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THE DISCHARGES OF CEREBELLAR GOLGI CELLS DURING LOCOMOTION IN THE CAT

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SUMMARY

1. Extracellular recordings have been obtained from 134 units in the paravermal cortex of lobule V in the anterior lobe of the cerebellum in free-to-move cats. Each unit discharged action potentials in a characteristic pattern with no complex spikes. Previous investigators have described such discharges and have assigned them to Golgi cells. We provide further evidence to support this identification.

2. In cats which were sitting quietly, each putative Golgi cell discharged tonically at a low rate (overall mean (±S.D.) was 14·5±7·3 spikes/s). Eighty-one of the neurones were also recorded during steady walking on a moving belt and the discharge rate then averaged 17·7 (S.D. ±19·4) spikes/s.

3. All eighty-one putative Golgi cells discharged rythmically during locomotion. Many different patterns of discharge were seen but as a population the neurones were most active in early stance and at the onset of the swing phase of the step cycle in the ipsilateral forelimb.

4. Over a range of different walking speeds (0·5–0·9 m/s) and of different uphill inclines (0–25 deg), putative Golgi cells discharged with similar patterns and rates, despite large changes in the vigour of the locomotor movements and in the amplitude of limb muscle electromyograms.

5. Groups of putative Golgi cells and of Purkinje cells recorded from restricted cortical regions produced discharges which fluctuated approximately in parallel during locomotion. However, a comparison of the activity patterns of pairs of closely adjacent Golgi and Purkinje cells revealed a wide variety of phase relations. The possible role of Golgi cells in determining the Purkinje cell output is discussed in the light of these findings.

INTRODUCTION

A profitable recent approach to investigating the role of the cerebellum in motor control has been to record the activity of single neurones during active movements. A striking fact emerging from these studies has been that a high proportion of cerebellar neurones display movement-related discharges. In the case of Purkinje

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cells, which are the output cells of the cerebellar cortex, such discharges have been found during skilled movements in primates (see Brooks & Thach, 1981, for review) and during locomotion and scratching in cats (Orlovsky, 1972; Udo, Matsukawa, Kamei, Minoda & Oda, 1981; Arshavsky, Orlovsky & Popova, 1984; Armstrong & Edgley, 1984*b*). One major contributor to determining the precise pattern of these discharges must be the nature of the impulse traffic in the cerebellar afferent pathways which terminate as mossy fibres and climbing fibres: many of these have been described and it is clear that both peripheral afferent and central 'efference copy' information are conveyed to the cerebellum in abundance (see Oscarsson, 1973; Bloedel & Courville, 1981).

However, the cerebellar cortex contains numerous inhibitory interneurones which can also influence the Purkinje cell output. These interneurones are of three main types: basket, stellate and Golgi cells. The basket and stellate cells receive excitatory input from granule cells and distribute postsynaptic inhibition to Purkinje cells. Golgi cells, by contrast, receive excitatory inputs directly from mossy fibres and also from the granule cells and in turn they postsynaptically inhibit the granule cells (see Eccles, Ito & Szentagothai, 1967; Ito, 1984). Little is known about the activity of these types of interneurone during motor behaviour, so their role in shaping Purkinje cell activity (i.e. the cortical output) remains unknown.

We have investigated the activity of one of these types of interneurone, namely the Golgi cell, the characteristic discharges of which have recently been described (Miles, Fuller, Braitman & Dow, 1980; Schulman & Bloom, 1981). In the present study, recordings were made from a large population of neurones with the same characteristics in awake cats and further evidence that they arise from Golgi cells is presented here. Most of the neurones were recorded during locomotion on a moving belt, in some cases at several different speeds and on different gradients. The locomotor-related activity of these neurones is described and is also compared with that of a substantial population of Purkinje cells from the same region of cortex. This comparison is used to infer possible roles of the Golgi cells in determining the Purkinje cell output.

An abstract of some of this work has been published (Edgley & Lidierth, 1985).

METHODS

Microelectrode recordings were made from twelve cats trained to accept handling and to walk steadily for brief periods on a moving belt. Details of the preparative surgery and the techniques for recording cerebellar unit discharges and limb muscle electromyograms (e.m.g.s) have been given in full in previous publications (Armstrong & Rawson, 1979; Armstrong & Drew, 1984; Armstrong & Edgley, 1984*a*).

Recordings of cerebellar unit activity and limb muscle e.m.g.s were fed to a tape-recorder (Racal Store 7D) for later analysis. The muscles studied included at least one extensor (lateral head of triceps brachii) and two or three flexor muscles from the ipsilateral forelimb (brachialis, biceps brachii, cleidobrachialis), together with the same muscles of the contralateral forelimb and the lateral gastrocnemius muscle of the ipsilateral hindlimb. Data analysis was performed using methods previously described (Armstrong & Drew, 1984; Armstrong & Edgley, 1984*a*). Briefly, determinations of the timings of unit discharges relative to the step cycle were made using computer-generated raster and post-event time histogram displays. In order to compare the discharges of different cells or a single cell during different types of locomotion the post-event time

histograms were normalized by using a bin width of 1/10th or 1/25th of the average step cycle duration. These displays could be triggered from the onsets of e.m.g. activity of any chosen muscle. In practice, the activity of the ipsilateral triceps brachii was used most frequently, as this muscle reliably produced one large burst of e.m.g. per step with clear onset and offset.

Locations of recording sites were determined histologically using either Merrill's (1974) technique of depositing iron from the microelectrode tip, or by passing current through the recording electrode to make small electrolytic lesions (5–20 μA for 20 s). To facilitate later location of these marks, larger lesions (20 μA for 30 s) were sometimes made after withdrawing the microelectrode by 1 mm. The cats showed no sign of being aware of the passage of this current. Following fixation, sections of the cerebellum were cut at 50 or 100 μm on a freezing microtome and were counterstained using cresyl violet or neutral red.

RESULTS

Identification and electrophysiological characteristics of Golgi cell discharges in the resting animal

Two distinct types of neural unit were commonly encountered in recordings from the cerebellar cortex of awake but passive cats. Most common were the discharges of Purkinje cells which were readily identifiable by the presence of the highly characteristic complex spikes (Eccles *et al.* 1967) which occur at low rates in the awake resting cat (1–2 spikes/s, Armstrong & Rawson, 1979). Most Purkinje cells also discharged simple spikes at much higher frequencies.

