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PROCESSING OF EYE MOVEMENT SIGNALS IN THE FLOCCULUS OF THE MONKEY

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SUMMARY

1. Extracellular recordings were made from afferents to the Purkinje cells of the flocculus of monkeys either spontaneously making saccadic eye movements (saccades) or trained to fixate a small visual target projected 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 a population of 108 units, eight were climbing fibres, seventy-one were mossy fibres, and twenty-nine were non-Purkinje cells. Based on their discharge patterns the latter two groups of units were categorized into one of four classes.

3. Long-lead burst units (twenty-two units) exhibited saccade-related discharges substantially before saccade onset (average: 113 msec). Most of these (twenty units) discharged for saccades in a particular direction, while the remainder exhibited discharges for saccades in all directions. All units were essentially silent between saccades.

4. Burst units (twenty-seven units) started discharging slightly before saccades (average: 6·9 msec). Discharges were associated with saccades in all directions (sixteen units) or in preferred directions (eleven units) and were not observed during periods of fixation.

5. Burst-tonic units (twenty-two units) were characterized by saccade-related burst and position-related intersaccadic tonic activity.

6. Tonic units (thirty-seven units) exhibited position-related tonic activity. The position-related activity in both burst-tonic and tonic units was observed only for fixation points within a specified region. The units were silent for fixation positions outside this region of preferred fixation.

INTRODUCTION

The elucidation of the role of the flocculus in gaze control has progressed with the investigation of Purkinje cell activity during saccades and periods of fixation (Noda & Suzuki, 1979*a*, *b*). The results of such studies raise questions concerning the neurophysiological basis for the observed changes in Purkinje cell activity. Are these discharge patterns simply reflexions of similar saccade-related activity in afferents to the Purkinje cells or are they the results of transformations occurring within the cortex of the flocculus? Also requiring clarification is the causal nature of the position-related changes in the tonic discharges of some Purkinje cells during steady fixation.

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Further delineation of floccular function, therefore, requires a knowledge of the input signals to the flocculus and of the transformations occurring within the cerebellar cortex and resulting in the discharge patterns observed in the output neurones, i.e. the Purkinje cells.

Connexions between the flocculus and certain brain-stem regions intimately related with oculomotor function implicate a role for the flocculus in supra-nuclear mechanisms related to gaze control. Early studies of the anatomical relationship between the flocculus and the brain stem indicated a reciprocal connexion between this portion of the cerebellum and the vestibular nuclei (Angaut & Brodal, 1967; Brodal, 1972*a*). More recent anatomical studies indicate that the flocculus is also reciprocally connected with the prepositus hypoglossal nucleus (Alley, Baker & Simpson, 1975) which is, in turn, reciprocally related to the nuclei of the oculomotor complex. A direct pathway from the oculomotor complex to the flocculus has also been discovered (Graybiel, 1977; Kotchabhakdi & Walberg, 1977). A comparison of the discharge patterns of the afferents to Purkinje cells during eye movements with those of neurones which are directly or indirectly connected to both the flocculus and oculomotor complex would aid in clarifying the functional relationships between the flocculus and these brain-stem oculomotor centres. Such a comparison, together with a consideration of the input–output relation of the flocculus, were the basis for implementing this study.

METHODS

Saccade-related activity was recorded in afferents to the Purkinje cells of the flocculus of six monkeys (*Macaca nemestrina*). The basis for identifying Purkinje cell units, and the surgical preparations, experimental conditions, procedures for training monkeys, method 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 papers (Noda & Suzuki, 1979*a*, *b*). Out of a total of 1488 units recorded, which exhibited saccade-related phasic changes in activity, 513 units were identified as Purkinje cells (Noda & Suzuki, 1979*a*). Of the remaining 975 units, a majority were probably Purkinje cells (Noda, Asoh & Shibagaki, 1977), but 125 units were considered not to be Purkinje cells, since their firing patterns differed from those observed it the identified Purkinje cells.

The activity analysed herein was recorded from 125 units classified as input fibres and as non-Purkinje cells, which are presumably stellate, basket or Golgi cells or all of these. Action potentials recorded from mossy fibres were typical axon spikes with sharp, non-inflected rising phases, while non-Purkinje cell spikes exhibited rising phases which were less steep than those of mossy fibres. These cells could be further distinguished from the fibres by the amplitude modulation sometimes observed in the high frequency burst associated with saccades in certain units.

Spontaneous Purkinje cell activity ranged from 30 to 150 spikes/sec and never decreased to zero spikes/sec in the identified Purkinje cells during periods of fixation, which were longer than 1 sec (Noda & Suzuki, 1979*a*, *b*). In contrast, for all non-Purkinje units (afferent fibres and interneurones), there existed some gaze position associated with cessation of firing. Some non-Purkinje units, in fact, were silent during all periods of fixation in any gaze position and were characterized by discharges only during saccades. The eye-movement-related discharge patterns observed in the non-Purkinje units, therefore, differed markedly from the discharge patterns observed in the identified Purkinje cells. Based on these differences, discharges of mossy and climbing fibre units could be distinguished from the firing patterns recorded from axons of the Purkinje cells.

Placement of the electrode in the flocculus was indicated by saccade-related burst activity observable in the oscilloscope at high magnification within the background and audible as a 'swishing' sound over the audio monitor. This sound was characteristic of the flocculus and always audible at appropriate levels of amplification. The approach to a Purkinje cell layer was heralded by an increase in tonic multiple discharges and advancement of the electrode into this zone of increased activity usually yielded an isolated Purkinje unit. Neighbouring the Purkinje cell layer was a layer wherein discharge patterns characteristic of mossy fibres were isolated from among the units responsible for the saccade-related increases in background 'noise' levels.

