventral portions of the dentate nucleus have been shown anatomically

(Angaut & Brodal, 1967; Haines, 1977). The same regions of the dentate nucleus project to the oculomotor complex (Rand, 1954; Carpenter & Strominger, 1964; Martin, King & Dom, 1974; Chan-Palay, Sweikhart, Van Itallie & Brown, 1976). Through the dentate nucleus, two channels possibly linking the flocculus to oculomotor function have been established anatomically. One is through the dentato-oculomotor direct and disynaptic route and the other is through the dentato-reticulo-oculomotor indirect and multisynaptic route (Chan-Palay *et al.* 1976). There are few neurophysiological data at present to conclude whether or not the direct flocculo-dentato oculomotor route subserves pause unit gating of oculomotor activity. To be sure, Gardner & Fuchs (1975) have recorded dentate burst units which increase activity 10–30 msec prior to saccades in all directions, but this observation, while encouraging, cannot act as the basis for any conclusion. Further study of this area is necessary and should prove fruitful in extending our understanding of the role of the flocculus in gaze control.

Does the flocculus initiate saccades?

The question now arises concerning the casual relation between the phasic changes in activity of floccular Purkinje cells and the initiation of saccades. The present study has shown that the majority of the Purkinje cells (82·5%) showed responses to saccades in all directions. Even among the cells showing directional selectivity for responses, examples of the preferred directions for individuals cells were found for all directions, suggesting that the flocculus may not play a major role in the control of saccade direction. In most Purkinje cells, while the activity changes preceded saccade onset, the onset-latency (measured from the last spike before the pause to saccade onset) showed considerable variation from cell to cell (Fig. 4*C*). Even within a cell, it varied from saccade to saccade (Fig. 4*B*). The responses occasionally started even after the onset of saccades in some units (see U458 of Fig. 4*B*). In the whole population of pause units, the onset-latency averaged 9·6 msec (± 6·8). This latency, however, does not reflect accurately the intracellular events involved with pause generation.

In considering pause and burst units, intracellular events in the two populations are, in theory, temporally compatible, despite the seeming difference in onset latencies. This can be shown by assuming an average frequency of 100 spikes/sec for floccular Purkinje cell discharges. If the saccade had not occurred, a theoretical spike following the last pre-pause spike would have appeared 0·4 msec after time zero (saccade onset) (9·6 msec − 10 msec = − 0·4 msec). In reality, the spike was suppressed because the saccade occurred. Therefore, the suppresion of discharges must have started between − 0·4 and 9·6 msec. Taking the middle of the range, the average lead time in the pause units may be estimated as 4·8 msec. This estimate is comparable with the average lead time of 3·8 msec (± 5·2) for the burst responses of the Purkinje cells, thereby reflecting similar chronologies in intracellular events (Fig. 5). The estimate also appears to be reasonable when a comparison is made with the afferent inputs to the Purkinje cells. The average lead time for the bursts of mossy fibre units recorded in the monkey flocculus was 6·9 msec (± 5·2) and that for interneurones was 4·2 msec (± 3·3) (Noda & Suzuki, 1979*b*).

In spite of prominent responses with close temporal relationships to saccades, the

value of the lead time does not strongly support the notion that the flocculus participates in the initiation of saccades. The lead time of floccular Purkinje cells appears to be too short to drive neurones of the oculomotor complex. The average burst lead time of the oculomotor neurones was 7·5 msec with a range of 4–10 msec (Robinson, 1970) and that of the abducens neurones, evaluated from the histogram of Luschei & Fuchs (1972, fig. 1), was 6·0 msec with a range of 3–11 msec. We know that other structures wherein saccade related activity is observed, such as the association cortex (Lynch, Yin, Talbot & Mountcastle, 1975), the internal medullary lamina of the thalamus (Schlag, Lehtinen & Schlag-Rey, 1974) and the superior colliculus (Schiller & Koerner, 1971; Wurtz & Goldberg, 1972) initiate saccade-related activity well before (50–150 msec) the onsets of saccades. Our own data (Noda & Suzuki, 1979*b*) indicated that the flocculus receives signals associated with impending saccades significantly before the onsets of saccades. For example, a group of mossy fibres started firing 100–200 msec before an eye movement with a peak in activity at the onsets of saccades. It is interesting to note that, in spite of such an early input of signals correlated with saccades, the output signals from the floccular Purkinje cells started only 4–5 msec before the onsets of saccades. As the long prelude (the discharges starting 100–200 mseec before the saccade) was observed in both mossy fibres and interneurones, the early eye movement signals must have been filtered out at the level of the Purkinje cells. The analysis of discharges of afferent units of the flocculus revealed that the pause in Purkinje cells was produced by a burst of impulses transferred through the mossy fibre system (Noda & Suzuki, 1979*b*). All these observations are in favour of a conclusion that the flocculus, or at least the majority of Purkinje cells, does not participate in the initiation of saccades. This agrees with the conclusions derived from stimulation (Ron & Robinson, 1973) and lesion experiments (Ferraro & Barrera, 1938; Westheimer & Blair, 1973; Robinson, 1974; Takemori & Cohen, 1974; Zee, Yamazaki & Gucer, 1978).

Function of the flocculus in eye movements

Although the flocculus may not initiate saccades, the intimate temporal relationships which are demonstrated in the present study between the Purkinje cell activity and the saccades strongly suggest that the flocculus must play a significant role in gaze control. We propose that the flocculus constitutes a locus for another 'pause and burst' complementary set of units and helps the oculomotor system, particularly in its fastidious function in gaze control. This circuit may not actually generate saccades but it may ensure the accuracy of eye movements, especially in their magnitudes, and, once a visual target is acquired, help the oculomotor system to maintain the target on the fovea.

The present study has shown that the pause duration of Purkinje cell activity was proportional to the saccade magnitude (Fig. 7). The ends of saccades were closely associated with the resumption of tonic activity, which in some units started with a significantly higher discharge rate (Fig. 3). All these Purkinje cell behaviours favour the proposed function of the flocculus. The higher discharge rate at the ends of saccades ensures a powerful initiation of the inhibitory influence upon target cells of floccular Purkinje cells. The discharges of these target cells would be sharply terminated by such inhibition, and discharges during the subsequent fixation period would

be prevented by the tonic Purkinje cell activity. For one reason or another, if the pause Purkinje cells do not resume their tonic activity at a proper time, the saccade will not end at the correct position. Ocular dysmetria is one of the frequently observed oculomotor symptoms in patients with cerebellar system disorders (Hoyt & Darroff, 1971). It consists of an initial conjugate 'overshoot' followed either by a single return or, more commonly, a brief small amplitude oscillation before the eyes come to rest. A saccade is made in the proper direction and of almost correct magnitude, but the accuracy is lacking. It is in the refinement of eye movement control and the delicate positioning of the eyes for fixation that the flocculus may play a role. In this respect, the high rate of discharge with regular inter-spike intervals observed in the Purkinje cells would be useful in exerting continuous inhibition on the target cells. The disruption of this inhibition would result in uncontrolled discharges of the target cells which in turn may cause difficulty in steady fixation. The oculomotor symptoms of cerebellar system disorders, such as opsoclonus and ocular flutter, are commonly considered to be manifestations of fixation disturbances.

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