A second, less frequently encountered type of unit was found close to, but not in, the Purkinje cell layers. Such units differed from the Purkinje cells in several important respects. Firstly, and most importantly, none of them ever discharged potentials resembling complex spikes. Secondly, their action potentials were of long duration, ranging from 0·8 to 2·0 ms (as compared to 0·3–1·0 ms for Purkinje cells, see Armstrong & Edgley, 1984*b*). The action potentials from three different units are illustrated in Fig. 1*A*. A third difference was that, although all of these units discharged tonically, their discharge rates were low. Figure 1*B* shows the discharges of the same three units recorded in passive, sitting cats and a discharge rate distribution histogram for 134 such units is illustrated in Fig. 2*A*. The mean rates estimated from a sample of 20 s or more in duration ranged from 1·7 to 43·5 spikes/s and the overall mean was 14·5 (S.D. $\pm$7·3) spikes/s. For comparison, Fig. 2*B* is a discharge rate distribution histogram for 129 Purkinje cells encountered in the same cortical area. The range of rates among the Purkinje cells is much wider and although some discharged very slowly (those which discharged mainly complex spikes) the overall mean rate was higher than the rate of any of the cells included in Fig. 2*A*. Figure 2*C* shows the distribution of modal interspike intervals (derived from interspike interval histograms) for both Purkinje cells and Golgi cells. The two distributions overlap to only a minor extent: most Purkinje cells discharged with modal intervals of 4–20 ms, while most putative Golgi cells discharged with modal intervals of between 20 and 80 ms. The fourth difference is the marked regularity of the discharges which is evident in Fig. 1*B* and which is in marked contrast to the irregular discharges of Purkinje cells (e.g. Armstrong & Rawson, 1979; Arshavsky, Orlovsky & Popova, 1984).

Though it is clear from the above that the units differ markedly from Purkinje cells, there are a number of other cerebellar cortical elements which might give rise

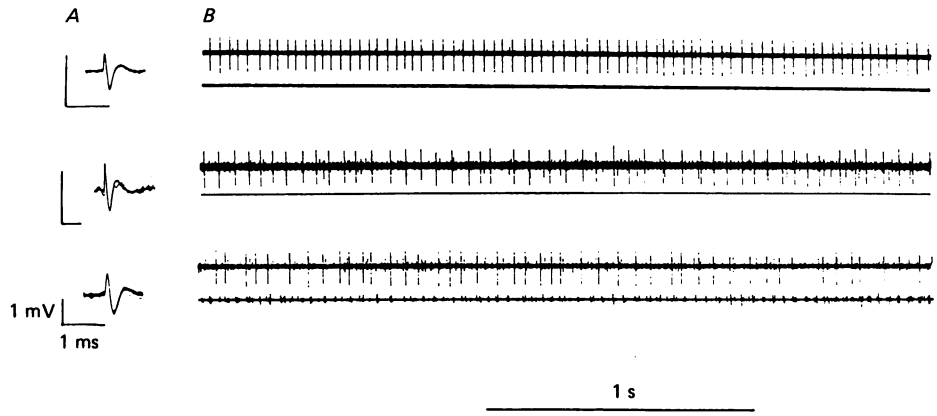

Fig. 1. The resting discharge of Golgi cells. *A* shows several superimposed traces of the action potentials in three Golgi cells while *B* shows the discharge in each cell in the resting animal. The lower traces in *B* are the e.m.g.s in the ipsilateral triceps brachii muscle. Negativity up in each case. Calibrations are 1 mV and 1 ms throughout. Note the different time base for the middle record in *A*.

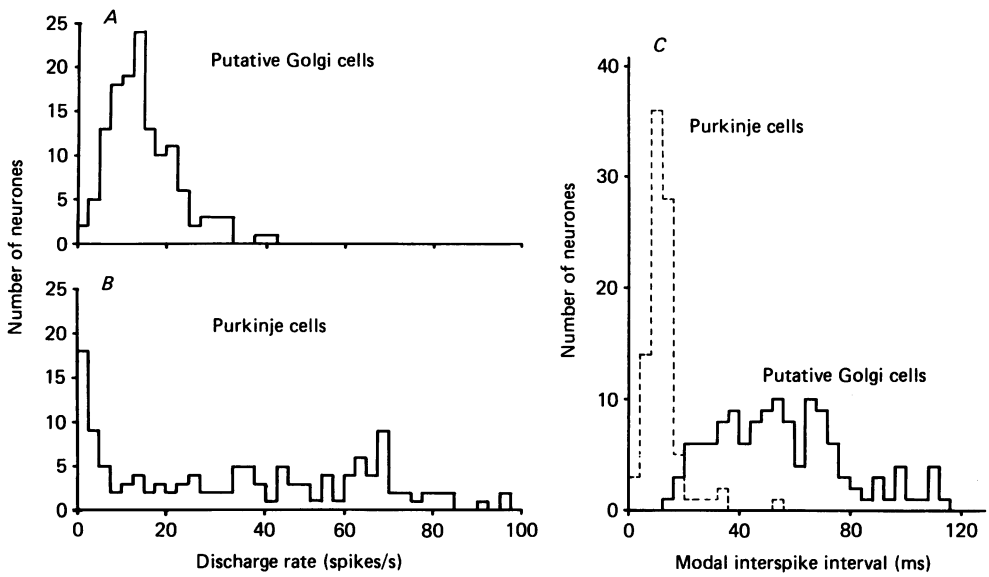

Fig. 2. Comparison of the resting discharge rates in 134 Golgi cells and in 129 Purkinje cells from the paravermal cortex of lobule V (Purkinje cell data are from Armstrong & Edgley, 1984*b*). *A* and *B* are frequency distribution histograms of the mean discharge rates in the Golgi cells ($n = 134$) and Purkinje cells ($n = 129$), respectively. *C* shows the frequency distributions of the modal interspike intervals in the same cells as in *A* and *B*.

to the observed potentials. However, several lines of evidence are available to help eliminate some of the possibilities. Several factors suggest that the discharges originate from neurone somata, rather than from axons: they were never encountered in the subcortical white matter, typical injury discharges and sometimes spike fractionation could be seen when the unit was damaged by the microelectrode and the

action potentials were of unusually long duration. Furthermore, the spikes were often large (up to 5 mV) and electrical contact could usually be maintained during electrode movements of more than 100 μm, suggesting an origin from large structures. These

