J. Physiol. (1984), **352**, *pp.* 403–424
With 9 text-figures
Printed in Great Britain

DISCHARGES OF PURKINJE CELLS IN THE PARAVERMAL PART OF THE CEREBELLAR ANTERIOR LOBE DURING LOCOMOTION IN THE CAT

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(*Received 3 January 1984*)

SUMMARY

1. Extracellular recordings were made from 124 Purkinje cells in the paravermal part of lobule V of the cerebellum in cats walking steadily at a speed of 0·5 m/s on a moving belt.

2. All cells tested had a tactile receptive field from which simple spikes could be evoked and 96% of these were on the ipsilateral forelimb.

3. Seventy-six of the cells were also studied whilst the animals sat or lay quietly without movement. Complex spikes were discharged at 1–2/s and these were accompanied by simple spikes in fifty-nine cells (78%); in the remaining cells there were no or few simple spikes. The over-all mean discharge rate (including both types of spike) was 37·8 ± 27 impulses/s (± S.D.).

4. During locomotion all cells discharged both types of spike and the over-all mean rate was 57·6 ± 29 impulses/s (± S.D.). In all cells but one, the frequency of the simple spikes was modulated rhythmically in time with the stepping movements but the phasing relative to the step cycle varied widely between cells. Peak rates also varied widely, the average being 91·5 ± 44 impulses/s (± S.D.). Most cells (63%) generated one period of accelerated discharge per step but others generated two (35%) or three (2%) such periods.

5. Despite the individual variations in discharge timing the population as a whole was considerably more active during the swing than the stance phase of the step cycle in the ipsilateral forelimb (68 impulses/s as compared with 49 impulses/s on average).

6. Thirty-four cells were electrophysiologically identified as lying in the c_1 zone of the cortex and twenty-five as being in the c_2 zone (nomenclature of Oscarsson, 1980). During locomotion, the population activity in the two zones differed slightly: activity in the c_1 population was phase advanced by approximately one-tenth of the step cycle.

7. The results are discussed, with particular emphasis on the finding that population activity in the Purkinje cells of the c_1 zone fluctuated during the step cycle in parallel with that in the part of nucleus interpositus to which they project.

INTRODUCTION

The present paper describes the patterns of impulse discharge among Purkinje cells in the paravermal part of lobule V in the anterior lobe of the cerebellum during the locomotion of cats walking for brief periods at steady speed on a moving belt. This part of the cerebellar cortex is the classical receiving area for inputs from the ipsilateral forelimb and lesions of it impair forelimb movements (Chambers & Sprague, 1955). Moreover, temporary cooling of the area during locomotion results in marked hyperflexions of the limb suggesting that it plays an active role in locomotor control (Udo, Matsukawa, Kamei & Oda, 1980). However, there have been no previous descriptions of the discharges of its Purkinje cells during locomotion although recordings have been made in other portions of the cerebellar cortex in high-decerebrate cat preparations stepping with the hind limbs only (Orlovsky, 1972*a*) or quadrupedally (Udo, Matsukawa, Kamei, Minoda & Oda, 1981).

The present recordings were carried out principally to throw light on the sources of input responsible for the rhythmic discharges found among neurones of an intracerebellar nucleus (nucleus interpositus) during locomotion under the same conditions (Armstrong & Edgley, 1984). As a population, cells located in the caudal part of nucleus interpositus anterior and with receptive fields on the ipsilateral forelimb discharged much more vigorously during the swing than the stance phase of the step cycle in the same limb. This parallels the findings of Orlovsky (1972*b*) for hind-limb-related interpositus neurones in decerebrate cats walking with the hind limbs only.

There are two major sources of input to interpositus neurones and either or both might be responsible for generating the rhythmic discharges observed by Armstrong & Edgley (1984). Monosynaptic excitation is provided by collaterals from some of the mossy-fibre and climbing-fibre afferents which pass around and through the nucleus *en route* to terminate in the overlying paravermal part of the cortex (see Chan-Palay, 1977; Bloedel & Courville, 1981 for references and discussion). In addition, Purkinje cells in the paravermal cortex monosynaptically inhibit the interpositus neurones via the highly convergent cerebellar corticonuclear projection (Ito, Yoshida, Obata, Kawai & Udo, 1970). The paravermal part of lobule V includes several of the sagittal strips or zones into which the cortex can be divided (see Voogd, 1969; Oscarsson, 1973, 1976, 1980). Of these, the c_1 and c_3 zones probably project to nucleus interpositus anterior and the c_2 zone to nucleus interpositus posterior (see Discussion for references).

As regards the relative roles of the two inputs, the former has not been investigated but Orlovsky (1972*a*) found that the discharges of hind-limb-related Purkinje cells in the paravermal part of lobule II and III of the anterior lobe occurred mainly opposite in phase to those of hind-limb-related interpositus neurones (i.e. their activity was greatest during stance). This is the pattern which would be expected if they played the major role in shaping the interpositus discharges by the process which Eccles (1973) has termed 'inhibitory sculpturing' (cf. Orlovsky & Shik, 1976).

In the present experiments, extracellular recordings have been made from many Purkinje cells, the large majority of which had tactile receptive fields restricted to or including the ipsilateral forelimb. Some were shown electrophysiologically to

belong to the c_1 cortical zone or to the c_2 zone. The former population can be presumed to have projected to (and therefore monosynaptically inhibited) the population of forelimb-related neurones in nucleus interpositus studied by Armstrong & Edgley (1984) which were encountered deeper in the same micro-electrode tracks.

METHODS

The Purkinje cells were recorded in the same cats as were used by Armstrong & Edgley (1984) for an investigation of the impulse activity in nucleus interpositus during locomotion.

The techniques for the animal training, the preparative surgery, the micro-electrode and electromyographic recordings, the receptive field determinations, the data processing and the histological controls were those of Armstrong & Edgley (1984).

Identification of Purkinje cells

As the micro-electrodes (glass-insulated tungsten electrodes) traversed the cerebellar cortical folds *en route* to nucleus interpositus, they inevitably passed through one or more cerebellar cortical layers. At such times, trains of extracellular action potentials were frequently recorded from single units, the majority of which were unequivocally identifiable as Purkinje cells because they discharged both complex spikes, which are generated by climbing fibre input, and simple spikes, which reflect input via the mossy fibre–granule cell–parallel fibre pathway (cf. for example Thach, 1967, 1970*a*; Armstrong & Rawson, 1979).

The locations of the micro-electrode tracks were verified histologically and they passed through the paravermal part of lobule V of the anterior lobe. The tracks were 3·0–5 mm lateral to the cerebellar mid line and must therefore have passed through one or other of the c_1, c_2 and c_3 cortical zones, each of which is a sagittally orientated strip of cortex approximately 1 mm wide. The c_1 zone is just lateral to the paravermal vein and the c_2 and c_3 zones are successively further lateral (see Voogd, 1969; Oscarsson, 1976, 1980). Most tracks were in the c_1 and c_2 zones.

Each of the c zones receives input via several spino-olivocerebellar pathways all of which terminate as climbing fibres and include a forelimb component (see Oscarsson, 1973, 1980). Stimulation of forelimb nerves therefore results in complex spikes in many Purkinje cells in all three zones. However, individual cells in the c_2 zone receive climbing fibre input from both forelimbs with latencies of 17 ms or longer (mediated via a path in the lateral funiculus of the cord or via an 'indirect' (long latency) path in the dorsal funiculus; Larson, Miller & Oscarsson, 1969*a*; Ekerot & Larson, 1979) while cells in the c_1 and c_3 zones receive input only from the ipsilateral forelimb at latencies which can be as short as 10 ms and are mostly less than 16 ms (mediated via a 'direct' (short latency) path in the dorsal funiculus or via a path in the dorsolateral funiculus; see Ekerot & Larson, 1979; Larson, Miller & Oscarsson, 1969*b*). It was therefore possible to assign some neurones to either the c_1 or the c_2 zone by examining the complex spikes evoked by weakly stimulating the right and left superficial radial nerves via electrodes implanted in the forearms (cf. Armstrong & Rawson, 1979). Stimuli were 0·1 ms pulses applied at 1 Hz and at intensities around or below the threshold for evoking a weak–visible flexion reflex. The animals ignored such stimuli and frequently dozed during their application.