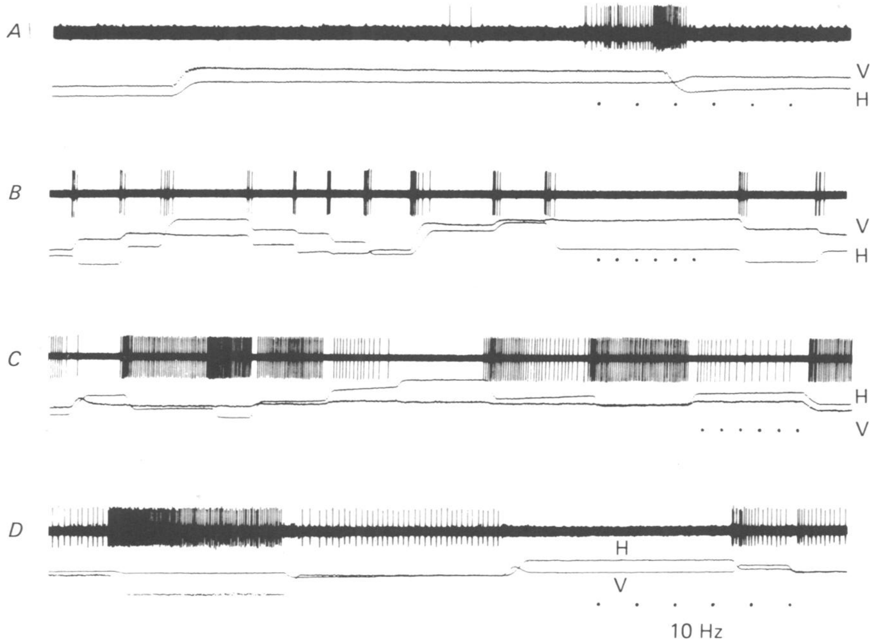

Fig. 1. Examples of discharge patterns recorded from mossy fibres in the monkey flocculus. *A*, long-lead burst of a mossy fibre. Note that bursts appeared with saccades only in a preferred direction. *B*, burst discharge of a mossy fibre. Note the lack of directional preference for the bursts and the absence of activity during fixation. *C*, burst-tonic activity in a mossy fibre. Note that bursts were observed with saccades in the preferred direction and pauses in the non-preferred direction. Beyond a position threshold, tonic activity changed with shifts of fixation points. *D*, tonic activity of a mossy fibre: this unit also showed position related changes in the level of tonic activity. H and V, horizontal and vertical electro-oculograms (e.o.g.s), respectively.

RESULTS

Classification

Saccade-related activity was observed in a population of 125 units composed of mossy fibres and non-Purkinje cerebellar neurones in the monkey flocculus. On the basis of their discharge patterns, a majority (110/125 units or 88 %) of these units could be categorized into four classes which are long-lead burst, burst, burst-tonic, and tonic units (Fig. 1). In addition, saccade-related discharges were present in eight units identified as climbing fibres on the basis of extremely low firing rates and discharge patterns equivalent to those observed for complex spikes in Punkinje cells. A few units exhibiting low frequency responses to saccades ($n = 4$) or bursts which followed saccade onsets ($n = 5$) are not considered in this paper. With respect to the

