J. Physiol. (1984), **351**, *pp.* 411–432
With 10 *text-figures*
Printed in Great Britain

DISCHARGES OF NUCLEUS INTERPOSITUS NEURONES DURING LOCOMOTION IN THE CAT

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(*Received 15 November 1983*)

SUMMARY

1. Extracellular recordings were made from ninety-five cerebellar nuclear neurones in the cat. All were studied during periods of steady walking at 0·5 m/s and most were also studied in the resting animal.

2. Most neurones were in nucleus interpositus anterior; forty-four cells were shown by antidromic invasion to project to the mid-brain.

3. Most neurones discharged tonically in the absence of overt movements and the mean rate was 42 impulses/s (S.D. ± 23). During locomotion the mean rate was 68 impulses/s (S.D. ± 32).

4. In all but seven neurones the discharge during locomotion was frequency modulated but in different neurones the depth of modulation varied from 5 to 161 impulses/s (mean 52 impulses/s; S.D. ± 30) and the time of peak discharge relative to the step cycle in the ipsilateral forelimb also varied widely.

5. Despite the individual differences the population as a whole was much more active during forelimb swing than during stance, both in numbers of neurones strongly active and in over-all average discharge rate (74 impulses/s as compared with 55).

6. Most neurones had tactile receptive fields on the ipsilateral forelimb while others received input from head and neck or from both ipsilateral limbs. The tendency to discharge preferentially during early swing was greatest for the first group, especially the subpopulations with receptive fields around or proximal to the elbow.

7. Cells encountered in close sequence during a micro-electrode track had similarly located receptive fields and usually showed similar patterns of discharge during locomotion.

8. These findings are discussed in relation to the suggestion by Orlovsky (1972*a*, *b*, *c*) that nucleus interpositus assists in regulating locomotion by evoking rubrospinal discharges which facilitate the flexor muscle activities produced by the spinal mechanisms reponsible for generating the swing phase of the step cycle.

INTRODUCTION

Nucleus interpositus is an important intracerebellar nucleus in mammals and it is generally agreed that as such it is important in movement control (e.g. Brooks & Thach, 1981). Its neurones project to and powerfully excite rubrospinal neurones and

also neurones of the ventrolateral thalamus which in turn project to the motor area of the cerebral cortex (see Brooks & Thach, 1981, for references). They receive monosynaptic inhibitory input from the Purkinje cells in the 'intermediate' (paravermal) part of the cerebellar cortex (Ito, Yoshida, Obata, Kawai & Udo, 1970; Voogd & Bigarre, 1980) and excitatory inputs from axon collaterals of those cerebellar afferent fibres which provide input to the intermediate cortex. These afferents are the climbing and mossy fibres which form the terminal stages of a variety of spino-cerebellar, cerebro-cerebellar and other cerebellar afferent pathways (see Bloedel & Courville, 1981).

Several studies have shown that interpositus neurones discharge in close temporal association with active movements of the forelimb both in cats (Burton & Onoda, 1978) and in monkeys (e.g. Thach, 1968, 1970; Harvey, Porter & Rawson, 1979) and a role in locomotor control is suggested by recordings made during the locomotion of decerebrate cats by Orlovsky (1972*a*). Orlovsky studied interpositus neurones with peripheral input from the ipsilateral hind limb and found that all discharged bursts of impulses which were phase-locked to the locomotor movements of the limb. Although different neurones discharged at different times in the step cycle, the population as a whole was most active during (and just in advance of) the swing phase of the step. The population activity in fact closely resembled that found for rubrospinal neurones under the same conditions and moreover the rhythmic discharges of rubral neurones were abolished by cerebellectomy (Orlovsky, 1972*b*).

Taken together with the finding that electrical stimulation of the red nucleus during decerebrate locomotion enhances the flexor muscle activity which generates the swing phase of the step (Orlovsky, 1972*c*), these observations suggested that nucleus interpositus contributes to controlling the swing phase at least in part by contributing excitatory input to flexor motoneurones via the rubrospinal tract. This hypothesis received support from later experiments on walking cats in which the functions of the forelimb-related part of the paravermal cortex were reversibly impaired by cooling: this led to hyperflexions of the forelimb, presumably because the interpositus neurones were subject to reduced inhibitory influences from the Purkinje cells (Udo, Matsukawa, Kamei & Oda, 1980).

While the results cited above provided Orlovsky with the basis for a coherent interpretation of the general role of interpositus neurones in locomotor control it must be noted that his interpositus recordings were obtained from decerebrate animals in which the nucleus was inevitably deprived of all inputs it may normally receive via the various (and substantial) cerebro-cerebellar pathways. Moreover the animals walked with hind limbs only and did not support their own weight. These factors may have appreciably influenced the discharge patterns observed because the firing of other cerebellar-related neurones (e.g. Deiters neurones contributing to the lateral vestibulospinal tract) apparently differs quite markedly in decerebrate cats depending on whether the locomotion involves all four limbs (Udo, Oda, Tanaka & Horikawa, 1976) or hind limbs only (Orlovsky, 1972*d*).

We have therefore recorded the discharges of interpositus neurones in chronically prepared cats trained to walk at controlled speeds on a moving belt. The neurones have been subgrouped according to their somatosensory peripheral receptive field and their discharge patterns during walking at 0·5 m/s have been characterized.

METHODS

The experiments were performed using nine cats trained to walk for brief periods on a belt moving at 0·5 m/s (a slow walking speed). At an initial operation performed using full general anaesthesia and aseptic precautions a small titanium chamber was affixed over a craniotomy which allowed access to the left side of the anterior lobe of the cerebellum. The dura was left intact and over-sealed with a layer of Medical Grade Elastomer (Dow Corning 382). The chamber was capped except during recording sessions when it carried a small autoclaveable micromanipulator used to advance glass-insulated tungsten micro-electrodes through the elastomer seal, the dura and the cerebellar cortex into the region of nucleus interpositus. Most single neurones were studied both during locomotion and during periods when the animal sat quietly on the experimenter's lap. The animals were not restrained during the recordings and gave no signs of any stress or discomfort. Details of the operative and recording techniques and of histological control procedures are given by Armstrong & Rawson (1979). Simultaneously with the cerebellar recordings electromyographic (e.m.g.) recordings of locomotor activity were made from selected flexor and extensor muscles of the fore- and hind limbs. The muscles studied were cleidobrachialis, brachialis, biceps brachii and triceps brachii (lateral head) in the ipsilateral forelimb, triceps brachii in the contralateral forelimb and sometimes vastus lateralis in the ipsilateral hind limb. These records were used to identify the stance and swing phases of the step cycle. The e.m.g. techniques are described in Armstrong & Drew (1984*a*, *b*).

The locomotor-related discharges of the interpositus neurones were subjected to computer-aided analysis (PDP 11-34) which included the construction of interspike interval histograms and of raster displays in which each line of the raster represented the discharges during one step cycle (duration typically 850 ms) and during the preceding 500 ms. Post-event time histograms were also constructed which showed the average pattern of neuronal discharge during a sequence of twenty steps. Our usual convention was to take the onset of the step cycle in the ipsilateral forelimb as occurring at the onset of the locomotor e.m.g. burst in triceps brachii muscle. Analysis was restricted to step sequences in which the gait was regular, i.e. in which step duration showed a coefficient of variance of less than 10%. Further details regarding data processing are given by Armstrong & Drew (1984*a*).

Whenever possible the somatosensory receptive fields of the neurones were defined by natural stimulation of mechanoreceptors in limbs and trunk as described by Armstrong & Drew (1984*b*). In addition an electrode implanted near the right red nucleus was often used to identify units antidromically as cerebellar efferent neurones (see Armstrong & Rawson, 1979). In some cases microstimulation via the micro-electrodes was used to evoke movements. Trains of ten 0·2 ms pulses at 330 Hz and intensities up to 80 μA were used. No signs of discomfort were ever seen.

After each experiment, sagittal sections of the cerebellum were inspected to verify the locations of the micro-electrode tracks (cf. Armstrong & Rawson, 1979).