RESULTS

Identification and subgrouping of neurones

Recordings were made from 124 Purkinje cells during periods of locomotion in which the animal walked steadily to maintain constant position on a belt moving at 0·5 m/s. Many were also recorded whilst the animal sat or lay quietly without making overt movements.

The action potentials of the different units ranged in amplitude from 0·4 to 2·2 mV and were usually negative–positive diphasic spikes though in some cases they were positive–negative. All units also discharged complex spikes, consisting of an initial

spike immediately followed for 3–10 ms by a succession of smaller spikes or (more usually) wavelets. Fig. 1*A–C* shows the discharges of three different units in the resting animal. Complex spikes are marked by filled circles and the units of Fig. 1*A* and *B* also discharged simple spikes. Most units resembled those of Fig. 1 in including obvious complex spikes in the background discharge, but in some cells complex and simple spikes could be reliably differentiated only when examined at

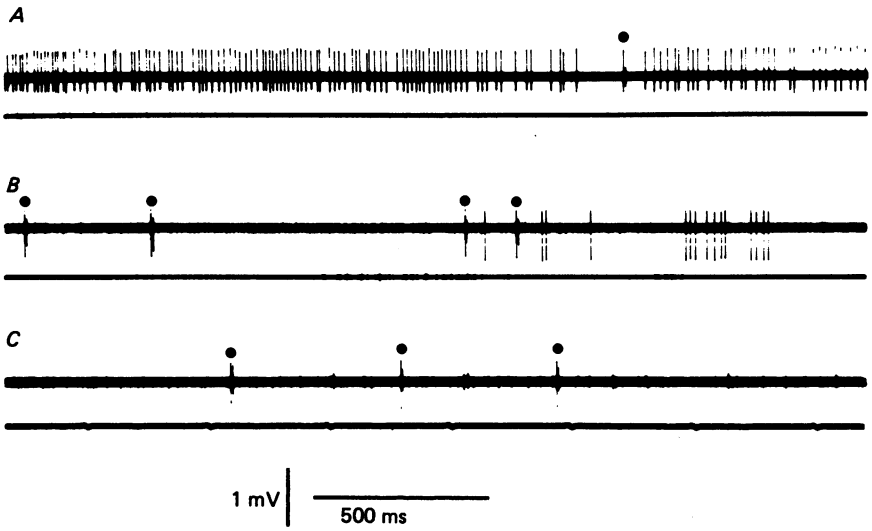

Fig. 1. Purkinje cell discharges in the absence of locomotion. The upper traces in *A*, *B* and *C* show extracellular action potentials recorded from three typical Purkinje cells during periods when the animal sat quietly without movement. Complex spikes are marked with filled circles. The lower traces show the e.m.g. signals recorded simultaneously from triceps brachii muscle in the ipsilateral forelimb. Voltage calibration represents 1 mV for the units, 2 mV for the e.m.g.s. Negative up in unit traces.

fast sweep speed. In a few units complex spikes could not be distinguished from simple spikes in the extracellular recordings but the unit was subsequently damaged by the micro-electrode and climbing-fibre excitatory post-synaptic potentials were revealed (cf. Armstrong & Rawson, 1979). In such cases it was assumed that complex spikes were present, but not distinguishable, during the extracellular recording, and the unit was accepted as a Purkinje cell.

Whenever units could be held long enough, an attempt was made to assign them to a particular cortical zone by studying the complex spikes evoked by weak stimulation of the superficial radial nerves (see Methods). Units were accepted as belonging to the c_2 zone if complex spikes were evoked from both right and left nerves at latencies between 16 and 25 ms. They were assigned to the c_1 zone if responses were evoked only from the ipsilateral nerve and at a latency of 12–16 ms. Examples of such responses are shown in Fig. 8*A* and *B*. In a few cases the identification was indirect in that an appropriate response was seen not in that cell but in another unit recorded immediately alongside. For many neurones no zonal identification was possible either because complex spikes could not be evoked from the nerves at the

weak stimulus intensities employed or because contact with the unit was lost. However, thirty-four neurones could be assigned to the c_1 zone and twenty-five others to the c_2 zone (see below).

Tactile receptive fields

Whenever possible somatosensory receptive fields were determined for the neurones by the manual application of stimuli such as brushing and bending hairs, light taps to the skin, palpation of deeper tissues and passive movement of joints. These stimuli were delivered while the animal sat or lay on the experimenter's lap and were accepted contentedly; they usually evoked purring.

Receptive field determinations were carried out for 111 cells and in all cases some area of the body surface could be found from which simple spikes could be evoked. The fields were sometimes small and well-defined (e.g. restricted to part of the forepaw) but in many cases they were very wide (e.g. covering most of the forelimb) and often had poorly definable edges. The responses evoked varied widely, from bursts of impulses in some units to small changes in the background rate in others. Even within a single neurone the response often varied considerably in intensity depending on the position of the stimulus within the receptive field area. Because of these characteristics the receptive fields were regarded only as indicating the region of the body from which the strongest tactile input was received (cf. Armstrong & Edgley, 1984) and are not described in detail.

Of the 111 neurones, five (4·5 %) had receptive fields centred on face, neck or back while the great majority (106; 95·5 %) had fields centred on some part of the ipsilateral forelimb. No fields were found for the hind-limb (see Discussion). Among the neurones with input from the forelimb there were thirteen (12 %) in which the receptive field encompassed the whole limb and it was not possible to define a region from which the responses were strongest. However, the remaining cells could be divided into twenty-one 'proximal' neurones in which the receptive field was confined to or centred on the shoulder or upper arm, twenty-eight 'elbow-related' neurones in which the field was confined to or centred on the region around the elbow and forty-four 'distal' neurones in which it was confined to or centred on the foot and/or wrist. Details regarding the impulse activity of these subpopulations during rest and during locomotion are given below.

Discharges in the resting animal

Seventy-six of the neurones studied during locomotion were also recorded during periods when the animal made no overt movements. Under these conditions fifty-nine neurones (78 %) discharged simple spikes tonically apart from occasional brief pauses (cf. Fig. 1*A*). Although the distribution of interspike intervals was fairly wide (cf. Armstrong & Rawson, 1979), indicating that the discharge was irregular, the mean rate of firing, as calculated using batches of 1000 successive intervals, was usually rather constant from batch to batch.

In most of the fifty-nine cells, complex spikes were also visible (see above and cf. Fig. 1*A*) but they always occurred at low rates, ranging from 1 to 2/s. Because in most cases the complex spikes could not reliably be discriminated from the simple spikes and because they usually made up a very small proportion of the total spikes

fired, these events were included with the simple spikes when values of discharge rate were calculated. Discharge rates were calculated after passing the action potential through a voltage-window-discriminator device and care was always taken that the device was triggered only by the initial spike of any complex spikes and not by the succeeding ripples or stunted spikes. Each complex spike was therefore counted as a single event.

