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ROLE OF MOTOR CORTEX IN CONTROL OF LOCOMOTION

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Summary

1. The activity of 252 motor cortex (MC) neurons (including 70 pyramidal tract neurons) was recorded extracellularly in the cat by means of a mobile electrode during free locomotion in a box.

2. The activity of 89% MC neurons was modulated during locomotion. The modulation was related to the stepping movements, since it increased in one stepping phase and decreased in the next.

3. MC neurons were also studied while the animal moved up a flat inclined surface, walking at different speeds, with a load of 85g attached to each forelimb, when the cat had to perform snakelike movements (turns) or walk on the flat surface placed in a horizontal plane. The pattern of MC neuron activity changed little under these conditions in comparison with uncomplicated locomotion.

4. The activity of 68 neurons was recorded in experiments with barriers and involving locomotion on a horizontal ladder which restricted the possible paw positions along the direction of locomotion. These tasks greatly affected the MC activity.

5. Neither bilateral MC lesion nor tetrodotoxin inactivation hampered uphill locomotion, walking along a moving floor, or locomotion involving turns and loaded forelimbs. On the contrary, it proved to be necessary for the MC to be intact for locomotion with space linked stepping limb movements (i.e. with barriers, on a ladder) to be possible.

6. Bilateral destruction of the ventrolateral nucleus of the thalamus (VL) resulted in a decrease in the rhythmical modulation of MC neurons during locomotion. After VL lesion the cat could walk quite well on the horizontal surface and uphill, at various speeds, with the forelimbs loaded; it could perform turns and could walk on the moving floor. The cat proved to be incapable, however, of walking with barriers and on the ladder.

Introduction

Locomotion under natural conditions always includes non-standard, "voluntary" components, which are necessary for overcoming obstacles, changing the direction of movements, and space orientation. In many cases, an animal has to carefully pick out the point at which its paw is to be placed. The system of reception with which the spinal locomotor generator itself is equipped is sufficient to ensure locomotion on a flat surface, but is not capable of adapting movements to a complex environment (Grillner and Rossignol, 1978). Natural locomotion is not possible without the contribution of supraspinal centres to the control of stepping movements. Commands from these centres reach the spinal mechanisms by various descending tracts (Asanuma, 1981; Armstrong, 1986; Arshavsky et al., 1986).

The activity of neurons in the reticulo-, vestibulo- and rubrospinal tracts during locomotion has been studied in decerebrated cats (Orlovsky, 1972 a & b; Orlovsky and Shik, 1976). These neurons were found to be rhythmically modulated, the modulation being related to the stepping rhythm. Similar results have been obtained on pyramidal tract cells in intact cats running on a treadmill band (Schmidt et al., 1976; Durelli et al., 1978; Palmer et al., 1980; Armstrong and Drew, 1984).

It is well known that the activity of motor cortex (MC) neurons changes during the performance of voluntary movements and in some cases, before the beginning of movements (Brooks and Stoney, 1971; Brooks, 1974; Conrad et al., 1974; Porter and Levis, 1975; Evarts and Tanji, 1976).

Lesion of the MC deprives an animal of the capacity to perform some voluntary limb movements, or at least interferes with the performance of these movements. But locomotion on a flat surface is still possible after this kind of lesion (Stepien et al., 1961; Denny-Brown, 1966; Burlachkova and Ioffé, 1978). Even complete removal of the cortex does not prevent locomotion on a treadmill or a flat surface (Orlovsky and Shik, 1976).

In the present study, we recorded the activity of MC neurons (including pyramidal tract neurons, PTNs) in a freely moving cat during locomotion. The external conditions for locomotion were varied as follows: (i) locomotion on a flat horizontal surface with no disturbances (which will be referred to as "normal" locomotion); (ii) the same as in (i) but with additional loading on some muscle groups; (iii) overcoming obstacles of various kinds

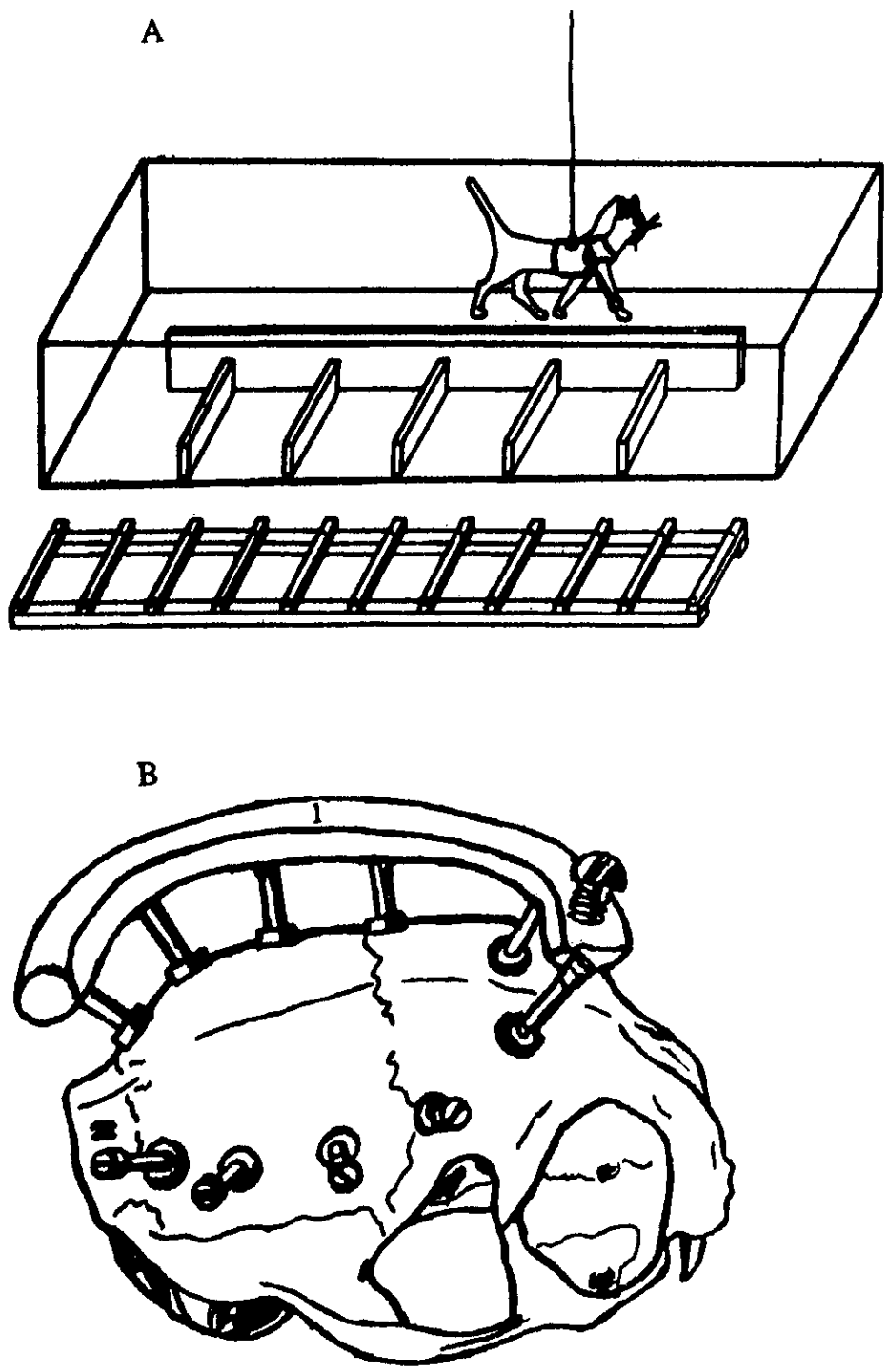

Fig.1. A: The experimental box was divided into two corridors (2.5 m long and 0.5 m wide); barriers or a horizontal ladder could be placed in one of them. The MC neuron recordings were carried out as the cat walked along the corridors. B: the cat's skull with a plastic base (1) fixed on it by means of screws (2). All the equipment for neuron recording was attached to the base.