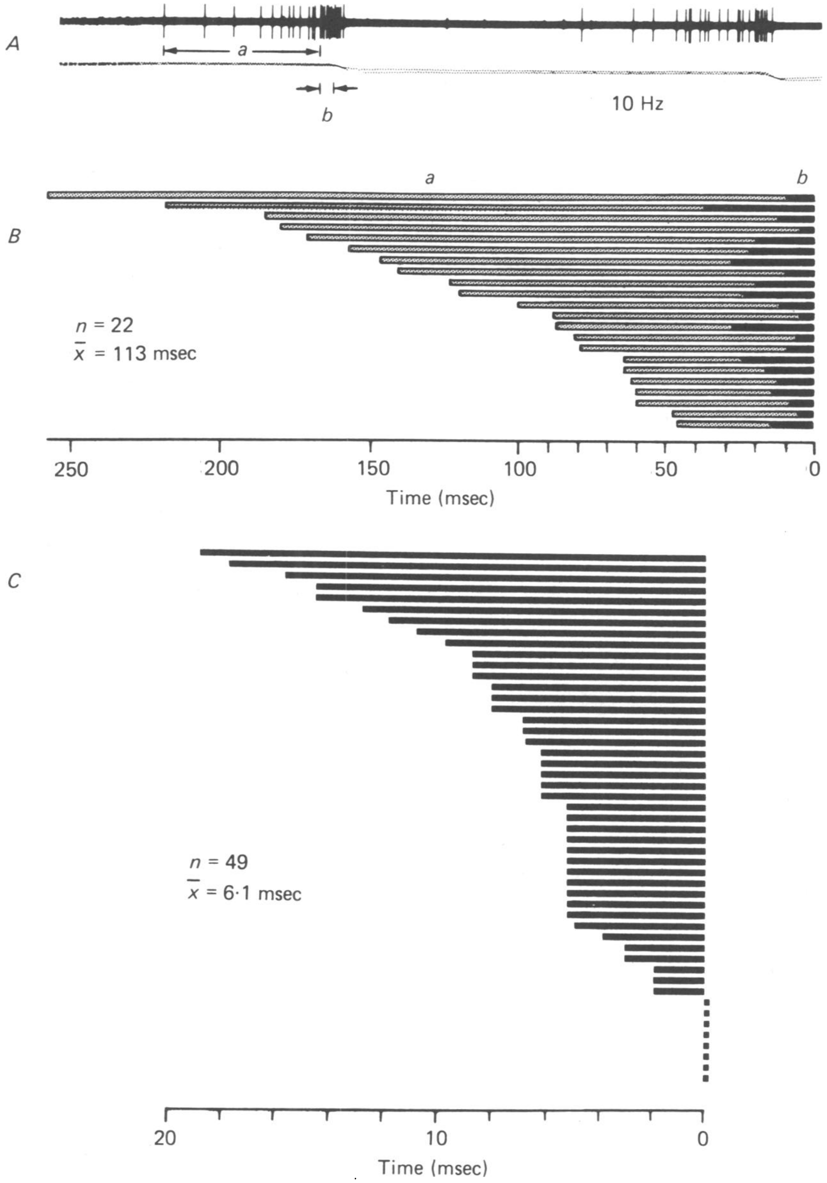

Fig. 2. Times from the onsets of saccade-related discharges to saccade onsets (lead times). *A*, an excerpt from the record of unit 82 illustrating the differentiation of prelude (*a*) from the pre-saccade portion of the burst (*b*). Distinguishing the prelude and burst discharges was sometimes somewhat arbitrary, but bursts could usually be differentiated by their higher discharge frequency. *B*, average prelude (light) and burst (dark) lead times are presented in bar form for all twenty-two long-lead burst units. Discharges were averaged over twenty or more saccades in the preferred directions. *C*, burst lead times for the combined population of burst units and the burst portion of burst-tonic units. The squares indicate a lead time of zero msec.

latter units, however, it may be noted that they were observed even in darkness, indicating that they were not the result of delayed visual input.

Long-lead burst units (Fig. 1*A*) were characterized by saccade-related high frequency bursts which slightly led saccade onsets and by relatively long duration 'preludes' of lower frequency discharges which preceded the bursts. Directional preference was commonly observed among this class of units. These units exhibited very little spontaneous activity and usually did not discharge during periods of fixation. *Burst units* (Fig. 1*B*) also responded with brusts which slightly preceded the onsets of saccades. In contrast to the long-lead burst units, directional preferences were less frequently observed. No discharges were observed during intersaccadic periods. *Burst-tonic units* (Fig. 1*C*) responded with a burst to saccades and were tonically active during some periods of fixation. The bursts portions of these units resembled the transient discharges of the burst units with respect to timing and duration. Burst-tonic units typically exhibited bursts only for saccades in a preferred direction. The level of tonic activity was related to eye position and increased with shifts of gaze in the same direction as the preferred direction for the bursts. *Tonic units* (Fig. 1*D*) were similar to burst-tonic units, but lacked consistent burst responses to rapid changes in fixation points.

Long-lead burst units

Twenty-two units were classified as long-lead burst units with an equal sampling of mossy fibres and non-Purkinje cells. An example of a long-lead burst mossy fibre is presented in Fig. 2, together with a bar diagram illustrating average times (lead times) from the onsets of preludes and bursts to saccade onsets for all the long-lead burst units (Fig. 2*B*). Based on the averages calculated for each unit, it was found that preludes preceded saccade onset by an average of 113 msec (47–260 msec) for the total sample of long-lead burst units. Average prelude lead time for mossy fibres was 117 msec, while non-Purkinje cell preludes led saccades by 109 msec on the average. The average burst-lead time was 14·3 msec (4–35 msec) for the total sample. For the mossy fibres, burst-lead time was 15·1 msec and for the non-Purkinje cells, the lead time was 13·6 msec on average.

The distinction between the prelude and burst discharge was sometimes ambiguous, but differences in the character of the discharges could be used to aid in the separation of the two components. The frequency of prelude activity was always lower than the frequency of burst discharges and the interspike interval within preludes often appeared to be more variable than for bursts. Within the prelude, discharge frequency increased gradually, while within the burst discharge rate increased more rapidly and attained a peak prior to the onsets of saccades, as exemplified by the histogram for a mossy fibre unit (Fig. 3*C*). The peak in the intraburst discharges for non-Purkinje cells similarly occurred at the beginning of bursts, although slightly later than for mossy fibres.

In twenty out of the twenty-two long-lead burst units, directional preferences were observed for saccade-related activity. The preferred directions were almost equally distributed among the ipsilateral (seven units), contralateral (six units) and vertical (seven units) directions with respect to the side of the recording. In Fig. 4*B*, saccade-related responses were plotted in polar co-ordinates for 124 consecutive

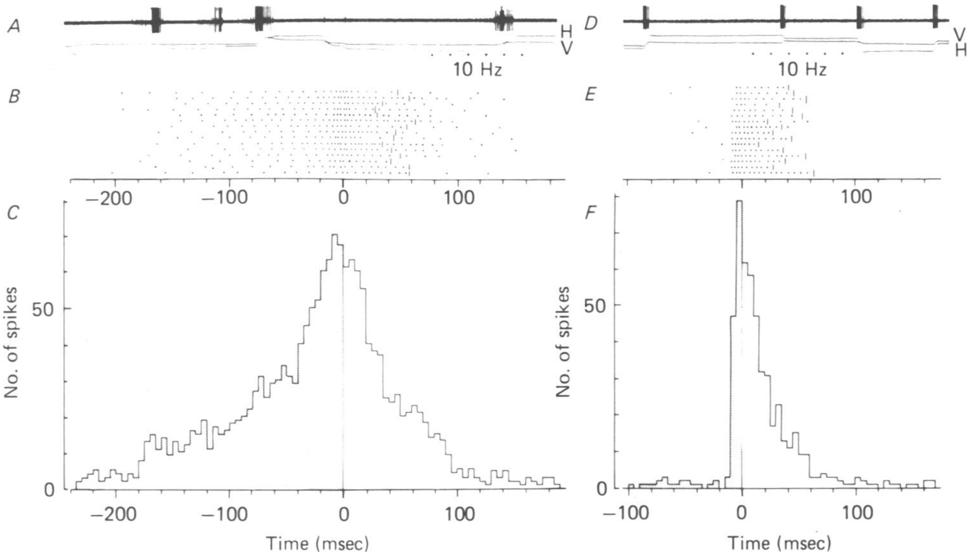

Fig. 3. *A*, example of long-lead burst discharges in a mossy fibre. *B*, raster constructed from the discharges to twenty saccades in the preferred direction of the unit in *A*. The discharges were aligned to saccade onset and the vertical lines indicate the ends of saccades. *C*, histogram illustrating the spike distribution of the long-lead burst discharges in the mossy fibre. Note the peak in the spike count prior to saccade onset. *D–F*, analogous to *A*, *B*, and *C* but for burst discharges in a mossy fibre.