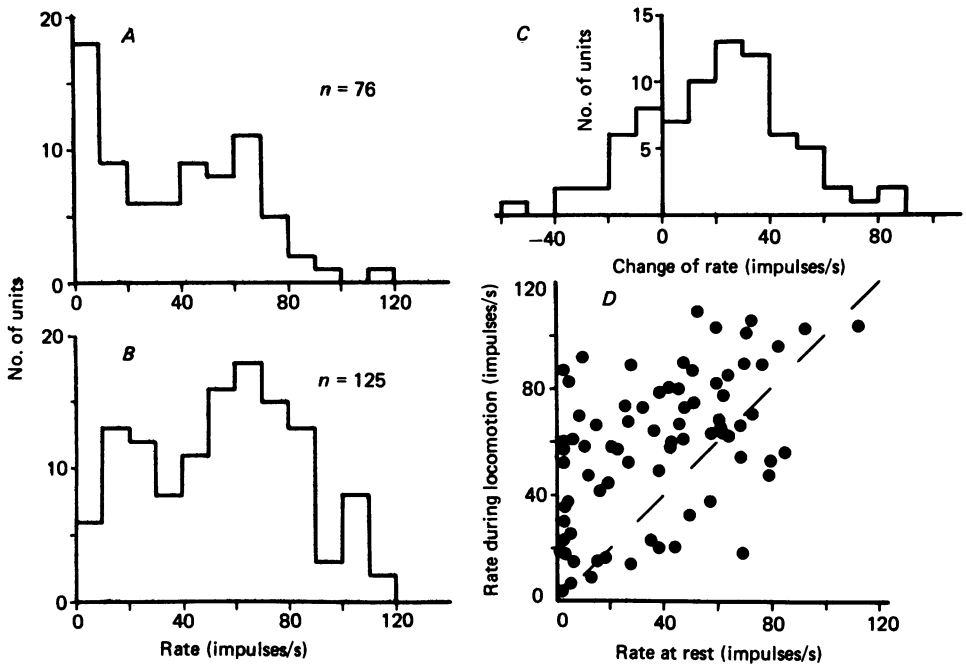

Fig. 2. Discharge rates of Purkinje cells during rest and locomotion. *A*, frequency-distribution histogram for the rates of the seventy-six Purkinje cells recorded during rest. *B*, frequency-distribution histogram for the rates of the 124 Purkinje cells (including those in *A*) recorded during locomotion at 0·5 m/s. *C*, frequency-distribution histogram for the differences in discharge rate between rest and locomotion for each of the neurones in *A*. Increases in discharge rate are plotted as positive, decreases as negative values. *D*, scattergram plotting the discharge rate during locomotion at 0·5 m/s (vertical axis) against that at rest, for each of the neurones recorded under both conditions. The diagonal dashed line represents no change.

In the remaining seventeen neurones (22 %) the discharge in the resting animal consisted either of complex spikes alone (cf. Fig. 1*C*) or of complex spikes interspersed with a small number of simple spikes which occurred singly or in short bursts (cf. Fig. 1*B*).

The frequency distribution for the discharge rates is shown for all seventy-six neurones in Fig. 2*A*, where it is evident that the range was very wide (from 1/s to 111/s). Except for the cells in the first bin (i.e. those discharging at < 10 impulses/s) complex spikes inevitably made only a small contribution to the discharge rate so that the values essentially reflect the level of simple spike activity. For the whole population the over-all rate was 37·8 ± 27 impulses/s (± S.D.) and when the neurones

were subgrouped according to cortical zone (c_1 or c_2) or according to the location of the receptive field within the forelimb, there were no statistically significant differences between the means for the different groups.

Discharge rates during locomotion at 0·5 m/s

All 124 neurones were studied during one or more periods of locomotion which included a sequence of twenty consecutive paces in which step duration had a coefficient of variation of less than 10 % and often less than 5 %. Step durations and the timing of the different phases of the step cycle were estimated from electromyographic (e.m.g.) records from limb muscles. In each animal the locomotor e.m.g.s of several muscles were recorded (see Armstrong & Edgley, 1984) but these always included the triceps brachii (lateral head) and brachialis muscles of the ipsilateral forelimb. Both have a single period of activity per step cycle and they function respectively as an extensor and flexor of the elbow. Each step cycle was taken to last from the onset of one locomotor burst in triceps brachii until the onset of the next. Within the step cycle the period from the onset of activity in triceps to that in brachialis muscle is referred to below as 'stance' while the period from the onset of activity in brachialis to that in triceps is referred to as 'swing'. This nomenclature is approximate because during locomotion under the present conditions foot placement actually occurs *ca.* 30 ms after the onset of triceps e.m.g. while foot lift occurs 30 to 45 ms after the onset of brachialis e.m.g. (see Armstrong & Drew, 1984). These errors are small however, because stance lasts an average of *ca.* 550 ms while swing lasts *ca.* 300 ms.

During locomotion all 124 Purkinje cells discharged complex spikes (in a few cases recognizable only when the micro-electrode damaged the cell), and the vast majority also discharged simple spikes. Complex spike activity during locomotion will be described fully in a subsequent paper.

Over-all levels of impulse activity (simple spikes plus complex spikes) ranged from 1 to 116 impulses/s and the frequency distribution of different rates is shown in Fig. 2*B*. Note that only six neurones (5 %) discharged at rates less than 10/s as compared with 24 % of cells during rest. This difference arises because in most of the seventeen cells which discharged mainly complex spikes during rest, the onset of locomotion was accompanied by the appearance of simple spikes. This change occurred without any alteration in the amplitude of the complex spikes so it is unlikely that it arose because of any artifactual depolarization of the cell brought about by damage due to movement of the micro-electrode tip relative to the neurone.

The mean discharge rate for the whole population was $57{\cdot}6 \pm 29$ impulses/s ($\pm$S.D.). When the neurones were subgrouped according to cortical zone or according to location of the receptive field on the forelimb, there were no statistically significant differences between the mean rates for the different subpopulations as assessed by Student's *t* test.

49 of the 124 neurones were studied during two or more sequences of twenty steady steps at 0·5 m/s. In more than half of these cells the discharge rates for these different sequences were very similar but in twenty cells (41 %) the greatest difference between the rates in different samples exceeded 10 impulses/s and in fourteen cells (29 %) it was 25 impulses/s or more. These shifts in the level of activity did not seem to reflect

any progressive damage caused by the micro-electrode tip because there was no change in spike shape or size. Moreover, although in some cases the highest rate was found for the latest sample, in other cases the highest rate was that for the earliest or for an intermediate sample. The fluctuations in activity level were not accompanied by any obvious behavioural change as judged from inspection of the animal or study of the e.m.g. records and the source of the variations therefore remains unknown. When they occurred the sample of activity chosen for Fig. 2*B* and elsewhere in Results (see below) was that in which the steps were most uniform (i.e. in which step duration showed the smallest coefficient of variation).

Comparison of Fig. 2*A* and *B* suggests that most of the seventy-six neurones studied during both rest and locomotion discharged faster during locomotion and this is verified by Fig. 2*C* which shows the frequency distribution of the individual differences in rate: only nineteen neurones (25 %) fired more slowly during locomotion than rest. Fig. 2*D* plots the individual rates during rest against the corresponding values during locomotion and it is clear that both increases and decreases were found for units with a wide range of rates during rest. The only exception is provided by the units with rates below 10 impulses/s during rest (i.e. those closest to the vertical axis in Fig. 2*D*). Because most of these discharged only complex spikes during rest and because simple spikes usually appeared during locomotion, the majority of these cells had increased activity during locomotion and in some cases the increases were very substantial.

Rhythmicity of the discharges during locomotion

Inspection of the impulse trains showed immediately that most neurones discharged more briskly at particular times during the step cycle: some discharged one or more discrete bursts of impulses separated by silent periods while others discharged throughout the step cycle but with rates consistently higher at some time(s) than at others. Examples of two neurones which discharged one burst of impulses per step are shown in Fig. 3*A* and *D*. That of Fig. 3*A* discharged at highest rate during the silent periods of the triceps brachii e.m.g. (in fact during the swing phase of the step in the ipsilateral forelimb) while that of Fig. 3*D* fired fastest during the locomotor e.m.g. burst in triceps brachii (i.e. during stance).

For each neurone the discharges during twenty regular steps were overlap averaged taking the onset of triceps brachii e.m.g. as a marker of the onset of the step cycle. The averages were displayed as post-event time histograms in which bin width was always 20 ms. Histograms for the units of Fig. 3*A* and *D* are shown in Fig. 3*B* and *E* respectively where the time axis has been made equal to *twice* the mean duration of the step cycle (cf. Armstrong & Edgley, 1984).

One advantage of the averaging procedure is well exemplified by Fig. 3*E*: comparison of this histogram with the raw data (Fig. 3*D*) shows that maximum discharge occurred just before and during the triceps e.m.g. but the histogram demonstrates that a few spikes were also usually discharged just after the end of triceps activity. These spikes are identifiable but not particularly obvious in Fig. 3*D*.