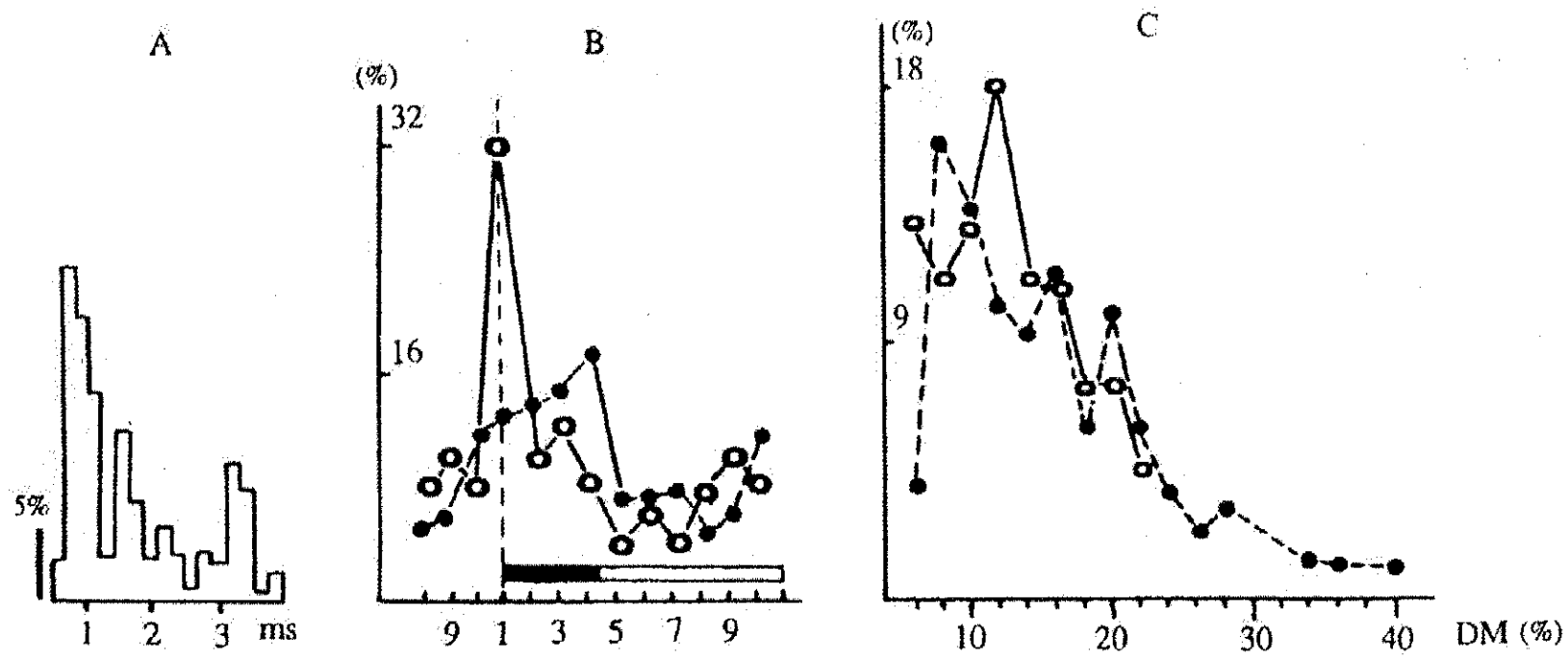

Fig. 2. A: Distribution of latent periods of antidromic responses. B and C: locomotion on the flat horizontal surface; B: distribution of points of maximum activity throughout the step cycle of the contralateral forelimb. The step was divided into 10 intervals, black and white bars - swing and stance phase, respectively. C: Distribution of values of depth of locomotor modulation (DM) open circles - PTNS, blackdots - non-PTNs.

during locomotion. We compared the activity of MC neurons under simple (i) and complicated conditions (ii) and (iii), assuming that the changes in the activity of MC neurons are likely to be related to changes in the task (a supraspinal "voluntary" component of movements) when changes in the movement itself (i.e. in the corresponding afferent inflow) are small.

Method

Seven cats, trained to walk or run inside a box in response to a sound signal, were used. A longitudinal wall divided the box into two corridors, each 2.5 meters long and 0.5 meters wide. On reaching the end of the one corridor, the cat returned taking the other one (Fig. 1A). Once training was completed, the cat underwent surgery, and a plastic base was fixed to its skull (without removing the skin) by means of radially inserted screws (Fig. 1B). A microdriver and an amplifier were then attached to the base. The bone and the dura above the MC (the area corresponding to the anterior and the rostral part of the posterior sigmoid gyrus) were removed, and the aperture was covered with a plastic plate. The plate had about 60-70 small holes, with thin glass tubes glued into them. The recording electrode was subsequently introduced through these tubes into the brain. A bipolar stimulating electrode was also implanted in the medullar pyramid (Snider-Niemer, 1960, coordinates P 10, R 1.5). The activity of MC neurons was recorded extracellularly by a mobile wolfram electrode (tip diameter about 5 μm) insulated with varnish. The movement of the forelimb contralateral to a MC cell was recorded by means of an electric tranducer attached to the limb, with which it was possible to distinguish between the stance and swing phases of the step. In other experiments, the stance phase duration was monitored by a contact attached to the paw. The signals were recorded on magnetic tape. When analyzing the neuronal activity, the step was divided into 10 intervals, and a post-event time histogram of spike distribution throughout the step was obtained for 10-50 successive steps. Besides, the mean value of the activity of a neuron in the step was assessed as well as the activity before locomotion. The difference between the maximum and minimum frequency in the step, divided by the mean frequency, was used as an index to the depth of rhythmic modulation.