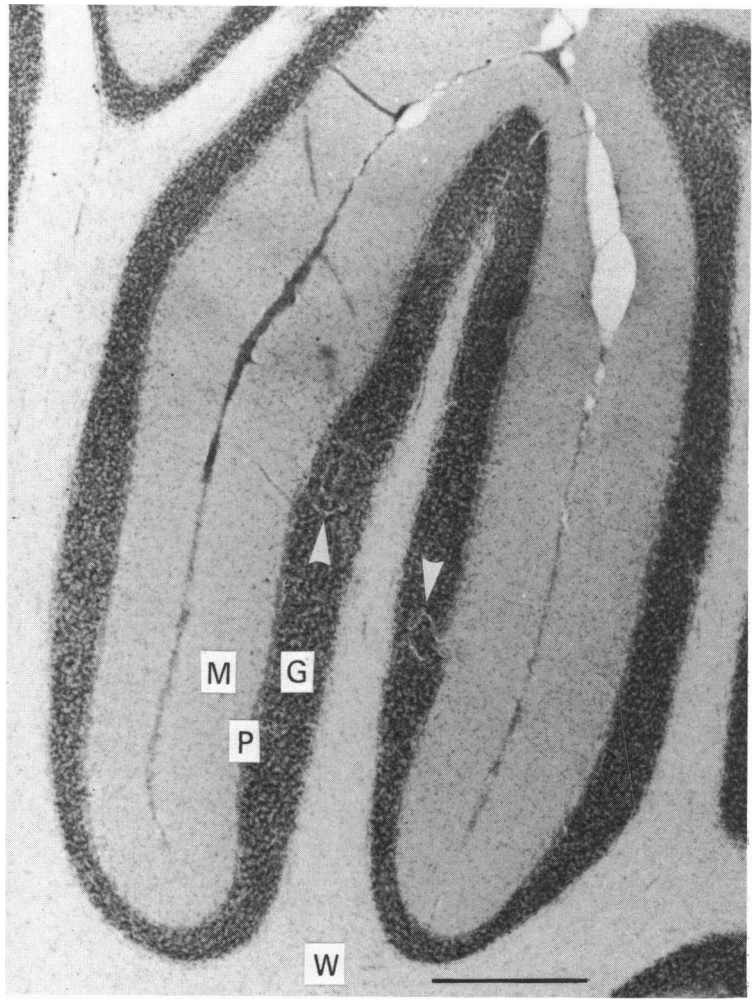

Fig. 3. Sagittal section of the cerebellum (50 μm thickness) showing the location of two microlesions (arrows) made at the sites from which two Golgi cells were recorded in a sodium pentobarbitone-anaesthetized cat. Abbreviations: M, molecular layer; P, Purkinje cell layer; G, granular layer; W, white matter. Calibration bar is 500 μm.

lines of evidence would seem to eliminate mossy fibre rosettes and granule cells as possibilities.

It appears therefore that these discharges originated from either the basket or stellate cells which lie directly above the Purkinje cells in the molecular layer or the Golgi cells which lie below them in the granular layer. Given the folded nature of the cerebellar cortex, it was often impossible to ascertain the precise location of neurones recorded in the depths of the cortex in relation to the cortical layers. However, in the

superficial parts of electrode tracks it was very noticeable that units of the regularly discharging type were found just deep to the Purkinje cell layer encountered or just superficial to the second, suggesting that they were Golgi cells. In order to determine their location with certainty, histological localizations were obtained as described in Methods. In all ten cases where the recording location was determined (three cases using iron deposition and four cases using microlesions made in sodium pentobarbitone-anaesthetized animals (40 mg/kg I.P., supplemented as necessary) plus three cases using microlesions in awake animals) it was found to lie in the granular layer. The experiments with anaesthesia were performed as terminal experiments on the animals which had been recorded from while awake. Note that the discharge properties of Golgi cells in the anaesthetized animal were similar to those in the awake animal, as were the shapes of the recorded action potentials (see Discussion). Two lesions made in the anaesthetized cat are shown in a single section of the cerebellum in Fig. 3. The evidence therefore supports the identification of these units as Golgi cells.

Peripheral receptive fields of Golgi cells

Whenever possible, somatosensory receptive fields were determined for the Golgi cells using weak tactile stimuli (pats, taps, hair brushing) applied while the animal sat quietly on the experimenter's knee. Such methods cannot allow a rigorously precise definition of receptive fields in awake animals (see Armstrong & Edgley, 1984*a*) but nevertheless provide a useful description of the tactile input to the neurone.

Ninety Golgi cells were examined in this manner and the discharges of all but three (3·3%) could be accelerated by tactile stimuli. Of the eighty-seven neurones which were influenced, almost all (85/87; 97·7%) had receptive fields which included the ipsilateral forelimb. One of the two neurones which lacked forelimb input was driven from the hindlimb, and the other from the face. Convergent inputs from the hindlimbs or face were occasionally found for those neurones with forelimb receptive fields (1 and 14%, respectively). Of thirty-six neurones tested for bilateral input, twenty-two (61%) received input from both forelimbs, usually from equivalent areas on each limb.

A particularly detailed evaluation of the receptive fields on the ipsilateral forelimb was performed in sixty-six cases and for forty-seven neurones (71%) the strongest input was from the distal part of the limb (i.e. below the elbow). All of the neurones with bilateral receptive fields were in this category.

These receptive fields bear a striking similarity to those of the Purkinje cells in this region of cortex (Armstrong & Edgley, 1984*b*; S. A. Edgley & M. Lidierth, in preparation). In particular, the fields of Purkinje cells and Golgi neurones recorded in close proximity in the same electrode tracks were similar.

Discharges of Golgi cells during locomotion

Recordings were obtained from a total of eighty-one Golgi cells while the animal walked steadily on a belt moving at between 0·4 and 0·7 m/s. All of these neurones were recorded during at least one period of twenty consecutive and regular steps. Discharge rates ranged from 1·6 to 48·5 spikes/s and a discharge rate distribution histogram is shown in Fig. 4*A*. The overall mean rate was 17·7 (S.D. $\pm$ 19·4) spikes/s

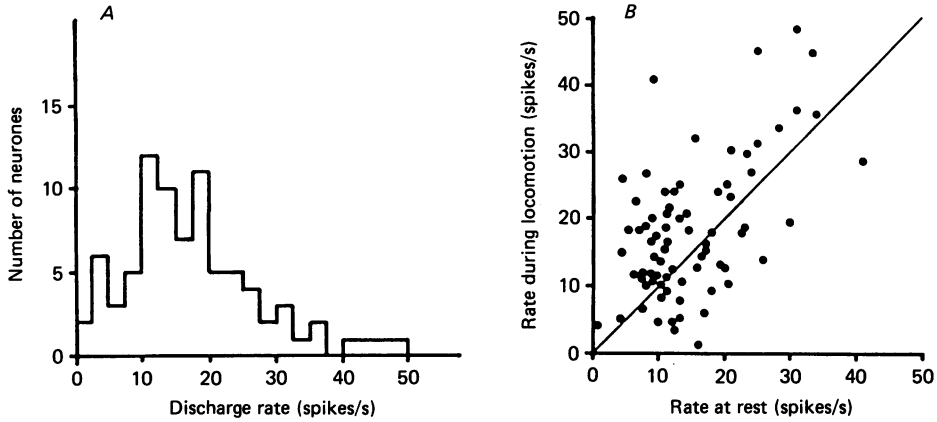

Fig. 4. The discharge rates of eighty-one Golgi cells during locomotion at 0·5–0·7 m/s. *A* shows the frequency distribution histogram of mean firing rates in the cells. *B* compares for each cell the mean rate during locomotion with that in the resting animal. Diagonal line is line of equality of rate.

