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Hindlimb muscle activity during unrestrained walking in cats with lesions of the lateral funiculi

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Abstract. In freely moving intact cats and cats with bilateral lesions of the lateral funiculi the foot contact signals and the activity of selected muscles operating at the ankle and knee joints were analysed during walking at moderate speed (0.4-1.0 m/s). No essential changes in the activity of the muscles gastrocnemius lateralis (GL), semitendinosus (ST) and vastus lateralis (VL) were found in operated animals. The tibialis anterior (TA) muscle activity had a shorter duration than the swing phase in operated animals and showed an impaired coactivation with gastrocnemius lateralis (GL) muscle at the end of the swing phase. Pilot experiments indicated that these deficits may be partly compensated for by peroneal nerve electrostimulation. Analysis of regression lines relating the swing duration to the step duration, determined from EMG records, confirmed our previous results, based on foot contact signals (Górska et al. 1993), showing that in cats with lateral funicular lesions the swing duration varies much more with the step duration than in intact animals.

Key words: locomotion, spinal cord, lateral funicular lesions, muscle control, step cycle structure, cat

INTRODUCTION

In our previous experiment (Górska et al. 1993) it was found that bilateral lesions of the lateral funiculi affected the hindlimb locomotor movements performed during unrestrained walking at moderate speed (0.4-1.0 m/s). The hindlimb step duration was longer than in intact cats by approximately 30-45% and the step cycle structure was changed: the values of the slopes of regression lines of the swing phase duration on the step cycle duration were markedly higher, while those of the stance phase were lower than in intact animals. Control lesion of dorsal columns did not produce any changes in the hindlimb movement parameters.

The main aim of the present study was to examine the influence of lateral funicular lesions on the activity of muscles operating at the ankle and knee joints and to find out whether the stronger relationship between the swing phase duration and the step duration observed in operated cats reflects some changes in the muscle control. In addition, in one cat we have performed a pilot study to see whether the electrostimulation of the peroneal nerve will give some improvement in gait of operated animals, similarly as it was found in some hemiplegic patients (Liberson et al. 1961, Vodovnik et al. 1985). Preliminary results have been published in an abstract form (Zmysłowski et al. 1992).

METHODS

Subjects and experimental procedure

The experiments were performed on two intact cats and three cats with bilateral lesions of the lateral funiculi performed at low thoracic level (T10-T12). The operated cats were the same as those described in the previous paper [for the extent of lesion see Fig. 1 in Górska et al. (1993)].

The experiments on the operated animals were performed 9-11 months after the surgery. The foot contact signals were recorded as described previously (Górska et al. 1992a,1993) i.e. the animals, with contact electrodes placed on the third toe pad of each foot, walked freely for a food reward, along a stationary walkway that was covered with soft copper wire netting connected to a 60 mV dc source.

The EMG was recorded from tibialis anterior (TA), gastrocnemius lateralis (GL), semitendinosus (ST) and vastus lateralis (VL) muscles with multi-stranded iridium-platinum wire electrodes (100 μm in diameter in teflon isolation). In each experimental session the electrodes were inserted into a mid-region of muscles (interelectrode distance was about 5 mm) with the use of hypodermic needles. The position of electrodes was checked by muscle electrostimulation. The EMG signals were amplified and filtered (30-500 Hz). All signals were monitored on an ink recorder (Mingograph) with paper speed of 50 mm/s, stored on a tape recorder (Racal), a/d converted with sampling rate 1000 samples/s and fed to the IBM PC AT computer. In each experimental session the activity of one or two pairs of antagonistic muscles in both hindlimbs were recorded. Each animal performed for 2-4 experimental sessions with EMG data for 100-150 steps collected in each session. As in our previous papers (Górska et al. 1992a,b,1993) the analysis was restricted to walk performed at moderate speed (0.4-1.0 m/s). The overall characteristic of gait in operated animals was similar to that described previously (Górska et al. 1993).

Data analysis

The following variables of locomotion were analysed: i. the swing, stance and step durations of each hindlimb, calculated from foot contact signals; ii. the duration of muscle activity in each investigated muscle determined from EMG records; iii. the time intervals between the onsets (offsets) of muscle activity in successive steps; iv. the time intervals between the onsets of muscle activity in each pair of antagonistic muscles.

The time measurement errors for the onsets and offsets of EMG and foot contact signals were 10 ms.