RESULTS

Action potential characteristics and location of the neurones

Extracellular recordings were made from a total of ninety-five neurones. In all cases stable records were obtained for at least one sequence of twenty consecutive steps during which the animal walked to maintain a constant position on a belt moving at 0·5 m/s. In most cases spike shape and size were constant for much longer periods ranging up to over an hour.

Most units yielded diphasic negative–positive action potentials which ranged in amplitude from 0·4 to 1·8 mV and in duration from 0·3 to 0·9 ms. Three typical examples are shown in Fig. 1*A*. That the recordings were from cell bodies rather than axons is probable because electrical contact was sometimes maintained during advances of the electrode tip which exceeded 100 μm. In addition slight A–B

inflexions were sometimes present on the rising phase of the action potentials and during injury discharges fractionation of the spike was observed.

Some neurones (44/95; 46%) were positively identified as cerebellar efferent neurones because they discharged a single action potential at short fixed latency in response to electrical stimulation of the ascending limb of the brachium conjunctivum

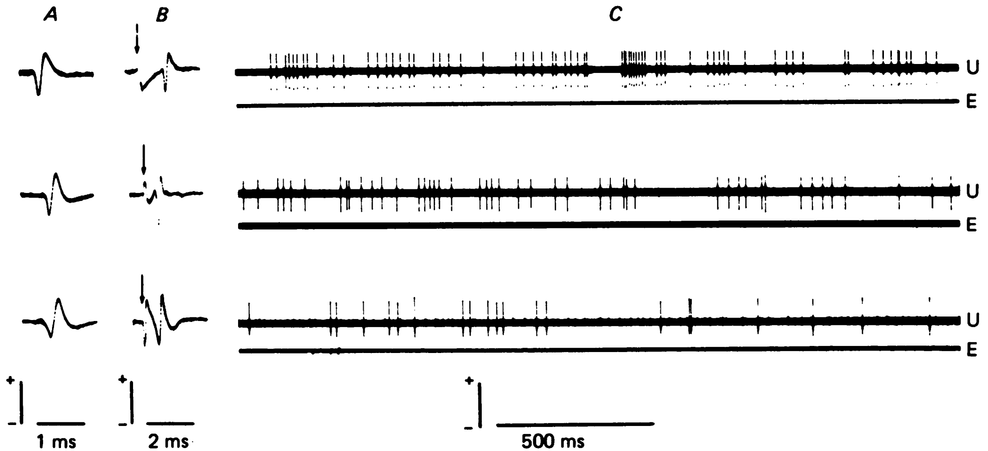

Fig. 1. Extracellular action potentials recorded from three typical interpositus neurones. *A*, fast-swept records showing the spontaneously occurring action potentials of three different neurones. Each record comprises several superimposed sweeps, pre-triggered to display the full shape of the spikes. *B*, antidromic action potentials of the same neurones generated by a mid-brain stimulus delivered at the arrow. *C*, discharges of the same three neurones recorded in the passive animal. In each case the unit record (U) is accompanied by the e.m.g. recorded simultaneously from the ipsilateral triceps brachii muscle (lateral head) (E). The voltage calibration equals 2 mV for all e.m.g. traces and 1 mV for all unit recordings. Note that positive is up in all unit traces.

(0·2 ms pulses) in the region of the contralateral (i.e. right) red nucleus. These responses were antidromically generated because they would follow frequencies of stimulation as high as 1000 Hz and were cancelled by natural discharges. The antidromic responses of the three neurones of Fig. 1*A* are illustrated in Fig. 1*B*. Antidromic latencies ranged from 0·4 to 1·5 ms and the frequency distribution of latencies was similar to that found by Armstrong & Rawson (1979).

Unfortunately mid-brain stimulation cannot discriminate between interpositus neurones and those of the other cerebellar nuclei (i.e. nucleus fastigius and nucleus lateralis) because all the nuclei provide projections to this region. However, the tracks entered the cerebellum in the paravermal part of lobule V of the anterior lobe between 3·5 and 5·0 mm lateral to the mid line (i.e. directly over nucleus interpositus). Moreover, in sagittal sections of the cerebellum (see Methods) the electrode tracks were marked by thin lines of gliosis and the large majority passed through the caudal half of nucleus interpositus anterior. In some brains a few tracks deviated into nucleus interpositus posterior or the medial portion of nucleus lateralis and because it is not possible to assign individual neurones to a particular track, an undeterminable (but presumably small) proportion of the neurones may have lain in these nuclei.

Receptive field characteristics

Whenever possible an attempt was made to determine a peripheral receptive field for each neurone by natural stimulation of mechanoreceptors over the whole surface of the body in the passive animal. Considerable care was taken to avoid eliciting any active movement which might be accompanied by 'motor' rather than 'sensory' discharges. For this reason the stimuli were confined to movements of hairs, light taps and light to firm pressures. For most neurones such stimuli were quite effective in modifying (usually accelerating) the resting discharge rate so that receptive fields could be located for eighty-three of the ninety-five neurones (87 %). Sharp boundaries could not usually be found for the fields and the intensity of the response elicited from different parts of the field frequently varied in a patchy and unpredictable manner. For this reason and because of the limited range of stimuli used the receptive field determinations should be interpreted only as defining the area of the body from which the strongest tactile input was received.

Most neurones (66/83; 80 %) had receptive fields which involved the ipsilateral forelimb and in forty-two cases (51 %) the field was apparently confined to that limb. These could be further subdivided into thirteen 'distal' neurones in which the field was centred on the foot and/or wrist, thirteen 'proximal' neurones in which the receptive field was centred around the upper arm and shoulder and sixteen cells with fields around the elbow region. A further twenty-four neurones (29 %) had wider receptive fields which included part or all of both ipsilateral limbs and sometimes the intervening trunk. In some cases the responses were briskest from the forelimb and in others from the hind limb. Finally seventeen neurones (20 %) had their strongest input from the face and/or neck.

Discharges in the absence of active movements

For seventy-three of the ninety-five neurones it was possible to record periods of discharge whilst the animal sat or lay quietly without overt movements. Only three neurones (4 %) were silent for long periods under these conditions. The remaining seventy units discharged irregularly but continuously apart from occasional periods of a few seconds when discharge ceased in some neurones. Examples of the tonic discharges of the three units in Fig. 1*A* and *B* are shown in Fig. 1*C*. At least one interspike interval histogram was constructed for each unit using a sample of 1000 successive intervals and these were used to obtain a value for the mean discharge rate. Values ranged widely from 2·1 to 105 impulses/s and the frequency distribution of rates is shown in Fig. 2*A*. The over-all mean rate in the population was 41·9 impulses/s (S.D. ± 23).

Discharge rates during locomotion

All ninety-five neurones were studied during at least one period of steady locomotion at a belt speed of 0·5 m/s, which corresponds to a comfortable walk (and a pace duration which is usually between 800 and 900 ms). The animals uniformly adopted a walking gait in which footfall in the hind limb preceded that in the forelimb, (by 10–20 % of the step cycle) rather than a pacing gait in which footfall occurs near-synchronously in the ipsilateral limbs (see Grillner, 1981).