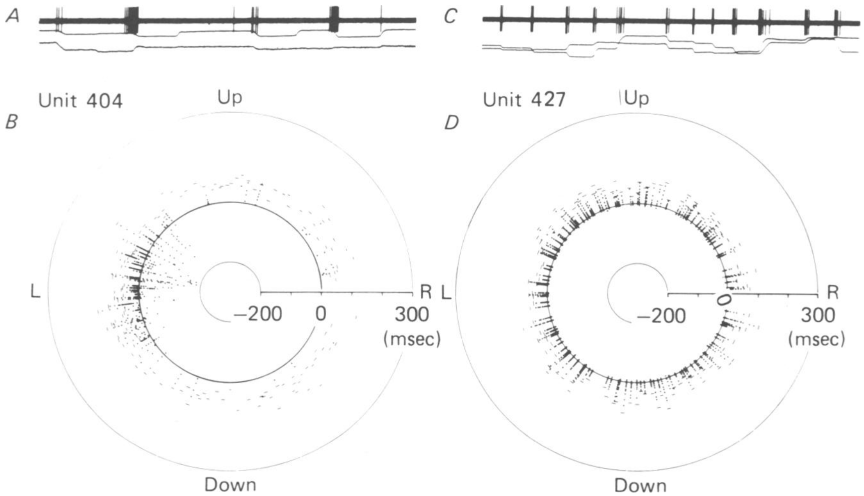

Fig. 4. *A* and *C*, excerpts from the records for a long-lead burst and a burst non-Purkinje cell, respectively. *B* and *D*, polar rasters constructed from the discharges associated with 124 saccades for each unit. The directions of the saccades are indicated by the radii along which the discharges are drawn. The zero msec circles indicate saccade onset and the small lines mark the ends of saccades. Note the difference in the degree of directional preference exhibited by the prelude and the burst for the long-lead burst unit (*B*).

saccades of a long-lead burst unit. The preferred direction for this unit was to the left (contralateral). It is interesting to note that the range of preferred directions associated with the prelude was narrower than that associated with the burst.

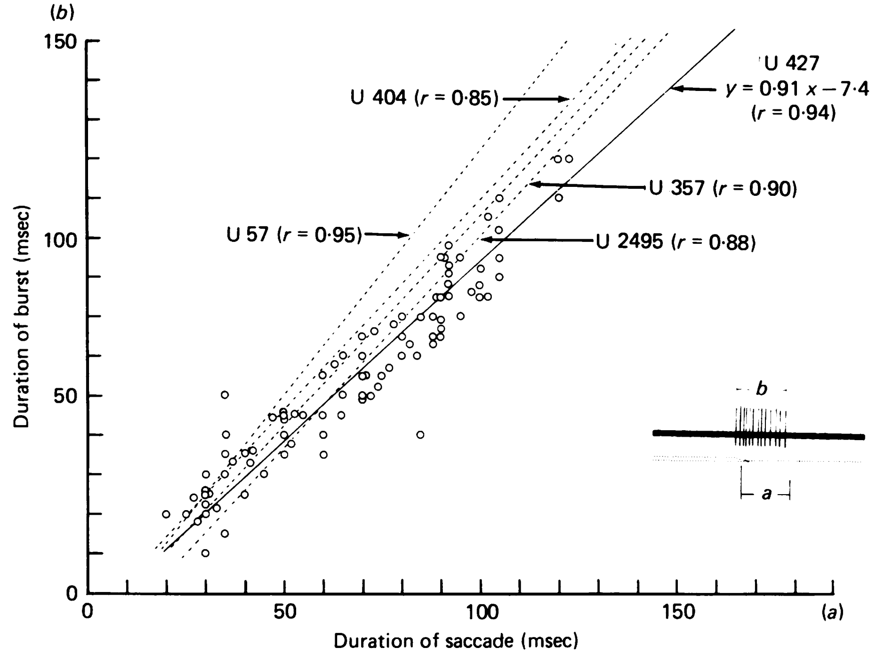

Fig. 5. Burst duration *vs.* saccade duration. The inset exemplifies the measurements of saccade duration (*a*), which is plotted on the abscissa, and burst duration (*b*), which is plotted on the ordinate. Duration values only for unit 427 are plotted (circles) and a linear regression line is drawn (continuous line). To avoid congestion, only linear regression lines are illustrated for four other units (dashed lines). r = correclation coefficient. U57, burst non-Purkinje cell. U357, burst-tonic mossy fibre. U404, long-lead burst non-Purkinje cell. U427, burst non-Purkinje cell. U2495, burst-tonic mossy fibre.

Burst units

A total of twenty-seven units were classified as burst units and twenty were recorded from mossy fibres and seven were from non-Purkinje cells. They were similar to long-lead burst units in that intraburst maximal firing occurred prior to saccade onset (Fig. 3*F*), but differed with respect to directional preferences (Fig. 4*D*). In more than half (sixteen out of twenty-seven units or 59%) of the burst unit population, transient discharges were observed for saccades in all directions; seven responded primarily for saccades in the contralateral direction, two preferred the ipsilateral and two the vertical directions.

Average times from burst onset to saccade onset, i.e. burst-lead times were measured for the burst units and the burst portions of the burst-tonic units with no significant difference found between the two populations. These data were therefore combined and the averaged burst lead times are presented in bar form in Fig. 2*C*. In the total sample, burst-lead times averaged 6·1 msec. Mossy fibre burst-lead times ranged from 0 to 19 msec and averaged 6·9 msec, while non-Purkinje cell lead times ranged from 0 to 9 msec and averaged 4·2 msec.

