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LOCOMOTOR-RELATED NEURONAL DISCHARGES IN CAT MOTOR CORTEX COMPARED WITH PERIPHERAL RECEPTIVE FIELDS AND EVOKED MOVEMENTS

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SUMMARY

1. Discharge patterns of motor cortical neurones in cats walking steadily on a moving belt have been compared with other functional characteristics of the neurones.

2. In forelimb motor cortex rhythmic discharges occurred in cells with peripheral receptive fields in all parts of the contralateral forelimb and also in cells with no discernible receptive field.

3. Cells discharging at similar times during the step cycle often had very different receptive fields and cells with similar receptive fields (including neighbouring cells) could discharge at similar or at quite different times.

4. In cells with a cutaneous receptive field including the forefoot the discharges during locomotion remained rhythmic (and their phasing relative to the step cycle was unchanged) when the response to mechanical stimulation in the receptive field was temporarily much reduced or abolished by local anaesthesia of the skin.

5. The proportion of neurones showing accelerated firing during different parts of the step cycle fluctuated more for antidromically identified pyramidal tract neurones (p.t.n.s) than for non-p.t.n.s and was highest during the second half of stance in the contralateral forelimb and lowest during swing.

6. When the neurones were subdivided according to the movement evoked by threshold electrical stimulation through the micro-electrode, p.t.n.s and non-p.t.n.s recorded by electrodes evoking elbow flexion showed a wide variety of discharge patterns. For p.t.n.s the discharge rate reached an average of 69 impulses/s during late stance and declined to an average of 26 impulses/s during swing.

INTRODUCTION

The preceding paper (Armstrong & Drew, 1984) described the discharge rates of motor cortical neurones in cats walking steadily on a moving belt. Most pyramidal tract neurones (p.t.n.s) and other neurones were rhythmically active but the timing

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of their maximal activity relative to the step cycle varied considerably in both 'forelimb' and 'hind-limb' areas of the cortex. This is not unexpected because the cells were widely distributed across the pericruciate cortex and presumably differed in their afferent and efferent connexions.

The present paper describes the range of discharge timing encountered in the forelimb motor cortex (i.e. coronal gyrus and lateral part of the anterior and posterior sigmoid gyri; see Armstrong & Drew, 1984 and cf. Nieoullon & Rispal-Padel, 1976) and compares these firing patterns with other information available for the neurones.

Firstly, a comparison was made with the peripheral receptive fields of the cells as revealed by the application of natural stimuli to the passive animal. This was done to determine whether cells with similarities in receptive field showed similarities in their patterns of locomotor-related discharge and vice versa. In fact, this was frequently not the case even for cells closely juxtaposed in the cortex.

The finding raises a question as to whether peripheral afferent inputs generated by the movements of locomotion play much part in determining the patterns of locomotor-related discharge. An approach to this question was therefore made for some neurones with cutaneous receptive fields on the contralateral forefoot by recording the discharges during locomotion both before and during local anaesthesia within the receptive field.

Attempts were also made to relate the discharge timings to any information which could be obtained regarding the *efferent* connexions of the neurones. Differences between p.t.n.s and non-p.t.n.s were first sought and an attempt was then made to subdivide the p.t.n.s according to their actions on the spinal cord. For this purpose the electromyographic (e.m.g.) signals recorded from a range of limb muscles were spike-trigger averaged (cf. Fetz, Cheney & German, 1976). Unfortunately, but not perhaps surprisingly (see Discussion), this failed to demonstrate a functional connexion between any one cell and any muscle tested. We therefore classified the neurones according to the type of movement evoked by threshold intracortical microstimulation via the recording electrodes (cf. Asanuma & Sakata, 1967) and attention was concentrated on cells recorded by electrodes which evoked flexions of the elbow.

METHODS

The procedures for animal training, for implanting cortical micro-electrodes and electromyogram (e.m.g.) leads, for data processing and for carrying out histological controls are fully described in the preceding paper (Armstrong & Drew, 1984).

For each unit the micro-electrode entry point into the cortex was known and p.t.n.s were identified via antidromic invasion from the medullary pyramid (Armstrong & Drew, 1983).

Determination of peripheral receptive fields

Peripheral receptive fields were tested both whilst the animals stood and whilst they lay on the experimenter's lap. Some fields were determined independently by two observers and their findings were in good agreement.

Stimuli included light brushing of hairs, light tapping of hairy and glabrous skin with blunt-ended probes, firm tapping on and palpation of muscle bellies, tendons, etc., and manual movement of joints. The animals were trained to accept these manoeuvres and determinations were made only when they were relaxed. Care was taken to avoid producing small 'startle' responses which might evoke movement-related rather than stimulus-related discharges. However, despite these precautions, it must be borne in mind that in free-to-move animals receptive fields cannot be defined nearly so precisely as in anaesthetized animals (cf. Baker, Tyner & Towe, 1971).

Responses to brief stimuli ranged from a single spike to a high-frequency burst of action potentials. Only in two neurones did any stimuli produce a clear reduction in the background discharge; these responses are not included here. The latencies of discharges evoked by natural stimulation were not determined.

Local anaesthesia

For some units with cutaneous receptive fields restricted to or including the contralateral forefoot the effect of temporary local anaesthesia within the receptive field was investigated. The locomotor-related discharges were recorded, the animal was briefly anaesthetized using a mixture of nitrous/oxide, oxygen and halothane, and a dental syringe was used to infiltrate the skin with 0·5–1·0 ml lignocaine plus 2 % adrenaline (Xylotox; Pharmaceutical Man. Co.). After recovery from the gaseous anaesthetic but before local anaesthesia declined the receptive field was retested and the unit discharges were recorded during locomotion at the same speed as before. Controls were occasionally carried out by recording before and after gaseous anaesthesia alone. In these cases there were no significant changes in the receptive field or the discharge pattern during locomotion.

Intracortical stimulation

The cortical micro-electrodes were also used to deliver brief trains of cathodal pulses from a constant-current stimulator in order to evoke movements. The anode was a stainless-steel wire implanted between the skull and temporalis muscle. Trains of eleven pulses (0·2 ms duration) at frequency 330 Hz and threshold intensity were employed. Movements evoked by electrodes which recorded cells with forelimb receptive fields were confined to the contralateral forelimb and were brief flicks. They were always observed whilst the animal was held in the same relaxed posture (supported under the belly and via the loose skin over neck and shoulders) with the limbs clear of any support. This reduced movement variability and facilitated inspection of all limbs. No adverse reactions to stimulation were ever observed. Maximum current used was 35 μA.

RESULTS

This report is based on recordings from the same neurones of the forelimb motor cortex (i.e. coronal gyrus and adjoining lateral parts of the anterior and posterior sigmoid gyri) as were studied in the preceding paper (Armstrong & Drew, 1984). For each cell the following information was available.

1. The discharge pattern during twenty successive paces at 0·5 m/s was characterized by constructing a post-event time histogram (p.e.t.h.) triggered from the onset of e.m.g. in muscle of the contralateral forelimb (lateral head of triceps brachii was used routinely; see Armstrong & Drew, 1984). Most neurones fired one discrete burst of impulses (or two bursts) per step; a smaller number fired throughout the step but with one or two periods of peak activity; the remainder were not frequency modulated during locomotion. For examples of p.e.t.h.s see Figs. 2 and 5 and also Armstrong & Drew (1984). The horizontal axis was always made to span a time equal to *twice* the duration of the step cycle.

2. The peripheral receptive field (if present) was carefully determined in the awake resting animal as described in Methods.

3. Most cells were tested for the presence of an antidromic response to stimulation of the ipsilateral medullary pyramid. Cells which gave a response are termed pyramidal tract neurones (p.t.n.s), unresponsive cells are termed non-p.t.n.s (cf. Armstrong & Drew, 1984).