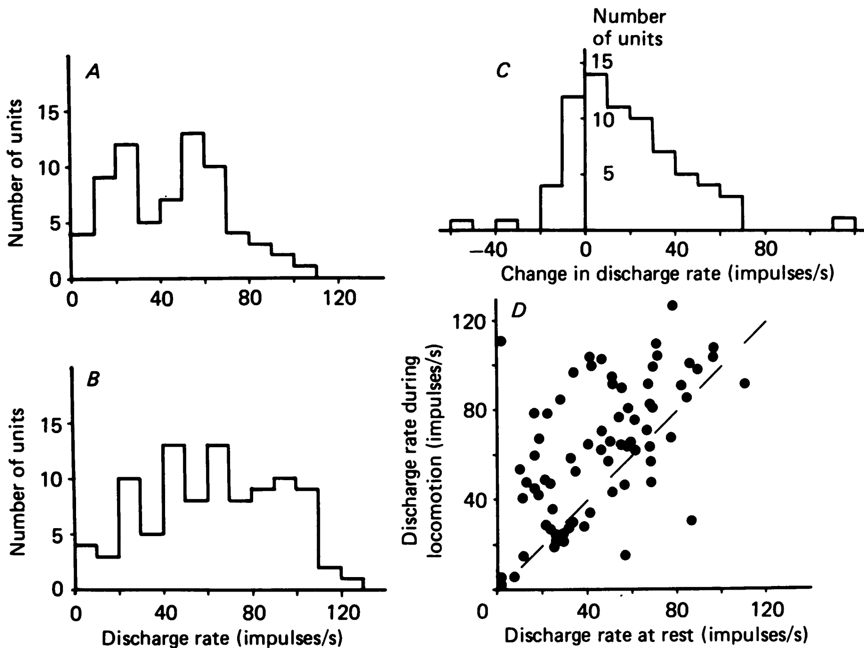

Fig. 2. Discharge rates of interpositus neurones during rest and locomotion. *A*, frequency distribution histogram for the discharge rates of seventy neurones in the resting animal. *B*, frequency distribution histogram for the discharge rates of ninety-five neurones (including those in *A*) during locomotion at 0·5 m/s. *C*, frequency distribution histogram for the change in discharge rate brought about in each of the neurones in *A* by the transition from rest to steady locomotion at 0·5 m/s. Increases in rate plotted as positive, decreases as negative values. *D*, scattergram plotting discharge rate at rest (horizontal axis) against rate during locomotion for each of the seventy neurones in *A* and *C*. Diagonal interrupted line is line of equal discharge.

The discharges of four typical neurones under these conditions are shown in Fig. 3*A–D*. The unit discharge (upper trace) is accompanied in each case by the e.m.g. recorded simultaneously from the lateral head of triceps brachii muscle in the ipsilateral forelimb (lower trace) and this allows the phasing of the discharges relative to the step cycle to be determined (see below). Under these conditions the ninety-five neurones were found to discharge at rates which ranged between 2·2 and 122 impulses/s. The over-all mean rate for the population was 68·4 impulses/s (S.D. ± 32) and the frequency distribution of rates is shown in Fig. 2*B*.

For forty-seven cells recordings were made during two or more periods of twenty regular steps usually some minutes apart. In most cells the discharge rates were almost identical in the different samples. However, in fifteen cases (32 %) the rates differed by more than 10 impulses/s and in five of these (11 %) they differed by more than 25 impulses/s. These changes were not accompanied by any obvious changes in locomotor performance or in the shape or size of the unit action potentials. In such cases the sample used in constructing Fig. 2*B* was that in which pace duration varied least.

Comparison of Fig. 2*A* and *B* indicates that in most neurones the discharge rate during walking was higher than during rest and this is confirmed by Fig. 2*C* which shows the frequency distribution for the changes in rate observed (increases plotted

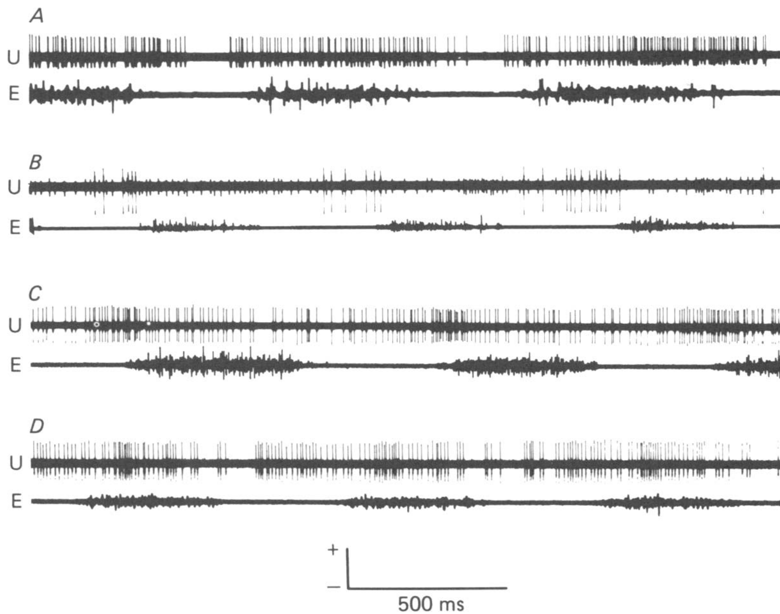

Fig. 3. Discharge of four typical interpositus neurones during locomotion at 0·5 m/s. In each of *A*, *B*, *C* and *D* trace U shows impulses discharged by a different unit during three successive paces. In each case the step cycles are indicated by trace E which shows the e.m.g. signal recorded from the lateral head of triceps brachii muscle in the ipsilateral forelimb. Vertical calibration is 1 mV for the units, 2 mV for the e.m.g. signals.

as positive values). The average change was an increase of 18·7 impulses/s (S.D. ± 25). The extent of change in individual units is indicated by Fig. 2*D* in which the rate during locomotion is plotted against that during rest for each unit. Fig. 2*D* reveals that changes could occur whatever the discharge rate during rest.

For the cell groups with differently located receptive fields there were no statistically significant differences between the average discharge rates, either at rest or during locomotion and the average changes in rate between rest and locomotion were likewise not significantly different.

Frequency modulation of discharges during locomotion

As shown by the examples in Fig. 3*A–D* many neurones discharged rhythmically during locomotion. Some discharged bursts of impulses alternating with silent periods but most fired throughout the step cycle, though more briskly at some time or times than at others. In order to investigate this periodic activity quantitatively a computer-aided analysis was performed in which the discharges during sequences of twenty successive steps were averaged, the results being presented as a post-event time histogram (see Methods and cf. Armstrong & Drew, 1984*a*). For convenience and uniformity the start of the step cycle was taken as the onset of the locomotor burst of e.m.g. in the ipsilateral triceps brachii muscle (extensor of the elbow). During locomotion at 0·5 m/s the period from the onset of triceps e.m.g. to the onset of e.m.g. in brachialis muscle (flexor of the elbow) occupies *ca.* the first 550 ms (*ca.* 67 %) of