Eye-movement-related bursts usually ended before the ends of saccades. The durations of the bursts were found to be highly correlated with the durations of the saccades (Fig. 5), with the two durations being approximately equal. With respect to this correlation, no differences were observed between burst and burst-tonic units nor between mossy fibres and non-Purkinje cells.

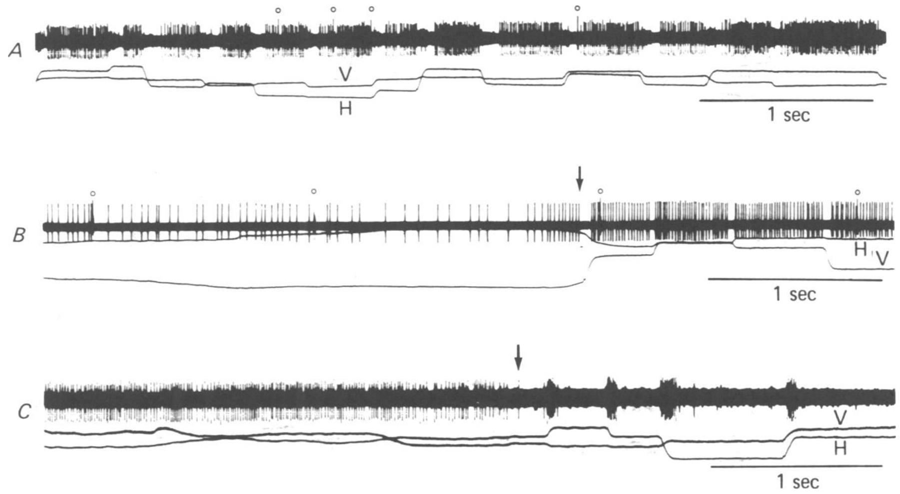

Fig. 6. Pause Purkinje cell and burst mossy fibre discharges during alert and drowsy states. *A*, pause Purkinje cell activity recorded with a micro-electrode having a relatively large tip exposure. Note the increased background activity present during saccade related pauses in Purkinje cell discharges. *B*, a different pause Purkinje cell recorded from with a higher impedance electrode. The monkey was initially drowsy and was roused by a handclap (arrow). Note the decreased level and the irregularity of the tonic activity when the animal was drowsy, in contrast to the high frequency, regular tonic discharges observed in the Purkinje cells of the alert monkey. Circles indicate complex spikes. *C*, mossy fibre discharges during drowsiness and after being roused with a handclap (arrow). The behaviour of the mossy fibre is opposite to that of the Purkinje cell. The bars in all the records indicate 1 sec.

Activity in Purkinje cells and burst units during drowsiness

A consistent observation when recording from the flocculus is the complementary behaviour of pause Purkinje cells (Noda & Suzuki, 1979*a*) and burst mossy fibres. When recording extracellularly with an electrode with a large tip exposure, the background 'swishing' sound associated with saccades is especially apparent. Soon after this 'swishing' is heard, a Purkinje cell layer is entered and saccade-related Purkinje cell activity is recorded. In pause units, the pauses in the Purkinje cell activity are associated with saccade-related increases in background noise or sometimes with transient multiple unit activity (Fig. 6*A*). Such increased background activity may correspond to the transient responses to eye movements observed in the burst inputs to the flocculus. With an electrode selected in an effort to isolate a unit from the intrapause multiple discharges, burst activity of a single fibre can be recorded occasionally. An example of such an isolated unit is shown in Fig. 6*C*. This observation raises the possibility of a complementary interaction between pauses and bursts, which is further supported by the contrasting discharge patterns of Purkinje cells and afferent burst units observed when the animal is drowsy. During such periods of drowsiness, Purkinje cell discharges become less frequent (Fig. 6*B*, prior to the arrow), while mossy fibre activity loses its transient character and becomes tonic (Fig. 6*C*, prior to the arrow). When the animal is roused with a handclap (arrow in Fig. 6*B* and *C*), Purkinje cell and mossy fibre activity again change in a complementary manner.

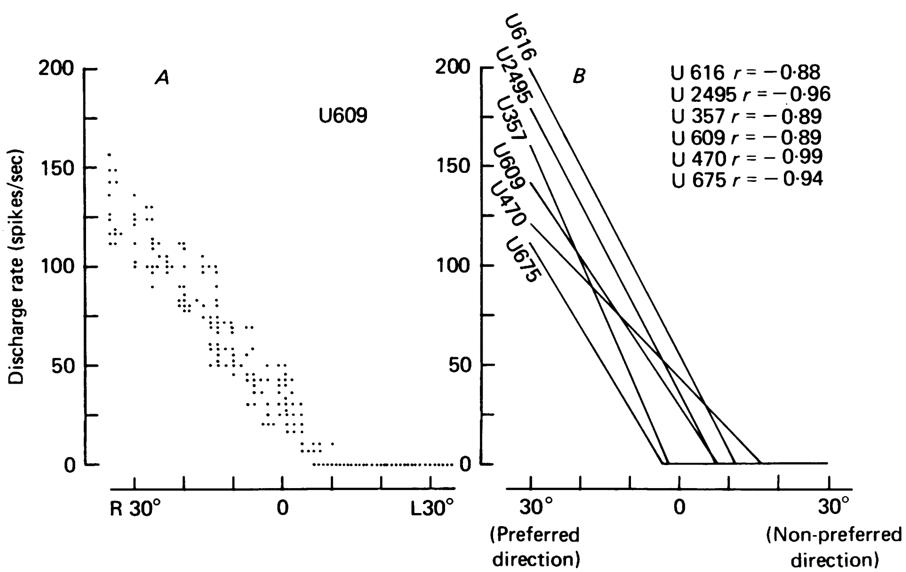

Fig. 7. Position related activity in mossy fibres and non-Purkinje cells. *A*, discharge rate of a mossy fibre (abscissa) graphed as a function of horizontal fixation position (ordinate). *B*, linear regression lines and corresponding correlation coefficients for the position related activity of six units. Most units began firing within 10° left or right (up or down) of the primary position. Mossy fibres: U357, U609, U616 and U2495. Non-Purkinje cells: U470 and U675.

