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Different forms of impairment of the fore-hindlimb coordination after partial spinal lesions in cats

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Abstract. Effects of large low thoracic (T10-T11) partial spinal lesions involving either the ventral quadrants of the spinal cord and, to a different extent the dorsolateral funiculi, or different extent of the lateral funiculi and/or the dorsal columns, on the fore-hindlimb coordination were examined in cats walking overground at moderate speeds. In both groups of operated cats, except those in which the lesion was essentially confined to dorsal columns, three different forms of impairment of fore-hindlimb coordination were observed, depending on the extent of lesion: (1) a change of locomotion towards pacing with preservation of the equality of rhythms in the fore- and the hindlimbs; (2) episodes of fore- and hindlimb rhythm dissociation and (3) a permanent dissociation of the fore- and hindlimb rhythms. A comparison of the results obtained in these two groups of operated cats points to the more important role played by the lateral funiculi, than by other parts of the spinal white matter, in controlling the fore-hindlimb coordination in cats.

Key words: locomotion, spinal lesion, fore-hindlimb coordination, cat

INTRODUCTION

Investigations of the effects of different spinal cord lesions on locomotion in cats have been focused thus far mainly on the study of hindlimb movements on a treadmill. Under such experimental conditions a complete transection of the spinal cord at a low thoracic level did not affect either the basic parameters of stepping or the basic patterns of hindlimb coordination (see Grillner 1981, for review). Coordinated locomotor activity of the forelimbs has been also demonstrated in a high spinal preparation (Miller and van der Meche 1976, Viala and Vidal 1978). In contrast, little information is available about the effects of spinal lesions on the fore-hindlimb coordination during locomotion. Two types of impairment of coordination between fore- and hindlimbs after partial spinal lesions have been described in the literature: a tendency for pacing with preservation of the equality of fore- and hindlimb rhythms, and a disruption of fore- and hindlimb rhythms. The first kind of impairment was originally described by English (1980), who found, using phase diagram analysis, a more frequent coupling of homolateral limbs in freely moving cats with bilateral lesions of the dorsal columns at the caudal thoracic level. A similar form of impairment, i.e. a tendency to pacing-like locomotion was found, by means of support pattern analysis, in our preliminary study on unrestrained locomotion in cats with large, low thoracic spinal lesions, sparing the dorsal columns and at least one dorsolateral or ventrolateral quadrant (Górska et al. 1993b). The operated animals manifested a predominance of support on homolateral limbs, accompanied by a reduction or absence of support on diagonal limbs. More extensive subtotal spinal lesions described in the literature caused a difference of the fore- and hindlimb rhythms in animals tested both on the treadmill (Eidelberg et al. 1981) and walking overground (Afelt 1974). Similar results were obtained by Kato et al. (1984) after serial bilateral hemisections of the spinal cord performed at two different levels.

In view of the paucity of data about the impairment of fore-hindlimb coordination after various partial spinal lesions, the aim of our experiments was to perform a detailed analysis of all forms of the impairment of fore-hindlimb coordination which could occur during unrestrained locomotion at moderate speeds in cats with different, usually large, partial lesions of the spinal cord at the low thoracic level. It will be shown that lesions, depending on their extent, elicited three distinct forms of impairment of the fore-hindlimb coordination: a change of locomotion towards pacing with the same locomotor rhythm of both girdles preserved, an intermediary form of impairment consisting of episodes of fore- and hindlimb rhythm dissociation, and a permanent dissociation of these rhythms. These three forms of impairment of the fore-hindlimb coordination have been recently described by us after lesions of the ventral and lateral parts of the spinal cord (Bem et al. 1995) and, in the present paper, we shall compare the effects of these lesions with lesions of the dorsolateral parts of the spinal cord[1]. It will be shown that both types of lesions, depending on their extent, elicited similar forms of impairment of the fore-hindlimb coordination.

METHODS

The experiments were performed on freely moving cats walking at moderate speed (0.4 to 1.0 m/s) along a 6-m-long and 1-m-wide walkway covered with soft copper-wire netting. One end of the netting was grounded while the other was connected to a 60-mV d.c. source. The distribution of the voltage along the walkway was linear. Contact electrodes fitted on the third toe pad of each paw allowed us to record the stance phases and to calculate the locomotor speed. From the recorded data only sequences consisting of at least 5 successive steps performed with an approximately constant velocity and without any obvious equilibrium deficits were taken for analysis. In each operated animal at least 150 steps (25-30 sequences) were analysed. For further details of experimental procedure, data collec-

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[1] A more detailed description of the effects of dorsolateral lesions on locomotion in cats in preparation.

tion, surgical procedure and methods of histological verification of lesions, see Górska et al. (1993a,b,c, Bem et al. 1995).