Variety of discharge timings relative to the step cycle

Comparison of the discharge timings in different cells was facilitated by using the p.e.t.h.s to determine that portion of the step cycle over which each unit displayed

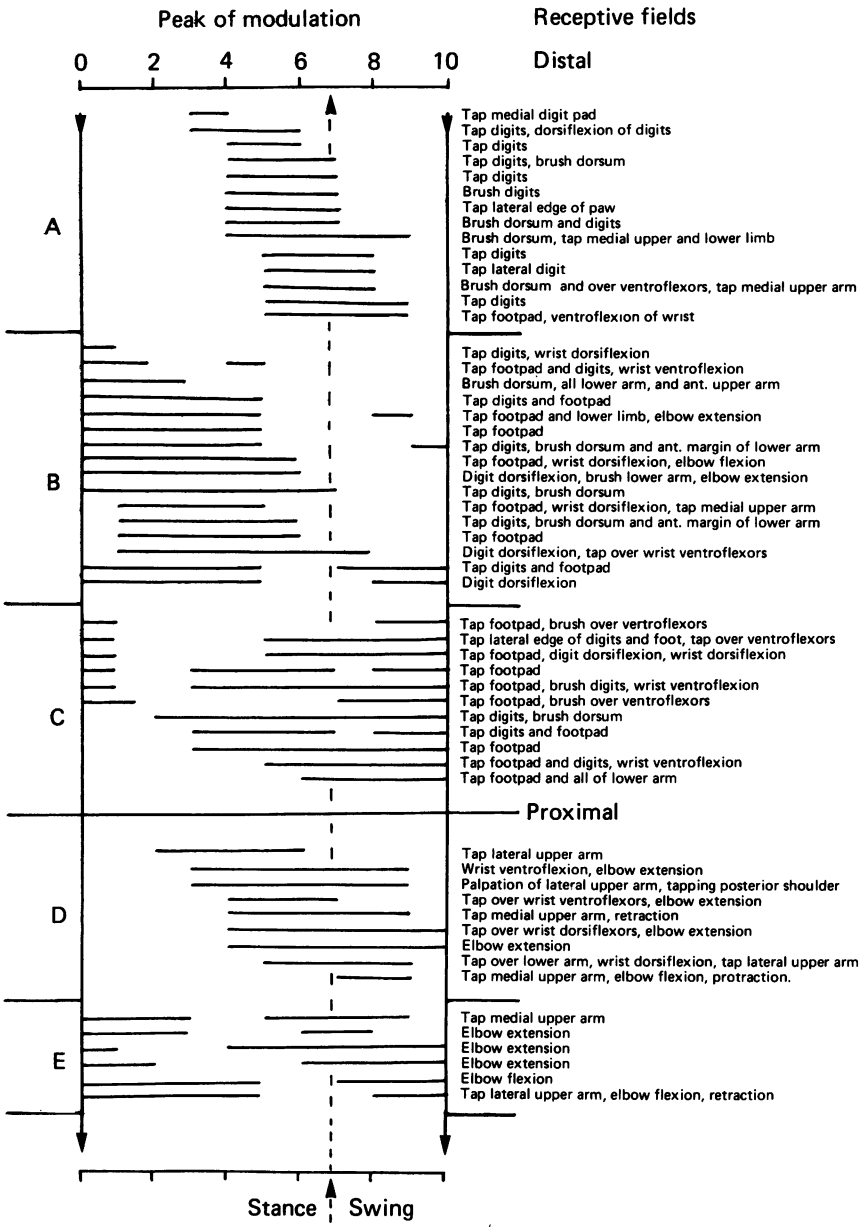

Fig. 1. Discharge phasings and receptive field data summarized for fifty-six motor cortical neurones which discharged rhythmically during locomotion and for which the receptive field lay on the contralateral forelimb. For each neurone this 'most active' period (see text) is represented on the left by a horizontal line. The step cycle is divided into ten equal epochs and the time of transition from stance to swing is shown by the vertical broken line. The peripheral stimuli which evoked discharges in the passive animal are indicated on the right. Note cells are grouped into forty-one in which the receptive field included the forefoot (distal cells) and fifteen in which the field did not include the foot (proximal cells). For the further subdivision into categories A–E see text. Note 'tap digits' implies tap to digit dorsum; 'tap footpad' implies tap to glabrous skin of the pads.

its highest frequency of discharge. This 'most-active' period was taken as the time during which the p.e.t.h. bin count exceeded the mean count by an amount equal to or greater than half the difference between the maximum and the mean counts.

The results of this procedure for fifty-six cells which discharged rhythmically during locomotion and had receptive fields on the contralateral forelimb are presented in the left-hand half of Fig. 1. For each cell the horizontal line shows the 'most-active' period during one step cycle (divided into ten equal time epochs). Inspection confirms immediately that the neurones showed considerable individuality, so that a wide range of timings is represented.

For cells which fired discrete bursts of impulses the lines in Fig. 1 represent the timing of the burst discharged during an 'average' step. Comparison with the original discharges showed good agreement between the duration of the individual bursts and the duration of the active period as estimated from the p.e.t.h. Also, in those fewer cases in which the unit discharged throughout the step but showed a rhythmic fluctuation in frequency, comparison with the original data showed that the periods of accelerated firing are well represented by the lines in Fig. 1.

In Fig. 1 the neurones have been divided into 'distal' cells in which the receptive field included the forefoot and 'proximal' cells in which the receptive field was located in more proximal parts of the limb. These two groups will be compared below but for the moment it should be noted that each of the two main groupings has been subdivided into subgroups respectively labelled A, B, C and D, E. This subgrouping is a purely empirical one which initially suggested itself simply from visual inspection of the locomotor-related discharge patterns. However, the distinction between groups A, B and C was confirmed when for those cells with one 'most-active' period per step the time of onset of this period was plotted against its time of offset. In the resulting scattergram (not shown) only two of the thirty-seven neurones concerned failed to fall into one of the three subgroups. These two are shown as the last two in group B.

Cells in group A became active during the second half of stance and ceased before (sometimes well before) the end of the step cycle. Group B includes cells discharging from at or shortly after the onset of the step cycle until (in most cases) the later part of the stance. The only exceptions are the last two cells illustrated (see above). Cells in group C were active between mid-stance or early flexion until at or shortly after the onset of the next step.

Among proximal cells each subgroup is less homogeneous but cells in group D mostly resembled those of group A whilst those in E included two like those of group C and two like the last two of group B.

Locomotor discharge patterns and peripheral receptive fields

It seemed desirable to try to account for the evident variety of discharge timings among the cortical neurones and to this end comparisons were made between the timings and the peripheral receptive fields of the neurones as determined with natural stimuli in the passive animal (see Methods). Most neurones were readily discharged by mechanical stimuli and the possibility therefore arises that peripheral inputs resulting from the movements of locomotion may be important in determining the patterns of rhythmic discharge during walking. If this were the case then neurones

with similar receptive fields might show similar behaviour during locomotion or vice versa.

In Fig. 1 the locomotor information for each cell is therefore accompanied on the right by information regarding the peripheral stimuli which evoked discharges in the resting animal. When more than one stimulus was effective, the most potent is listed first. The receptive field data are necessarily given only briefly but more complete information is provided for some cells by the figurines in Figs. 2 and 5. It should be noted that 'brush' in Fig. 1 implies discharges evoked by movement of hairs and also that the 'taps' which feature prominently were light and should mainly have excited cutaneous receptors, although it cannot be excluded that deeper receptors were sometimes also excited. Inspection of the receptive field data in Fig. 1 shows immediately that the cells exhibited very considerable individuality in terms of the type of adequate stimulus and also in terms of receptive field location. Nevertheless, some similarities within groups and differences between groups can be detected. Thus, of the fourteen cells in group A all except two were excited only by 'probably cutaneous' stimuli (i.e. hair brushing and/or light taps) but only one was driven by such stimuli applied to the main footpad. By contrast, eight of the sixteen in group B responded to taps to this structure as did nine out of the eleven in group C. However, while group C resembled group A in that most cells (eight of eleven) had 'probably cutaneous' receptive fields, group B differed in that eight of its sixteen cells could be driven by passive movement of joints (but also in seven of the eight, by cutaneous stimuli).