The relationships between the step phases and the muscle activity durations and the intralimb muscle coordination were evaluated with the first order regression (least square method) and correlation analysis. For each pair of variables the slope of the regression line (a), the correlation coefficient (r) and the coefficients of determination (r^2) were calculated. The latter coefficient determines the portion of the total variation of the dependent variable which is explained by the linear regression model. In all the cases about 100 points were used to fit each regression line.

The statistical significance of the values of a, r and r^2 and of the differences between these values in intact and operated animals were determined with the analysis of variance. The slopes of all linear regression lines and of the coefficients r and r^2 presented in this paper were statistically significant ($P<0.001$). Because none of the animals showed statistically significant differences between the left and right limbs, all the data presented in this paper were from the left hindlimb.

Electrostimulation

Since in all operated cats the main motor deficit appeared in TA activity, one animal (No 121) at the end of testing was subjected to electrostimulation of the left peroneal nerve to verify whether this treatment leads to improvement of TA activity. The electrostimulation was carried out while the animal was resting quietly in a hammock with hindlimbs pendant. Rectangular, unipolar pulses of 0.7 ms duration and with the frequency of 50 imp/s in a 1 s long series followed by pauses of 1 s duration were applied through AgClAg surface electrodes. The cathode was positioned over the point where the peroneal nerve branches into the deep and superficial nerves. The anode was about 2 cm away from this point. The stimulating current was adjusted to obtain ankle dorsiflexion (about 15 deg). The animal tolerated the stimulation very well with no signs of discomfort. The stimulation was continued for 4 weeks (5 times a week) with 20-30 min daily sessions. Thereafter, the hindlimb locomotor movements were re-examined in two sessions (about 100 steps in each) with the usual procedure of EMG and foot contact recordings.

RESULTS

Step cycle structure

The step cycle structure, determined from foot contact signals, was affected in operated cats in the same way as previously described (Górska et al. 1993). The slopes of regression lines (a) relating the swing duration to the step duration were much steeper ($P<0.001$) in operated than in intact cats (Table I) and relatively similar to the slopes of regression lines for the stance phase (1-a). This means that in operated cats the swing and stance phase varied with the step cycle nearly in the same way. The coefficients of correlation between the swing phase and the step cycle duration were also significantly ($P<0.001$) greater in operated cats, as were the coefficients of determination (r^2) (Table I).

TABLE I

Ranges of the slopes of regression lines (a), of the coefficients of correlation (r) and of the coefficients of determination (r^2) relating the swing duration to the step cycle duration in intact and operated cats. Data from foot contact signals. Asterisks denote statistically significant differences between intact and operated cats. All significant differences were at the $P<0.001$ level

Cats	a	r	r^2
Intact	0.15-0.18	0.55-0.60	0.30-0.36
Operated	0.39-0.48*	0.77-0.83*	0.59-0.69*

Activity of the flexor and extensor muscles acting at the ankle and knee joints

The activity of the ankle flexor muscle (TA) was affected in operated animals, whereas the activities of GL, ST and VL did not show any obvious changes between intact and operated animals.

M. TIBIALIS ANTERIOR

In intact cats the swing phase, measured from foot contact signals, began almost simultaneously with the TA activity, from 10 ms before up to 10 ms after the onset of TA activity. In operated cats the TA activity could start slightly later, from 10 ms before up to 40 ms after the beginning of the swing phase.

The TA activity in intact animals consisted of two bursts separated either by an interval of lower activity or by a short-lasting (20-40 ms) pause (Fig. 1). The second burst, which appeared at the end of the swing phase, lasted from 10 to 60 ms and its maximal amplitude was smaller than the amplitude of the first burst. The second burst of TA activity appeared in 90% of steps in intact animals and, when present, always coincided with the beginning of GL activity, leading to coactivation of these antagonistic muscles. This coactivation preceded the onset of the stance phase which usually (in 90% of steps) took place just before or just after the end of TA activity. In operated cats the second burst of TA activity and the coactivation of TA and GL occurred much more seldom than in intact animals (in about 30% of steps vs. 90% in intact animals). Moreover, the second burst had often a residual form and consisted of single spike-like activity (Fig. 1).

In operated cats the mean duration of TA activity was shorter than the mean swing duration by about 40 ms, while in intact cats these two values were nearly equal. The mean duration of TA activity and the mean duration of the swing phase in operated cats were 308±78 ms and 353±59 ms (*t*-test, $P<0.001$), respectively. In intact cats the corresponding values were 298±47 ms and 300±32 ms.