The impairment of the fore-hindlimb coordination was investigated in two groups of operated cats: one which we shall call for simplicity ventrolateral (VL) and another dorsolateral (DL). The lesions performed in each cat of both groups are shown schematically in Fig. 1B. Both groups of operated animals were tested 5-6 months postoperatively, except for cats in which the lesion was essentially confined to dorsal columns (Nos 125 and 126), which were tested 2 weeks after surgery.

RESULTS AND DISCUSSION

Figure 1A shows the percentages of sequences with different types of fore-hindlimb coordination performed by each operated cat i.e. with equal rhythm of the fore- and hindlimbs, with episodes of fore- and hindlimb dissociation and with permanent dissociation of fore- and hindlimb rhythms (see Bem et al. 1995, for the method of computer selection of each of these three kinds of sequences). Within each group of the operated animals there was, in general, a correlation between the extent of the lesion and the pattern of fore-hindlimb coordination: smaller lesions elicited no differences in the locomotor rhythms of both girdles, more extensive lesions - episodes of fore- and hindlimb dissociation, while the most extensive lesions - a permanent dissociation of the fore- and hindlimb rhythms.

Equal rhythms of fore- and hindlimbs

Figure 2 shows the timing of the onsets of stance phases in a sequence of steps with equal rhythms of the fore- and hindlimbs in a cat walking with similar speeds before (A) and after (B) surgery. As shown in this Figure, both before and after surgery the changes in the step cycle durations, if present, occurred approximately at the same time in both girdles and the order of limb movements was "transverse" (Howell 1944, Gray 1968) i.e. the movements of the hindlimbs (either putting them down or lifting off, not illustrated) were preceded by a movement of the diagonal forelimb and followed by a movement of homolateral forelimb.