Another difference between groups relates to the spatial extent of the receptive fields: in group A twelve of the fourteen and in group C all of the receptive fields were confined to foot and forearm whilst in group B five of the sixteen cells had fields including the elbow region or upper arm.

As regards the 'proximal' cells of groups D and E, five of the six in group E responded only to stimuli involving tissues associated with the elbow joint. However, in seven of the nine cells in group D excitation was produced from the wrist and/or shoulder regions as well as from around the elbow.

These associations indicate that cells with similarities in the timing of their discharges during locomotion sometimes show similarities in their receptive field characteristics, but equally it is obvious that the relationships are only probabilistic. Moreover, cells with very different receptive fields may show similarities in locomotor pattern. This is readily seen from Fig. 1 where some cells in groups A and D show such similarities despite the fact that only those in A had receptive fields involving the foot (cf. also groups C and E).

Cells varied widely in respect of the duration as well as the timing of their 'active period' and in general the deeper the frequency modulation the shorter the active period in Fig. 1. Over-all, cells with 'distal' receptive fields were more deeply modulated than those with 'proximal' fields.

Cells not frequency modulated during walking made up *ca.* 20% of the whole population (see Armstrong & Drew, 1984). Such cells are omitted from Fig. 1, but they numbered one in ten of 'distal' cells and one in four of 'proximal' cells. Fig. 1 also omits eleven cells for which no receptive field could be found; nine of these were frequency modulated during walking (see also below).

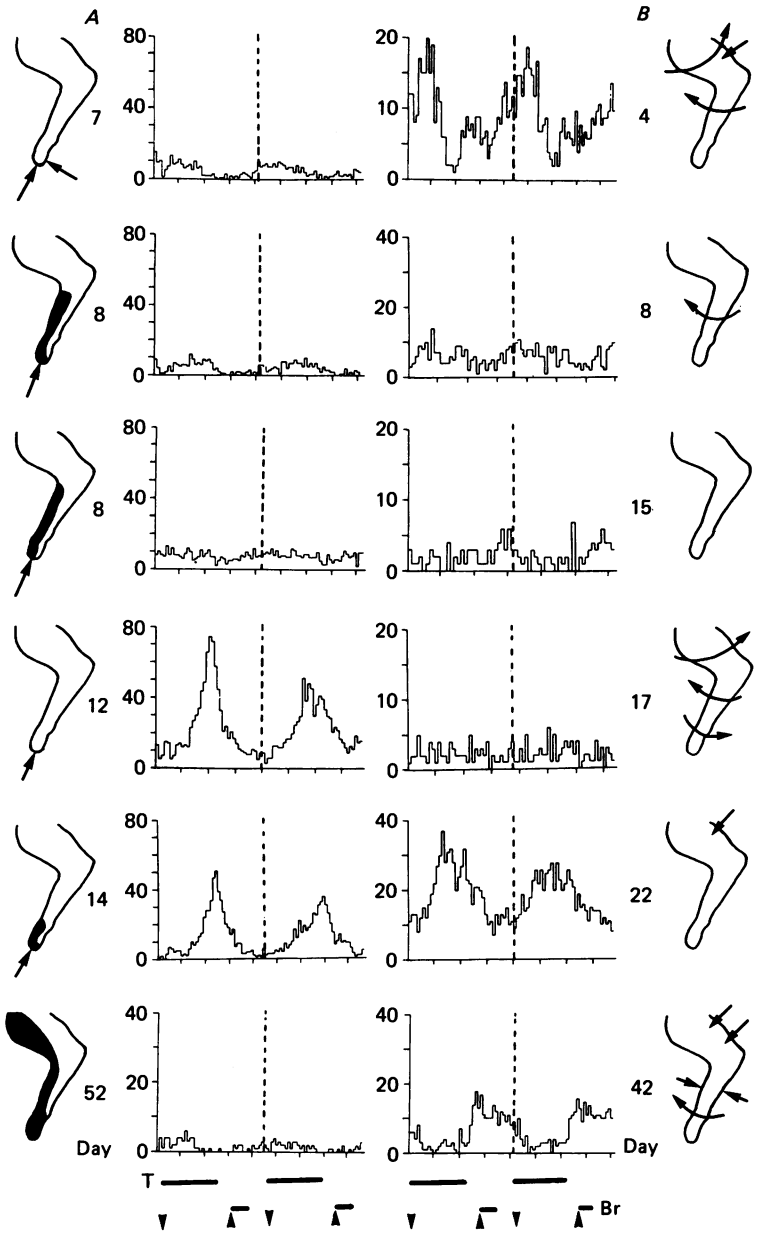

Fig. 2. Receptive fields and discharge patterns during locomotion (at 0·5 m/s). *A* and *B* each show six neurones recorded on one micro-electrode. Day of recording is indicated. Note in *A* that the two cells on day 8 were recorded simultaneously. Each p.e.t.h. comprises the discharges during twenty successive steps. Vertical axis, impulses per bin; bin width 20 ms. Horizontal axis is equal to *twice* mean duration of step cycle. Start of step was taken as onset of e.m.g. in lateral head of contralateral triceps brachii (cf. Armstrong & Drew, 1983). Horizontal lines beneath p.e.t.h.s show approximate duration of e.m.g. in triceps brachii (T) and brachialis (Br) muscles. Downward and upward arrowheads indicate footfall and foot lift respectively. On the figurines a curved arrow implies that passive movement of the joint nearest to the arrow discharged the cell; a straight arrow implies a tap; shaded areas indicate brushing hairs.

Locomotor-related discharges of closely juxtaposed neurones

Neurones closely juxtaposed in the cortex might be expected to have synaptic inputs in common and previous studies have shown they usually have receptive fields which are similar in location, though not necessarily in modality (see Discussion for references). In view of such findings it is of interest to determine whether they also display similar patterns of locomotor-related discharge. We have therefore compared the discharges of cells recorded by the same implanted microwire, because such cells are presumably quite close neighbours (see Armstrong & Drew, 1983).

There were in fact ten microwires from which recordings were made during locomotion from between two and six cells; two of these wires were in the hind-limb motor cortex (i.e. medial part of the posterior sigmoid gyrus; cf. Nieoullon & Rispal-Padel, 1976).

Results from two electrodes which recorded six cells each are shown in Fig. 2*A* and *B*. The discharge during locomotion is shown as a p.e.t.h. which spans two complete step cycles so that the vertical dashed line indicates the transition from one step to the next (cf. Armstrong & Drew, 1984). The receptive field is shown on a figurine of the contralateral forelimb and the recording day is also stated.

On electrode *A* three cells showed somewhat similar discharge patterns (day 7, day 8 first cell, day 52) and two other cells (days 12 and 14) also showed similar phasing. However, the patterns for the triad and the pair were very different and the pair also differed markedly from the second cell of day 8 which showed only faint frequency modulation (note that the two day 8 cells were recorded simultaneously).

The cells of Fig. 2*B* are even more heterogeneous; indeed no two seem at all similar, with the possible exception of those of days 4 and 8 where the phasing shows some similarity although the depth of modulation is very different. Considerable heterogeneity was also evident for other electrodes, as may be seen from Fig. 3 which presents the results for all ten in more compressed form (electrodes O and X are *A* and *B* of Fig. 2).