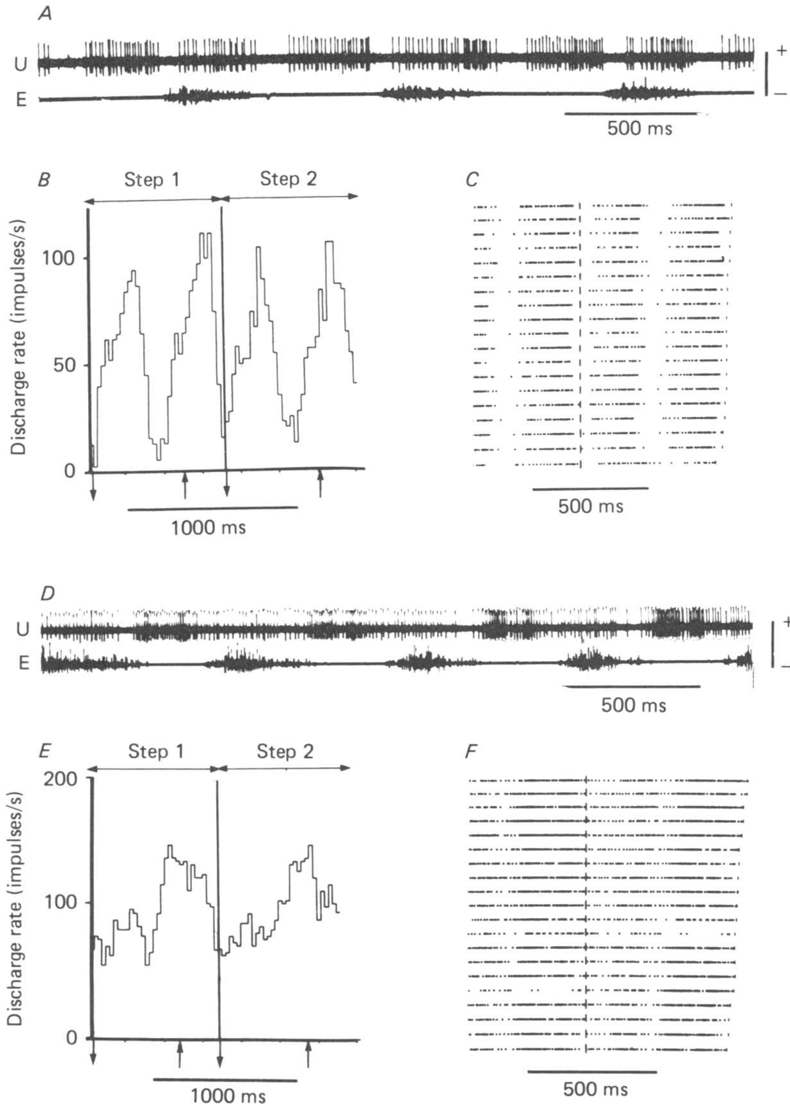

Fig. 4. Displays of the impulse activity of two interpositus neurones during locomotion at 0·5 m/s. One unit shown in *A*, *B* and *C* and a second in *D*, *E* and *F*. *A* and *D* each show the unit discharges (trace U) and the triceps brachii e.m.g. (trace E) during a few successive paces. Voltage calibration is 1 mV for the unit traces and 2 mV for the e.m.g.s. *B* and *E* each show a post-event time histogram which overlap averages the unit discharges during a sequence of twenty paces including those shown in *A* and *D* respectively. In each case the time axis begins at the time of onset of the locomotor burst of e.m.g. in triceps brachii. The time axis spans *twice* the average duration of a step cycle so that one step is shown on each side of the vertical line which bisects the histogram. Note that the approximate time of placement and lift of the ipsilateral forefoot are shown by the downward and upward arrows respectively. In each pace stance is therefore to the left of the upward arrow and swing is to the right. Bin width in each case is 20 ms. *C* and *F* are raster displays of the same discharges which make up *B* and *E* respectively. The vertical interrupted line marks the onset of locomotor e.m.g. in triceps brachii so that each line of the raster shows one complete pace (to right) plus the preceding 500 ms. Note that the paces are rank ordered by duration with longest at top.

the step cycle and is referred to in the present account as stance. Swing denotes the 33 % of the step remaining after brachialis onset. This usage of the terms stance and swing is an approximate one because a combined cinematographic and e.m.g. analysis (see Armstrong & Drew, 1984*a*) has shown that during locomotion at 0·5 m/s foot placement in fact occurs slightly (*ca*. 30 ms) later than the onset of e.m.g. activity in triceps brachii muscle, while foot lift occurs slightly (30–45 ms) after the onset in brachialis.

Post-event histograms for two representative neurones are included in Fig. 4. For each unit a short section of filmed record (Fig. 4*A* and *D*) shows the action potentials discharged during a few successive paces (upper trace) together with the locomotor e.m.g. recorded from triceps brachii (cf. Fig. 3). Below this record the post-event time histogram is shown to the left (Fig. 4*B* and *E*). In both units it includes the paces shown above plus other paces to a total of twenty and the horizontal axis has been adjusted to span *two* complete step cycles. It is clear from these displays that the neurone of Fig. 4*A* generated many more impulses during mid-stance and mid-swing than at other times while that in Fig. 4*B* was most active at the onset of swing.

It should be noted that when more than one histogram was constructed for the same unit using different batches of steps the timing of the peaks and troughs was always identical, even in those units for which the mean discharge rate was most widely different (i.e. the fifteen cells in which rate differed by more than 10 impulses/s).

In both Fig. 4*B* and *E* the histogram is accompanied on the right by a raster display based on the same batch of data. The vertical interrupted line marks the onset of activity in triceps brachii muscle so that each line of the display represents the discharges during a single pace plus the preceding 500 ms. The paces are not shown in their order of occurrence but were rank ordered according to duration with the longest pace at the top. These displays provide a qualitative impression of the pace-by-pace variability in the discharges and in Fig. 4*C* it is evident that their timing was rather uniform but that the number of impulses per burst varied somewhat. In Fig. 4*F* the second unit also behaves fairly uniformly from pace to pace but in one step (twelfth from the top) there was a marked reduction in activity throughout the step and the high-frequency activity normally present in swing was absent. Similar temporary breaks in the rhythmic discharge were found in some other units and were also noted by Orlovsky (1972*a*). A quantitative index of the degree of pace-by-pace variability in the behaviour of each unit could be obtained by determining the discharge rate during each step and calculating the coefficient of variance for the twenty values. In sixty-three cells (66 %) the value was less than 20 %. For a neurone discharging at an average of 68 impulses/s (the over-all mean rate for the population) this implies a standard deviation of less than 13·5 impulses/s. In nine neurones (10 %) the coefficient exceeded 50 % but most of these were slowly firing cells (< 15 impulses/s) in which a difference of two or three impulses per pace represents a substantial proportional change in discharge rate.

In addition to these visual displays each histogram was divided into ten time segments of equal duration and the mean rate of discharge was calculated for each. The highest value is termed the peak rate during the step (see below). It should be noted that this value is an average for twenty steps and represents the rate during

a period of 80–90 ms depending on the precise step duration (which showed some variation between samples and between different animals).

Among the ninety-five units the peak rates ranged widely from 5 to 169 impulses/s and a frequency distribution for the different values is shown in Fig. 5*A*. The over-all mean for the whole population was 89·4 impulses/s (S.D. ± 38). To determine whether

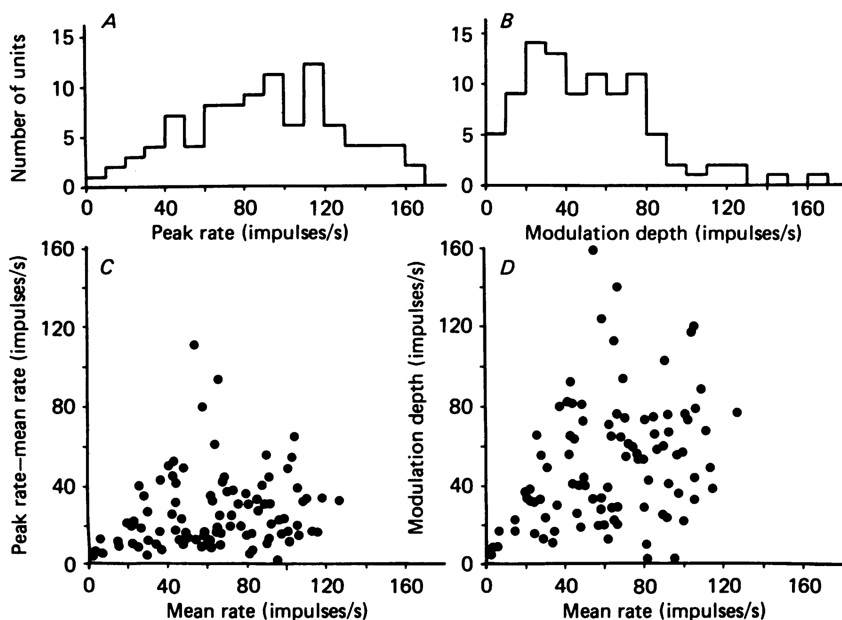

Fig. 5. Discharge parameters of all ninety-five interpositus neurones during locomotion at 0·5 m/s. *A*, frequency distribution histogram for the peak rates of discharge. Peak rate defined as the rate during that tenth of the step cycle when the unit discharged fastest (see text). *B*, frequency distribution for the extent to which each unit showed frequency modulation of the discharge rate during locomotion. Index of modulation used was the rate difference (in impulses/s) between those tenths of the step when the unit was most and least active. *C*, scattergram plotting mean rate of discharge (horizontal axis) against the amount by which the peak rate exceeds the mean rate (vertical axis). *D*, scattergram plotting mean rate for each unit (horizontal axis) against modulation depth defined as in *B* (vertical axis).

the highest peak rates were achieved by those cells with the highest over-all level of activity, in each cell the difference between the peak rate and the mean rate was plotted against the mean rate. The resulting scattergram is shown in Fig. 5*C* where it is evident that there was no clear-cut relationship. Some cells with low levels of over-all activity reached quite high peak rates (because they generated one short burst per step and were otherwise almost silent), and, conversely, other cells discharged throughout the step but did not achieve particularly high peak rates (because only a modest level of frequency modulation was superimposed on the tonic discharge).