Results

Locomotion on the horizontal flat surface

The activity of 252 MC neurons was recorded during locomotion on the flat horizontal surface ("normal locomotion"). Among these there were 70 PTNs which responded to high-frequency antidromic stimulation of the pyramidal tract. The distribution of the latency of antidromic responses is shown in Fig. 2A. The conduction speed of PTN

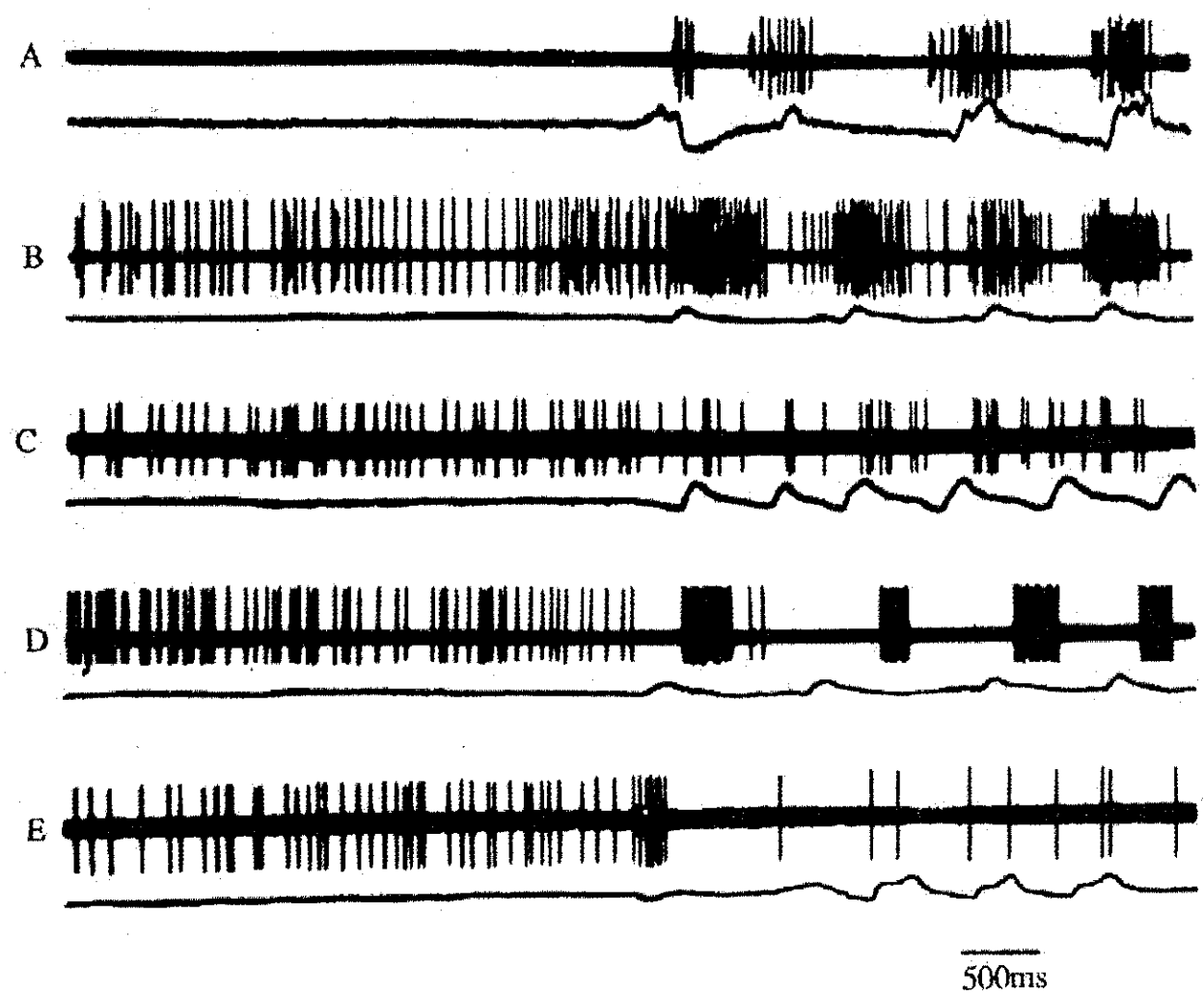

Fig. 3. Examples of activity of MC neurons before and during locomotion (flat horizontal surface). Bottom lines monitor the movement of a contralateral forelimb in rostro-caudal direction. Strongly modulated units (A, B, D), a unit without any clear rhythmical modulation (C) and a unit with decreased firing during locomotion (E) are shown.

axons ranged from 13 to 83 m/sec. Since we found no marked difference between the activity of PTNs and that of non-PTNs, the results of these two groups will be presented together except for a few cases which will be specially indicated. Seventy MC neurons had somatic receptive fields, i.e. they could be activated by tactile stimuli, by muscle squeezing or by passive joint movements.

The activity of 222 (89%) MC neurons was modulated during locomotion in relation to the stepping movements: it increased in one step phase and decreased in the next (Fig. 3). The maximum activity in 65% of "modulated" neurons coincided with the swing phase of the contralateral forelimb, and in 35% of neurons, with the stance phase. Fig. 2B shows the phase distribution of points showing maximum activity, for PTNs and non-PTNs. Most PTNs showed maximum activity at the beginning of the swing phase (black bar), while the maxima of most non-PTNs were distributed throughout the swing phase. The depth of modulation of PTNs and non-PTNs did not differ on the average but the maximum value with PTNs was 25%, while with non-PTNs it could reach 35-40% (Fig. 2C).

In the absence of locomotion, the discharge frequency of MC neurons was 1-30/sec, with an average of 9.8 ± 1 sec (Mean ± SD). The average activity (M ± m) of 34% of the neurons showed no change during the transition from standing to locomotion. In 36% of the neurons, the mean firing-rate increased about two-fold, and in 20% it even increased 3-5-fold. The activity of 10% of the neurons decreased to about half the initial level during locomotion.

We analyzed the activity of modulated neurons just before the first step performed by the contralateral forelimb. For this purpose, we counted the number of spikes in each 100 msec interval during the 2 sec period preceding the swing phase of the first step. No change in the activity of 70% of the neurons (34 out of 54) was observed during this period. The activity of 14 (25%) neurons increased and that of 2 neurons decreased. No rhythmical modulation of activity was observed in MC neurons before the onset of locomotion (Fig. 3).

Locomotion uphill, at various speeds, involving turns, loaded forelimbs, and locomotion on a moving floor

The power developed by the locomotor system of an animal increases in the case of uphill locomotion, provided the speed remains the same. Does any difference in the activity of MC neurons accompany the change in the power developed by limb muscles?

The activity of 37 MC neurons (including 21 PTNs) was recorded when the cat moved up the flat inclined (10°) surface. The average activity over the step cycle and the de of its modulation in 20 (55%) neurons during uphill locomotion were practically the same as in normal locomotion (Fig. 4A). In 10 (27%) neurons the average activity increased by 78 ± 16% during uphill as compared with normal locomotion. An increase in the depth of modulation was observed in 7 (19%) neurons, amounting on the average to 56 ± 19%. The changes in activity during uphill locomotion in all the neurons recorded are shown in the graph in Fig. 7A (see legend for explanation).