Burst-tonic and tonic units

Position-related activity was observed in nearly half (fifty-nine out of 125 units or 47 %) of all the non-Purkinje units sampled from the flocculus. This position information was reflected in the tonic discharges of twenty-two burst-tonic and thirty-seven tonic units. Of the twenty-two burst-tonic units, fifteen were recorded from mossy fibres and seven were from non-Purkinje cells. The thirty-seven tonic units included twenty-one mossy fibre units and sixteen non-Purkinje cell units. When discharge frequency is graphed as a function of horizontal or vertical fixation positions (Fig. 7), a point on the fixation axis exists beyond which a unit begins to discharge. This point defines the position threshold and each unit was characterized by such a point, i.e. all burst-tonic or tonic units had a zone of fixation positions associated with zero activity. In agreement with Lisberger & Fuchs (1978), a majority of the units were found to have position thresholds within ±10° of the primary position (Fig. 7*B*). Once the direction of the gaze shifted beyond the position threshold into the region of preferred fixation, the level of tonic activity increases almost linearly with eye positions, with a greater increment in frequency observed for extremes, 25–30°. Such a relationship was observed in 78% of the burst-tonic and tonic units. In the remaining 22% of the units, discharge frequency was not monotonically related to fixation position, but was typically all-or-none with a certain fixation point again defining a position threshold. Once the threshold was crossed, tonic activity was observed whose frequency was independent of fixation position.

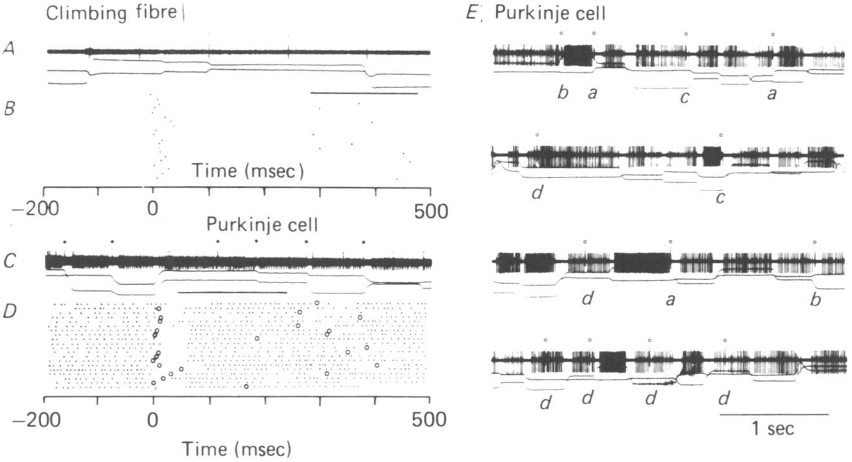

Fig. 8. Climbing fibre discharges and Purkinje cell complex spikes. *A*, saccade-related climbing fibre discharges. *B*, raster constructed from the climbing fibre discharges associated with twenty saccades and aligned to saccade onset. *C*, example of a pause Purkinje cell. Dots denote complex spikes. *D*, raster constructed from the discharges to twenty saccades for the unit exemplified in *C*. Circles indicate the occurrence of complex spikes. *E*, an extended excerpt from the record of another Purkinje cell. Note the lack of an intimate temporal relationship between complex spike and pause occurrence. Complex spikes. indicated by circles, occur at the beginning (*a*), in the middle (*b*) or before (*c*) pauses in Purkinje cell activity, in addition to occurring during periods of fixation (*d*). The bars in *A*, *C*, and *E* indicate 1 sec.

For a combined population of burst-tonic and tonic units, increasing tonic levels of activity were observed for saccades in the ipsilateral direction in twenty-nine units, the contralateral in twenty-seven units and the vertical directions in three units. These figures are comparable with those of Lisberger & Fuchs (1978) with the exception of a little less preference for vertical directions in the present sample.

Climbing fibres and complex spike occurrence

The saccade-related discharges observed in eight units potentially correspond to activity of climbing fibres. Recordings were believed to be from climbing fibres if they were of low frequency, i.e. discharging once every second, and if their spike distributions were analogous to those for complex discharges observed in Purkinje cell units. The climbing fibre unit shown in Fig. 8*A* discharged on average once every second. The raster (Fig. 8*B*) illustrates the saccade-related responses, with postsaccadic discharges due either to subsequent saccades or to non-saccade-related firing. A marked similarity is apparent between the occurence of the climbing fibre discharges and the Purkinje cell complex spikes indicated by circles in Fig. 8*D*. Some of the climbing fibre and complex spike discharges in the Figure are positively related to saccades. However, their occurrence within an eye movement period is not related uniquely to either the onset or end of saccades. Discharges are observed at the beginning and at intermediate time during a saccade (Fig. 8*E*, *a* and *b*, respectively). With respect to pause Purkinje cells, the occurrence of a complex discharge at any time during a saccade indicates the lack of a causal relation between climbing fibre activity and Purkinje cell pauses. The saccade-related climbing fibre responses were observed even in the dark, indicating that they were not associated with the visual input which has been observed in climbing fibres of the rabbit (Maekawa & Simpson, 1973) and cat (Simpson, Precht & Llinás, 1974).