The duration of TA activity in operated cats varied less with the swing phase duration than in intact animals. The values of the slope of regression lines relating the swing phase duration, determined from foot contact signals (TS), to the TA activity duration (TT) were significantly ($P<0.001$) lower in operated cats (range 0.51-0.77) than in intact ones (range 0.96-0.99) (Table II, Fig. 2). These relationships were also weaker as shown by significantly ($P<0.001$) lower values of the coefficients r and r^2 in operated animals (Table II).

M. GASTROCNEMIUS LATERALIS

The overall activity of the GL muscle was similar in intact and operated cats. In intact animals the stance phase began 10-80 ms after the onset of GL activity and terminated 20-120 ms after its offset. The maximal amplitude was reached during the first 15% of the muscle activity. In some cases a second, short burst in GL activity appeared after the termination of the main burst. In operated animals the time shifts between the GL activity and the stance

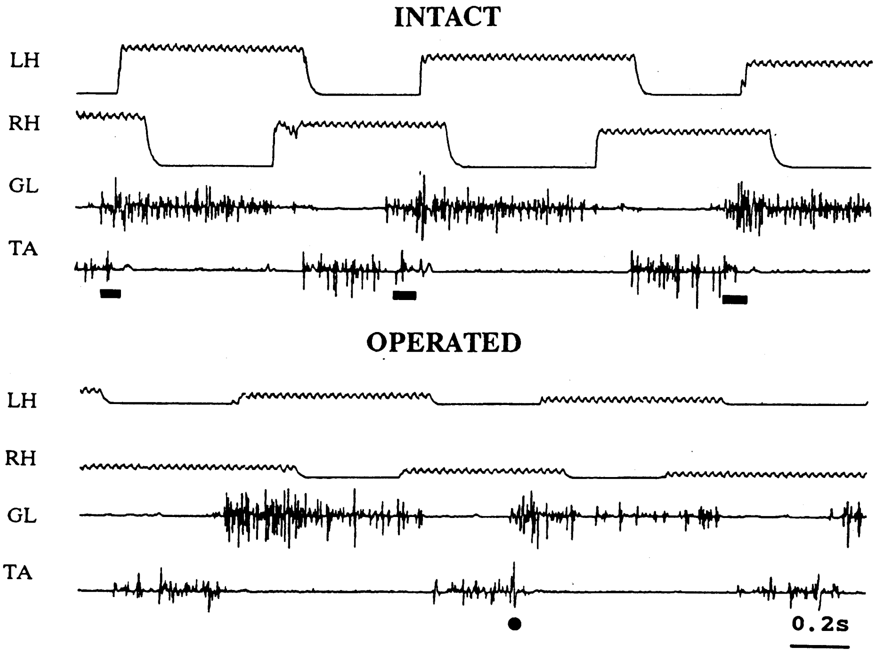

Fig. 1. Foot contact signals of the left (LH) and right (RH) hindlimbs and raw EMG of the left mm. gastrocnemius lateralis (GL) and tibialis anterior (TA) in an intact and an operated cat. Upper deflections in the LH and RH records denote the stance phases. Note the presence of coactivation in the TA and GL muscles in all steps in the intact animal (the second bursts in TA activity is marked by bars), the lack of this coactivation in the 1st and 3rd step in the operated animal and a residual coactivation in the 2nd step (the residual second burst in TA activity is marked by a dot).

TABLE II

Ranges of the slopes of regression lines (a), of the correlation coefficients (r) and of the coefficients of determination (r^2) relating the step phases durations to the duration of the corresponding muscle activity in intact (N) and operated (O) animals. TS, swing duration; TSU, stance duration. TT, duration of m. tibialis anterior activity; TG, duration of m. gastrocnemius lateralis activity; TST, duration of m. semitendinosus activity; TV, duration of m. vastus lateralis activity. Denotation of statistically significant differences as in Table I

Regression		a	r	r^2
TS on TT	N	0.96-0.99	0.91	0.85
	O	0.51-0.77*	0.72-0.78*	0.52-0.61*
TSU on TG	N	0.94-1.03	0.96-0.97	0.92-0.94
	O	0.95-0.98	0.93-0.95	0.86-0.90
TS on TST	N	0.89-1.04	0.87-0.89	0.77-0.79
	O	0.97-1.02	0.79-0.89	0.62-0.79
TSU on TV	N	0.97-1.00	0.93-0.97	0.86-0.94
	O	0.82-0.99	0.94-0.95	0.88-0.90

phase onsets and offsets were similar to those in intact cats. In the EMG records of some steps in operated animals, irregular pauses appeared, which might suggest that the muscle was activated in different way than in intact cats (Fig. 1).