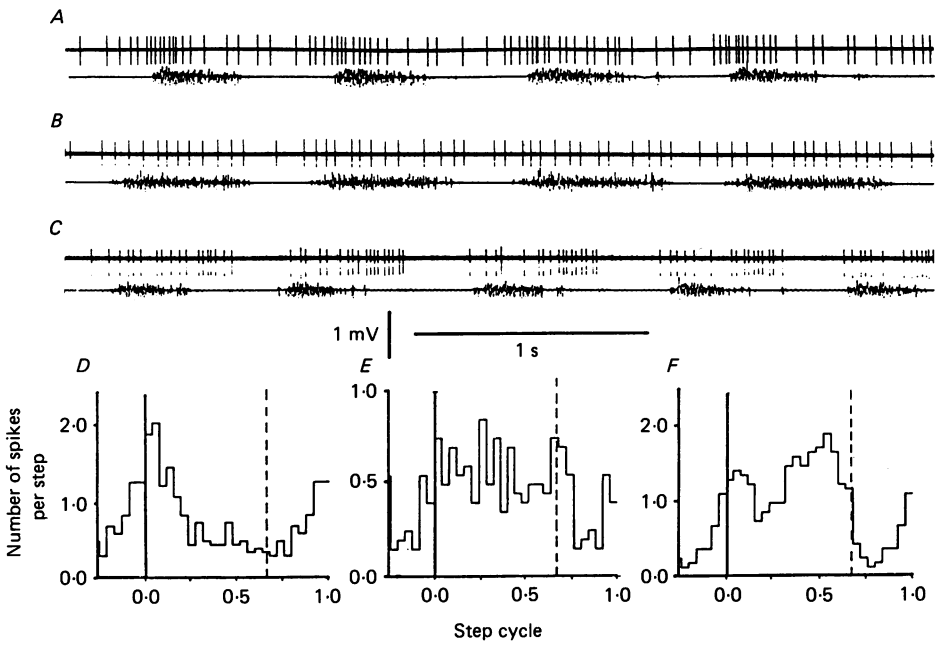

Fig. 5. Frequency modulation of the discharges of three Golgi cells during locomotion. *A*, *B* and *C* each show the discharge of a Golgi cell (upper trace) together with the e.m.g. from the ipsilateral triceps brachii muscle (lower trace). Calibrations below *C* apply to the unit discharges throughout *A*, *B* and *C*. *D*, *E* and *F* show post-event time histograms for the three cells in *A*–*C*. The zero time reference is the time of onset of the ipsilateral triceps brachii e.m.g. and the dashed vertical line indicates the time of transition between the stance and swing phases of the step cycle in the ipsilateral forelimb. Step durations are normalized. Bin width is one-twenty-fifth of the step cycle. Each histogram includes twenty successive steps.

which is not significantly higher (Student's t test, $P > 0{\cdot}05$) than the mean rate in the passive animal. However, most individual neurones discharged at different rates at rest and during locomotion, as can be seen from Fig. 4*B*. Although many neurones discharged faster during locomotion, this change was not accompanied by the appearance of interspike intervals of less than 10 ms.

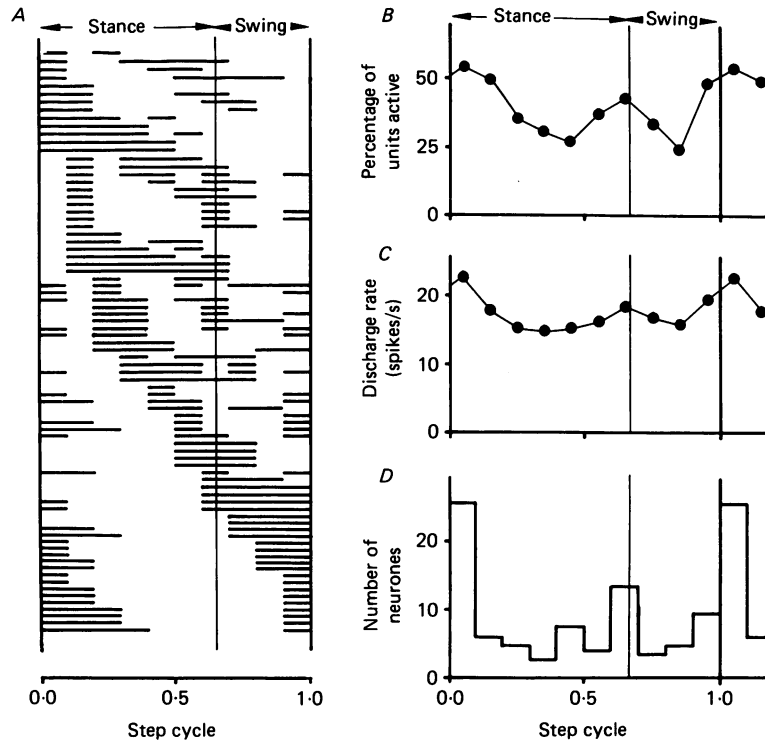

Fig. 6. Summary of the activity patterns in all eighty-one Golgi cells during locomotion. The horizontal axis in each diagram shows the normalized step cycle with the onset of the e.m.g. in the ipsilateral triceps brachii as the zero reference. *A*, the continuous horizontal lines show the active periods (see text) in each of the eighty-one neurones while *B* shows the percentage of cells that were active in each tenth of the step. *C* shows the mean discharge rate and *D* the number of cells discharging at peak rate during each tenth of the step.