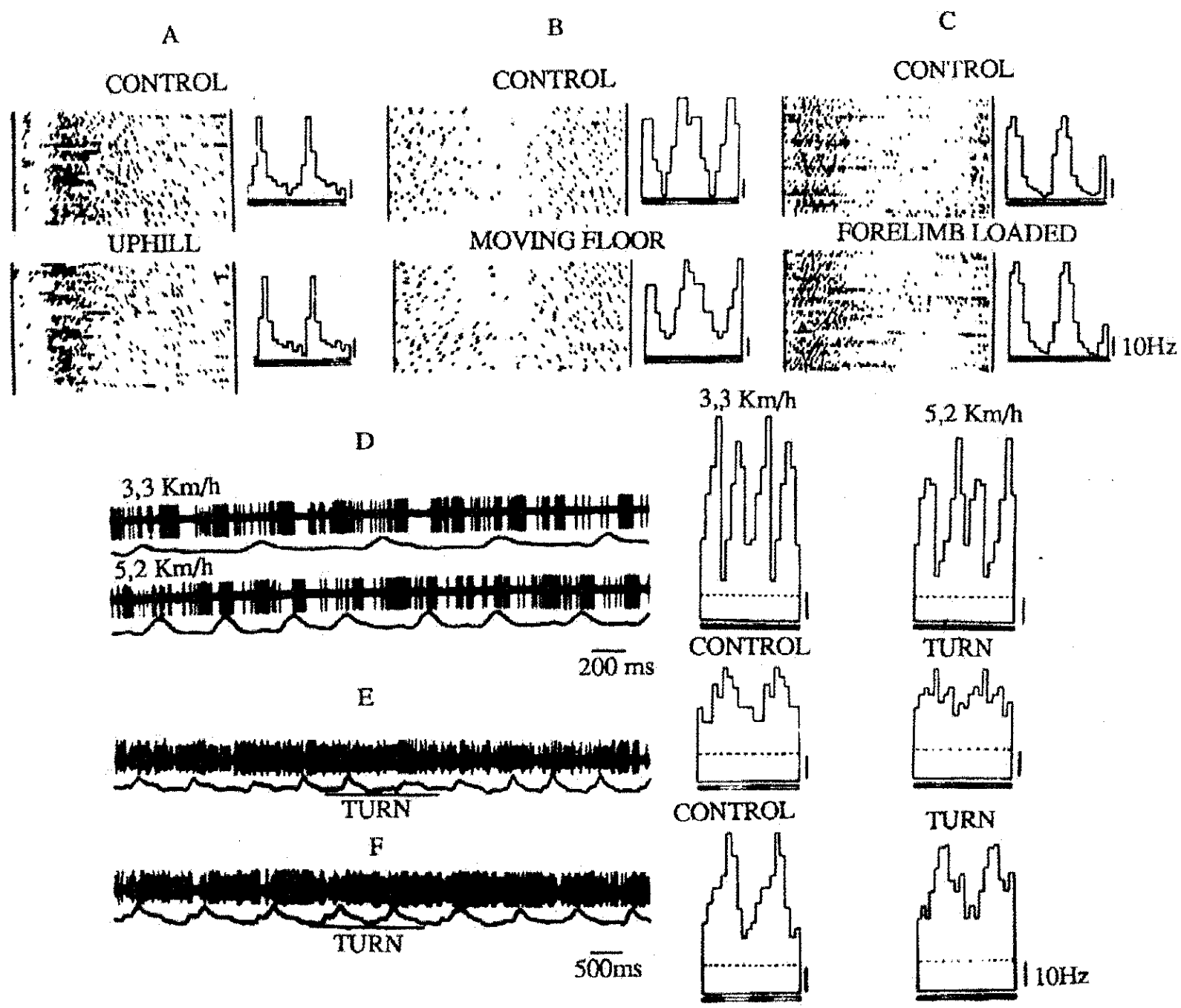

Fig. 4. A - C: examples of activity of MC neurons under various conditions. For each neuron the activity is shown during normal, simple locomotion (Control) and when conditions for locomotion were changed. In A, cat walked uphill (10°); in B it walked on the moving floor (side-to-side movements with frequency of 0.8/sec amplitude of 60 cm); in C with loads (85 g) attached to the elbows. The activity of each neuron is presented in the form of a raster, i.e. sequence of spikes in a cycle, for 30 successive steps. Each spike is represented by a short line: the inclination of the line indicates the phase of the step (right - swing, left - stance). A post-event time histogram of the firing frequency (throughout the step cycle), corresponding to the raster, is also presented. D: activity of MC neuron in a subject walking at two different speeds and corresponding phase distribution of spike activity. E, F: activity of two MC neurons (E and F) when a cat performed the turn (marked by a bar). As a control, in phase distributions, the activity before and after the turn was used. In D - F, the dashed line in the phase distribution indicates the average activity of a neuron before locomotion. A black bar under the phase distribution marks the swing phase of the forelimb contralateral to a neuron.

In our experiments, an animal sometimes spontaneously change its speed, which allowed us to compare the neuron activity at various speeds of locomotion. Fig. 4D illustrates locomotion at speeds of up to roughly twice the lowest speed. The average activity of a neuron, as well as the depth of its modulation, (see the histogram in Fig. 4D), changed little with the increase in the speed. This was also true of the other neurons tested (n = 7).

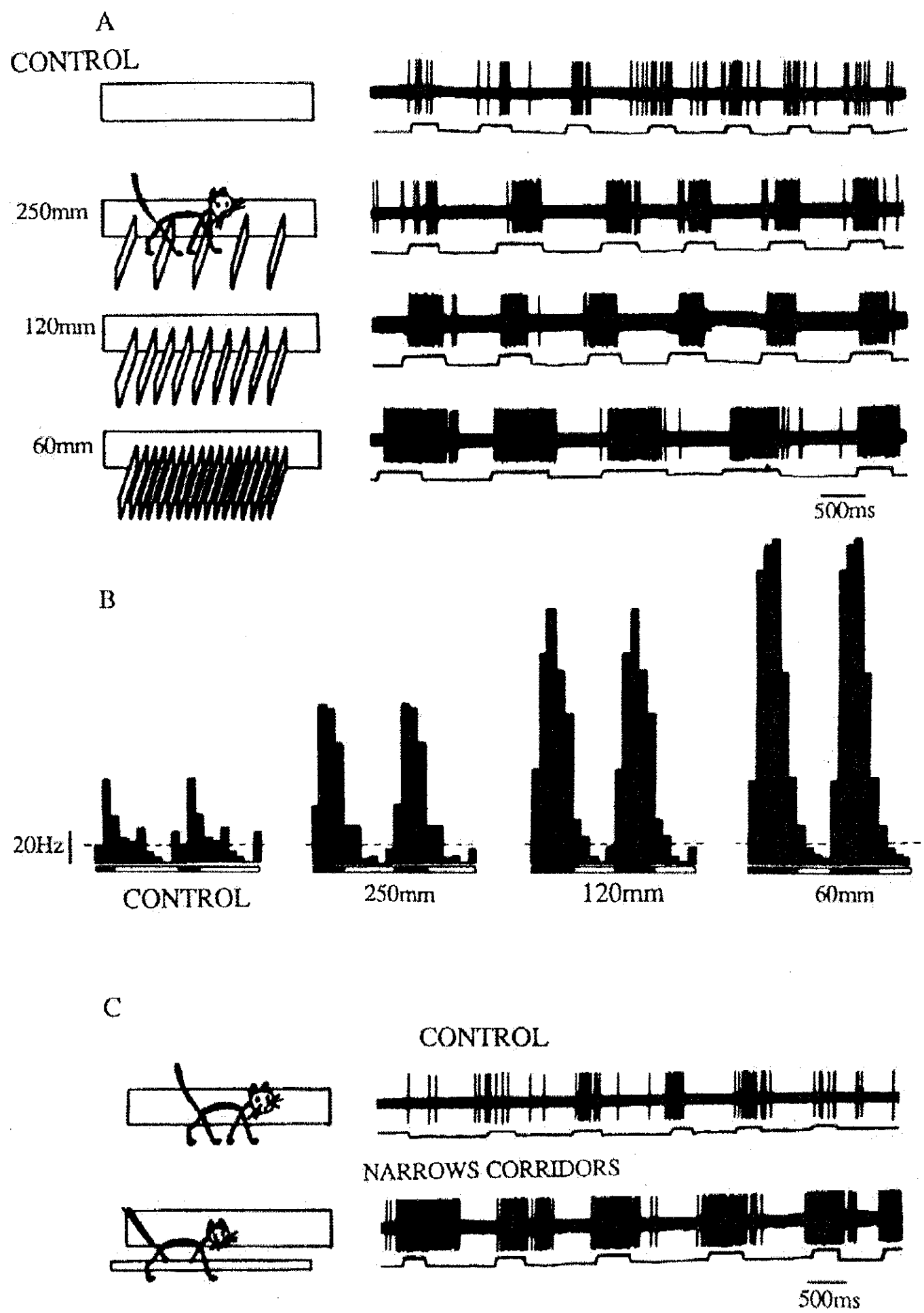

Fig. 5. Changes in the activity of a PTN with restrictions of possible limb positions when stepping. In A, a cat initially walked with no obstacles (Control), and then the barriers (70 mm in height, interbarrier distance as indicated) were arranged in the box. Corresponding phase distributions of the neuron activity are shown in B. C: after locomotion under normal conditions (Control), a longitudinal rod forming two narrow corridors (for left and right limbs) was placed on the floor. In A and C, the bottom trace shows the stance and swing phases of the forelimb contralateral to a neuron. (Deflection down and up, respectively).