Both in intact and in operated animals the relationships between the stance duration (TSU), measured from foot contact signals, and the duration of GL activity (TG) were similar (Table II, Fig. 2). The values of the slopes of the regression lines in both groups of cats were nearly 1.0 and the correlation coefficients above 0.93.

M. SEMITENDINOSUS

The activity of this muscle in intact animals could consist of two bursts, one associated with the onset of the swing phase and the second with the swing termination. When present, the amplitude of the second burst was much smaller than that of the first burst. The second burst in ST activity predominated in steps of short duration, performed at speeds approaching 1 m/s. In operated animals the second burst in ST was usually absent (Forssberg at al. 1980). The swing phase started during the first 60 ms of ST activity both in intact and operated cats and terminated between 100 and 250 ms after the first burst offset in intact animals, and between 100 and 300 ms in operated cats. The relationships between the swing duration (TS) and the duration of ST activity (the first burst only) (TST) were similar in intact and operated animals (Fig. 4 and Table II). The slopes of the regression lines were close to 1.0 and the coefficients of correlations ranged between 0.80 and 0.90.

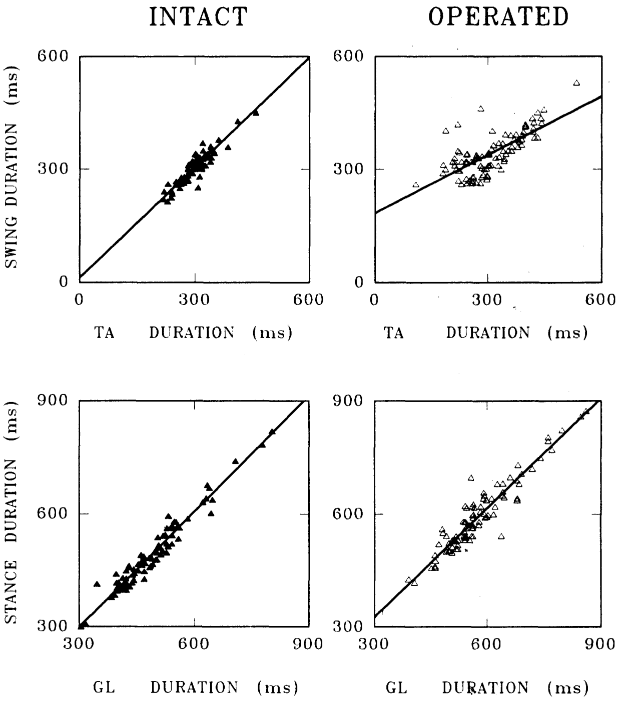

Fig. 2. Relationships between the swing duration and the duration of m. tibialis anterior (TA) activity and between the stance duration and the duration of m. gastrocnemius lateralis (GL) activity in an intact and an operated cat. Note that in the vast majority of steps in the operated cat the TA activity was shorter than the swing phase.

M. VASTUS LATERALIS

In intact cats the stance phase usually began at the onset of VL activity but in some steps, with longer duration, it could begin up to 100 ms after the onset of VL activity. The stance phase terminated