Filmed recordings from three Golgi cells during locomotion are illustrated in Fig. 5*A–C*. Each discharged in a rhythmic pattern which was time-locked to the step cycle. The extent of this rhythmicity is not easily quantified in recordings such as those in Fig. 5*A–C*, so the discharges were further analysed by averaging them over twenty step cycles (see Methods) and constructing post-event time histograms. Those prepared for the neurones in Fig. 5*A*, *B* and *C* are shown in Fig. 5*D*, *E* and *F*, respectively. Values for the average discharge rate of each neurone during each tenth of the step cycle were taken from similar histograms constructed with a bin width of one-tenth of the average step cycle duration (cf. Armstrong & Edgley, 1984*a*, *b*). This process allows a determination of the peak discharge rate (from the

tenth during which the neurone discharged at its highest rate) and of the minimum rate (from the tenth when the neurone discharged least). Units were considered to discharge in a frequency-modulated manner when either the peak or minimum rate differed from the overall mean rate by 10% or more (see Armstrong & Edgley,

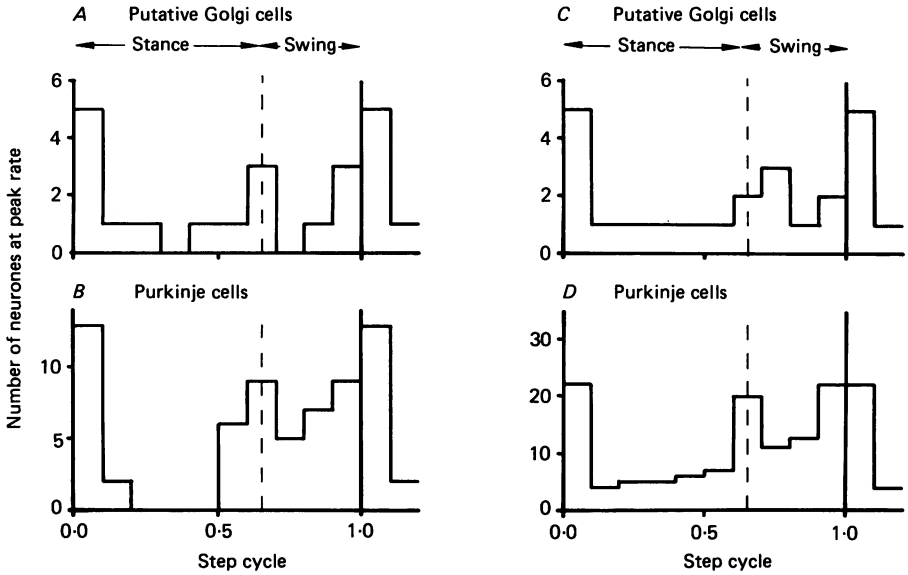

Fig. 7. Comparison of the step-related activity in the populations of Golgi cells and Purkinje cells recorded in close proximity in the paravermal cortex of lobule V. *A* and *B* show the number of neurones achieving peak rate in each tenth of the step in sixteen Golgi cells and forty-nine Purkinje cells recorded from a single animal. *C* and *D* are similar plots for eighteen Golgi cells and 115 Purkinje cells recorded in the medial part of the paravermal cortex in nine animals.

1984*a*, *b*). Using this definition, all eighty-one neurones discharged in a frequency-modulated pattern during locomotion. However, the extent of the modulation varied widely: many neurones discharged throughout the step though at varying rates, while 33% were silent during one or more tenths of the step.

The discharge timing of the Golgi cells as a population was assessed using an approach similar to that used by Armstrong & Edgley (1984*a*, *b*) to describe the activity of Purkinje cells. Firstly, each neurone was considered to be 'active' during the tenths of the step when its discharge rate exceeded the average rate by 10% or more. On this basis, thirty-seven neurones (46%) had one 'active' period in each step, a further thirty-four neurones (42%) had two such periods and eight (10%) had three. In Fig. 6*A* the active periods of each of the putative Golgi cells is represented by a horizontal line and the vertical lines show the timing of the step cycle: a very wide range of different patterns of activity is apparent. These data are transformed in Fig. 6*B* to illustrate the proportion of neurones active during each tenth of the step. Two broad peaks are present: the largest occurs at the onset of stance and the second occurs at the onset of swing; substantially fewer neurones were active in the middle of the stance and swing phases. The average discharge rate of the whole population of neurones during each tenth of the step is plotted in Fig. 6*C*, and Fig. 6*D*

is a histogram showing the number of neurones discharging at peak rate during each tenth of the step. Each of these displays reveals a similar pattern, with most activity in the population occurring early in stance and at the transition from stance to swing.

The relationship between the discharges of Golgi cells and those of Purkinje cells

One aspect of the putative Golgi cells discharges which is of particular interest is their relationship to the activity of nearby Purkinje cells, since this might give an indication of their role in modifying the cerebellar cortical output. A comparison of the activities of putative Golgi cells and Purkinje cells has been made in two ways: firstly by comparing the activities of groups of neurones recorded from restricted areas of cortex and secondly by comparing the discharges of pairs of neurones recorded in close succession in single electrode penetrations.

The results of the former approach are illustrated in Fig. 7. Figure 7*A* and *B* shows the times of peak activity for a group of sixteen Golgi cells and a group of forty-nine Purkinje cells, respectively. All were recorded from a single cat in which the recording chamber was fixed over the lateral part of the intermediate zone (c2 and c3 zones, see Ekerot & Larson, 1979). The activity of the two groups is similar: both show high activity at the times of transfer between stance and swing (i.e. at approximately the times of foot placement and foot lift). A similar comparison is made in Fig. 7*C* and *D* for groups of eighteen Golgi cells and 115 Purkinje cells, respectively, which were recorded from the medial part of the intermediate zone (c1 and c2 zones) in nine cats. Again the discharge patterns of the two groups of neurones are similar. These data therefore show that the peak of activity in the Golgi cell population generally coincides with that of the local Purkinje cells.

The approach used above has obvious limitations, however, in that the recordings were made in regions of cortex where individual neurones, of both types, could discharge with widely differing patterns. Comparing the discharges of closely adjacent neurones may overcome these problems, although it is technically more difficult. In twelve cases recordings were obtained from Purkinje cells in close proximity to one of the Golgi cells. Neurones were considered to be in close proximity when their recording locations were less than 200 μm apart in the same electrode penetration. In these cases the discharge patterns have been compared using post-event time histograms. This approach yielded equivocal results: in three pairs the discharges were in phase (compare the upper and lower histograms of Fig. 8*A* and *B*) and the peak activities coincided while in seven cases they did not coincide but were phase shifted (Fig. 8*C* and *D*). In the remaining two cases there was no clear relationship. These data show that the phase relationship between individual Golgi and Purkinje cells which are close neighbours in the cortex is variable.