Figs. 2 and 3 also provide an opportunity to explore the relationship between receptive field and locomotor discharge for groups of cells which are close neighbours. Here it may be noted that the cells of days 12 and 14 in Fig. 2*A* were both excited strongly by taps to the tips of the toes (brushing the hairy skin on the foot dorsum also excited the second cell, but less strongly) and they also produced rather similar p.e.t.h.s. The two cells of day 8 also had very similar receptive fields and both were weakly modulated during locomotion, generating more impulses during stance than swing (only just detectable for the second cell). Other cases in which cells with similarities in receptive field generated similar p.e.t.h.s may be seen in Fig. 3 (for example, the first and third cells from electrode R, the first two from Y and the three from Z).

However, further inspection shows that such parallel similarities were not invariably present. Thus, in Fig. 2*A* the cells of days 7 and 12 had virtually identical receptive fields but very different p.e.t.h.s, whilst in Fig. 3 the first two cells from S were excited by the same peripheral stimuli but their locomotor-related discharges were very different. Equally, cells with similar locomotor discharges did not always have similar

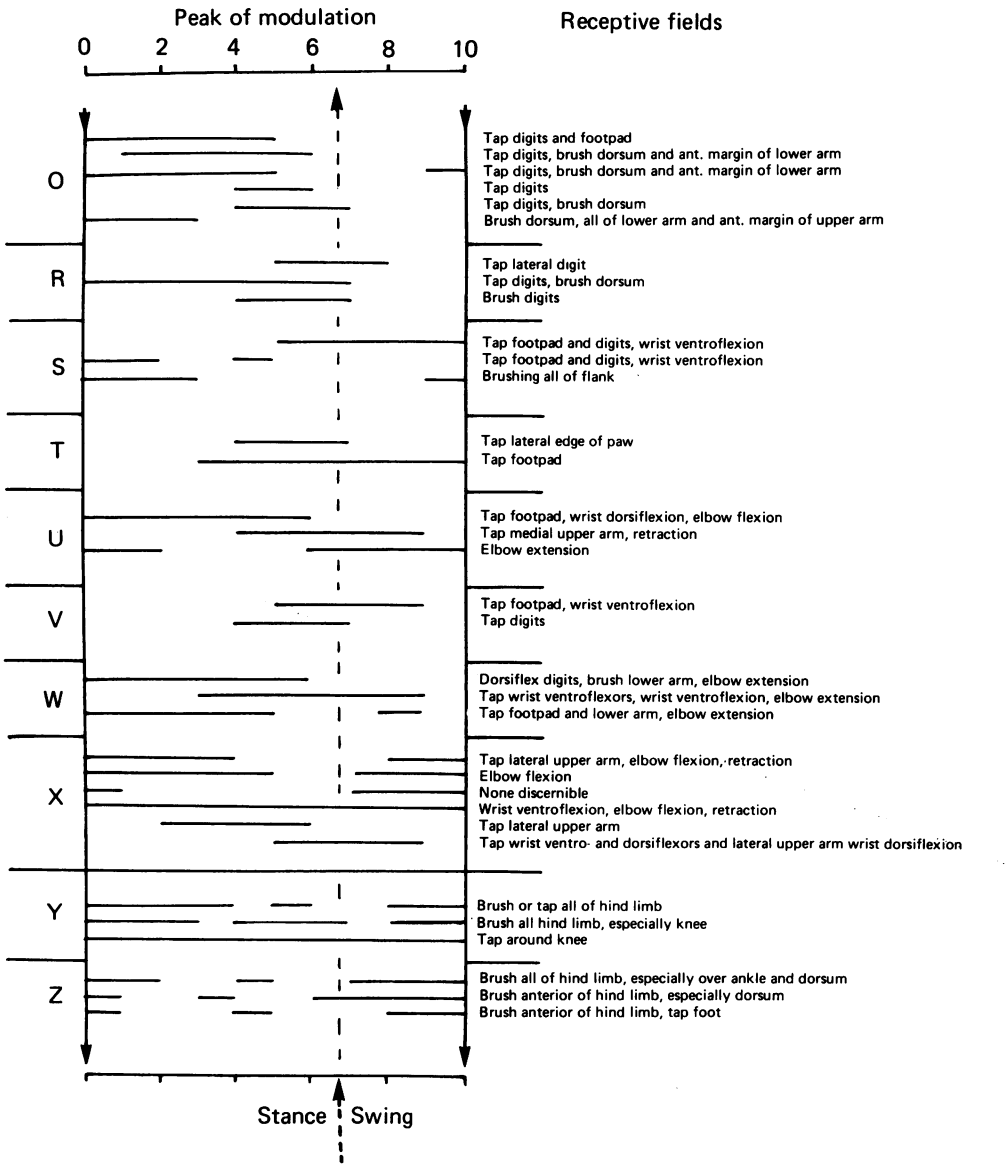

Fig. 3. Locomotor-related discharge patterns and receptive fields for thirty-four neurones recorded on ten different micro-electrodes (O to Z). Conventions for locomotor discharges as in Fig. 1. Note electrodes O and X are respectively *A* and *B* of Fig. 2. Note also that Y and Z were in the hind-limb motor cortex (i.e. medial part of posterior sigmoid gyrus).

receptive fields. Those from days 7 and 52 in Fig. 2*A*, for example, had very different receptive fields (see also in Fig. 3 the two cells from electrode V).

It may also be noted that cells readily discharged from the periphery were not necessarily modulated strongly, or indeed in some cases at all (e.g. the cell of day 17 in Fig. 2*B*). This was so even when the receptive fields were such that they were

likely to be stimulated at some phase of the step cycle (e.g. included taps to the main footpad or passive movement of digits, wrist or elbow). The converse was also noted, i.e. that cells with no discernible receptive field were modulated, sometimes weakly as in the day 15 cell in Fig. 2*B*, and sometimes very strongly, as in some cells recorded on wires yielding only one cell.

Collectively, these findings give no clear evidence to suggest that inputs from the peripheral receptive field are necessarily a major factor in generating the rhythmic discharges during locomotion.

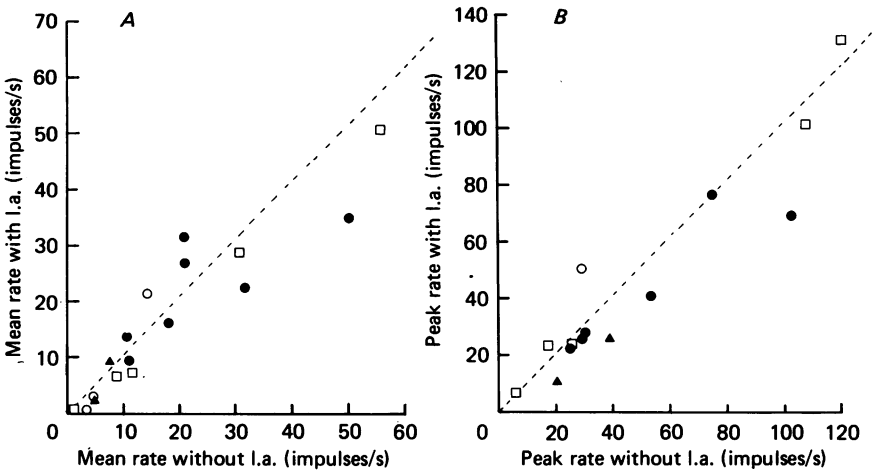

Fig. 4. *A* plots mean discharge rate during locomotion with local anaesthesia (l.a., vertical axis) against mean rate during normal locomotion (horizontal axis) at the same speed (0·5 m/s) for seventeen neurones. *B* is a similar plot of peak rates for those neurones in *A* which were frequency modulated during locomotion. Note one fast-axon p.t.n. is omitted for which peak rate decreased from 180 to 100 impulses/s during local anaesthesia. ●, fast-axon p.t.n.s; ○, slow-axon p.t.n.s; □, non-p.t.n.s; ▲, unidentified neurones. Fast-axon p.t.n.s are those in which the axonal conduction velocity exceeded 21 m/s; slow-axon p.t.n.s conducted at between 9 and 21 m/s (cf. Armstrong & Drew, 1983).