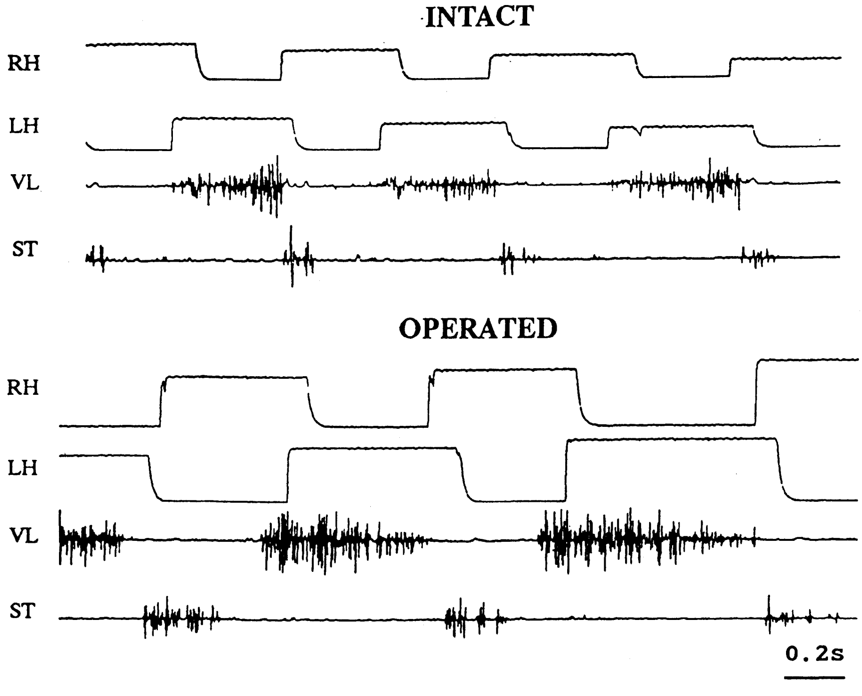

Fig. 3. Foot contact signals of the right (RH) and left (LH) hindlimb and raw EMG of the left mm. vastus lateralis (VL) and semitendinosus (ST) in an intact and an operated cat. Upper deflections in the RH and LH records denote the stance phases.

between 0 and 100 ms after the offset of VL activity. In operated cats the timing of the VL activity was the same as in intact cats. Both in intact and operated animals, two forms of activity in VL were observed: one, with a burst of high amplitude at the beginning of muscle activity and a second, with such a burst near the end of muscle activity (Fig. 3). Similar data have been obtained by other authors (Forssberg et al. 1980, Bradley and Smith 1988a, 1988b). The first type of muscle activation occurred more often in steps of shorter duration. The relationships between the stance duration (TSU), measured from foot contact signals, and the duration of VL activity (TV) were essentially similar in intact and operated animals (Fig. 4 and Table II). In both groups of cats the values of the slopes of the regression lines were close to 1.0 and the correlations above 0.90.

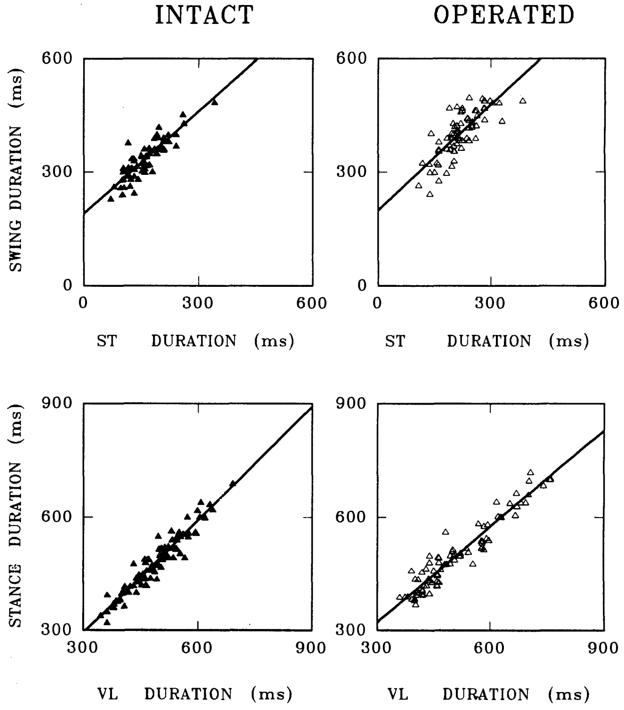

Fig. 4. Relationships between the swing phase duration and the duration of m. semitendinosus (ST) activity, and between the stance phase duration and the duration of m. vastus lateralis (VL) activity in an intact and an operated cat.

Coordination of muscle activity within the step cycle

Since the results presented above could not explain changes in the step cycle structure observed in operated animals (cf. Table I) we have also analysed