Discharges of Golgi cells during locomotion at different speeds

As all of the putative Golgi cells discharged in relation to locomotor movements, it is of interest to know how their activity varied during different locomotor conditions. To this end, whenever stability permitted, recordings were made during walking at different speeds. Stable recordings were obtained from fourteen Golgi cells during locomotion at both 0·5 m/s (a slow, steady walk) and at 0·9 m/s (a hurried walk). The pace durations at these speeds averaged 803 (S.D. $\pm$80) and 582 (S.D. $\pm$43)

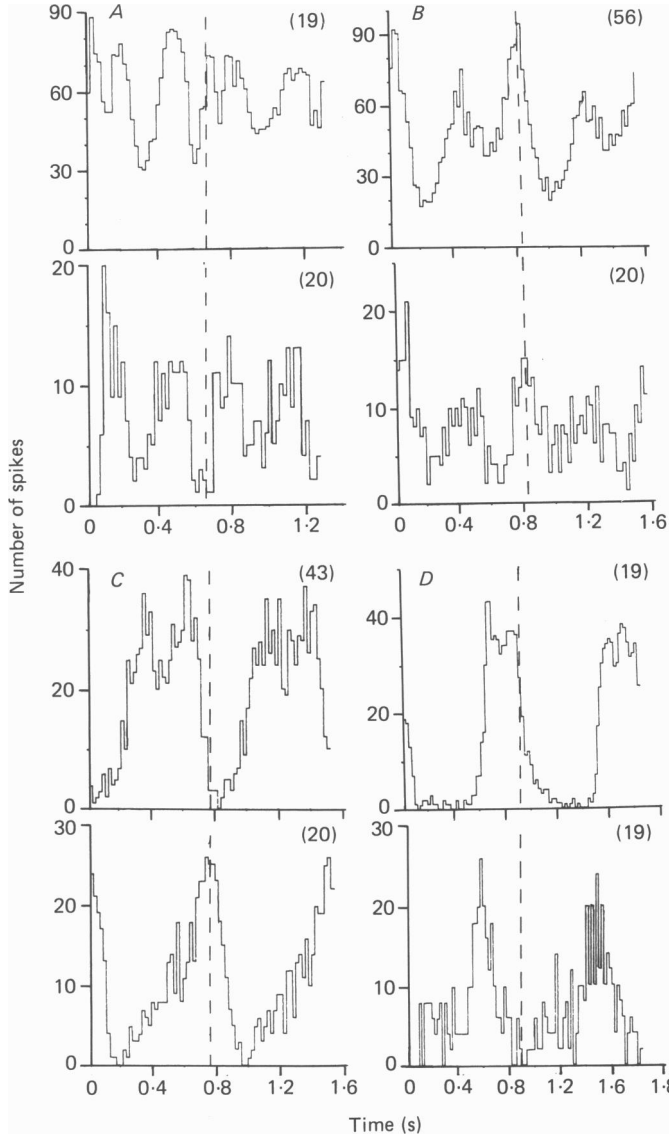

Fig. 8. Comparison of the discharge patterns of pairs of closely adjacent Golgi cells and Purkinje cells during locomotion. *A–D* each show the post-event time histogram of a Golgi cell (lower) and an adjacent Purkinje cell (upper). Both recordings were made at electrode positions less than 200 μm apart. Bin width is 20 ms in each case and *two* step cycles are shown in each histogram; the dashed vertical line indicates the average point at which the first cycle was completed. The numbers to the right of each histogram (in parentheses) show the numbers of steps used to construct the histograms.

ms, respectively. Compared to 0·5 m/s, the velocity of limb movement is considerably higher during locomotion at 0·9 m/s and the amplitudes of the limb muscle e.m.g. bursts are considerably larger (D. M. Armstrong & S. A. Edgley, in preparation).

Comparisons of the discharge patterns of each neurone during locomotion at the

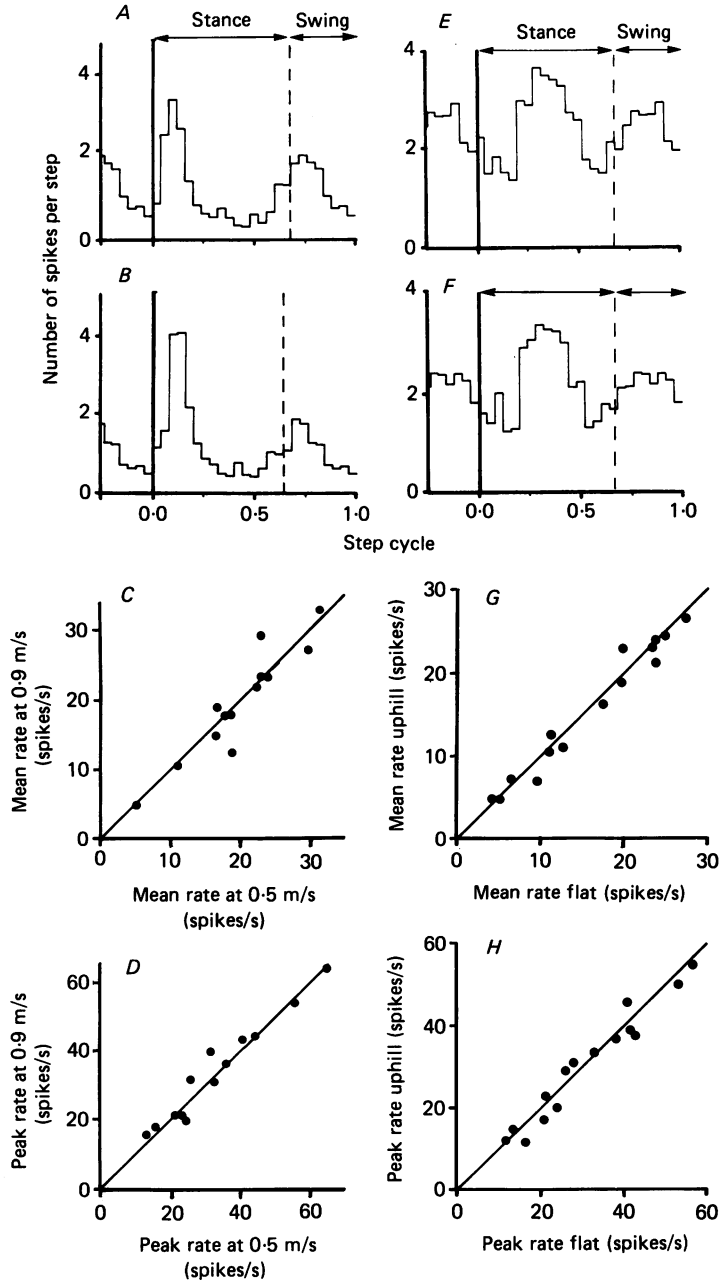

Fig. 9. *A* and *B* show the post-event time histograms of a Golgi cell during locomotion at 0·5 m/s (*A*) and 0·9 m/s (*B*), while *C* and *D* compare the mean rate and peak rate, respectively, for thirteen Golgi cells during locomotion at these speeds. In *E* and *F*, similar plots compare the activity of a Golgi cell during locomotion on a horizontal belt and an incline of 20 deg. *G* and *H*, as *C* and *D* but for fifteen cells during locomotion on the flat or on a 20–25 deg incline. Note that the diagonals in *C*, *D*, *G* and *H* represent no change in discharge rate.