A second, perhaps more important advantage is that the histograms can be used to measure the discharge rate achieved at different times during an 'average step'. This can be done for each 20 ms bin, but for greater convenience the computer was

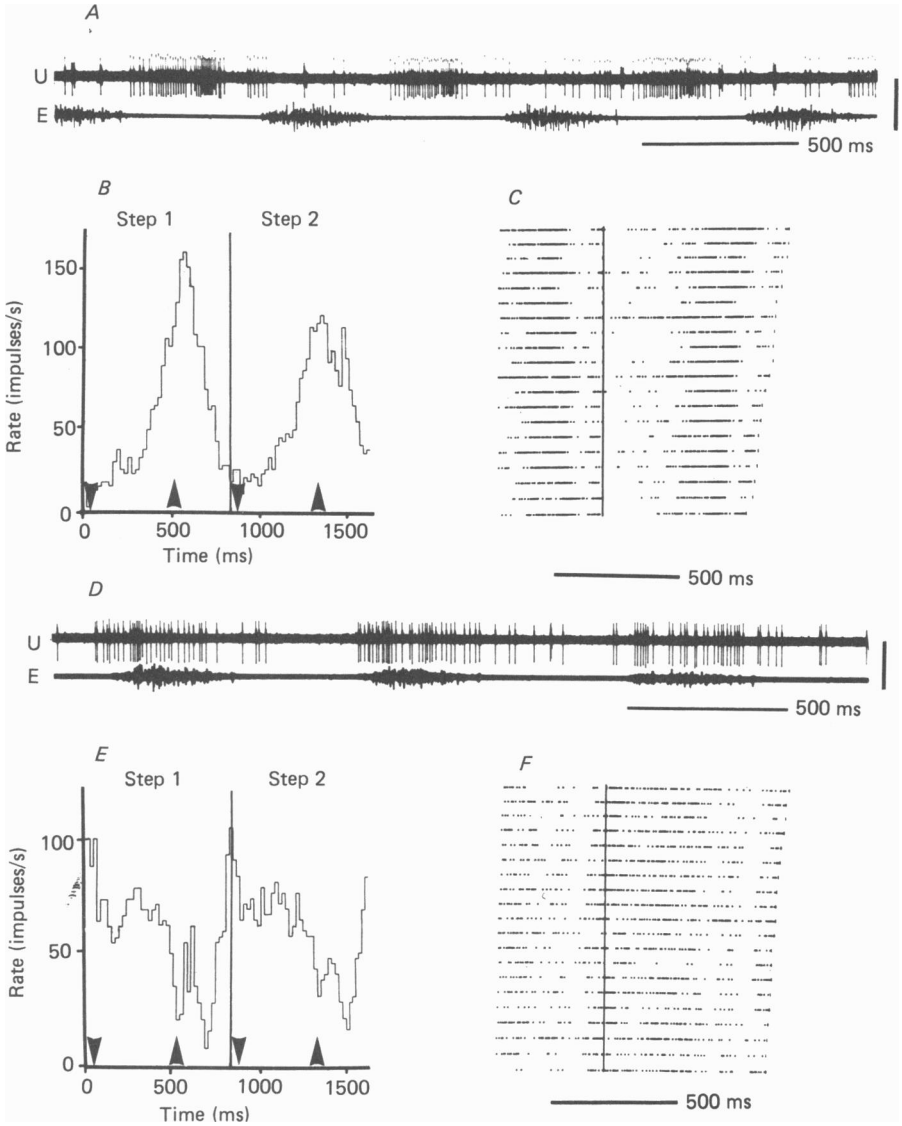

Fig. 3. Discharges of two Purkinje cells during locomotion at 0·5 m/s. *A* and *D* each show the discharges of a unit (trace U) and the e.m.g. activity recorded from triceps brachii muscle (trace E) during three successive paces. The voltage calibration bars represent 1 mV (negative up) for the unit recording and 2 mV for the e.m.g. recording. *B* and *E* each show a post-event time histogram, made by overlap averaging the discharges of the units shown in *A* and *D* over a sequence of twenty paces. In both histograms the time axis begins at the time of onset of e.m.g. activity in triceps brachii. The time axis has been scaled to equal *twice* the average pace duration so that one step is shown to either side of the vertical line which bisects the histogram. Note that the approximate times of foot lift and foot placement are shown by the upward and downward arrows respectively. Bin width is 20 ms in each case. *C* and *F* are dot-raster displays constructed from the same data used to construct *B* and *E* respectively. The vertical line represents the time of onset of e.m.g. activity in triceps brachii in each pace and each line of the raster shows the discharges during one complete pace and the preceding 500 ms. The paces are not shown in chronological order but have been rank ordered according to duration with the longest at the top.

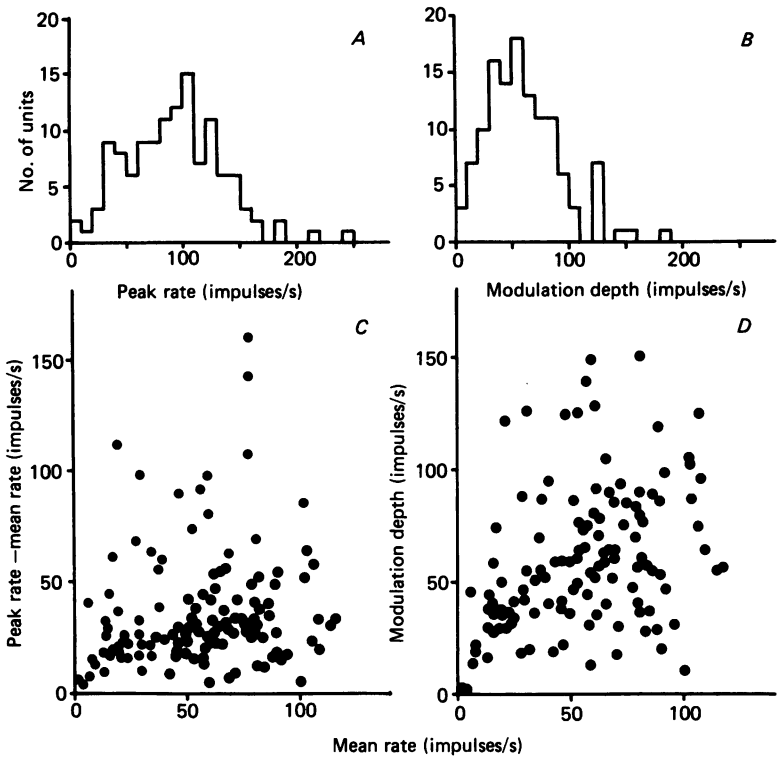

Fig. 4. Discharge parameters of the 124 Purkinje cells during locomotion at 0·5 m/s. *A*, frequency distribution for the peak rates of discharge (as defined in text). *B*, frequency distribution for the depths of frequency modulation (see text) of the discharge rate during locomotion. *C*, scattergram showing the relationship between mean discharge rate (horizontal axis) and the amount by which the peak rate exceeded the mean rate (vertical axis). *D*, scattergram showing the relationship between modulation depth (vertical axis) and mean rate.

programmed to divide the step into tenths and calculate the discharge rate during each tenth. In the present paper (cf. Armstrong & Edgley, 1984) a neurone was arbitrarily taken as frequency modulated (i.e. as discharging rhythmically) if in at least one of the tenths the rate was at least 10% higher or lower than the mean for the whole step cycle. On this basis, all but 1 of the 124 neurones was frequency modulated during locomotion, though the extent (depth) of the modulation varied considerably between units (see below).

For each unit, the peak rate was taken as that during the tenth of the step when activity was greatest. The resultant values varied very widely from 2 to 242 impulses/s and the frequency distribution of different values is shown in Fig. 4*A*. The over-all mean was 91·5 ± 44 impulses/s (± S.D.). Fig. 4*C* plots the mean rate for each cell against the difference between peak and mean rates: the correlation between these two values is clearly weak and large differences were sometimes found for cells with low over-all levels of activity. Such cells were those which displayed one brief burst of impulses per step and were otherwise almost silent.

In each cell an approximate index of the depth of frequency modulation was

obtained by subtracting the rate during the tenth of the step when the cell was least active from the peak rate. A frequency-distribution histogram of the resultant values is shown in Fig. 4*B*. They ranged from a few impulses/s up to 185 impulses/s with an over-all mean of 64·2 ± 40 impulses/s (± S.D.). Fig. 4*D* demonstrates that the depth of frequency modulation was only weakly correlated with mean rate indicating that strongly rhythmic discharges were not confined to cells showing any particular level of over-all activity.