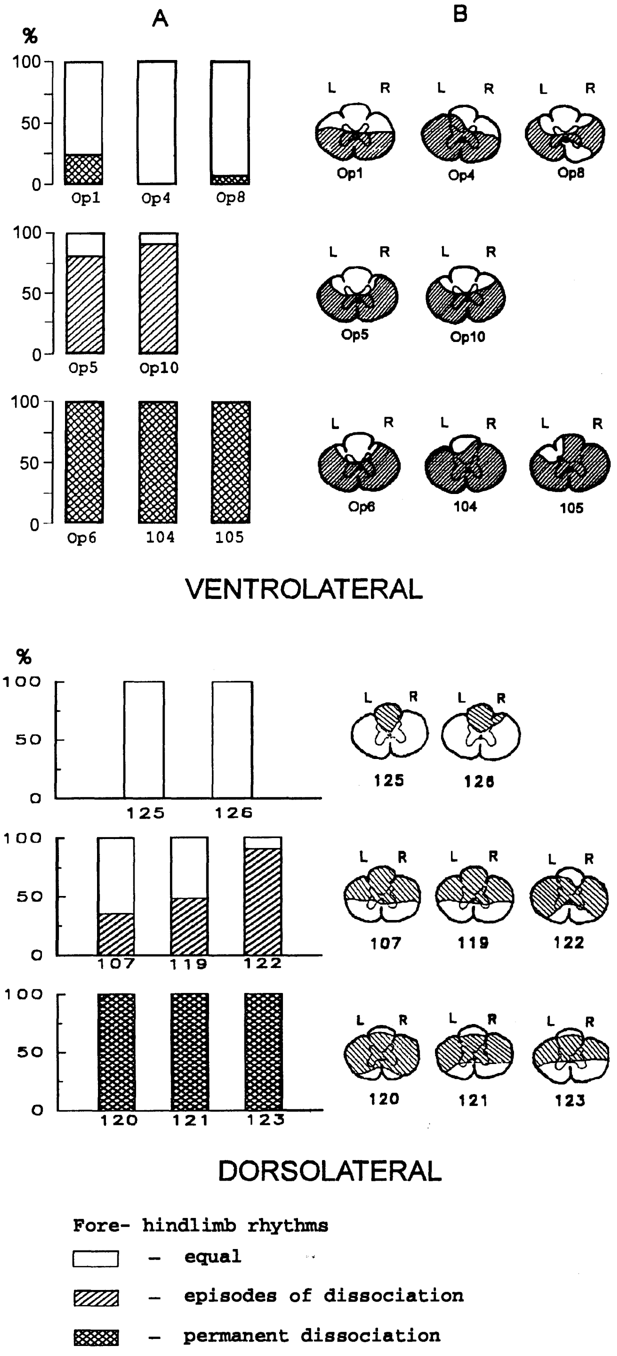

Fig. 1. A, percentage of sequences showing different patterns of fore- and hindlimb rhythms in individual cats from the ventrolateral and dorsolateral group (for explanation of symbols see bottom of the Figure). B, schematic representation of the extent of lesion (hatched) in each operated cat. Numbers in A and B denote individual animals.

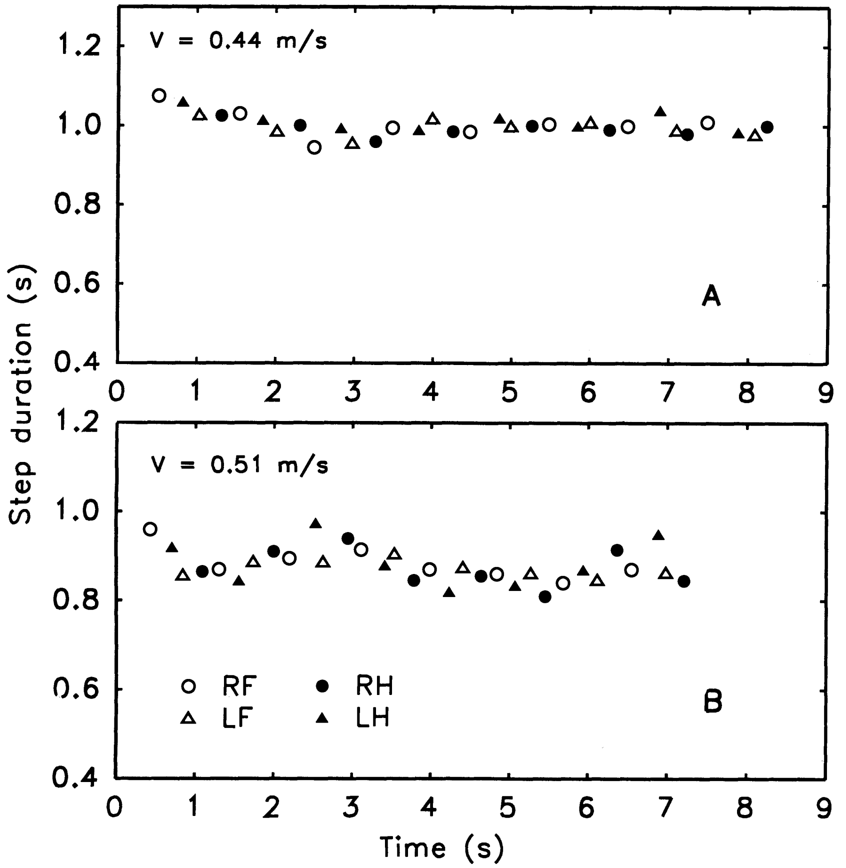

Fig. 2. Timing of the onsets of stance phases in a cat (No 107DL) before (A) and after (B) surgery walking with an equal rhythm of the fore- and hindlimbs. Abscissae: the time from the onset of the analysed sequence. Ordinates: step cycle durations of particular limbs (see symbols in the insert in Fig. 1B). Note that in A and B the order of limb movements is transverse (Gray 1968) i.e. right forelimb (RF), left hindlimb (LH), left forelimb (LF), right hindlimb (RH) and so on (see also the left hand diagram (T) at the bottom of Fig. 5).

Although the locomotion in operated animals walking with the same rhythm of both girdles looked apparently normal, the analysis of the duration of various support phases in the four-limb step cycle showed a change in operated animals. Figure 3A and B compares the sequence and the mean relative duration of support phases occurring during one step in intact animals (N), cats with lesions essentially restricted to the dorsal columns (DC), with dorsolateral (DL) and ventrolateral (VL) lesions walking with the same rhythm of both girdles.