Effect of local anaesthesia within the peripheral receptive field

To investigate the possible role of peripheral inputs during locomotion more directly, local anaesthetic was applied in the receptive field as described in Methods. Study was restricted to seventeen cells which had cutaneous receptive fields confined to or including the distal part of the limb (i.e. foot, wrist and lower forearm) and in which the anaesthetic produced no changes in the locomotion evident from observation of the movement or inspection of the e.m.g. signals from several limb muscles (including flexors and extensors of digits, wrist and elbow).

Ten of these cells were p.t.n.s, five were non-p.t.n.s and two were unidentified. Their discharge rates during locomotion before and during local anaesthesia are compared in Fig. 4*A*; twelve showed some reduction in rate while five showed some increase. In absolute terms the largest change was a decrease of 16·5 impulses/s, and no other cell changed by as much as 10 impulses/s. However, because most discharged fairly slowly some of the changes are more substantial in percentage terms. One very slowly firing p.t.n. was almost silenced.

Of the seventeen cells sixteen discharged rhythmically during locomotion and for fifteen of these the peak firing rates with and without local anaesthesia are shown in Fig. 4*B* and legend (one cell fired so slowly that a realistic peak rate could not be estimated from the p.e.t.h.). Again, the changes wrought by the anaesthetic were modest in absolute terms except in three p.t.n.s: two fast-axon p.t.n.s showed substantial decreases (80 and 30 impulses/s) (see Fig. 4*B* and legend).

However, the most striking finding was that, without exception, local anaesthesia failed to abolish the rhythmic discharges during locomotion. This is clearly seen from Fig. 5 which presents results from six cells including three p.t.n.s (Fig. 5*A*, *E* and *F*), two non-p.t.n.s (*B*, *D*) and one unidentified neurone (*C*). In each case the peripheral receptive field and the locomotor p.e.t.h. are shown for normal conditions (above) and for the period of local anaesthesia (below). In four of these cells (Fig. 5*A*, *C*, *D* and *F*) the response to peripheral stimulation was very much reduced (though not entirely abolished), but although the depth of frequency modulation during locomotion was somewhat decreased the cells still discharged rhythmically and with the same timing relative to the step cycle. In the other two cells (Fig. 5*B* and *E*) the results were even more striking: discharges could no longer be evoked from the receptive field but both cells were still frequency modulated during walking. In the cell of Fig. 5*C* both mean and peak rate were reduced but in that of Fig. 5*E* neither was changed. The results for the remaining cells were essentially similar to those in Fig. 5 but it should be noted that the Figure includes the cell which showed the largest absolute increase in mean rate (Fig. 5*E*) and the two cells with the largest absolute reductions in both mean and peak rate (Fig. 5*A* and *F*).

In the cells of Fig. 5*A* and *F* the response to stimulation in the area of the original receptive field was reduced but the originally localized field on the toes became replaced by a 'sock'-type field which extended above the wrist. Similar observations were made in a few other cells and are of considerable interest insofar as they suggest that the spatial extent of some receptive fields is dynamically determined by central neural mechanisms (cf. Brooks, Rudomin & Slayman, 1961; Baker *et al.* 1971).

The one cell (see above) which did not fire rhythmically during locomotion under normal conditions became weakly modulated during anaesthesia even though its mean rate was reduced; peak discharge occurred at the transition of stance to swing.

Locomotor discharges and the efferent functions of the neurones

It is obviously possible that cortical neurones of different functional types may discharge differently during locomotion. It therefore seemed worthwhile to determine whether there was any systematic difference in timing between the locomotor-related discharges of p.t.n.s and non-p.t.n.s. Analysis was confined to neurones located in the forelimb motor cortex and recorded via micro-electrodes which yielded movements of the contralateral forelimb when used to stimulate the cortex. Brief trains of cathodal pulses (11 at 330 Hz) were employed (see Methods) and movement thresholds ranged from 5 to 35 μA. Movements observed included ventroflexion and dorsiflexion at the wrist, flexion and extension at the elbow and a variety of movements at the shoulder joint including abduction, retraction and protraction of the forelimb.

Initially the step cycle was divided into ten equal epochs and we determined the proportions of p.t.n.s and non-p.t.n.s which were 'most active' (same criteria as in

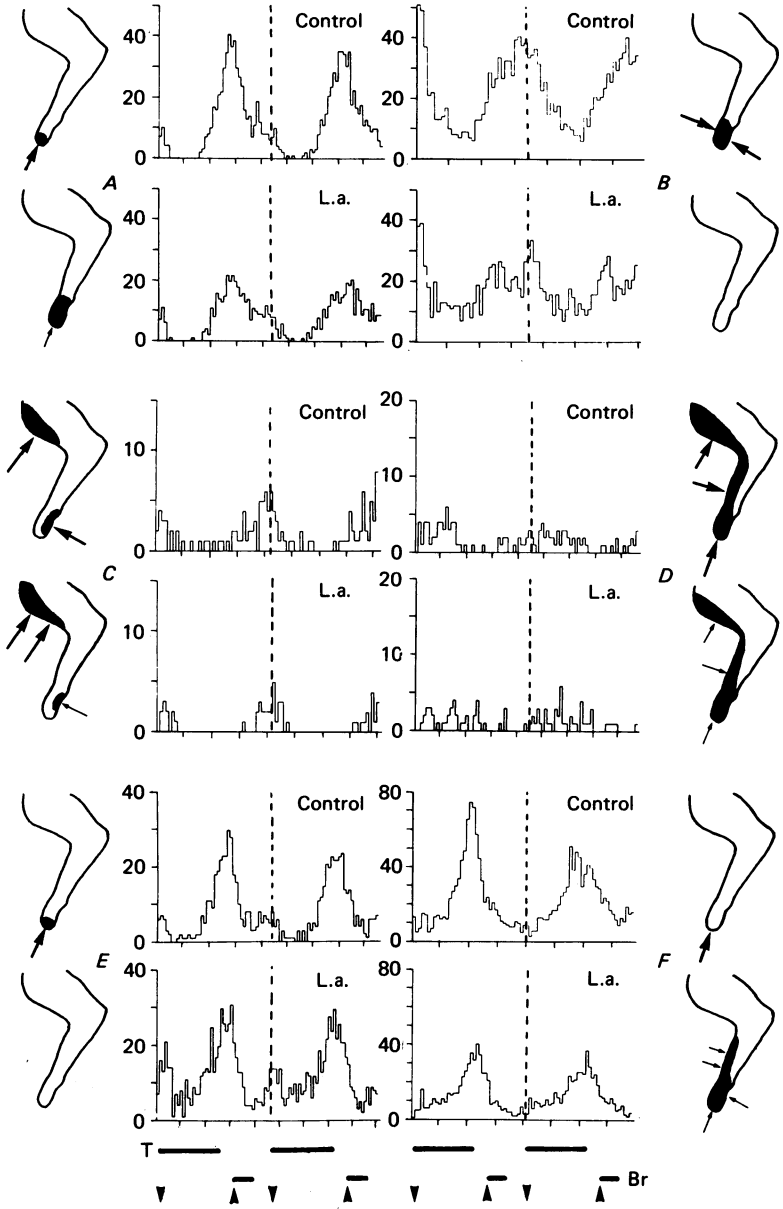

Fig. 5. Effect of cutaneous anaesthesia on locomotor-related discharge and on receptive field characteristics. *A–F* are six different cells. In each case figurines show receptive field before (upper) and during (lower) local anaesthesia (l.a.). P.e.t.h.s show the discharge pattern during locomotion before (upper) and during (lower) local anaesthesia. Conventions are as in Fig.2 except that in the l.a. Figurines the smaller arrows (*A*, *C*, *D* and *F*) indicate a much diminished response to same stimulus.