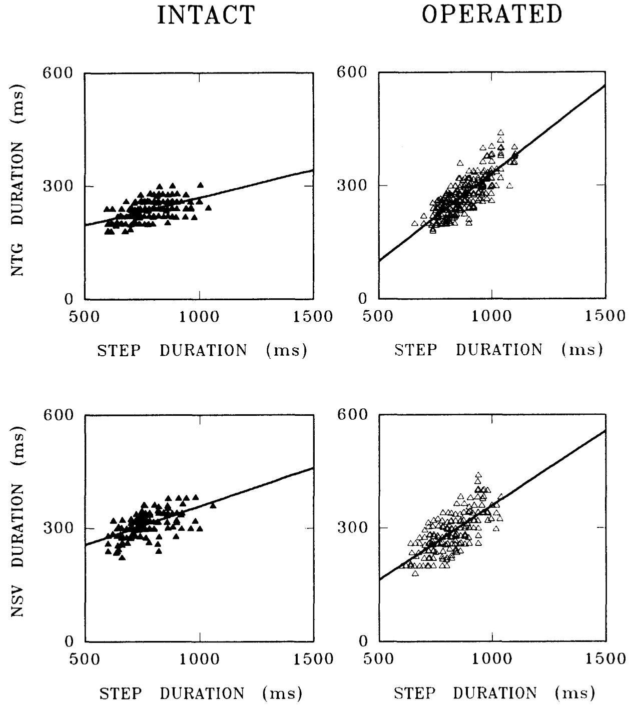

Fig. 5. Time intervals between the onsets of activity of mm. tibialis anterior and gastrocnemius lateralis (NTG), and between the onsets of activity of mm. semitendinosus and vastus lateralis (NSV) as a function of the step duration (measured from the onsets of successive TA and ST activities, respectively) in an intact and an operated cat.

the relationships of the step cycle and its phases with the activity of various muscles and the coordination of the activity of antagonistic muscles.

TA AND GL MUSCLES

No differences between intact and operated animals were found with respect to the relationships between the following variables associated with the onsets of the swing phase: intervals between successive onsets of swing phases (determined by foot contact signals), intervals between successive onsets of TA activities and intervals between successive offsets of GL activities. The same applied to variables associated with the beginning of the stance phase, i.e., intervals between successive onsets of stance phases, intervals between successive onsets of GL activities and intervals between successive offsets of TA activities. The slopes of the regression lines for all these relationships ranged in intact and operated animals between 0.90 and 1.07, while the correlation coefficients ranged between 0.90 and 0.98. These results show that the timing of step phase onsets and offsets was synchronized with the timing of the corresponding muscle activity onsets and offsets in a similar way both in intact and operated cats.

TABLE III

Ranges of the slopes of regression lines (a), of the correlation coefficients (r) and of the coefficients of determination (r^2) relating the time intervals between the onsets of activities of a pair of antagonistic muscles to the step duration in intact (N) and operated (O) animals. NTG, time interval between the onsets of mm. tibialis anterior and gastrocnemius lateralis activity; NSV, time interval between the onsets of mm. semitendinosus and vastus lateralis activity. TC, step duration measured from successive onsets of EMG of TA or ST, respectively. Denotation of statistically significant differences as in Table I

Regression		a	r	r^2
NTG on TC	N	0.14-0.17	0.53-0.58	0.29-0.34
	O	0.32-0.46*	0.57-0.80*	0.32-0.64*
NSV on TC	N	0.16-0.20	0.39-0.58	0.15-0.34
	O	0.38-0.52*	0.69-0.74*	0.48-0.55*

Different results were obtained for the regressions relating time intervals between the onsets of TA and GL activities (i.e., the events associated with the swing phase onset and offset) to time intervals between onsets of successive TA activities (i.e., the step cycle durations measured from the EMG of TA). The slopes of the regression lines relating these variables (NTG on TC) were significantly ($P<0.001$) steeper in operated than in intact animals, and the coefficients r and r^2 were significantly ($P<0.001$) greater (Fig. 5 and Table III). The differences between these parameters in intact and operated animals were similar to those obtained in both groups of animals for the relationships between the swing phase and the step cycle durations estimated from foot contact signals (cf. Table I).

ST AND VL MUSCLES

The analysis of relationships similar to those described above, performed for ST and VL muscles, gave nearly the same results. In both intact and operated cats the slopes of regression lines relating intervals between onsets of successive swing and of successive stance phases and the onsets and offsets of ST and VL activities ranged between 0.88 and 1.06, while the correlation coefficients ranged between 0.87 and 0.99. On the other hand, as in the case of TA and GL muscles, the slopes of the regression lines relating time intervals between the onsets of ST and VL activities (i.e., the intervals determining the swing phase duration) to intervals between successive onsets of ST activities (i.e., the step durations measured from EMG of ST) were significantly ($P<0.001$) steeper in operated than in intact cats and the corresponding correlation coefficients were significantly ($P<0.001$) greater (Fig. 5 and Table III-NSV on TC).