It is clear from Fig. 5*A* and *C* (and from Figs. 3 and 4) that not all cells showed equal degrees of frequency modulation during locomotion and the extent of the

modulation in the different cells was therefore investigated quantitatively. To this end a depth of modulation was calculated for each cell as the difference between the peak rate and the rate during the tenth of the step when the unit discharged least (minimum rate). This index varied between cells from 2 to 161 impulses/s (mean 52 impulses/s; S.D. ±30) and a distribution histogram for the different values is shown in Fig. 5*B*. For each cell the depth of modulation was also plotted against the mean rate to produce the scattergram of Fig. 5*D*. This demonstrates there was no close correlation between mean rate and depth of modulation, at least among neurones with mean rates above 20 impulses/s.

It is obvious from Fig. 5*B* and *D* that there were some cells in which the discharge rate during locomotion was modulated by only very small amounts. Units were therefore arbitrarily included as being rhythmically active only if either the peak or the minimum rate differed from the mean by 10% or more. Thus, for example a cell discharging at 70 impulses/s would be included provided that the peak rate was at least 77 impulses/s or the minimum rate did not exceed 63 impulses/s. On this basis no fewer than eighty-seven neurones (92%) were rhythmically active.

Discharge phasings relative to the step cycle

Among the eighty-seven rhythmically active neurones fifty-one cells (57%) showed one period of accelerated discharge per step cycle, thirty-five (39%) showed two such periods and three (3%) had three such periods. Just as the neurones varied widely in mean rate, peak rate and depth of modulation they also showed considerable individuality in the timing of these accelerations relative to the step cycle in the ipsilateral forelimb. This is evident both from inspection of the actual discharges (see Figs. 3 and 4) and from comparison of the post-event time histograms for different units (see Fig. 4*A* and *B*). However, such comparisons are not easily made for large numbers of units and a display was therefore devised which is more compact than the histogram, though inevitably it provides less information. The method used was to determine in which part of the step cycle the discharge rate exceeded the mean rate by 10% or more. This period (or periods) was taken as the 'active' period and in Fig. 6*A* these are represented as horizontal lines for all eighty-seven frequency-modulated neurones. A similar approach has previously been used by Orlovsky (1972*a*, *b*, *d*) and by Armstrong & Drew (1983*b*). Fig. 6*A* demonstrates that there was a very wide variety of discharge timings among the population. However, it is also evident that more units were active at some times than at others. This variation can be quantitated by counting the cells active in each tenth of the step cycle and expressing this number as a percentage of the total studied. The result is shown in Fig. 6*B* which demonstrates that this percentage fluctuates quite substantially during the step from as high as 51% during swing to as low as 19% in mid-stance.

One limitation of this method of treating the discharges is that, for those cells which were active during a considerable proportion of the step cycle, it fails to identify the time of peak activity with any precision. As an alternative, therefore, Fig. 6*C* shows in histogram form the number of modulated neurones which reached their peak rate during each tenth of the step cycle. Again, the number reaches a maximum of nineteen in late swing and is as low as two in mid-stance.

The modes of presentation used in Fig. 6*B* and *C* have the advantage that each

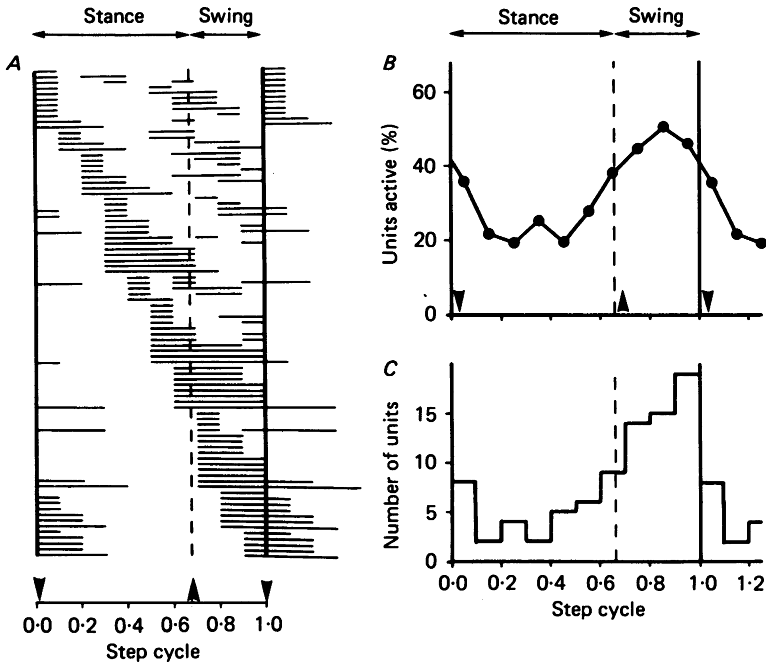

Fig. 6. Timing of interpositus neuronal discharges relative to the step cycle in the ipsilateral forelimb. *A*, horizontal lines represent the 'active' periods (see text) in each of the eighty-seven neurones which discharged rhythmically in time with the step cycle. Vertical interrupted line marks the time of onset of e.m.g. in brachialis muscle (elbow flexor) in the ipsilateral forelimb. Downward and upward arrows respectively mark the approximate time of foot placement and lift in the ipsilateral forelimb. *B*, shows how the proportion of neurones discharging strongly (i.e. active as defined in the text) fluctuated during the step cycle. Same neurones as in *A*. *C*, shows how the number of neurones discharging at peak rate (see text) fluctuated during the step cycle. Note that for neurones which displayed two or three active periods per step only the highest peak is represented and that three cells with no well-defined peak have been omitted.

neurone is treated as an equivalent unit but equally they ignore the fact that some neurones discharged much more rapidly than others. It is therefore possible that the neurones most active during swing might have lower discharge rates than those most active in stance. If this were the case then in terms of total impulses per unit time the output of the nucleus during stance might equal or even exceed that during swing, in spite of the variation revealed by Fig. 6*B* and *C*. This possibility was explored by summing the discharge rates for all cells during each tenth of the step cycle and dividing these totals by the number of cells so as to derive an average rate for each tenth. This provides a representation of the behaviour of the 'average neurone' in the population during the step cycle. The result for all ninety-five neurones is presented in Fig. 7 and shows that the average rate is at its maximum (74 impulses/s) in mid-swing and its minimum (55 impulses/s) in mid-stance. The fluctuation thus parallels that in Fig. 6*B* and although its amplitude is smaller it must be remembered both that unmodulated neurones are now included and also that Fig. 6*B* inevitably over-emphasizes the fluctuation in nuclear output because it ignores the fact that

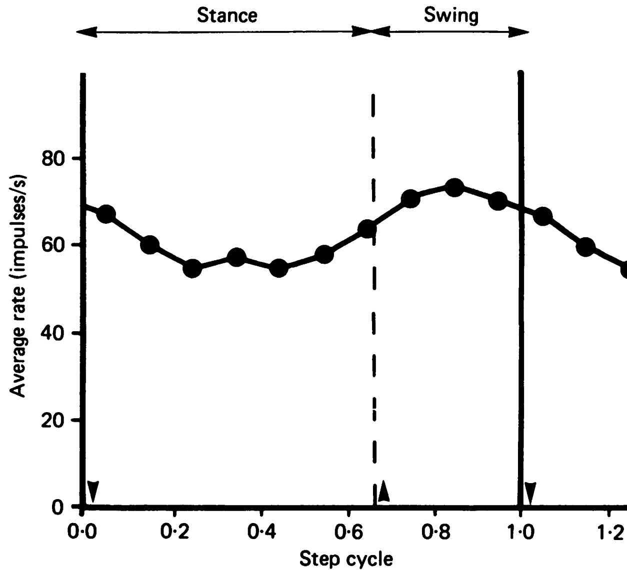

Fig. 7. Curve showing the fluctuation of the average discharge rate amongst the population of ninety-five interpositus neurones between different tenths of the step cycle (see text). Downward arrows indicate the approximate time of placement and upward arrow the approximate time of lift for the ipsilateral forefoot. The interrupted vertical line marks the average time of onset of e.m.g. activity in the elbow flexor muscle brachialis (i.e. the point of transition from stance to swing as defined in the text).

outside their active period most cells continued to discharge or were silent for only part of the time.