two speeds were made using post-event time histograms with a bin width of 1/25th the step cycle duration. Most cells (11/14: 79%) discharged with similar timing patterns at both speeds (relative to the overall duration of the step cycle). Post-event time histograms for one such neurone are shown for locomotion at 0·5 m/s in Fig. 9*A* and for locomotion at 0·9 m/s in Fig. 9*B*. Two of the three remaining neurones discharged with broadly similar patterns at the two speeds but with some differences in the shapes of the post-event time histograms. The activity timings for the other neurone differed widely between the two speeds.

Like the discharge timings, the discharge rates of most neurones were also similar during locomotion at the two speeds as is shown by the comparisons made in Fig. 9*C* and *D*. In Fig. 9*C* the mean rate value during locomotion at 0·9 m/s is plotted against the corresponding value during locomotion at 0·5 m/s for each of the fourteen neurones. In Fig. 9*D* the peak rate values are similarly plotted. In both graphs most points lie close to the diagonals, which represent no change. Taken as a population, the putative Golgi cells discharged with slightly higher mean discharge rates during locomotion at 0·9 m/s but the increase was small (averaging 0·3 (S.D. ±3·2) spikes/s). The peak rate values showed a slightly larger increase (averaging 1·15 (S.D. ±3·4) spikes/s).

Discharges of Golgi cells during locomotion on different gradients

Recordings were also obtained from fifteen neurones during locomotion on a belt inclined at 20–25 deg. During locomotion at 0·5 m/s on such steep gradients the timings of the step cycle events and limb muscle e.m.g. bursts were essentially similar to those seen during locomotion on a horizontal surface. However, the amplitudes of the e.m.g. bursts (both flexor and extensor) were greatly increased, presumably indicating an increased production of muscle force.

All fifteen Golgi cells discharged with strikingly similar patterns during locomotion uphill and on the flat. Post-event time histograms are shown for a cell during locomotion both on the flat (Fig. 9*E*) and on the inclined belt (Fig. 9*F*) and the similarity in discharge pattern is most striking. The similarity extended to discharge rate as well as timing and in Fig. 9*G* and *H* the mean and peak rates during locomotion on an incline have been plotted against the values during locomotion on the flat for all fifteen neurones. All points lie close to the diagonals which represent no change. The largest individual difference in mean rate was an increase of 3·1 spikes/s, but on average the putative Golgi cells discharged with very slightly lower mean rate (by 0·3 (S.D. ±1·4) spikes/s) during locomotion on the incline. For peak rate the largest individual difference was an increase of 5·5 spikes/s on the gradient but again, on average, uphill walking was accompanied by a slight decrease amounting to 0·82 (S.D. ±3·2) spikes/s.

DISCUSSION

Identification of the discharges of Golgi cells

Each of the neurones described above discharged in a characteristic manner which clearly differed from that which is typical of Purkinje cells. The discharge properties in fact bore a very close resemblance to those previously attributed to Golgi cells in

anaesthetized cats (Eccles, Llinás & Sasaki, 1966*a*) and rodents (Schulman & Bloom, 1981) and in alert primates (Miles *et al.* 1980). Each of these reports described discharge rates in the range 15–32 spikes/s which is lower than the values found for most Purkinje cells, which usually attain 40–50 spikes/s and in some cases 100 spikes/s (see Brooks & Thach, 1981; Armstrong & Edgley, 1984*b*). The characteristic regularity of the discharges and the absence of interspike intervals less than 10 ms was also noted in the studies referred to above. These discharge properties contrast strongly with those of Purkinje cells which are highly irregular and which produce interspike interval distributions which are usually strongly skewed with a peak consisting of short intervals and a tail made up of longer intervals (see e.g. Armstrong & Rawson, 1979).

In view of the lack of complex spikes and the differing discharge characteristics, it is highly improbable that the discharges originated from Purkinje cells. This view is also supported by the fact that when units of this type were recorded in the b-zone cortex (the lateral vermis) they were never antidromically activated by electrical stimuli delivered in Deiters' nucleus, whereas many of the surrounding Purkinje cells (which are known to project to Deiters' nucleus) could be activated by such stimuli (D. M. Armstrong & G. Andersson, personal communication). Both Schulman & Bloom (1981) and Miles *et al.* (1980) marked the recording sites at which units similar to those described here were recorded and concluded that the units lay in the granule cell layer, as was confirmed in the present study. Since the action potentials were large and stable and of long duration, it seems highly unlikely that they could have arisen from mossy fibre terminals or from granule cells, both of which discharge brief spikes at high frequencies and which are usually difficult to isolate (Lisberger & Fuchs, 1978; Miles *et al.* 1980). The conclusion of Schulman & Bloom (1981) and of Miles *et al.* (1980) that the discharges originate from Golgi cells therefore seems the most logical.

The responses of Golgi cells to the electrical activation of cerebellar afferents in anaesthetized or decerebrated cats have been described by Eccles *et al.* (1966*a*). In response to electrical stimulation of the parallel fibres some Golgi cells discharged with instantaneous frequencies up to 1000 spikes/s. However, in the present study interspike intervals of less than 10 ms were seldom seen even during vigorous locomotion or strong tactile stimulation.

Unequivocal proof that the slow regular discharges originate from Golgi cells must await studies in which the recorded neurones are marked by intracellular staining. In fact intracellular recordings have been made from cortical neurones in awake cats which were subsequently shown to be Golgi cells (Nahvi, Woody, Tzebelikos & Ribak, 1980). The discharges of such units were unusual in that they comprised of a small initial spike, which was often inactivated, immediately followed by a full action potential. No such feature was ever seen preceding the extracellularly recorded action potentials of the present investigation. Unfortunately Nahvi *et al.* (1980) do not describe the spontaneous discharge patterns of the neurones they recorded so a comparison with the present cells is not possible.