Locomotion uphill, as well as locomotion at increased speed, requires greater limb muscle activity (in both flexors and extensors) (Orlovsky et al., 1966). It is therefore surprising that the activity of MC neurons changed so little under these conditions.

In another series of experiments, a load of 85 g was attached to each forelimb at the distal part of the elbow. During locomotion with the load, the average activity in 7 MC neurons (over the 11 tested) increased by 60 ± 10%; in 1 neuron it decreased; in 3 neurons, it remained the same. The depth of modulation in 5 neurons (45%) incrased by 30 ± 1%; in 3 neurons it decreased by 37 ± 7%; and in 2 neurons, it did not change. Fig. 4B shows an example of the neuron in which the pattern of activity persisted in spite of the load. The effects of the load upon all the neurons tested are shown in Fig. 7C.

On reaching the end of a corridor in the box, the cat turned and continued running, taking the other corridor. The beginning and the end of the turn were monitored by means of photodiodes. In a series of special experiments, a series of partitions was placed in the box in such a manner that a cat had to perform snake-like body movements, turning to the right, then to the left, and so on. The step length during the turn differed from that produced while walking straight ahead: it increased in the case of the "outer" limbs and decreased in that of the "inner" ones. If compared to incomplicated locomotion, the average activity during the turns increased by 56 ± 11% in 52 (70%) neurons (out of the 75 modulated MC neurons tested); in 7 neurons it decreased by 30 ± 3%; and in 17 (23%) neurons, it remained the same. The depth of modulation in 24 (32%) neurons increased by 64 ± 9%; in 16 (21%) neurons it decreased by 32 ± 3% and in 35 (47%) neurons, it did not change. Examples of turns are shown in Fig. 4E, F. The data on all the neurons tested in one cat are summarized in Fig. 7B.

In a special series of experiments, the supporting surface was made unstable. For this purpose, the whole box with a walking cat was put on a platform performing sine oscillations in a horizontal plane (the period was 1.3 sec, and the amplitude, 60 cm). The direction of the oscillations was perpendicular to that of locomotion. Under these conditions, the pattern of stepping movements (joint angles, muscle forces, etc.) varied continuously and considerably. Nevertheless, the pattern of MC neuron activity changed little as compared to simple locomotion. In most of the 35 MC neurons tested (including 19 PTNs), neither the average activity nor the depth of modulation changed. In only 7 (20%) neurons was a change in pattern observed. In 3 of these, the average activity increased by 112 ± 36%. The depth of modulation increased in 2 neurons and decreased in 4, the change being 49 ± 10%. Fig. 4C shows the activity of a PTN during locomotion on stable and unstable supporting surfaces, and the histograms of spike activity for these two cases. The persistence of the pattern of activity observed in most MC neurons is also illustrated in Fig. 7D.

Summarizing the results presented in this section, we should like to emphasize that most of the variations and complications of locomotion we used, i.e., different speeds, uphill movement, turns, movement of the floor, and additional loading of the forelimbs, resulted in relatively little change in the pattern of rhythmic activity of MC neurons. This will become more obvious later, when we come to report the great changes in the pattern which occurred under visually controlled locomotion conditions.

Influence of destruction and TTX inactivation of MC upon locomotion on a flat surface

At the end of each experiment, we destroyed the MC bilaterally. Under nembutal anesthesia the MC grey matter was sucked out until the white matter became visible under the holes used previously for the recording electrodes. The capacity of animals for locomotion was tested within two days of the MC ablation. Another method for inactivating the MC consisted of poisoning the cortex by bilateral application of tetrodotoxin (TTX) (5 μl, 10^{-4} mol, Armstrong and Drew, 1984). The drug was injected through a needle which replaced the recording electrode. Recording of MC neurons at a distance of 2 mm from the needle tip showed that their electric activity disappeared within about 10 min of the TTX injection. At that time the capacity of an animal for locomotion was tested.

Animals deprived of the MC, as well as those with the MC inactivated with TTX, seemed to have no difficulty in performing the whole range of our tests: normal locomotion