Frequency modulations after subgrouping the neurones by receptive field location

In Figs. 6 and 7 the interpositus neurones have been treated as a single population but in fact they can be subgrouped according to receptive field location (see above) and there is evidence that this subgrouping has functional significance for the normal operation of the nucleus (see Discussion).

Displays similar to those of Figs. 6 and 7 were therefore prepared separately for cells with forelimb receptive fields, face and neck receptive fields and receptive fields which included both forelimb and hind limb. These are shown in Fig. 8, where *A–C* show the results for forelimb-related cells and *D–G* show those for face and neck cells (open symbols) and for cells receiving both fore- and hind-limb input (filled symbols). Because the forelimb-related group was large, comprising forty-two neurones (one-half of the cells for which receptive fields were defined), it is not surprising to find that it behaved quite similarly to the over-all population except that the fluctuation in proportion of neurones active is larger (from 62 % in mid-swing to 12 % just before mid-stance).

By contrast, the subpopulation of face/neck-related cells showed little fluctuation either in proportion of cells active or in average rate, even though most of the individual neurones were frequency modulated.

Cells receiving input from both ipsilateral limbs were also usually modulated and

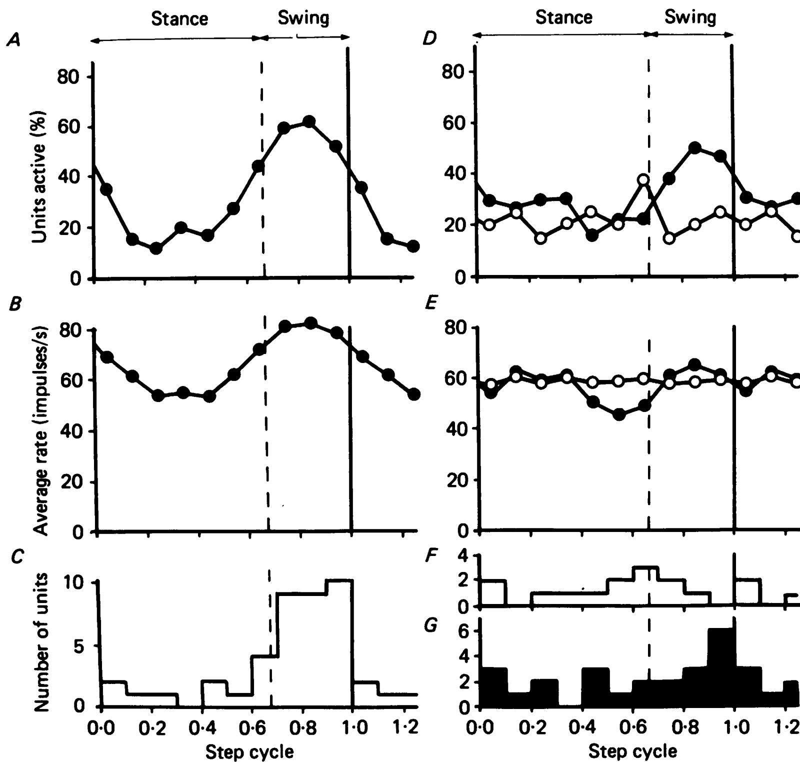

Fig. 8. Population activity during locomotion for interpositus neurones with differently located receptive fields. *A–C* respectively show proportion of cells active (cf. Fig. 6*B*), average discharge rate (cf. Fig. 7) and number of cells discharging at peak rate (cf. Fig. 6*C*) for the forty-two neurones with forelimb receptive fields. *D* and *E* are similar plots to *A* and *B* but for cells with face/neck receptive fields (open symbols; $n = 17$) and with input from both fore- and hind limbs (filled symbols; $n = 24$). *F* and *G* are similar to *C* but for face/neck and forelimb/hind-limb cells respectively.

the number active was again greatest at mid-swing and least in mid-stance. However, by comparison with the forelimb-related subgroup more cells were active in early stance and the average rate showed less fluctuation during the step cycle. This arose primarily because the cells showed a particularly wide variety of discharge timings and because the population included many of the cells which were active twice per step cycle.

To determine whether there were differences in population activity between the subgroups of neurones with receptive fields in different parts of the forelimb the curves shown in Fig. 9 were prepared. Fig. 9*A–C* refers to the elbow-related subgroup whilst the filled and open symbols in Fig. 9*D–G* refer respectively to the proximal and distal subgroups. Comparison shows that the proximal and elbow-related cells behaved rather similarly. However, although the distal population resembled the others in being most active during swing, its activity level was also quite high during the second half of stance (see Discussion).

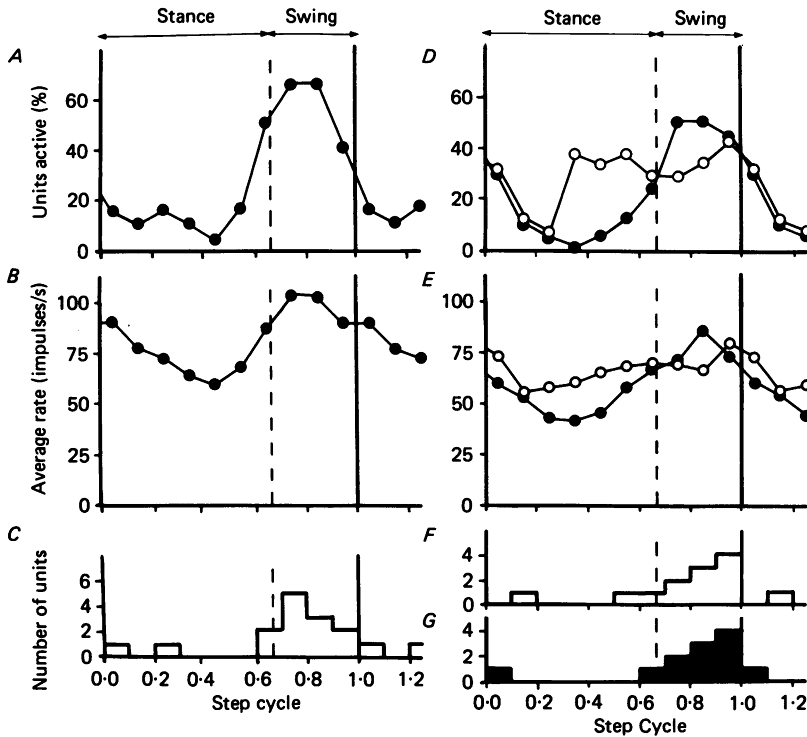

Fig. 9. Population activity during locomotion among subgroups of neurones with receptive fields centred in different parts of the ipsilateral forelimb. Plots are similar to those of Fig. 8. *A–C* are for neurones with receptive fields centred on the elbow ($n = 16$). *D* and *E* are similar to *A* and *B* respectively but for cells with distal fields (open symbols; $n = 13$) and proximal fields (filled symbols; $n = 13$). *F* and *G* are similar to *C* but for distal and proximal cells respectively.