Taken together these results show that the stronger relationship between the swing phase and step cycle durations observed in operated animals can not be explained as due to the disturbances in muscle control because the coordination of step phases with muscles was not affected in operated animals. What was affected were the parameters determining the step cycle structure i.e., the timing of the onsets of activity of the antagonistic muscles with respect to the step cycle duration.

Effects of electrostimulation

In the operated cat in which the peroneal nerve was stimulated (see Material and Methods section) re-examination of locomotion showed some improvement in the hindlimb movements. The number of steps in which coactivation of TA and GL was observed (and the second burst in the TA activity) increased from about 30% to about 60% of steps and the pattern of TA activity approached that observed in intact cats. In line with this finding was a change in the slope of regression line relating the swing phase and the TA activity durations (0.88 vs. 0.51 obtained before electrostimulation) and in the the corresponding correlation coefficient (0.89 vs. 0.72 before electrostimulation). Moreover, the slope of the regression line relating the swing phase duration to the step cycle duration determined from foot contact signals, tended to decrease (from 0.46 before to 0.35 after electrostimulation), which suggested that the positive effect of peroneal nerve stimulation was not restricted to the TA activity.

DISCUSSION

The results of the present study fully confirm our previous data, based on foot contact analysis (Majczyński et al. 1990, Górska et al. 1993), showing that in intact cats walking overground at moderate speeds (0.4-1.0 m/s) bilateral lesions of the lateral funiculi produce changes of the step cycle structure. At the same time they show that the stronger relationship between the swing phase duration and the step duration observed in operated cats can not be attributed to an abnormal pattern of muscle activity, at least of the muscles investigated in the present experiment. The temporal relationships between the onsets or offsets of activity of TA, GL, ST and VL and the transitions between the step phases were similar in intact and operated cats as were the relationships between the durations of the step phases and the durations of activity of the corresponding muscles (except for TA muscle).

The major difference between intact and operated animals consisted in a stronger relationship between the time intervals determined by the onsets of activity of antagonistic muscles at a given joint (TA and GL, ST and VL), that corresponded to the swing phase duration, and the step cycle duration, determined by successive onsets of TA or ST activity, respectively. The values of the slopes of the regression lines, the correlation coefficients and the coefficients of determination for these relationships were much greater in operated than in intact cats and were similar to those obtained from foot contact signals both in the present (cf. Table I and III) and the previous experiment (Górska et al. 1993). This suggests that the changes in operated animals were not due to the deficits in muscle coordination but, presumably, to some alterations in the mode of operation of spinal neuronal networks controlling the step cycle structure. It is also worth stressing that the deficits observed in operated animals had a very stable character, since they did not diminish during a 6-7 month interval that elapsed between the previous and the present experiments. During this period the animals could freely practice locomotion in a large housing room.

The most important feature of the step cycle structure after lateral funicular lesions consisted of nearly equal slopes of the regression lines relating the swing and stance phase durations to the step cycle duration. Much steeper slope of the regression line of the stance phase than of the swing phase on the locomotor speed and/or cycle duration is a fundamental feature of the step cycle structure in intact animals. This plays a crucial role in the adjustment of gait to locomotor speed, because shortening of the step cycle occurs mainly at the cost of the stance phase (for reviews see Grillner 1975, 1981, Wetzel and Stuart 1976). Therefore, in the case of similar slopes of the regression lines for the swing and stance phases, as was observed after lateral funicular lesions, the adjustment of animals to locomotor speed will be altered, since the duration of body support on two hindlimbs would be constant, irrespectively of the animal speed. This might have been one of the reasons why the operated cats were never seen to trot because in this kind of gait the double hindlimb support is absent.

Although the mechanisms of changes in the step cycle structure after lateral funicular lesions remain to be established, these effects seem to be connected with the destruction of some pathways running in the lateral funiculi, especially in its dorsal parts. No changes in the slopes of the regression lines relating the hindlimb swing, stance and step durations to the locomotor speed were found in our previous pilot study (Górska et al. 1992b) with extensive lesions of the spinal cord as long as the major portions of dorsolateral funiculi, at least on one side, were left intact. Subtotal spinal lesions, sparing only small parts of dorsolateral funiculi led to a significant decrease of the slopes of the regression lines of the stance and step durations on locomotor speed, compared to intact animals. These results suggest that pathways running in the dorsal parts of the dorsolateral funiculi, (e.g., the dorsal spinocerebellar tract, the dorsal reticulospinal tract, the cortico- and rubrospinal tracts, the descending monoaminergic pathways etc.), may play an important role in a proper adjustment of the hindlimb step cycle parameters to changes in locomotor speed and, thus, in the maintenance of the proper step cycle structure. However, the role of other pathways can not be excluded, since lesions destroying major portion of the dorsolateral funiculi combined with the preservation of one ventral quadrant did not lead to disturbances in the adjustment of the step cycle phases to the locomotor speed (Górska et al. 1992b).