Although the post-event time histograms and measurements derived from them have the usual advantages of averaging techniques, they also inevitably obscure any pace-to-pace variations in the pattern of discharge. For this reason each histogram was accompanied by a raster-type display of the spike data in which each dot represented an action potential and each line of the raster represented the discharges during one complete step plus those in the preceding 500 ms period. Rasters for the units of Fig. 3*A* and *D* are shown as Fig. 3*C* and *F* respectively. The steps are not shown in their order of occurrence but rank ordered by duration with the longest pace at the top. The rasters confirm and extend what is visible in the raw records, namely that step by step variations did in fact occur. They were usually modest but occasionally substantial. Thus, in Fig. 3*C* there is a high level of activity during the seventh pace from the top and in Fig. 3*F* there is an unusually low level of activity in the thirteenth pace from the top. A quantitative measure of the variability was therefore obtained by calculating the discharge rate during each of the twenty steps and then calculating the coefficient of variation of these rate values. In most cells this was less than 25 % but in twenty-one cells (17 %) it exceeded 50 %. However, in seventeen of the twenty-one, the over-all mean rate during the twenty steps was less than 20 impulses/s and at such levels of activity even a small change in the number of spikes per pace will produce a large change in mean rate and therefore a large coefficient of variation.

As already mentioned, forty-nine cells were studied during more than one batch of twenty paces and in a proportion of these there were quite substantial differences in over-all discharge rate between the different samples (see above). However, it was striking that, except in one cell, the timings of the peaks and troughs in the histogram display were the same in all samples.

Timing of the discharges relative to the step cycle

The cells of Fig. 3*A* and *D* discharged at quite different, indeed opposite, times during the step cycle and in the population as a whole the cells varied very widely in this respect. Some indication of the degree of variability encountered is given in Fig. 5 in which raw data and histograms are shown for three other neurones.

To facilitate comparisons between the discharge timings for the whole population the approach used by Armstrong & Edgley (1984) was employed (cf. also Orlovsky, 1972*a*, *b*). In each neurone the firing rate during each tenth of the step was determined and the 'active period' (or periods) was taken as being those tenths when the rate exceeded the mean rate by 10 % or more. The results for all 123 rhythmically active neurones are given in Fig. 6*A*, where for each cell active periods are represented by appropriately placed lines. The range of behaviour is clearly very wide: not only were there some units 'active' during each tenth of the step, there were also differences

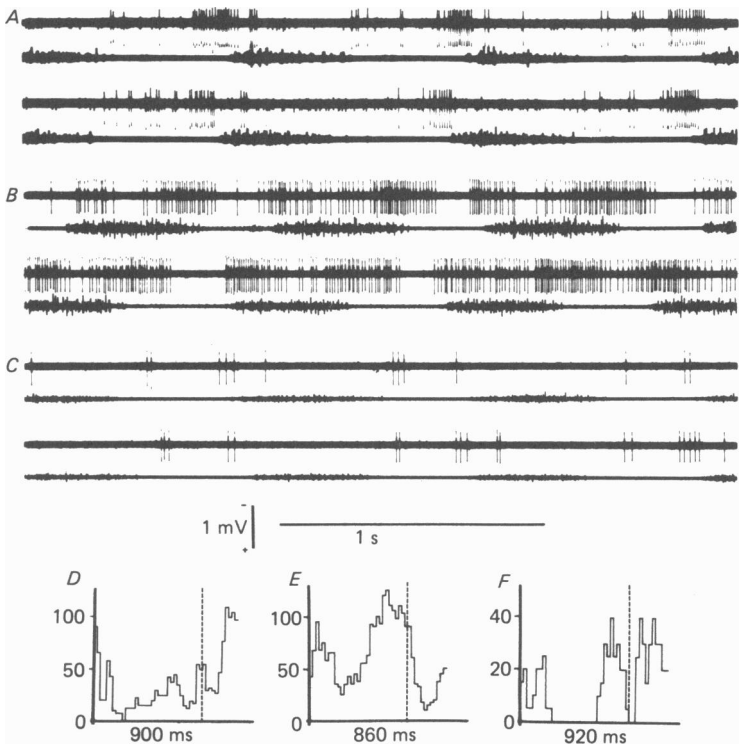

Fig. 5. Discharges of three further Purkinje cells during locomotion at 0·5 m/s. *A*, *B* and *C*, discharges of three different Purkinje cells during locomotion. In each case the unit recordings are accompanied by the simultaneously recorded e.m.g. activity from triceps brachii. Two sequences of three paces each are shown for each unit. The voltage calibration bar is 1 mV for the units (negative up) and 2 mV for the e.m.g. records. *D*, *E* and *F*, post-event time histograms made by averaging the discharges of the neurones in *A*, *B* and *C* over twenty steps each. Note that the horizontal axes represent the duration of a *single* step cycle, the average durations of which are shown below each histogram. The dashed vertical lines represent the time of onset of activity in the major elbow flexor muscles.

in the number of active periods per cell (cf. also Fig. 5). Seventy-seven neurones (63 %) had one active period, forty-three (35 %) had two and three (2 %) had three. Despite this variability, many of the neurones which became active early in stance did so only briefly and frequently became active again later, while neurones becoming active from late stance onwards usually did so for one longer period.

From Fig. 6*A* the proportions of neurones active during each tenth of the step cycle can be found and these are shown in Fig. 6*B*. The percentage active was only 20 % in mid-stance but rose sharply in late stance to reach 50 % in late swing.

As pointed out with reference to interpositus neurones by Armstrong & Edgley (1984), curves like Fig. 6*B* have the disadvantage that no account is taken of the wide variations in over-all level of activity which exist between units. For this reason the discharge rates during each tenth of the step cycle were averaged for all units to provide the curve of Fig. 6*C* which again indicates that, as a whole, the Purkinje cell population discharged more during swing (maximum 68 impulses/s in late swing) than during stance (*ca.* 49 impulses/s in mid-stance).

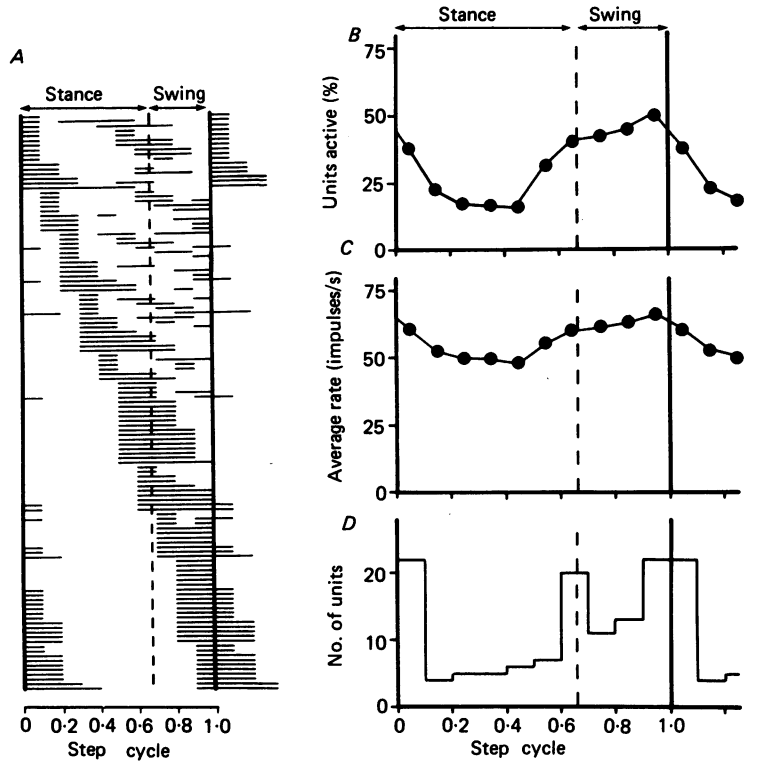

Fig. 6. The timing of the activity in the Purkinje cells in relation to the step cycle in the ipsilateral forelimb. *A*, lines representing the active periods of each of the 123 Purkinje cells which discharged rhythmically during locomotion. The continuous vertical lines represent the onset of e.m.g. activity in triceps brachii, the dashed vertical line represents the time of onset of e.m.g. activity in brachialis muscle (elbow flexor). *B*, plot showing the fluctuation in the proportion of neurones active (see text) during different tenths of the step. Same neurones as in *A*. *C*, the average discharge rate of the Purkinje cell population (all cells) during each tenth of the step cycle. *D*, the number of neurones attaining their peak discharge rate during each tenth of the step cycle. Note that this histogram only includes those neurones with a clearly defined time of peak discharge.