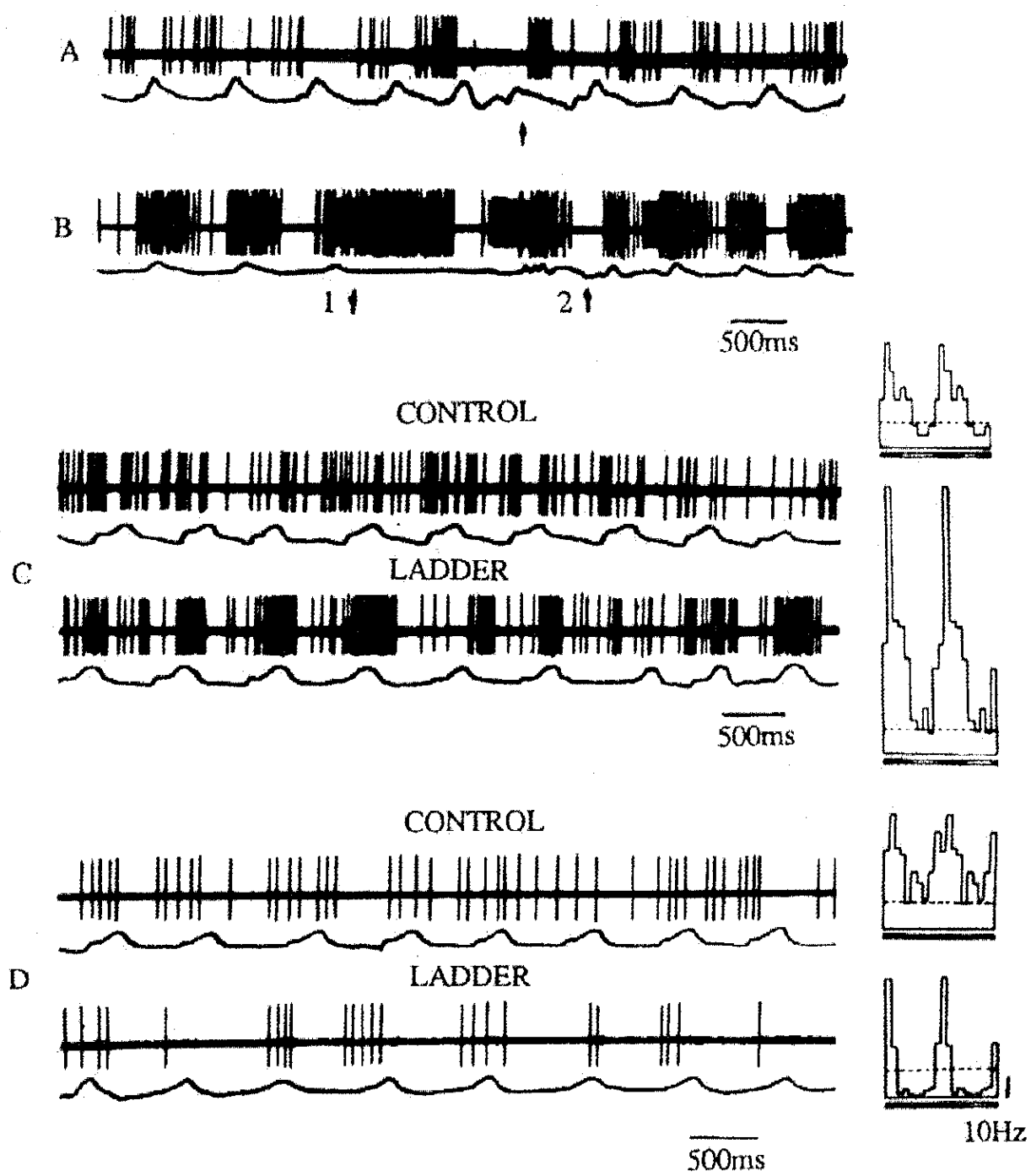

Fig. 6. A, B: activity of various PTNs in a cat overcoming a single barrier (height 70 mm in A and 200 mm in B). The arrow in A indicates the moment at which the contralateral forelimb was above the barrier. The first arrow in B indicates the moment when an animal stopped before the barrier, the second one indicates that when the cat jumped over the barrier. C, D: changes of the activity of two PTNs in a subject walking on the horizontal ladder (interrung distance, 250 mm) as compared to normal locomotion (Control). Corresponding post-event time histogram are presented on the right. In the first unit, the depth of modulation increased due to the growth of a maximum activity, and in the second unit, due to the decrease in activity in between the maximums.

at various speeds, locomotion uphill, locomotion on a moving floor, locomotion with additional loading of the forelimbs, and turns. This is in agreement with the results obtained by other authors (Stepien et al., 1961; Denny-Brown, 1966), who have demonstrated that bilateral MC lesion does not disturb locomotion on a flat surface.

Walking with specially restricted limb positions

Several series of experiments were carried out, in which a cat had to use its visual system for controlling (or correcting) its stepping movements.

I. Walking with barriers. We restricted the possible paw positions on the floor along the X axis (the direction of locomotion) by arranging barriers along the cat's path (the height of the barriers was 70 mm, and the distance between successive barriers 250 mm or less, Fig. 5A). In order to walk along the box, an animal had to step over the barriers and to place its paw in between them.

The activity of 68 MC neurons, including 12 PTNs, was recorded in the experiments with barriers (interbarrier interval, 250 mm). The average activity during locomotion with

barriers differed from that in normal locomotion in 54 (79%) MC neurons. In 34 neurons (including 7 PTNs) it increased by 75 ± 15%; in 20 neurons (including 4 PTNs) it decreased by 30 ± 4%. The depth of modulation changed in 57 (84%) MC neurons. It increased in 40 (59%) neurons (including 9 (75%) PTNs). In the case of non-PTNs, the increase was 35 ± 5%; in that of PTNs, 67 ± 32%. In 17 (25%) neurons (including 1 PTN) the depth of modulation decreased by 21 ± 3%. The results obtained in one cat are shown in Fig. 7E.

The deepening of modulation observed in most MC neurons in subjects overcoming barriers was determined by two factors: (i) an increase in the firing rate during the phase of the maximum activity and (ii) an inhibition of the discharge in between the maxima. Usually (in 91% of cases) the phases of maximum activity were the same in both normal and complex locomotion, as in the case of the neuron shown in Fig. 5A.

In a few experiments, we tested the activity of the same MC neuron not only with a 250 mm interbarrier interval but with shorter intervals as well, i.e. such that the animal had to perform stepping with greater accuracy. In all the neurons tested the average activity and depth of modulation increased with the shortening of the interbarrier interval, as in the case shown in Fig. 5 A, B.

In this series of experiments we used not only regularly arranged barriers but, in a few cases, a single barrier, with a view to investigating what strategies an animal used to overcome the obstacle. When the height of a barrier was the same (70-90mm) as in the experiments described above, an animal could overcome it without interrupting a normal sequence of steps, as shown in Fig. 6A, but the amplitude of movement at the joints increased in the step with the obstacle (visual observation). As can be seen in Fig. 6A, a MC neuron burst was more intense in the step with the obstacle, but its phase remained unchanged. When the height of a barrier was 200mm, the animal stopped in front of it and then jumped over it; in this case, the regular modulation of MC neurons was disturbed and then resumed with the beginning of regular stepping (Fig. 6B).

2. Walking on a ladder. We used a horizontal ladder with 50 mm rungs, the distance between successive rungs being 250 mm (i.e. equal to an average cat's step). When walking on the ladder, the possible positions of a limb landing on the supporting surface were farther restricted along the X axis, as compared to walking with barriers. The activity of 108 MC neurons was recorded in a subject walking on the ladder. Among these, there were 24 PTNs and 7 neurons responding antidromically to stimulation of the ipsilateral N. ruber (corticorubral neurons, CRNs). Examples of recordings are shown in Fig. 6 C, D.

In a subject walking on the ladder, as compared to normal locomotion, the average activity changed in 88 (81%) MC neurons. In 77 (71%) neurons it increased by 56 ± 6%; and in 11 (10%) neurons it decreased by 28 ± 4%. The depth of modulation was also altered in 87 (80%) MC neurons (including 19 (80%) PTNs and 6 (88%) CRNs). In 61 (56%) neurons (including 12 (50%) PTNs and 4 (57%) CRNs) it increased by 40 ± 3%; in the case of PTNs the increase being 46 ± 8%; in that of CRNs, 34 ± 18%; and in that of nonidentified MC neurons, 36 ± 5%. The depth of modulation decreased in 26 neurons (including 7 PTNs and 2 CRNs) by 35 ± 4%.

During locomotion on the ladder, the deepening of modulation observed in most MC neurons resulted from the same causes as in walking with barriers, i.e. the increase in firing rate in the phase of maximum activity (Fig. 6C) and/or inhibition of the discharge in the phase of minimum activity (Fig. 6D). The phases of maximum and minimum activity persisted in the overwhelming majority of neurons, as in the examples given in Fig. 6 C, D.

3. Walking along two narrow corridors for left and right limbs. We restricted the possible limb positions along the Y axis (perpendicular to the direction of locomotion) by disposing a long longitudinal rod on the box floor in such a manner that only narrow corridors (50 mm width) between the rod and the box walls were left free for the animal to place its feet (Fig. 5C). Ten neurons were tested in these experiments, and their activity was compared to that recorded during normal locomotion. In 8 neurons, both the average activity and the depth of modulation increased (by 50 ± 3% and 70 ± 5%, respectively) during locomotion along narrow corridors, as shown in the example in Fig. 5C.