Fig. 1) during each epoch. The results for a total of fifty-five neurones (thirty-three p.t.n.s, twenty-two non-p.t.n.s; unidentified cells excluded) are shown in Fig. 6*A*, where the p.t.n.s are represented by filled circles and non-p.t.n.s by open circles. As in

Figs. 1 and 3 the vertical dashed line indicates the mean time at which foot lift occurred (determined as explained in Armstrong & Drew, 1984), so that stance occupies the period to the left of the line and swing the period to the right. The number of p.t.n.s showing accelerated discharge rises to a maximum of 77 % in the second half of the stance and subsequently declines during swing to a minimum of 27 % near the end of the step cycle. The proportion of non-p.t.n.s also fluctuates (to a slightly smaller extent) but the curve lags that for p.t.n.s by approximately one-tenth of a step cycle.

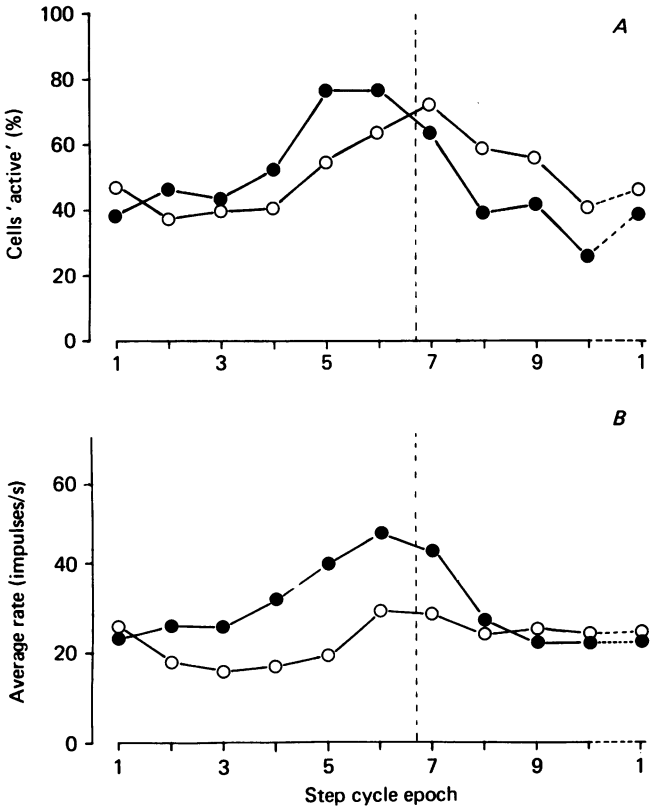

Fig. 6. Population activity curves during the step cycle for p.t.n.s and non-p.t.n.s in the forelimb motor cortex. *A* shows the proportion of p.t.n.s (●; $n = 33$) and non-p.t.n.s (○; $n = 22$) active during each successive tenth of the step cycle (duration *ca.* 85 ms). *B* shows the discharge rate of the 'average' p.t.n. (●; $n = 33$) and non-p.t.n. (○; $n = 22$) during the step cycle (see text).

In constructing Fig. 6*A* each neurone has been regarded as equivalent in the sense that no account has been taken of the fact that they discharged at a wide variety of different rates (see Armstrong & Drew, 1984). The possibility thus exists that neurones active in late stance might be those which discharged slowly while those active in swing might be those discharging at high rates (or vice versa). We therefore also determined how the over-all level of discharge in each of the two cell populations fluctuated during the step cycle. The cycle was again divided into ten equal epochs and the p.e.t.h.s were used to measure the firing rate of each cell during each epoch.

The values in each epoch were then summed for all cells and divided by the number of cells in the population. A similar procedure has previously been used by Orlovsky (1972*a–c*) and can be regarded as defining the discharge rate of the 'average neurone' in the sample during the step.

The results for the same p.t.n.s and non-p.t.n.s as in Fig. 6*A* are shown in Fig. 6*B*. For both types of cell the rate fluctuated during the step cycle though to a more marked extent in the p.t.n.s. Comparison with Fig. 6*A* shows that the time course of the fluctuations in rate paralleled very closely that for the proportion of cells which were 'most active'. The amplitude of fluctuation was also similar so that in late stance, when the proportion of p.t.n.s active was approximately double that in swing, the average discharge rate was approximately twice that during swing.

Behaviour of neurones from electrodes evoking elbow flexion

The neurones in Fig. 6 were recorded by electrodes from which a wide variety of different wrist, elbow and shoulder movements was obtained using threshold electrical stimulation. It is likely, therefore, that they lay in cortical loci with a variety of responsibilities in relation to movement control and initiation. As a result it is probable that the axons of the p.t.n.s involved varied widely in terms of their spinal destinations. Thus it is not unexpected that they should discharge at a variety of different times during the step cycle and it is possible that a population of cells more homogeneous in terms of their efferent functions might behave more uniformly.

This possibility was explored by subdividing the neurones according to the nature of the threshold movement evoked from the corresponding micro-electrode. Unfortunately, a reasonably sizable subpopulation of cells was available only for elbow flexion (because this movement was the commonest to be evoked from electrodes which also yielded unit recordings).

Fig. 7*A* shows the discharge timings of all twenty-five neurones (thirteen p.t.n.s and twelve non-p.t.n.s) recorded via electrodes which evoked elbow flexion, and it is evident that they varied greatly. Indeed comparison with the left half of Fig. 1 shows that examples are included from each subgroup in that Figure. Nevertheless, the proportion of cells active fluctuated during the step cycle as may be seen from Fig. 7*B* in which p.t.n.s (●) and non-p.t.n.s (○) are plotted separately. Comparison with the corresponding plots in Fig. 6*A* shows a marked similarity for each cell type, in terms of both the timing and the amplitude of the fluctuations. There is therefore no evidence to suggest any marked difference in timing between the selected and unselected populations.

When the discharge rates of the neurones were taken into account by plotting the rate for the 'average neurone' in the same way as in Fig. 6*B*, the results shown in Fig. 7*C* were obtained. Comparison shows that the plots for both p.t.n.s and non-p.t.n.s were broadly similar to the corresponding plots in Fig. 6*B*, but it is noticeable that the rate for the average p.t.n. fluctuated very strongly from a maximum of 69 impulses/s in late stance to a minimum of 26 impulses/s, a level which was maintained throughout the swing phase. The corresponding values in Fig. 6*B* are 47 and 23 impulses/s, which indicates that restricting the sample of p.t.n.s to those recorded via electrodes which yielded elbow flexion has selected from among the larger population a subgroup which collectively fires particularly vigorously during the second half of stance.

This is confirmed by Fig. 7*D* (●) which shows the corresponding plot for those p.t.n.s of Fig. 6 which remain after removal of the 'elbow flexion' group (i.e. those recorded via electrodes yielding threshold movements other than elbow flexion). The population rate still increases in late stance but the fluctuation is much reduced, being from 35 impulses/s at peak to 21 impulses/s in mid-swing. By contrast, restricting the sample of non-p.t.n.s had little effect on the curve of population discharge for these neurones (compare open circles in Figs. 6*B*, 7*C* and *D*).