Our results concerning the EMG analysis in intact cats are, in general, similar to those reported by other authors (Rasmussen et al. 1978, Forssberg et al. 1980, Grillner 1981, Halbertsma 1983, Bradley and Smith 1988a, Naito et al. 1990). In operated animals only TA activity showed some impairment. Its activity was shorter than the swing phase and the TA and GL muscle coactivation was affected. The second burst at the end of TA activity, which coactivated with the onset of GL activity, was present in intact animals in 90% of steps, whereas in operated animals it was observed only in 30% of steps, and if present, it had often a residual form. Shortening of TA activity had no influence on the swing duration, because this phase depended mainly on the ST activity. However, the lack of coactivation of TA and GL muscles was probably responsible for a tendency for foot dropping at the end of the swing phase occurring in operated animals, as the muscular torques produced by TA and GL muscles were not balanced. The coactivation of TA and GL muscles in normal kittens and its lack in spinal kittens was reported by Bradley and Smith (1988a,b). Rasmussen et al. (1978) found TA and GL coactivation in adult intact cats. Lovely et al. (1990) described the overlap of activity between TA and the soleus muscle in treadmill-exercised adult spinal cats.

The deficits in TA activity observed in operated cats could be partly compensated for by peroneal nerve electrostimulation. Our pilot study showed that after a series of sessions with electrostimulation, the duration of TA activity increased and its coactivation with the GL muscle improved as shown by a greater percent of steps with the second burst. The method of peroneal nerve electrostimulation was introduced into clinic by Liberson et al. (1961) mainly in order to improve the gait of hemiplegic patients by strengthening the dorsiflexion of the foot and thus diminishing the foot drop. It appeared, however, that stimulation of this nerve gave more generalized effects on the human gait, not limited to the activity of TA muscle. Similar tendency was observed in our stimulated cat in which the slope of the regression line of the swing duration on the step duration somewhat decreased after stimulation. Since the method of stimulation of the peroneal nerve gives positive results only in about 50% of patients with foot drop (Vodovnik et al. 1985) the use of this method in an animal model might help the understanding the mechanisms underlying its restorative effects and the constraints on its effectiveness after various CNS lesions.

Changes in the step cycle structure found in the present study after partial spinal lesions are at variance with the lack of major alterations in the treadmill hindlimb stepping parameters described in animals with complete spinal transection (Barbeau and Rossignol 1987, Naito et al. 1990). Results somewhat similar to ours were, however, obtained by Lovely et al. (1990). It has been found that spinal cats, subjected to intensive hindlimb treadmill training, walked at a lower range of speed and exhibited an increase in the swing and hip flexion durations as well as a shortened time of support on both hindlimbs. An increase in the swing phase and step cycle duration by noradrenergic and serotonergic drugs was also reported by Barbeau and Rossignol (1991).

The stronger impairment of the step cycle structure obtained by us after partial spinal lesion than that described for treadmill stepping in spinal animals may be related to some factors inherent to treadmill testing, such as the enforced stepping or an increased sensory inflow from the hindlimbs, which may compensate the lack of supraspinal input. The improvement of the hindlimb movement parameters in the cat with peroneal nerve stimulation support the latter hypothesis. On the other hand, it is also conceivable that partial lesions of the spinal cord, as opposed to complete spinalization, may create different forms of interactions between parts of spinal circuitry controlling the swing and stance phases, due to canceling some supraspinal and propriospinal influences and some ascending feedback systems. Our experiments also suggest that the GL, ST and VL muscles are less dependent on supraspinal input than the TA muscle. This would be in agreement with data showing that the corticospinal and rubrospinal tracts control to a larger extent the distal and flexor muscles than the proximal and extensor muscles (Kuypers 1964).

Further experiments are required to establish which mechanisms and structures play a substantial role in the process of programming the step cycle structure.

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