In intact animals, due to a different timing of the stance phases in each limb, the step can be divided into 8 different support phases with the support on three limbs (phases II, IV, VI and VIII) alternating with the support on two limbs: homolateral (phases I and V) and diagonal (phases III and VII). The order of these phases corresponds to that described already by Muybridge (1957), Howell (1944) and Gray (1968) for animals walking at moderate speed and in our intact cats steps with such sequences of support phases occurred in 90-99% of cases. The relative duration of each of the support phases was essentially similar, with the support phases on two hind- and one forelimb being about 5% shorter than other support phases (Górska et al. 1993a).

A similar analysis performed on operated animals walking with the same rhythms of both girdles showed a change in their way of walking, except for cats with lesions essentially confined to the dorsal columns (cf. Fig. 1B cats Nos 125 and 126) which, when tested two weeks after surgery, did not appear to be affected, as shown by a similar sequence and relative durations of particular support phases as in intact cats (cf. Fig. 3 cats N and DC). In contrast, cats with dorsolateral (DL) and ventrolateral (VL) lesions differed in their way of walking. The main difference consisted in an increase (by 50 to 69%) of the relative durations of the supports on homolateral limbs (phase I and V) and a disappearance or almost complete reduction of the phases of support on diagonal limbs (phases III and VII in intact ani-