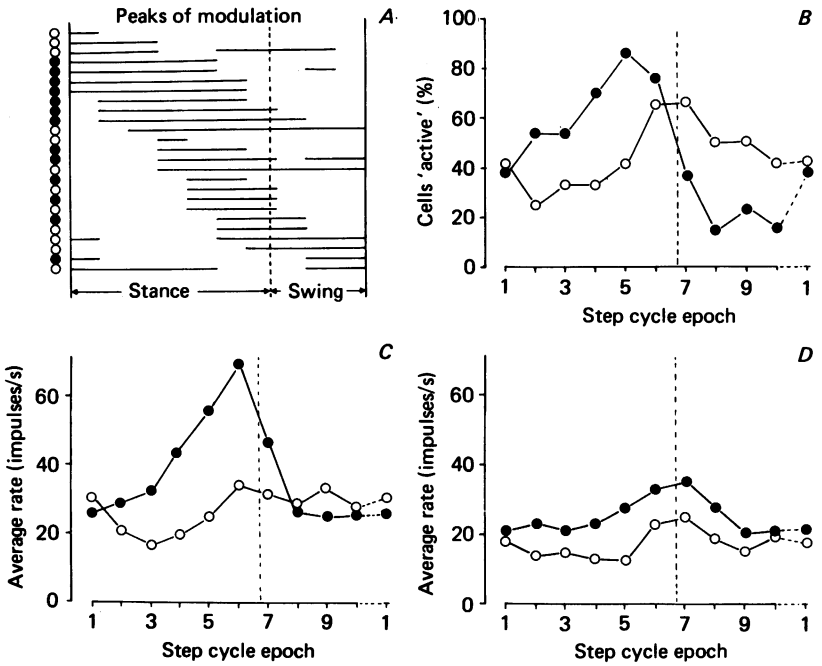

Fig. 7. Discharge characteristics during locomotion for p.t.n.s (●) and non-p.t.n.s (○). *A* shows the discharge phasings for each of twenty-five neurones (thirteen p.t.n.s and twelve non-p.t.n.s) recorded via electrodes through which stimulation evoked flick-flexions at the contralateral elbow. Display conventions as in Figs. 1 and 3. *B* shows for the same cells as in *A* how the proportion of cells active fluctuated during the step cycle. *C* shows how the average rate for the same p.t.n.s and non-p.t.n.s as in *A* and *B* fluctuated during the step cycle. *D* is similar to *C* but shows the average rate for the cells in Fig. 6 (twenty p.t.n.s and ten non-p.t.n.s) which remain after removal of those in Fig. 7*A–C* (i.e. cells recorded via electrodes evoking movements other than elbow flexion).

DISCUSSION

The preceding paper (Armstrong & Drew, 1984) reported that most motor cortical neurones discharge rhythmically during locomotion, albeit at a wide variety of rates. The present paper shows in addition that in the forelimb area of the motor cortex the neurones discharge with an equally wide variety of timings relative to the step cycle in the contralateral forelimb. This individuality of behaviour must arise because the cells receive different patterns of input and it is obviously desirable that the sources should be identified. Several, perhaps many, are presumably involved but one obvious possibility is receptors in the moving limb. Most cells were readily discharged by natural mechanical stimuli applied to the contralateral forelimb in the passive

animal and many cells had receptive fields involving stimuli of a kind likely to arise during locomotion (e.g. light tactile stimulation of the footpads, movement of joints). Moreover previous studies of primary afferent neurones have shown that many low-threshold mechanoreceptors, both cutaneous and muscular, in the hind limb are strongly excited during locomotion (Severin, 1970; Prochazka, Westerman & Ziccone, 1976; Loeb, Bak & Duysens, 1977). The same is presumably true of the forelimb and it is *a priori* likely that such inputs will be transmitted to the motor cortex unless it is postulated that the somatosensory pathways to the cortex are shut down during active movements (see below).

In the present experiments cells with 'proximal' receptive fields (i.e. fields not involving the foot) tended to be less strongly frequency modulated during locomotion than cells with 'distal' receptive fields (i.e. fields involving the foot). However, this apart, the results failed to demonstrate any simple and obvious relation between peripheral input and the discharge characteristics during walking. Some cells with well-defined receptive fields did not discharge rhythmically whilst others for which no field could be detected did so. Moreover, among those frequency-modulated cells with receptive fields no close correlation was detected between the locomotor-related discharge pattern and the nature (location, type of effective stimulus) of the receptive field. Efforts to detect any such correlation were undoubtedly hampered by the striking diversity found in respect of both these characteristics, but nevertheless it is clear that among cells most readily discharged by a particular stimulus (e.g. gentle taps) to a particular part of the limb (e.g. the tips of the digits) some discharged at a similar time during the step cycle while others discharged at quite different times.

It is of course possible that when comparisons are attempted for cells scattered across the forelimb motor cortex any tendency for a similarity in receptive field to lead to a similarity in the locomotor-related discharge might be masked by differences between the many other inputs which undoubtedly converge onto each neurone. For this reason special attention was paid to several small groups of cells, each recorded by a single implanted microwire. Histological evidence (see Armstrong & Drew, 1984) indicates that such cells must be quite close neighbours and this was consistent with the finding that, in agreement with previous studies (e.g. Welt, Aschoff, Kameda & Brooks, 1967; Asanuma, Stoney & Abzug, 1968; and see also Asanuma, 1975), the large majority of such cells had receptive fields which overlapped at least partially. However, whilst some cells were similar in respect both of receptive field and of locomotor-related discharge timing others with receptive fields very similar in location and stimulus type discharged at different (sometimes non-overlapping) times during the step cycle. This suggests that the rhythmic discharges were not primarily a response to input from the receptive field, though it does not of course exclude the possibility that peripheral inputs made some contribution to determining the pattern of discharge. As a corollary, it seems likely that juxtaposed cells with similar receptive fields can nevertheless receive very different patterns of input from other (undefined) sources.

Independent confirmation of the view that peripheral inputs are not the main factor in shaping the locomotor-related discharges derives from the experiments with local anaesthesia. The procedure usually led to some change in the discharge and more often than not this was a reduction in mean rate and in peak rate. However, the changes

were usually modest (see Fig. 4) and in no case did anaesthesia abolish a rhythmic discharge or alter its phasing. In most cases the response to receptive field stimulation was severely reduced rather than abolished but occasionally it was completely blocked and even in these cases the rhythmic discharge during walking showed little change. It therefore seems unlikely, at least for neurones with cutaneous receptive fields including or restricted to the foot, that peripheral inputs generated from the receptive field by the limb movements are a major source of the locomotor-related rhythms.

The implications are twofold. First it is possible, as suggested by Palmer, Marks & Bak (1981), that transmission in paths from skin to motor cortex is reduced during locomotion. This would accord with the finding that somato-sensory evoked potentials are much reduced in actively moving as compared with resting animals (Ghez & Pisa, 1972; Coulter, 1974).

Secondly, whatever inputs give rise to the locomotor rhythms they are presumably mainly central in origin. Prolonged discussion of possible sources would not be profitable but one deserving mention is the intracellular nuclei which provide substantial projections to motor cortex via the ventro-lateral thalamus. Orlovsky (1972*a*) has shown that fastigial and interpositus neurones discharge rhythmically in decerebrate walking cats and similar rhythms are present in interpositus neurones in intact cats (Huett, 1980; S. A. Edgley, personal communication). Peripheral input may play some role in controlling these discharges but is presumably not essential because similar rhythmic discharges occur in interpositus neurones during the 'fictive' locomotion and rhythmic scratching of paralysed animals (Viala, Coston & Buser, 1970; Antziferova, Arshavsky, Orlovsky & Pavlova, 1980; Arshavsky, Orlovsky, Pavlova & Perret, 1980). Moreover, in actively moving monkeys tactile inputs from the moving limb apparently exert little effect on interpositus neurones discharging in relation to the movement (Harvey, Porter & Rawson, 1979).

Arshavksy, Berkenblit, Fukson, Gelfand & Orlovsky (1972) have shown that locomotor-related rhythmic discharges are still present in the ventral spino-cerebellar tract after section of the lumbar dorsal roots and have therefore proposed that this path (together with reticulo-cerebellar paths) forwards information to the cerebellum regarding the rhythmic activity of spinal interneurones which collectively constitute pattern generators for locomotor movements. It is thus possible that the rhythmic activity of motor cortical neurones during locomotion is to some extent sustained by rhythmic inputs forwarded from spinal pattern generators via pathways through the cerebellum. Conversely, because such a high proportion of p.t.n.s and non-p.t.n.s is rhythmically active during locomotion it is highly probable that rhythmic inputs reach the cerebellum via descending (cerebro-cerebellar) pathways as well as via ascending paths such as the ventral and dorsal spino-cerebellar tracts and their forelimb homologues.