Because some cells were active for a substantial fraction of the step cycle, a third measure of population activity relative to the step cycle was obtained by determining the number of neurones reaching their peak rate in each tenth of the step cycle and the results are shown in Fig. 6*D*. Only 115 neurones are represented because in a few cases there was no clearly defined peak. Fig. 6*D* illustrates that few neurones achieved peak rate during mid-stance; many more neurones did so during swing and at the times of transition between stance and swing.

The rhythmic activity within different Purkinje cell subpopulations

Plots similar to those of Fig. 6*B*, *C* and *D* were constructed separately for the proximal, elbow-related and distal subgroups of Purkinje cells and the results are shown in Fig. 7. In each subgroup the cells varied widely in discharge pattern but for all three groups the plots for proportion of cells active and for average discharge rate both indicate that the population activity was substantially greater during swing

(and the earliest part of stance) than during most of stance. Activity increased slightly earlier among the proximal cells than among the others and the histograms showing times of peak discharge confirm this since the number of cells discharging at peak rate in late stance was highest in this subgroup.

Because the Purkinje cells of the c_1 and c_2 cortical zones are known to project to different parts of nucleus interpositus (see Discussion), plots similar to those of Fig. 7

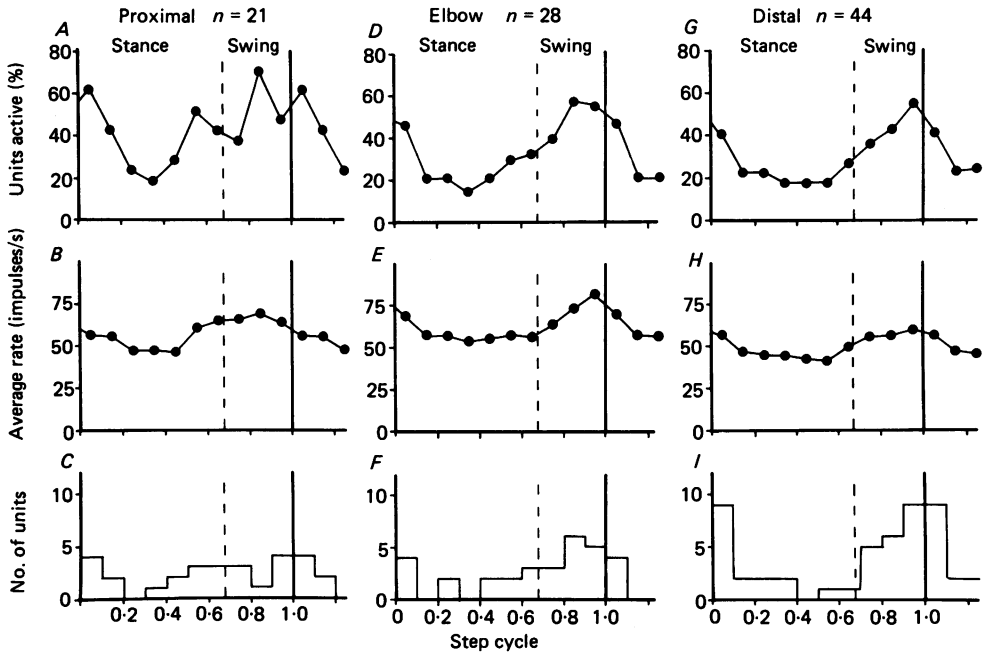

Fig. 7. The timing of the activity in the subpopulations of Purkinje cells with receptive fields centred on different parts of the ipsilateral forelimb. *A*, *B* and *C*, plots similar to those in Fig. 6*B*, *C* and *D* respectively, made for the group of twenty-one Purkinje cells with receptive fields on the proximal part of the ipsilateral forelimb. *D*, *E* and *F*, plots similar to those in *A–C* made for the twenty-eight Purkinje cells with receptive fields centred on the elbow. *G*, *H* and *I*, similar plots to those in *A–C* and *D–F* made for the forty-four neurones with receptive fields centred on the distal part of the forelimb.

were also prepared for those subgroups of cells electrophysiologically identified (see above) as belonging to one or other of the two zones. These are shown in Fig. 8 where *A*, *C*, *E* and *G* and *B*, *D*, *F* and *H* refer to c_1 and c_2 neurones respectively. Both subgroups were more active during swing than during stance and the activity fluctuated to a similar extent in terms both of proportion of cells active (cf. Fig. 8*C* and *D*) and of average rate (cf. Fig. 8*E* and *F*). The only noticeable difference between the two zones is that the level of activity begins to rise (and reaches its maximum) about one-tenth of a step cycle earlier in the c_1 subgroup. A shift in the same direction is also evident in the histograms showing the times at which each neurone reached its peak rate (cf. Fig. 8*G* and *H*).

Among the individual cells making up the two subpopulations there were no

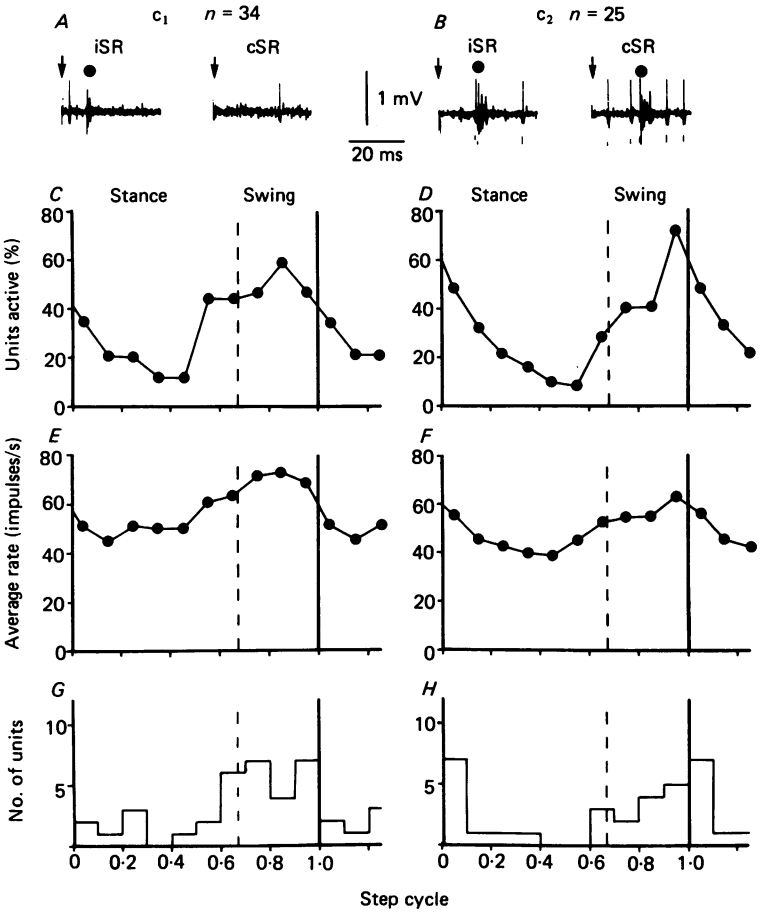

Fig. 8. The timing of the activity of the Purkinje cell populations identified as belonging to the c_1 and c_2 zones (see text). *A* and *B*, responses of a c_1 and c_2 neurone respectively, to stimulation of the superficial radial nerves at low intensity. Where evoked, the complex spikes are marked with filled circles. Stimuli marked by arrows. *C*, *E* and *G*, are plots similar to those in Fig. 6*B*, *C* and *D* respectively, but made for the population of thirty-four Purkinje cells shown to lie in the c_1 zone. *D*, *F* and *G*, are similar plots to those in Fig. 6*B*, *C* and *D* respectively, made for the twenty-five neurones shown to lie in the c_2 zone. iSR and cSR are respectively the ipsilateral and contralateral superficial radial nerves (see Methods).

systematic differences in discharge pattern (e.g. in number of 'peaks' per step) and in each population, as for the receptive field subgroups, a variety of discharge timings and of depths of modulation was represented.