DISCUSSION

(1) *Input pathways*

Anatomical studies implicate a functional relationship between the flocculus and brain-stem areas involved with gaze control. Vestibular inputs to the flocculus indicate that this portion of the cerebellum participates in the control of the vestibulo-ocular reflex (Brodal, 1972*b*; Ito, 1974), while olivary inputs have been shown to communicate visual information to the flocculus (Maekawa & Simpson, 1973). In addition to these inputs, the perihypoglossal complex, the inferior central nucleus of the Raphe and the lateral reticular nucleus are known to project to the flocculus in the rabbit (Alley, 1977). Similar projections have been demonstrated in the cat and monkey with an additional finding that there are direct afferents to the flocculus arising in the oculomotor complex (Graybiel, 1977; Kotchabhakdi & Walberg, 1977).

Physiological observations indicate that the nucleus prepositus hypoglossi receives visual, eye and neck movement information (Gresty & Baker, 1976) and suggests that such sensori-motor information is further communicated to the flocculus. Little is known of the inferior central nucleus of the raphe, but it is interesting to note that this nucleus is located next to the nucleus raphe pontis (Carpenter, 1976), where the brain-stem pause units intimately involved with saccade initiation are believed to exist (Keller, 1977). Of the afferents to the lateral reticular nucleus, the superior collicular inputs (Kawamura, Brodal & Hoddevik, 1974) are notable because of the known collicular participation in the control of eye movements and the possible existence of a tecto-reticulo-floccular pathway. Comparisons between eye-movement-related neuronal activity recorded in these areas and discharge patterns observed in afferents to the flocculus are enlightening.

(2) *Possible flocculus–brain stem inter-relations*

Long-lead bursts associated with saccades have been reported for units only in the thalamic internal medullary lamina (Schlag & Schlag-Rey, 1977), the superior colliculus (Schiller & Koerner, 1971; Wurtz & Goldberg, 1972; Sparks & Pollack, 1976), and the paramedian pontine reticular formation (p.p.r.f.) (Luschei & Fuchs, 1972; Keller, 1974). The agreement between lead times for long-lead burst units in the superior colliculus and such units in the flocculus suggests the possibility of saccade-related information reaching the flocculus from the superior colliculus. Compatible with this possibility is the finding that the superior colliculus projects to the lateral reticular nucleus (Kawamura *et al.* 1974), which in turn projects to the flocculus, implicating some functional involvement between the superior colliculus and the flocculus.

Long-lead burst neurones of the p.p.r.f. have been shown to receive short latency excitatory inputs from the superior colliculus (Raybourn & Keller, 1977). Although direct pathways have not been found either from the superior colliculus or the p.p.r.f. to the flocculus, the similarities between the saccade-related long-lead burst units in all three areas indicate that activity preceding eye movements on the order of hundreds of milliseconds may reach the flocculus from the superior colliculus either via or independent of the p.p.r.f.

Burst units are also found in the p.p.r.f. (Luschei & Fuchs, 1972; Keller, 1974) and a notable similarity to burst units in floccular afferents is their comparable behaviour during periods of drowsiness. Activity in burst units of both areas is characterized by a transition from saccade-related phasic discharges to irregular tonic activity as the monkey's eyes start to wander and drift about (Keller, 1976; this paper, Fig. 6).

Transient discharges were observed for saccades in all directions in 59 % of the floccular burst non-Purkinje units. In contrast, similar units recorded in the p.p.r.f. constituted 31 % (Keller, 1974) or 34 % (Luschei & Fuchs, 1972) of the burst neurones. An important observation concerning the p.p.r.f. burst units was the lack of units discharging for purely contralateral or vertical saccades. There was a similar tendency for neurones in the vestibular nuclei (Miles, 1974). The discharges of the burst neurones of the mesencephalic reticular formation were associated with a predominantly vertical component of saccades (Büttner, Hepp & Henn, 1977; King & Fuchs, 1977).

In the p.p.r.f., burst-lead times ranged from 3 to 13 msec with a mode between 8 and 9 msec (Luschei & Fuchs, 1972) or ranged from 7 to 12 msec and averaged 9 msec (Keller, 1974). Lead times for burst units of the vestibular nuclei ranged from 5 to 15 msec (Miles, 1974) which matched the range observed for burst units of the mesencephalic reticular formation (Büttner *et al.* 1977). Burst-lead times for mossy fibres in the flocculus averaged 6·9 msec in our population and 6·3 msec in the sample of Lisberger & Fuchs (1978).

The preferred directions and temporal characteristics observed for burst neurones of the pontine and mesencephalic reticular formations implicate a convergence of burst signals onto cells from which burst mossy fibres originate. With respect to encompassing all examples of directional preferences, the pontine and mesencephalic reticular formations are complementary and the integration of saccade-related phasic activity from each structure would result in bursts associated with saccades in all directions. Burst-lead times for reticular and mossy fibre burst units are consistent with the possibility of a polysynaptic pathway between the reticular formation and the flocculus.

Burst-tonic and tonic discharge patterns are observed in units within many of the structures intimately associated with eye movements. Both patterns have been recorded in neurones of the superior and medial vestibular nuclei (Miles, 1974;

Keller & Daniels, 1975; Fuchs & Kimm, 1975), the p.p.r.f. (Luschei & Fuchs, 1972; Keller, 1974) and the prepositus hypoglossal nucleus (Baker, Gresty & Berthoz, 1975). Burst-tonic and tonic mossy fibres of the flocculus share some characteristics with similar cell types in the vestibular nuclei and the prepositus hypoglossal nucleus (Fuchs & Kimm, 1975; Baker *et al.* 1975) reflecting the anatomically proven projections from these structures to the flocculus.

Burst-tonic units in the vestibular and prepositus hypoglossal nuclei and the p.p.r.f. resemble floccular mossy fibre burst-tonic units in that burst durations approximate saccade durations. Comparing the vestibular nuclear neurones and mossy fibre burst-tonic units in the flocculus, agreement also exists with respect to burst-lead times. In the distribution of burst-lead times for vestibular burst-tonic neurones, Fuchs & Kimm (1975) observed a modal point between 6 and 8 msec which agrees well with the average lead time of 6·9 msec calculated for mossy fibres in the present study. Baker *et al.* (1975) observed that burst-tonic neurones in the prepositus hypoglossal nucleus sometimes exhibited burst lead times of up to 20 msec. This is compatable with the 0–19 msec range for lead times found in the mossy fibres of the flocculus. Burst-tonic units in all structures are similar in that they exhibit pauses for saccades in non-preferred directions. Although burst-tonic and tonic activity have been observed in the p.p.r.f. (Luschei & Fuchs, 1972; Keller, 1974), further characterization of these units is required before conclusions can be made concerning the possibility of the p.p.r.f. as an indirect source of such activity in mossy fibres.