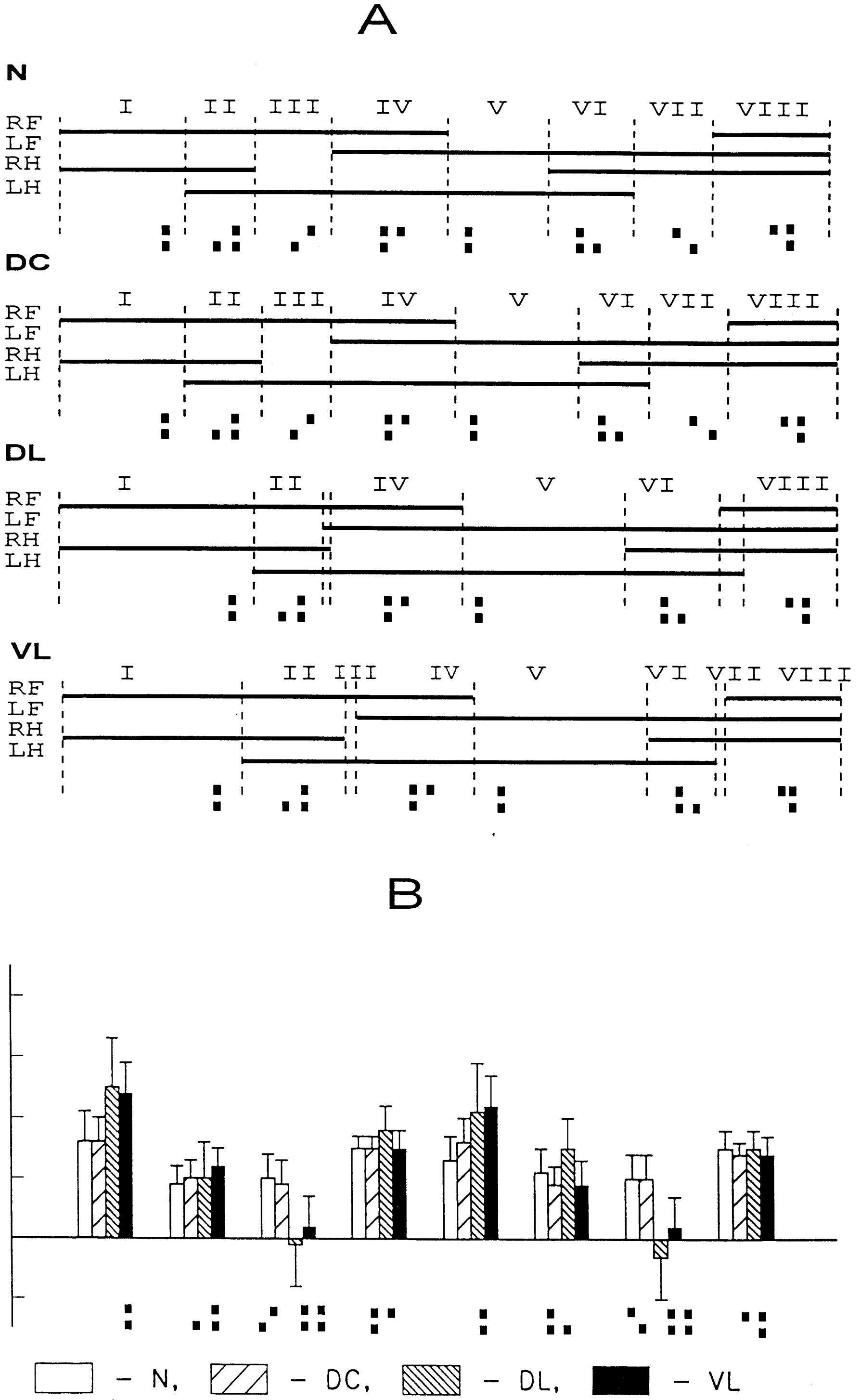

Fig. 3. A, sequence and mean relative durations of the support phases in intact animals (N), cats with lesions essentially restricted to dorsal columns (DC), cats with dorsolateral (DL) and ventrolateral (VL) lesions walking with equal rhythm of both girdles (cf. Fig. 1). Horizontal bars denote the stance phase of each limb and open spaces the swing phase. RF, LF, RH and LH indicate right forelimb, left forelimb, right hindlimb and left hindlimb, respectively. Vertical broken lines indicate the durations of the successive support phases which are denoted by Roman numerals. In each phase filled rectangles indicate the supporting limbs. B, means and SD of particular support phases in the four groups of cats represented in Fig. 3A. Note lack of diagonal supports in cats with DL lesion and their replacements by supports on four limbs due to a prior onset of the forelimb stance phase than of the diagonal hindlimb swing phase (cf. Fig. 3A) which is shown by negative mean values.

mals). This effect was more accentuated in cats with dorsolateral (DL) than with ventrolateral (VL) lesions and in the former group of operated animals phases of diagonal support were often replaced by phases of support on four limbs, due to a prior onset of the forelimb stance phase than of the diagonal hindlimb swing phase (cf. Fig. 3A cats N and DL). Other phases of support were essentially unchanged (cf. Fig. 3B). The increase in the relative durations of phases of support on homolateral limbs and the substantial reduction or absence of phases of support on diagonal limbs changed the gait of operated animals towards pacing that is a kind of gait in which the movements of homolateral limbs are synchronized.

The mechanisms of a greater synchronization of homolateral limbs in operated cats are at present unknown. The pacing type of gait is rarely encountered in intact animals except for camels and giraffes (Gray 1968). It is worth stressing, however, that in operated animals the coordination within each girdle, i.e. in both fore- and in both hindlimbs was not at all or only very little affected by the surgery as shown by the unchanged duration of the swing and stance phases and phase shifts between homologous limbs (Górska et al. 1993b, Bem et al. 1995). Thus the changes in the fore-hindlimb coordination in DL and VL groups were the result of a shift in time between the movements of both girdles, so that the time intervals between the diagonal limbs become increased (cf. the onsets of swing phases in LF and RH and in RF and LH in Fig. 3A), while those between the homolateral limbs decreased (cf. onsets of swing phases in RH and RF and in LH and LF in the same Figure) as compared to intact animals. The increased delay between the onsets of swing in diagonal limbs led to a significant reduction or disappearance of the support on diagonal limbs, so that lifting the hindlimb off the ground in operated animals took place approximately at the same time (VL cats) or even after (DL cats) the diagonal forelimb was put on the ground, i.e. when an additional support of the body was assured. Such a strategy might have been also aimed to counteract the deficits in the equilibrium control observed in both groups of operated cats. The increase of the time intervals between the movements of diagonal limbs would suggest an attenuation of crossed facilitatory influences which might coordinate the activity between both girdles in intact cats as suggested by Orsal et al. (1990). Another possibility is that instead of crossed pathways between both girdles, the ipsilateral pathways connecting the brachial and lumbar enlargements had been less effective as judged by the longer time intervals between the onsets of the swing phases in the forelimb and the onsets of stance phases in the ipsilateral hindlimb (cf. LF → LH and RF → RH in Fig. 3A). Irrespective of the mechanisms involved in the change of coupling between the fore- and hindlimbs in our operated animals, the greater synchronization of homolateral limbs hampered them to change the gait from a walk into a trot, which requires a synchronization of diagonal limbs.