DISCUSSION

Tactile receptive fields

In all tested neurones it was possible to detect a peripheral receptive field from which natural stimulation of mechanoreceptors modified the background discharge. All such fields involved the forelimb and no hind-limb fields were found, but this is

not surprising because the neurones were within the classical forelimb area of the cat cerebellar cortex. Most fields were rather wide, 'vague' edged and response intensity varied from place to place in the field. To some extent this diffuseness may reflect the problems of using manually applied stimuli together with the difficulty of detecting subtle changes in firing rate in those cells (the majority) which displayed a vigorous but irregular background discharge of simple spikes. However, very similar receptive field characteristics were noted in awake cats by Thach (1967) and in monkeys by Harvey, Porter & Rawson (1977).

Discharge rates

In two previous studies, the average discharge rates for Purkinje cells in awake and resting cats have been given as 48/s (Hobson & McCarley, 1972) and 44/s (Armstrong & Rawson, 1979), these values referring to simple spikes only. In the present study, both simple and complex spikes were counted but in agreement with the previous workers rates for complex spikes were 1–2/s so that our population average of 37·8 impulses/s only slightly over-estimates the rate for simple spikes alone. In awake, but passive, monkeys Thach (1970*a*) and Mano (1970) have reported similar discharge rates of 48/s and 28/s respectively.

During walking the level of activity was considerably higher than at rest (mean of 57·6 impulses/s) and the increase was entirely due to augmented simple spike activity. There are no previous studies in awake cats with which this level can be compared but in high-decerebrate cat preparations, Purkinje cells in other parts of the cortex discharge at comparable rates during locomotion. Thus Udo *et al.* (1981) reported an average rate of about 60 impulses/s among Purkinje cells in the lateral part of the vermis in lobule V (i.e. in the b zone; see Voogd, 1969; Oscarsson, 1976, 1980), while Orlovsky (1972*a*) reported a rate of approximately 75 impulses/s among hind-limb-related Purkinje cells in the paravermal part of lobules II and III.

It is interesting to note that Orlovsky (1972*a*) also reported an over-all average rate of 39 impulses/s for the Purkinje cells in his decerebrate preparations in the intervals between bouts of locomotion. This value is strikingly similar to our finding for the resting animal (see above). This agreement is perhaps surprising because nucleus interpositus neurones were much less active in the decerebrate preparation than in awake cats during both rest and locomotion (cf. Orlovsky, 1972*b*; Armstrong & Edgley, 1984).

All but one of the 124 Purkinje cells were considered to discharge rhythmically during locomotion. Similarly, Udo *et al.* (1981) also reported that the large majority (142/145 neurones) of Purkinje cells in the b zone discharged rhythmically during quadrupedal decerebrate locomotion. By contrast, Orlovsky (1972*a*) reported that only 67% of paravermal Purkinje cells discharged rhythmically during hind-limb stepping in decerebrate cats. This difference may have arisen because it is sometimes difficult, purely by visual inspection of spike trains, to detect frequency modulations superimposed on an irregular background discharge. Alternatively, the difference may have arisen because the Purkinje cells in Orlovsky's preparations received abnormal patterns of afferent input owing to the fact that the animals stepped only with the hind limbs and did not support their own weight.

In Orlovsky's experiments, 86% of those cells which were rhythmically active discharged one burst of impulses per step while the remaining 14% discharged two

bursts. In the present experiments, most neurones (63 %) likewise showed one period of accelerated firing per step but 35 % showed two such periods and a few showed three. The reasons for this difference are unclear. However, a similar difference was found for interpositus neurones and possible explanations were discussed by Armstrong & Edgley (1984); similar factors presumably operate in respect of the Purkinje cells.

However, the most striking difference between our findings and those of Orlovsky relates to the timing of the maxima and minima in the impulse activity of the Purkinje cells when taken as a population. In the present study, the population was considerably more active during swing than stance whereas Orlovsky reported a quite different finding: population activity peaked in early stance and was least at the onset of swing. Orlovsky's recordings were from hind-limb-related cells whereas ours had forelimb receptive fields but in nucleus interpositus the forelimb-related neurones studied by Armstrong & Edgley (1984) were very similar in population behaviour to the hind-limb-related cells studied by Orlovsky (1972*b*). We had therefore expected to find a comparable similarity for the Purkinje cells. One possible (but speculative) explanation is that some or all of Orlovsky's recordings were made not in the paravermal cortex but in the b zone in the lateral part of the vermis. This is not improbable because they were collected from lobules II and III which are deep below the cerebellar surface and are narrow mediolaterally. Udo *et al.* (1981) have shown that both hind-limb- and forelimb-related Purkinje cells in the b zone usually discharge most strongly at around the onset of stance.

Functional relationship between the Purkinje cells and interpositus neurones during locomotion

Purkinje cells in the paravermal part of the anterior lobe project to and monosynaptically inhibit the neurones of nucleus interpositus and it is therefore important to compare the activity of the Purkinje cells with those of the neurones of nucleus interpositus anterior which were recorded in the same experiments (Armstrong & Edgley, 1984).

Most anatomical investigations of the cerebellar corticonuclear projection agree that the c_1 and c_3 cortical zones project to nucleus interpositus anterior and the c_2 zone to nucleus interpositus posterior (see Voogd, 1969; Haines & Rubertone, 1976; Voogd & Bigarre, 1980; Armstrong, Gregory, Schild & Trott, 1982, and unpublished observations; but cf. Dietrichs, 1981). Moreover, they also indicate that it is the c_1 zone which provides the major cortical input to the (medial) part of nucleus interpositus anterior through which most of the micro-electrode tracks passed in the study of Armstrong & Edgley (1984). It is therefore appropriate to compare the population activity of the c_1 zone Purkinje cells with that of the interpositus neurones which had forelimb receptive fields. In fact, as shown in Fig. 9, the Purkinje cells of the c_1 zone and the forelimb-related interpositus neurones showed remarkably similar patterns of population activity during locomotion. In both cases the proportion of cells active (Fig. 9*A*) and the average rate (Fig. 9*B*) were at a minimum in mid-stance, rose rapidly in late stance and reached a peak in mid-swing before declining at around the onset of the next step. Moreover, the large majority of cells of both types reached their peak rate during swing (cf. Fig. 9*C* and *D*).

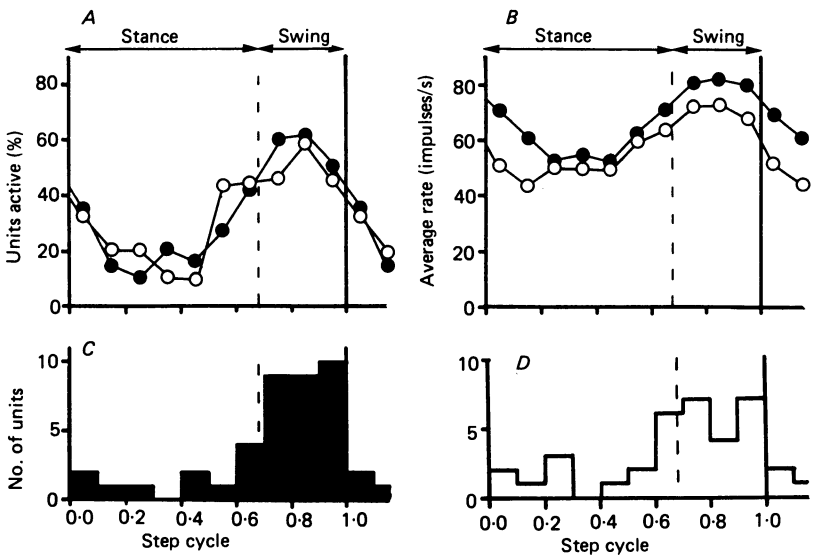

Fig. 9. Comparison of the timing of the activity in the population of thirty-four Purkinje cells identified as belonging to c_1 zone, with the timing of the activity in a population of forelimb-related neurones of nucleus interpositus anterior (from Armstrong & Edgley, 1984). *A*, plots showing the proportion of neurones in each population 'active' during each tenth of the step cycle. Open circles, c_1 Purkinje cell population; filled circles, the population of interpositus neurones. *B*, the fluctuation in discharge rate amongst the two populations during the course of the step cycle. Open circles represent the Purkinje cells of the c_1 zone; and filled circles the interpositus neurones. *C* and *D*, histograms showing the number of neurones attaining their peak discharge rate during each tenth of the step cycle, for the interpositus neurones and the Purkinje cells of the c_1 zone respectively.