Locomotor-related discharges and the efferent organization in motor cortex

Approximately 60 % of the neurones were antidromically identified as p.t.n.s and thus their natural orthodromic discharges were presumably conducted into the pyramidal tract. With the proviso that the cell sample was heavily biased towards p.t.n.s with fast axons (two-thirds conducted at > 21 m/s), the results therefore

indicate that during steady locomotion the activity in that part of the pyramidal tract which arises in the forelimb motor cortex is greatest during the second half of stance in the contralateral forelimb. This is so whether the activity is measured in terms of the number of axons showing accelerated firing or in terms of the discharge rate in the average p.t.n. (see Fig. 6).

The identity of the non-p.t.n.s is obviously a matter for conjecture but because most neurones were in the deeper layers of the cortex (see Armstrong & Drew, 1984) many were probably cortical efferent neurones of some kind. Over-all, their activity lagged behind that of the p.t.n.s so they are unlikely as a class to have been driving the p.t.n.s via any direct and excitatory intracortical connexion.

As explained in the Introduction and Results we attempted to determine whether cells exerting similar spinal actions showed any similarity in their locomotor-related discharge patterns. In the monkey Fetz *et al.* (1976) have demonstrated that spinal connexions established by individual p.t.n.s can often be revealed functionally by spike-trigger averaging the e.m.g.s from a wide variety of muscles. Such p.t.n.s can then be classified according to the identity of the α-motoneurone pools whose excitability they influence. However, no positive results were obtained from this procedure in the present experiments, presumably because the technique is *a priori* unlikely to succeed when the connexion between the cortical neurones and the α-motoneurones is mainly indirect via one or more spinal interneurones as is the case in the cat (e.g. Lloyd, 1941; Illert, Lundberg & Tanaka, 1976).

The neurons were therefore subdivided according to the nature of the movement evoked by intracortical stimulation via the micro-electrodes, an approach which is not altogether satisfactory since even threshold movements are likely to result from the excitation of a substantial population of cortical neurones (see Asanuma, 1975; Phillips & Porter, 1977). These need not necessarily be entirely uniform in their influence on the cord and the recorded unit might chance to be atypical in this respect.

Unfortunately, the only suitably substantial subgroup comprised cells recorded via electrodes yielding elbow flexion. These showed a range of locomotor-related discharge timings quite similar to that in the whole sample. Two alternative conclusions are possible: either the method of subgrouping was inadequate so that the cells remained heterogeneous with respect to their projections, or cells capable of facilitating the same group of synergistic muscles (i.e. elbow flexors) do indeed display a wide range of discharge patterns.

Despite the variations in individual behaviour there were nevertheless substantial fluctuations in the numbers of p.t.n.s and non-p.t.n.s active at different times in the step (see Figs. 6 and 7). This resembles the findings of Orlovsky (1972*b*, *c*) for rubro-spinal and vestibulo-spinal neurones projecting to the lumbar enlargement. In decerebrate cats the population activity of the rubro-spinal neurones rose in late stance and peaked during swing whilst that of the vestibulo-spinal neurones increased progressively during swing and peaked early in stance, declining thereafter. These and other findings are taken to indicate that rubro-spinal discharges augment the force developed by the flexor muscles thereby assisting the spinal mechanisms which generate the swing phase of the step; the vestibulo-spinal tract acts similarly in relation to stance (Orlovsky, 1972*b–d*).

Given the similarities in functional organization which exist between the spinal

stages of the rubro-spinal and cortico-spinal tracts (see Brodal, 1981) it might be predicted that p.t.n.s recorded via electrodes evoking elbow flexion would be most active during early swing when the flexor muscles are most active. However, the number active and the discharge rate in fact reached maximum in the second half of stance and declined rapidly to a minimum during swing. By contrast, the activity of non-p.t.n.s recorded from such electrodes peaked later in stance and throughout swing remained at a higher level than was reached during the first two-thirds of stance.

While the activity pattern for non-p.t.n.s shows some resemblance to that found for rubro-spinal neurones, that for the p.t.n.s certainly does not correspond at all well with what would be predicted, unless there is a substantial delay between cortical discharge and the onset of any resultant change in muscle activity. In monkeys executing signal-initiated arm movements several studies (e.g. Evarts, 1966, 1972; Porter & Lewis, 1975) have in fact shown that there is an appreciable delay between the onset of firing in p.t.n.s related to the task and the onset of e.m.g. activity. However, the delay is of the order of 80 ms whereas in the present experiments the onset of e.m.g. in the elbow flexors occurred at least 350 ms after the population discharge rate for p.t.n.s began to increase and just after this rate reached its peak.

It may be recalled here that the peak rates of cortical neurones did not usually increase either when walking speed increased or when the animals walked uphill (see Armstrong & Drew, 1984). This behaviour again differs from that of rubro-spinal neurones which discharge 'more vigorously' during more vigorous (decerebrate) locomotion (Orlovsky, 1972*b*) and again suggests that the pyramidal outflow is not primarily involved in augmenting the activity of flexor motoneurones so as to assist in producing the swing phase.

The above argument does not of course exclude the possibility that some *individual* p.t.n.s contribute towards initiating and controlling elbow flexion, and indeed a few were most active during swing. However, it does seem likely that if as a population the p.t.n.s play any active role in locomotor control then their major direct action under the present conditions is to control some aspect of spinal cord activity other than the discharge of flexor α-motoneurones. In view of the multiplicity of actions which the cortico-spinal tract is known to exert on the cord (including regulation of the inflow of somatosensory information: see Lundberg (1975) and Asanuma (1981) for references and discussions) it is unprofitable to speculate much further. However, it may be significant that peak activity among the p.t.n.s recorded from electrodes yielding elbow flexion in fact occurs during the same tenth of the step cycle (i.e. the sixth) as the termination of e.m.g. in the elbow extensor triceps brachii (which precedes foot lift by approximately 120 ms during walking at 0·5 m/s: see Armstrong & Drew, 1984). It is therefore possible tentatively to suggest that the role of these p.t.n.s may include helping to determine the time at which elbow extensor activity ceases (via a presumed excitatory action on spinal inhibitory interneurones). Given that locomotor adaptation is achieved through variations in the duration of stance much more than swing (see Grillner, 1974), this is a not an unlikely responsibility for p.t.n.s. Such an action would be essentially an influence over timing in the step cycle (cf. Armstrong & Drew, 1984) and it would be consistent with the observation that in the decerebrate cat electrical stimulation of the pyramidal tract is capable

of resetting the (hind-limb) step cycle; in fact stimulation during stance led to premature termination of the locomotor burst in an extensor (lateral gastocnemius) and to an earlier (and larger) burst in an antagonistic flexor muscle (tibialis anterior) (Orlovsky, 1972*d*).

The suggestion above would also be in excellent accord with the observation (Eidelberg & Yu, 1981) that lesions of cat motor cortex or pyramid lead to an inappropriate increase in stance duration, swing being little changed; this has indeed been interpreted as indicating a loss of descending inhibitory control over the limb extensors.

Finally it may be noted that brief intracortical stimulation (10 pulses at 330 Hz) through implanted micro-electrodes is often capable during locomotion of producing a complete temporary break in the activity of elbow extensors. This inhibitory action can occur at latencies as short as 7 ms after the first stimulus and at stimulus intensities as low as 3–10 μA (D. M. Armstrong & T. Drew, unpublished).

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