Table 1

Percentage of MC neurons in which a change in activity (as compared to that recorded during normal locomotion) accompanied the performance of complex locomotor tasks.

	Uphill	Various speeds	Loaded forelimbs	Turns	Moving floor	Barriers	Ladder	Narrow Corridors
Change in average activity	27	10	60	70	9	79	81	60
Change in depth of modulation	19	8	45	53	17	84	80	72

The main results of this and preceding sections are summarized in Table 1, which shows the percentage of MC neurons in which a change in activity accompanied various complications of the locomotor task. One can see that **Barriers, Ladder** and **Narrow Corridor** are the tasks which most affected the MC activity. In all these tasks, an animal had to link its stepping movements to the coordinates of the outer space.

Influence of destruction and TTX inactivation of MC on locomotion involving space-linked limb movements

Bilateral MC lesion and TTX inactivation hampered neither uphill locomotion, locomotion along the moving floor, nor locomotion with loaded forelimbs (see above). On the contrary, the intact state of the MC proved to be necessary for locomotion involving space-linked stepping limb movements to be possible.

After the MC ablation or TTX inactivation, the animal could no longer step over obstacles (it knocked them over). It could not walk on the ladder either (it missed the rungs and fell down). The cat failed to place its paws at the appropriate points for 5-7 days after the MC lesion, then its attempts became more successful, and within about one week the animal managed to carry out all the locomotor tasks without making any mistakes.

Influence of destruction of N. ventralis lateralis thalami on locomotion and on activity of MC neurons

One of the main inputs to the MC is through the ventrolateral nucleus of the thalamus (VL), which transmits signals from the cerebellum and basal ganglia (Strick and Sterling, 1974). We tried to eliminate this input by destroying the VL bilaterally. For this purpose a macroelectrode was inserted into the VL region stereotaxically and a current of 3 mA was delivered through it for 30 sec. Histological inspection confirmed the destruction of the VL. The results obtained in this animal are presented below.

On the day following the VL lesion the cat could walk quite well on the horizontal surface and uphill, at various speeds, with a loaded forelimb; it could perform turns and walk on the moving floor. On the contrary, the cat proved to be incapable of walking with barriers or on the ladder. The cat's mistakes while stepping were the same as after the MC destruction (see above): it could not step over an obstacle and missed the rungs of the ladder. For about 3 days the animal was completely unable to perform stepping placing its paws accurately. Then its attempts became more successful, and within one week it could overcome the obstacles with only a few mistakes.

In this cat we recorded the activity of 19 MC neurons before the VL lesion and that of 66 MC neurons after the lesion. Comparing the behaviour of MC neurons before and after

the VL destruction, one can see an increase (76%) in their average activity (17 ± 1 versus 9.7 ± 1 per sec) and a decrease (36%) in the depth of modulation (8.5 ± 1 versus 11.6 ± 1). The activity of MC neurons was also recorded on the 4th day when the operated cat made the first attempts to walk on the ladder. In this case as well, the average activity increased while the depth of modulation remained small (Fig. 8).

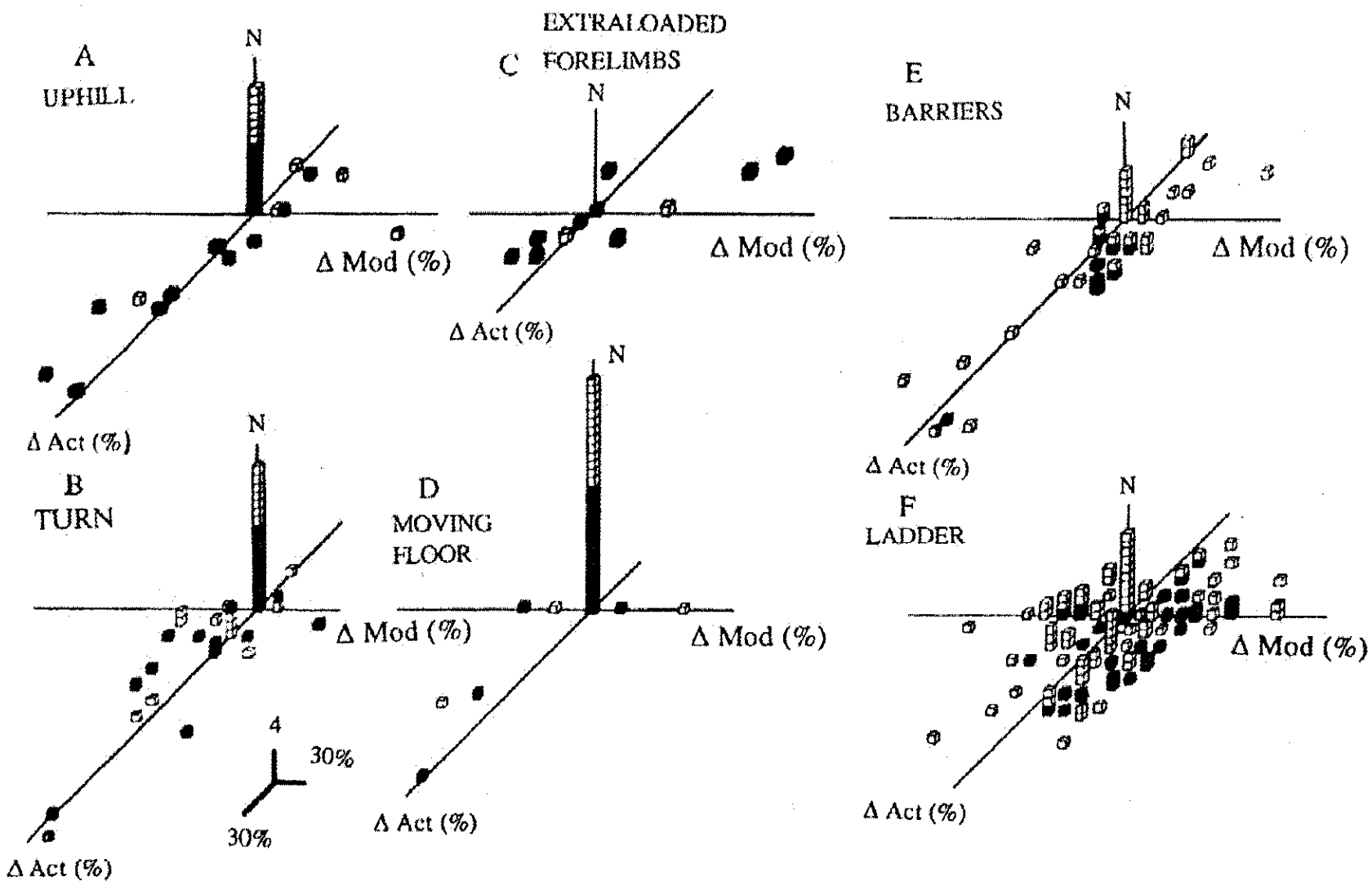

Fig. 7. Changes in the activity of MC neurons with complex locomotor tasks, as compared to normal locomotion. Horizontal axes: change in the average activity (Act) and the depths of modulation (Mod); vertical axis: number of neurons. In the graph each neuron is shown as a cube (black, PTN; white, non-PTN). One can see that in cases A, B, C and D most neurons did not change their pattern of activity, while in E (barriers) and F (ladder) the majority of neurons showed a change in either the average activity, or the depth of modulation, or both these characteristics.