Locomotor-related discharges and receptive fields of spatially related neurones

When micro-electrodes were advanced through the nucleus it was sometimes possible to record several neurones (up to eight) in a single track. Unfortunately, the design of the manipulator did not allow the distances between units to be measured accurately but note was taken whenever units were encountered in close succession. In such cases the neurones almost invariably had receptive fields in the same part of the body. In a single track, therefore, two or three neurones with input from both ipsilateral limbs or from a particular area of the head and neck might be followed by two or three more with input from a particular area of the ipsilateral forelimb. These observations suggest a degree of somatotopy within the nucleus (cf. Eccles, Rantucci, Rosen, Scheid & Taborikova, 1974) and it therefore seemed worthwhile to compare the locomotor-related discharge patterns of those neurones which were encountered close together. Representative results for three such groups of three cells each are shown in histogram form in Fig. 10 where there are obvious similarities within each group (and equally obvious differences between the groups). The cells of Fig. 10*A–C*

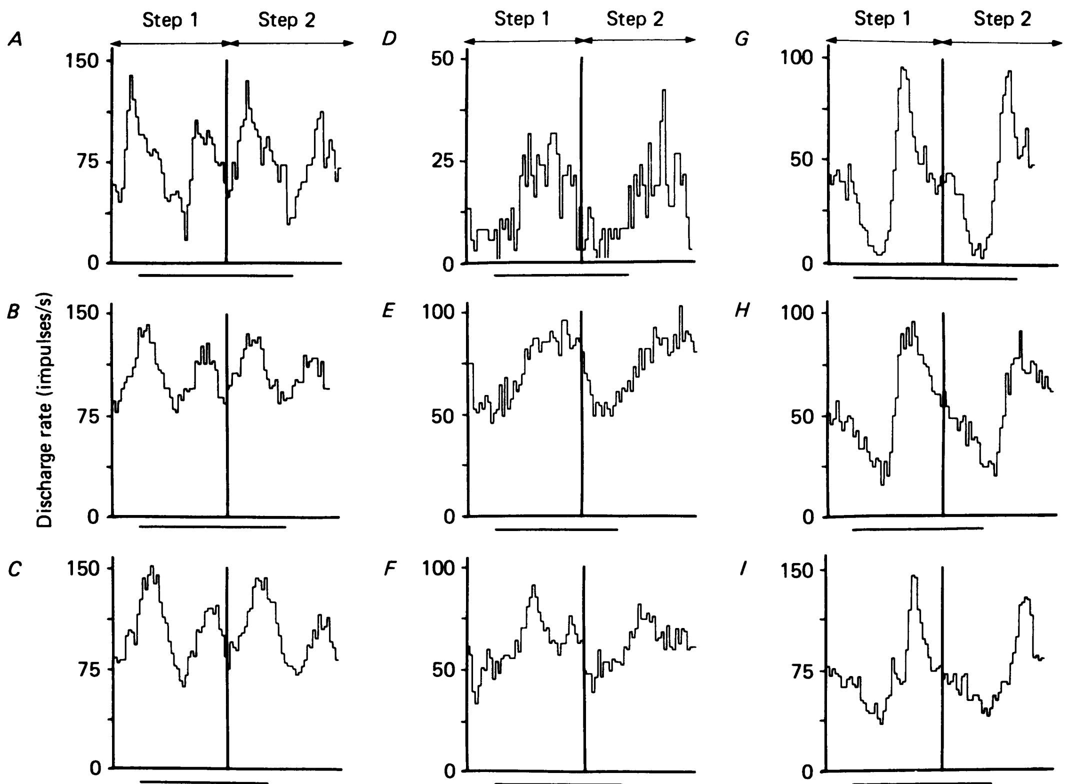

Fig. 10. Discharge patterns during locomotion for small groups of cells encountered in close succession during three different micro-electrode tracks through nucleus interpositus. *A–C* represent three different neurones recorded in a single track with *A* the most superficially located and *C* the deepest. Similarly for *D–F* and for *G–I*. Each histogram is based on the discharges during twenty steps and in each case the horizontal (time) axis spans two complete steps which are separated by the vertical line bisecting the histogram. Bin width 20 ms in all cases. Time calibration beneath each histogram is 1 s. In all cases the triggering event was onset of locomotor e.m.g. in triceps brachii of ipsilateral forelimb.

all received input from both ipsilateral limbs while those of *D–F* all received forelimb input. Unfortunately receptive field determinations were not made for the cells in *G–I*.

Movements evoked by microstimulation

When two or more cells with similar receptive fields were encountered in succession the micro-electrode tip was subsequently positioned as nearly as possible in the centre of the population and attempts were made to evoke movements by electrical stimulation (see Methods). In nine cases movements could be evoked by currents not exceeding 70 μA; threshold was 70 μA in one case and 12–50 μA in the remaining eight cases. In the two cases in which the cells (two in one case, three in the other) had receptive fields on the face and neck the evoked movements were twitches of muscles in the face or face and neck. By contrast, in the four cases in which (two to four) cells had fields confined to the ipsilateral forelimb the movements were flexions of

the same limb. Finally, in the three cases involving (three to seven) cells with input from both ipsilateral limbs flexion movements at the elbow and knee were evoked with the same threshold. Collectively these findings suggest that areas of the nucleus receiving input from a particular part of the body are likely to give rise to movements involving the same part (see Discussion).

DISCUSSION

Discharge rates in the resting animal

In the absence of overt movements most neurones generated a tonic, though irregular, discharge and the levels of activity (range 2–105 impulses/s, over-all mean 42 impulses/s) were very similar to those found in awake cats by previous workers, who have reported over-all means of 34 (Armstrong & Rawson, 1979), 41 (Cody, Brantingham-Moore & Richardson, 1981) and 39 impulses/s (Palmer, 1979). They are also similar to the rates found in awake monkeys by Thach (1970) who quotes an over-all mean of 37 impulses/s and by Harvey *et al.* (1979) who found that most cells fired at 30–50 impulses/s.

Somatosensory receptive fields

Receptive fields have previously been studied extensively in decerebrate paralysed cats by Eccles *et al.* (1974*a*) and by Eccles, Rosen, Scheid & Taborikova (1974*c*). These authors also found that the forelimb was frequently represented (in 89 % of cells) but they encountered forelimb/hind-limb convergence more often (in 60 % as compared with our 29 % of cells). They also found 11 % of neurones with fields restricted to the hind limb while we found none. To some extent these differences may be ascribable to their ability to assess responses quantitatively but they probably also reflect the fact that they sampled widely in the nucleus whereas most of our tracks were in the caudal part of interpositus anterior (i.e. near the centre of the nucleus). Other workers using cats (Larsen & Yumiya, 1979) and monkeys (see Brooks & Thach, 1981) have also concluded that forelimb inputs predominate in the middle of the nucleus.

Neurones with receptive fields centred on the foot and/or wrist comprised less than one-third (13/42) of the cells with 'forelimb' receptive fields (cf. Larsen & Yumiya, 1979). If there is congruence between the tactile and 'motor' somatotopies within nucleus interpositus (see below) this finding would fit well with the observation that forelimb movements evoked by microstimulating in the nucleus occur mostly at elbow or shoulder, wrist movements being relatively infrequent (Schultz, Montgomery & Marini, 1979; cf. also Udo *et al.* 1980).

Cells recorded in close succession in an electrode track usually had similar receptive fields (cf. Larsen & Yumiya, 1979) indicating that the 'patchy' somatotopy detectable in the decerebrate cat (e.g. Eccles *et al.* 1974*a*) is maintained in the awake animal.

Discharges during locomotion

We have located no previous reports concerning discharge rates during the locomotion of intact cats but Orlovsky (1972*a*) has described the discharges of twenty-seven interpositus neurones during hind-limb stepping in high decerebrate cats. The average rate during locomotion was 40 impulses/s which is considerably

lower than the rate found here. However, Orlovsky also reported a low discharge rate in the periods between bursts of locomotion (12 impulses/s, cf. our 42 impulses/s). A low resting rate of 23 impulses/s was also reported for decerebrate cats by Arshavsky, Orlovsky, Pavlova & Perret (1980). These low values might reflect a loss of inputs normally received via descending pathways but other factors may be involved because an average rate of 43 impulses/s was reported for decerebrate cats by Eccles, Rosen, Scheid & Taborikova (1974*b*).

An important difference between our results and those of Orlovsky (1972*a*) is that he found that most interpositus neurones did not discharge rhythmically during locomotion. However, all cells with hind-limb receptive fields were rhythmically active and the non-rhythmic neurones were those without input from the hind limb. This suggests that the difference may have arisen because Orlovsky's animals walked with the hind limbs only.

Another difference is that many neurones in the present study discharged throughout much of the step cycle while Orlovsky found discrete 'packets' (i.e. bursts) of impulses separated by silent periods. Moreover, although many of our cells showed a single period of high-frequency activity per step no fewer than 29% generated two such periods (and a few produced three). Orlovsky found only three cells (11%) which produced two bursts per step, the remainder firing one burst, usually during the swing phase. These differences may have arisen because in Orlovsky's animals the forelimbs moved only weakly or were immobilized (and part of the body weight was taken by external supports). Another possible source of difference may be that we used computer-averaging techniques while Orlovsky (1972*a*) relied on visual inspection of the spike trains. Similar explanations have been suggested to account for parallel differences encountered in studies of the locomotor-related discharges of vestibulospinal neurones in Deiters nucleus (cf. Orlovsky, 1972*d*; Udo *et al.* 1976).