Discharges of Golgi cells in the absence of movement

All of the Golgi cells discharged tonically while the cats rested on the experimenter's knee but it should be noted that small active movements of the limbs and head generally occurred during these recordings because the cats were playful and curious. The tonic discharge is therefore best described as having been present during periods when there were no substantial movements. Eccles, Llinás & Sasaki (1966*b*) have described a depression of granule cell excitability lasting more than 100 ms which was attributed to the inhibitory action of Golgi cells. It therefore seems that in the resting animal, the granule cells experience a degree of tonic inhibition (and the Purkinje cells a tonic disfacilitation) due to the activity in Golgi cells.

Discharges of Golgi cells during locomotion

Unlike the Purkinje cells of the intermediate zone of the cortex, most of which discharge faster during locomotion than during rest (Armstrong & Edgley, 1984*b*), the discharge rates of many Golgi cells were lower, and the overall average rate for the population was not significantly different, from that during rest. As the Golgi cells are not thought to be inhibited by basket or stellate cells (Hamori & Szentagothai, 1966), the lower discharge rates of some neurones can be ascribed either to increased inhibitory input mediated via the Purkinje cell collaterals or to disfacilitation due to reduction in their excitatory input from mossy fibres or granule cells.

All eighty-one investigated Golgi cells discharged rhythmically during locomotion suggesting that they play an active role in cortical information processing. In this respect they resembled the paravermal Purkinje cells, most of which also discharged rhythmically during locomotion (Armstrong & Edgley, 1984*b*; S. A. Edgley & M. Lidierth, in preparation). Presumably the discharges of both types of neurone are governed to a large extent by activity in the mossy fibre afferents. The present finding that the discharges of all the Golgi cells were modulated contrasts somewhat with that of Miles *et al.* (1981) who reported that the discharges of 40% of the Golgi cells recorded in the flocculus were unrelated to eye position or movement, whereas the discharges of all but 7% of the local Purkinje cells were so related. One factor contributing to this discrepancy could be that locomotion requires the participation of a great many muscles and may therefore engage the entire paravermal cortex, whereas a particular vestibulo-ocular reflex paradigm may engage only specific parts of the flocculus.

Individual Golgi cells discharged with different patterns during locomotion (Fig. 6*A* and *B*) and even among cells with similar receptive fields a wide range of different patterns was seen. The cytoarchitecture of the cortex is well known: each Golgi is thought to occupy a separate cortical territory, so that the dendritic and axonal arborizations of each neurone are non-overlapping (Eccles *et al.* 1967; Palkovits, Magyar & Szentagothai, 1971). As a consequence of this arrangement, the granule cells can be divided into small colonies, each of which will be influenced by a single Golgi cell. The individuality of Golgi cell behaviour therefore implies that different colonies of granule cells will have different patterns of Golgi cell inhibition during locomotion.

In view of the fact that granule cell axons extend for several millimetres along the

cerebellar folia (e.g. Brand, Dahl & Mugnaini, 1976) it is difficult to speculate as to how the Golgi cell system might influence Purkinje cell activity. However, there have been recent suggestions that the ascending limb of the granule cell axon might exert a much more powerful influence on the Purkinje cells than the parallel fibre branches (Llinás, 1982; Bower & Woolston, 1983). If this is the case then the heterogeneity of the discharge patterns of Golgi cells would suggest that the granule cell inputs to different small groups of Purkinje cells are under different patterns of inhibitory control during locomotion.

The role of the Golgi cells in determining Purkinje cell activity

Although studies of the present type are unlikely to provide precise details of cortical information processing, nevertheless they may provide some first indications of how it might occur. From the analysis of the discharge patterns of groups of neurones recorded in the same cortical area, the impression is that, overall, the activities of Golgi cells and Purkinje cells tend to co-vary during locomotion (Fig. 7). This would suggest that Golgi cell activity will tend to limit the extent of the frequency modulation among the Purkinje cells and, as a consequence, Golgi cells seem unlikely to play a role in the generation or enhancement of the modulation patterns of Purkinje cells. However, the limitations of this approach are obvious: the recordings were made in a relatively large region of cortex (a cylinder of cortex approximately 2 mm in diameter), in which both individual Purkinje cells and Golgi cells discharge with different patterns during stepping. A comparison of the activity patterns of closely adjacent neurones should give more accurate information regarding the Golgi cell–Purkinje cell relationship. As there are fewer Golgi cells than Purkinje cells (Eccles *et al.* 1967; Lange, 1974) and as they have large axonal arborizations, there is a good chance that a Golgi cell located less than 200 μm from a particular Purkinje cell will influence that cell and its near neighbours. However, the results obtained by comparing such closely neighbouring cells were equivocal: there appears to be no unique relationship between the activities of the two types of cell (Fig. 8). Assuming that the Golgi cells influence the Purkinje cells nearest to them most powerfully (see above), the present results suggest that in some cases Golgi cell disfacilitation is greatest at the time of peak discharge of the Purkinje cells, whereas in other cases it is greatest at the time of minimum activity. It therefore seems likely that the role of the Golgi cells *vis-à-vis* the Purkinje cells is not restricted to simply damping or restraining the extent of their frequency modulation.

Discharges of Golgi cells during locomotion at different speeds and on different gradients

During locomotion at different speeds or on different gradients, almost all Golgi cells behaved similarly in that the patterns and rates of discharge were essentially unaltered under all of the conditions tested. It therefore appears that their disfacilitatory influence on the Purkinje cells would vary little over the range of speeds and gradients investigated. This is somewhat surprising since the limb muscle e.m.g. activities differed greatly in amplitude under the different conditions. Mossy fibre afferents projecting to this area of cortex arise from many sources (see Oscarsson, 1973; Bloedel & Courville, 1981) and many are thought to provide the cerebellum

with information regarding the progress of movements. Considerable alterations in the activity of these afferents might therefore be expected as the speed or angle of the belt was varied. Our observations suggest, however, that the net input to the Golgi cells was virtually unchanged, both in pattern and in strength.

The behaviour of these neurones closely parallels the behaviour of Purkinje cells (and their target interpositus neurones), most of which also discharged with similar patterns and rates over this range of speeds (D. M. Armstrong & S. A. Edgley, unpublished observations). As both the Purkinje cells and the putative Golgi cells discharged similarly under these conditions it appears that the mossy fibre input to the intermediate zone of the cortex remains essentially similar when either the speed or incline of the moving belt is altered.

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