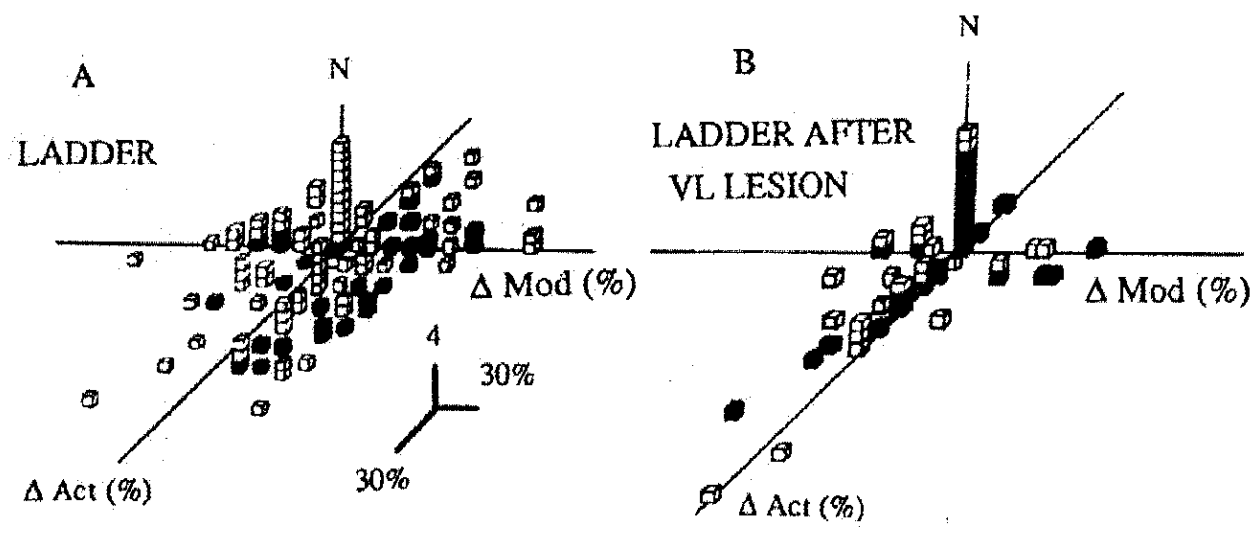

Fig. 8. The effect of VL destruction. A: changes in the activity of MC neurons in subjects walking on the ladder as compared to normal locomotion (repetition of Fig. 7F). B: the same after bilateral VL destruction. One can see that transition from normal locomotion to walking on the ladder, after the VL lesion, is not accompanied by any increase in the depth of modulation but only by an increase in the average activity level.

Discussion

Uncomplicated locomotion. When a cat walked directly on the flat horizontal surface with no obstacles, the activity of most MC cells (both PTNs and non-PTNs) was rhythmically modulated, the modulation being related to the rhythm of the stepping movements. This rhythmic modulation arose only with the onset of locomotion. In some MC neurons, however, a tonic change in activity, could be observed prior to the first step. This change seems to be associated with the postural ajustments involved in the transition from standing to locomotion.

Various MC neurons showed maximum activity in various step phases, but the majority of them were more active in the swing phase of the corresponding limb. This is in agreement with the commonly held view that the pyramidal tract exerts its action mainly on the limb flexors (Brooks and Stoney, 1971; Asanuma, 1981).

Our results, as far as simple locomotion of freely moving cats is concerned, are in complete agreement with those obtained on cats walking on a treadmill band (Armstrong and Drew, 1984a): in both cases, most MC cells were modulated, the maximum overall activity being in the swing phase.

What is the source of the rhythmic signals modulating the activity of MC neurons? Armstrong and Drew have demonstrated (by blocking corresponding nerves with novocaine) that elimination of afferent flow from the receptive field of MC neurons did not abolish the rhythmic modulation of this neuron (Armstrong and Drew, 1984b). This finding suggests that the source of modulatory signals is not at the periphery but rather in the central neuronal mechanisms.

In experiments on decerebrated cats walking on a treadmill band (Asanuma, 1981), it has been demonstrated that neurons of various descending tracts of the brainstem are rhythmically modulated in relation with the stepping cycle. The source of modulatory signals proved to be the spinal neuronal mechanism generating the stepping rhythm. It was also found that spinal influences upon the neurons of descending tracts were mediated by the cerebellum. It seems likely that MC neurons receive the modulatory commands via the same route since their rhythmical modulation was found to decrease considerably after destruction of the VL, the nucleus mediating cerebellar influences upon the MC.

Locomotion with various loads. During locomotion at higher speeds or uphill, limb muscles have to develop more force which is provided by an additional excitation of the appropriate motoneurons. The present study shows that the pattern of MC neuron activity changes little with the increase in the load upon the motor apparatus. In a minority of neurons only, there were changes in the average activity, and in an even smaller number of neurons, in the depth of modulation. These results are in agreement with those obtained in connection with treadmill locomotion, with a cat walking at various speeds or uphill (Armstrong and Drew, 1984a).

We also observed here that the pattern of activity of MC neurons changed little when locomotion was complicated in other ways, namely when a cat performed turns and when it walked on the moving floor. Without doubt, in these cases not only the afferent activity of the spinal mechanisms but also the afferent flow from various limb receptors changed. The fact that the pattern of activity of MC neurons changes little under these conditions means first, that the afferent signals from limb receptors do not play a decisive role in modulating the MC neurons. This provides further confirmation of the idea that modulation of MC neurons originates at central level. Secondly, the persistence of the MC output pattern, while changing the spinal cord afferent activity, suggests that the MC does not participate in the control of stepping movements in the locomotor tasks considered above. This suggestion is further supported by the fact that the destruction of the MC did not hamper the performance of these locomotor tasks.

Locomotion involving space-linked limb movements. The main finding in the present study is that the pattern of activity of most MC neurons changed dramatically when an animal had to perform stepping movements with accuracy, i.e. had to take into account,

when stepping, the peculiarities of the surrounding space. Since the information concerning these peculiarities was obtained via the visual system, one may conclude that the activity of MC neurons changes considerably when the visual system is involved in the control of locomotion.

Since destruction of the MC makes an animal incapable of performing space-linked stepping (Barrier and Ladder tests), it seems very likely that the activity of pyramidal tract neurons, involving very pronounced rhythmical modulation, as observed in these experiments, constitutes the cortical commands addressed to the spinal stepping mechanisms. These commands suitably adjust the operation of the spinal mechanisms to external conditions. This is in agreement with Hancock's point of view (1985).

Do the brain mechanisms (those of the MC in particular) replace the spinal mechanisms involved in locomotion when an animal performs stepping movements under visual control? In our opinion, they do not replace the spinal mechanisms, which in all kinds of locomotion determine the sequence of muscle contractions for a given limb and interlimb coordination, as well as the stepping rhythm. This point of view is based on the fact that the phase of activity of most MC neurons in the step cycle does not change when locomotion falls under visual control. Besides, the decrease in the rhythmic modulation of MC neurons observed after the VL lesion indicates that this rhythmicity has an external (as regards the MC) origin. We would like to extrapolate to the MC the hypothesis (Arshavsky et al., 1986) that all the commands addressed from the brain to the spinal mechanisms during locomotion must take the current state of the spinal mechanisms, i.e. the phase of the locomotor cycle, into account. Only on this condition can the highest brain centres correct stepping movements without disturbing the basic locomotor pattern.

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