(3) *Input–output transformations*

It has been shown in a preceding paper (Noda & Suzuki, 1979*a*) that the great majority of Purkinje cells in the flocculus stop firing slightly before the onset and throughout the period of a saccade. During steady fixation, Purkinje cells maintain high levels of tonic discharges which change in relation to eye positions in some cells. It has also been shown that the regularity of tonic discharges reflects the degree of stability in eye position during fixation (Noda & Suzuki, 1979*b*). As Purkinje cells constitute the only output from the flocculus and exert inhibitory synaptic action upon their direct target cells (see Eccles, Ito & Szentágothai, 1967 for a review), the flocculus seems to exert a tonic inhibitory influence upon the oculomotor system and helps to maintain stable retinal images during steady fixation. The tonic inhibition is suddenly removed with saccades. This may produce a disinhibitory action upon the target cells and result in bursts with very precise temporal relationships with the duration of saccades. The degree of inhibitory influence varies with changes in fixation points, implicating the flocculus as a source of eye position information for the oculomotor system (Noda & Suzuki, 1979*b*). The flocculus may thus ensure the accuracy of eye movements and help to maintain a visual target on the fovea.

The present study has indicated that the flocculus receives eye movement and position information from the brain stem and transforms it into such discharge patterns as observed in the Purkinje cells (Noda & Suzuki, 1979*a*). From a straightforward consideration of the mossy fibre-granule cell-Purkinje cell pathway, one would expect the afferent bursts to be translated into saccade-related bursts in the Purkinje cells and such is probably the case for burst and possibly for burst-pause Purkinje cells. Since the majority of Purkinje cells pause during saccades, while the majority of mossy fibres exhibit bursts, it is conceivable that the transient cessation in Purkinje cell tonic activity may also reflect the burst activity observed in floccular afferents.

Eccles *et al.* (1967) have proposed three quite distinct inhibitory mechanisms in the cerebellar cortex. In the first mechanism, the mossy fibre input, via granule cell activation, excites basket cells which in turn inhibit Purkinje cells. This inhibitory action of basket cells is intense as a consequence of the characteristic terminations of basket cell axons around the Purkinje cell somata. The second and third mechanisms involve Golgi cells which provide negative feed-back loops which inhibit granule cells. Since Purkinje cells discharge spontaneously even in the deafferented preparation (see Eccles, *et al.* 1967 for a review), it would be difficult to explain the complete suppression of Purkinje cell activity as resulting solely from an inhibition of input signals at the granule cell level. Considering the magnitude of the number of parallel fibres converging on a given Purkinje cell, the direct inhibition of the Purkinje cell would appear to be a more efficient mechanism for pause generation than inhibition of all the converging granule cells. Since Golgi cells do not directly inhibit Purkinje cells, it would appear that the pauses in Purkinje cells are produced primarily by the burst of mossy fibre discharges acting through basket cell activation.

A consideration of the characteristics of the input signals entering the flocculus supports the hypothesis of a causal relationship between bursts in afferents and pauses in Purkinje cells. Of the mossy fibre population, nearly half (thirty-one out of sixty-seven units or 46·2 %) exhibited saccade-related bursts and no intersaccadic activity. Within burst-tonic mossy fibres (fifteen out of sixty-seven units or 22·4 %), the intraburst frequency was usually more than five times greater than the frequency of the intersaccadic tonic activity. Depending on eye position, intersaccadic periods of zero activity were also observed in mossy fibres exhibiting tonic activity. Thus, the total number of impulses being carried to the flocculus by the mossy fibres is enormously greater during saccades than during fixation. Activity in afferents to the flocculus will exert an excitatory influence on both basket and Purkinje cells, since both cell types are innervated by a 'beam' of parallel fibers (Eccles *et al.* 1967). During intersaccadic periods, however, the excitatory impulses to the basket cells may cause predominantly subthreshold excitation, and Purkinje cell activity would be the primary reflexion of excitatory input entering through the parallel fibres. During saccades, on the other hand, the number of impulses entering the flocculus increase substantially and basket cells are strongly activated, resulting in the generation of a burst of inhibitory impulses which would cause the complete suppression of Purkinje cell activity. Due to possible differences in the thresholds of individual basket cells, variations in the patterns of inhibition produced by the basket cells would occur and be responsible for the pause or burst variation of Purkinje cell responses to saccades.

The tonic levels of discharges in some Purkinje cells were proportional to eye positions in a certain plane. Such position-related discharges implicate a role of the flocculus in maintaining eye position, especially in eccentric gaze (Noda & Suzuki, 1979*b*). The data in the present study indicate that eye position information is supplied by the mossy fibres to the flocculus. This information, however, has to be integrated by the processing circuitry of the flocculus. Position-related Purkinje cell output signals differ strikingly from the mossy fibre inputs in that the Purkinje cell activity encompassed almost the entire range of eye positions, whereas in mossy fibres the tonic level of activity was proportional to eye positions only within a limited range. Below the 'position threshold' all burst-tonic or tonic mossy fibre units were completely silent. The convergence onto Purkinje cells of units from the population of burst-tonic and tonic units which show all-or-nothing position dependent activity with different position thresholds would also contribute to the full range of position information. Convergence of such seemingly limited eye position information, conveyed by individual channels of mossy fibres, may result in the full range of position-related activity observed in Purkinje cells.

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