The range of peak discharge rates in the present study (5–169 impulses/s) implies that many neurones fired briskly even at the relatively slow speed of locomotion studied and the range is strikingly similar to that of 50–150 impulses/s quoted for most of his cells by Orlovsky (1972*a*).

Regarding the sources of synaptic input which evoked the rhythmic discharges no information is available from the present results. However, large numbers of rhythmically discharging Purkinje cells were found in the overlying cortex (D. M. Armstrong & S. A. Edgley, unpublished observations) so it is highly likely that the inhibitory input from these neurones played a part in shaping the interpositus activity, by the process which Eccles (1973) has termed 'inhibitory sculpturing'. The relative importance of this mechanism as compared with the excitatory inputs which presumably arrive via the nuclear collaterals of cerebellar afferent fibres will be discussed in a future paper (D. M. Armstrong & S. A. Edgley, in preparation).

Possible motor significance of the interpositus discharges

Almost half the neurones projected to the mid-brain and were therefore cerebellar output neurones. In addition it is likely that many of the remaining (untested) cells were also output neurones because in a previous study 95% of interpositus cells could be antidromically invaded from the mid-brain (Armstrong & Rawson, 1979).

Many previous studies indicate that interpositus outputs result primarily in augmented activity in flexor muscles of the limbs. Thus, Chambers & Sprague (1955) showed that interpositus lesions led to limb hypoflexions (especially at elbow and knee) during locomotion while, conversely, lesions of the overlying cortex led to hyperflexions presumably by reducing the inhibitory input from the Purkinje cells (see also Udo *et al.* 1980). Other studies have shown both in cats (Asanuma & Hunsperger, 1975; Giuffrida, Li Volsi, Panto Perciavalle, Sapienza & Urbano, 1980) and monkeys (Schultz *et al.* 1979) that microstimulation in the nucleus leads to contractions most often of flexor muscles.

The route by which interpositus exerts its motor effects has also been investigated in detail. Its influence might be relayed via the rubrospinal and/or the corticospinal tract (see Introduction) but in cats limb muscle contractions evoked by microstimulation within the nucleus appear to be generated entirely via the rubrospinal tract (Asanuma & Hunsperger, 1975; Giuffrida *et al.* 1980).

That the interposito-rubrospinal pathway has a detailed somatotopical organization is known from experiments in which microstimulation of different afferent fibres to nucleus interpositus (e.g. Perciavalle, Santangelo, Sapienza, Serapide & Urbano, 1979) and at different sites in both interpositus (e.g. Giuffrida *et al.* 1980) and the red nucleus (Ghez, 1975) evoked contractions of different single muscles in the limbs.

Several lines of evidence indicate also that within interpositus in the cat the sensory and movement somatotopies are essentially congruent. First, Orlovsky (1972*b*) found for rubrospinal neurones which projected to the lumbosacral cord and discharged rhythmically during hind-limb locomotion that the rhythm was abolished by cerebellectomy. It is therefore likely that these neurones were driven by the interpositus cells which were frequency modulated during hind-limb movements and the latter were invariably those in receipt of hind-limb peripheral input (cf. the parallel findings made for 'fictive' scratching by Arshavsky, Orlovsky, Pavlova & Perret, 1978, 1980). Secondly, Larsen & Yumiya (1980) found that lesions of the cerebellar peduncles much reduced the responses of red nucleus neurones to somatosensory inputs suggesting that these responses were mediated mainly via nucleus interpositus (cf. also Nishioka & Nakahama, 1973). Because the sensory and motor representations within the red nucleus are both detailed and congruent it follows that rubrospinal neurones influencing particular parts of the musculature must receive their sensory inputs via interpositus neurones with receptive fields localized to the same areas of the body. Thirdly, Burton & Onoda (1978) found that interpositus neurones discharging just in advance of a voluntary flexion of the forelimb received peripheral input from that limb and often from no other part of the body. Fourthly, when microstimulation was carried out in the present experiments the movements evoked involved those parts of the body which were represented in the receptive fields of the neurones recorded near the stimulating locus.

This last finding must be regarded with some caution because of the risk that the movements resulted from stimulation of fibres of passage rather than nearby cell bodies. Such fibres might include cerebellar afferent fibres passing through the nucleus or providing collaterals to it and/or interpositus axons arising from cell bodies some distance from the locus of stimulation.

In light of the above evidence it is very probable that those interpositus neurones with forelimb receptive fields were (via the rubrospinal tract) facilitating the spinal

mechanisms which control the flexor musculature of the same limb. Like Orlovsky's hind-limb-related cells the individual neurones showed a wide range of discharge timings relative to the step cycle but activity in the population as a whole was least in mid-stance, rose sharply towards the end of stance and reached a maximum during swing. This pattern is remarkably similar to that found by Orlovsky for hind-limb-related cells both in interpositus and the red nucleus. He pointed out that it is just what would be expected if the discharges helped to control swing by regulating the contraction of the limb flexor muscles (many of which develop e.m.g. activity together at the very end of stance and remain active throughout the first two-thirds of swing).

Orlovsky also studied the effects of electrical stimulation within the red nucleus during locomotion (1972*c*) and provided that stimuli were applied near the onset of swing there was a marked increase in the locomotor e.m.g. in flexor muscles. Extensors were unaffected and muscle timings were unchanged. He concluded that the interposito-rubrospinal system normally acts to facilitate hind-limb swing by augmenting the forces developed by the flexor muscles, but without changing the basic rhythm of the stepping (i.e. it reinforces the stepping rhythm laid down by the spinal pattern generators for locomotor movements of the limbs).

Our results strongly support the extension of Orlovsky's scheme to the control of the forelimb during normal locomotion. Presumably the step-by-step variations evident in the discharges of individual neurones (see Results) represent, at least in part, a means by which the influence of the nucleus is subtly varied from step to step. However, additional experiments will be needed to show the extent to which such variations exert any adaptive influence over the stepping movements and also to account for the marked individuality in the behaviour of the different neurones.

It may be noted that the population pattern seen for forelimb-related neurones as a whole (see Fig. 8) primarily reflects that for the twenty-nine cells with receptive fields around or above the elbow (see Fig. 9). The thirteen cells with receptive fields centred on the foot and/or wrist behaved rather differently. This cannot yet be explained but may reflect the fact that during locomotion the many muscles acting on the wrist and foot contract with a wide variety of timings relative to the step cycle (English, 1978). In particular the flexors do not show the near-synchrony evident among large flexors acting at the elbow and shoulder.

Unfortunately, the motor role of the neurones showing forelimb/hind-limb convergence cannot profitably be discussed: further analysis will require experiments in which the movements of the fore- and hind limbs are dissociated as in the experiments of Orlovsky. Nor can a role be assigned to the cells with face/neck receptive fields in the absence of information regarding any locomotor activity which may occur in the corresponding areas of the musculature.

Finally, the interpositus neurones provide monosynaptic excitation to the ventrolateral thalamus as well as the red nucleus. The connexion is powerful and the thalamic neurones provide mono- and disynaptic excitation to pyramidal tract neurones of the motor cortex (see Brooks & Thach, 1981 for references). We were surprised therefore that the population activity for the interpositus neurones with receptive fields centred on the elbow was almost precisely opposite in phase to that of a subgroup of pyramidal tract neurones recorded via motor cortical electrodes at which threshold microstimulation evoked elbow flexion (Armstrong & Drew, 1984*b*; see the filled circles in their Fig. 7*B* and *C*). However, this reciprocal relationship is in excellent accord with the recent conclusion by Li Volsi, Pacitti, Perciavalle, Sapienza & Urbano (1982) that, via axon collaterals which they provide to the

thalamic ventrolateral nucleus, 'interpositus nuleus efferents which activate a particular muscle via the rubrospinal path inhibit the discharge of pyramidal neurons controlling that muscle'.

We thank Ms L. Gregory and Mr C. Makepeace respectively for their excellent technical and photographic services and Mrs A. Lear and Mrs B. Schields for typing. Dr Edgley was supported by the M.R.C.

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