The procedure we have adopted of 'pooling' the results from large numbers of individual cells, which showed a wide variety of locomotor-related discharge patterns, is open to the objection that it may grossly over-simplify the functional relationship existing between the Purkinje cells and their target neurones. However, the cerebellar corticonuclear projection is spatially very convergent (see Allen & Tsukuhara, 1974, for references and discussion) so that temporally converging the activities of cells recorded at different times but under the same conditions of locomotion therefore provides a real if approximate parallel to what must occur from instant to instant during cerebellar function.

It should be noted that only those Purkinje cells which responded to weak stimulation of the superficial radial nerves could be assigned to a particular zone. Zonal identification was therefore possible only for cells with receptive fields within the skin territory innervated by that nerve. However, this selectivity is unlikely to have produced any gross distortion in the profile of the population activity within the c_1 zone because the alternative grouping of the cells by receptive field location revealed broadly similar profiles for the 'distal', 'proximal' and 'elbow-related' subgroups (see Fig. 7). The fact that activity in the c_1 zone was slightly phase advanced over the c_2 zone (see below) seems to reflect the fact that in electrode tracks which passed through the c_1 zone, proximal receptive fields were much commoner

than they were in tracks through the c_2 zone and as a population the proximal cells were slightly phase advanced over distal and elbow-related cells.

By contrast with our results, the interpositus and Purkinje cell populations in Orlovsky's experiments (1972*a*, *b*) discharged almost opposite in phase. This was interpreted as showing that the period of reduced interpositus activity was a response to a raised level of inhibitory input from the Purkinje cells. Conversely, the period of accelerated activity was interpreted as a disinhibitory phenomenon resulting from decreased discharge of the Purkinje cells (see Orlovsky & Shik, 1976). Perhaps the most important aspect of the present results is that they throw this interpretation into doubt and demonstrate instead that when the interpositus neurones develop their highest level of activity they do so *in the face of* an increased inhibitory input from the Purkinje cells. This finding carries two important corollaries. First, it implies that rather than *sustaining* the rhythmic activity of the interpositus neurones, the Purkinje cells act to *restrain* or 'damp' it (cf. Brooks & Thach, 1981). Secondly, it implies that the period of accelerated interpositus activity is primarily a response to excitatory inputs. These might conceivably be provided by afferents terminating in the nucleus without reaching the cortex but current evidence suggests they are provided by collateral branches of some of the climbing-fibre and mossy-fibre afferents which pass on to terminate in the paravermal cortex (see for example Chan-Palay, 1977; Bloedel & Courville, 1981).

The view which emerges, of the cortex acting as a restraint on a cerebellar output generated primarily via the cerebellar afferent collaterals, offers the attractively efficient organizational feature that the cortex exerts its greatest (inhibitory) effect on the nuclear neurones just when they are most active and therefore exerting their greatest influence on their extracerebellar targets.

The considerations above are of sufficient theoretical importance that it is worthwhile to consider whether the view is supported by other evidence and first, we may note that work by Orlovsky (1972*c*), on Deiters nucleus appears to offer no support. This nucleus lies outside the cerebellum but, like nucleus interpositus, it receives inhibitory input from Purkinje cells (in the b zone) and excitatory input from cerebellar afferent collaterals. Its neurones also discharge rhythmically during decerebrate locomotion (maximum activity during stance). However, although removal of the Purkinje cell input by cerebellectomy raised the discharge rate during locomotion (presumably by disinhibition) it also abolished or greatly weakened the rhythmic character of the discharges. Orlovsky took this to indicate that the excitatory input from the cerebellar afferent collaterals is approximately constant in level throughout the step cycle so that the normal rhythms are almost entirely imposed by the Purkinje cells which alternately inhibit and disinhibit the Deiters neurones.

However, this deduction is in conflict with other findings. Thus, although Udo, Oda, Tanaka & Horikawa (1976) have confirmed that hind-limb-related Deiters neurones are most active early in stance they also found that cooling the b zone of the cortex to reversibly inactivate the Purkinje cells *enhanced* rather than reduced the frequency modulation. Furthermore, as noted above, forelimb-related Purkinje cells in the b zone are usually most active at around the onset of stance and recently it has been demonstrated that Deiters neurones projecting to the cervical enlargement (i.e.

forelimb-related) are also most active in early stance (Udo, Kamei, Matsukawa & Tanaka, 1982). The authors do not comment directly on this in-phase relationship between the Purkinje cells and Deiters neurones but the parallel with our findings is striking.

Secondly, two studies of paravermal Purkinje cells and interpositus neurones in monkeys can be regarded as supporting an in-phase mode of operation. Mortimer (1973) found that during 'startle' movements, evoked by acoustic stimuli, the earliest changes in both types of cell were increases in discharge rate which occurred almost simultaneously. Similarly, at the onset of signal-initiated arm movements the commonest initial change among task-related neurones of both types was an increase in rate (Thach, 1970*a*, *b*).

Thirdly, in the present experiments the transition from rest to locomotion was accompanied by an increased average rate in both cell populations. This implies not only an excitation of both populations but also that excitatory inputs to the interpositus neurones were sufficient to more than offset the effect of the increased inhibitory input from the Purkinje cells.

Finally, support is also provided by the motor effects of temporarily cooling the paravermal part of lobule V during the locomotion of the decerebrate or awake cats (Udo *et al.* 1980). Cooling led to temporary increases in the amplitude and duration of the locomotor bursts of e.m.g. in forelimb flexor muscles and to hyperflexions of the limb during swing, presumably because Purkinje cell activity was reduced and activity in the interpositorubrospinal path correspondingly increased. Effects on the stance phase and extensor muscle activity were small, which accords with our finding that at this time activity is at its least in both the Purkinje cells and the interpositus neurones.

Locomotion and the zonal organization of the cerebellar cortex

We cannot comment in comparable detail on the functional significance of the rhythmic discharges of the Purkinje cells in the c_2 zone because recordings were not made from the relevant nucleus (nucleus interpositus posterior). However, Oscarsson (1976, 1980) has concluded that each cortical zone subserves a distinct motor function and our recordings from the c_2 zone are therefore useful because they can be compared with those in the adjacent c_1 zone. In fact, the population activity in the two zones did not differ strikingly although the activity in the c_2 zone appeared to lag that in the c_1 zone by approximately one-tenth of a step cycle. The significance of this remains unknown. However, comparison with the work of Udo *et al.* (1981) indicates that there is a much greater difference in population activity between the b zone and either of the c zones because most Purkinje cells of the b zone generate two peaks of activity per step and population activity in this zone is greatest just before the onset of stance and during the early part of this phase. Most probably the general function of this zone in relation to its target nucleus (i.e. Deiters nucleus) is qualitatively similar to that which we suggest for the c_1 zone in relation to nucleus interpositus anterior, namely to restrain the effects which the nucleus exerts on motor mechanisms within the spinal cord. In the case of Deiters nucleus the latter would appear to include extensor mechanisms which contribute to the stance phase of the step while in the case of interpositus they include flexor mechanisms contributing to the swing phase.

We wish to thank Ms L. Gregory, Mrs A. Lear and Mr C. Makpeace for their excellent services respectively as technician, typist and photographer. Dr Edgley was supported by the Medical Research Council of Great Britain.

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