Episodes of fore- and hindlimb rhythm dissociation

The next pattern of impairment of the fore-hindlimb coordination, present in both groups of operated animals, consisted of short lasting episodes of rhythm dissociation (cf. Fig. 1). Figure 4 shows the timing of the onsets of fore- and hindlimb stance phases in a pass with two such episodes. During the episode, the step cycle durations of the hindlimbs suddenly increased and after reaching a maximum gradually decreased, which was associated with opposite changes in the forelimbs.

A more detailed analysis of episodes of rhythm dissociation showed that they occurred in a very stereotyped manner (Fig. 5). The episodes always appeared at the background of small (20-40 ms) difference in the rhythms of both girdles, the hindlimb step cycle being longer than that of the forelimb. At the beginning the animal used the usual transverse (T) order of limb movements, which due to a small difference in the fore- and hindlimb step cycle durations changed into pacing. Once the animal reached this type of coordination, the differences in the rhythms of the fore- and hindlimbs suddenly in-

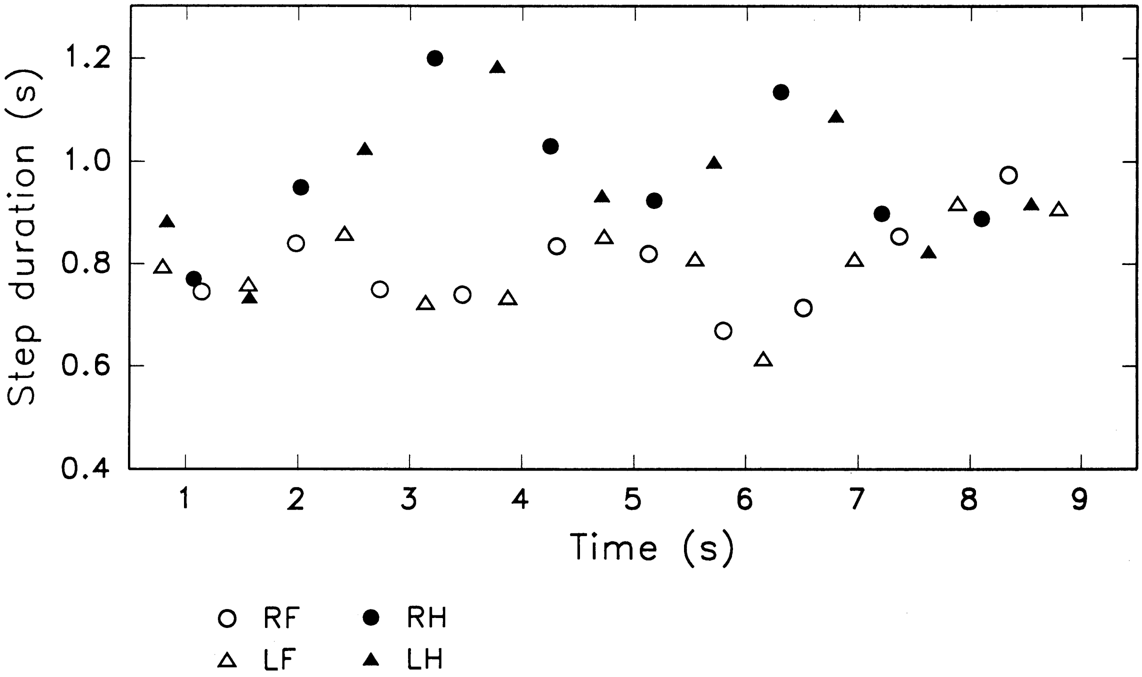

Fig. 4. Timing of the onsets of stance phases in an operated cat (No 107DL) with two episodes of rhythm dissociation during one pass. Abscissa and ordinate as in Fig. 2. For symbols of particular limbs see bottom of the Figure.

creased: the step cycle durations in the hindlimbs increased, while those of the forelimbs decreased, resulting in an increasing difference of rhythms. This increase of rhythm difference was associated with the "lateral" (L) order of limb movements (Howell 1944, Gray 1968), i.e. the movements of the hindlimbs were preceded by a movement of homolateral forelimb and followed by a movement of diagonal forelimb (see diagram marked L at the bottom of the Figure) until two successive forelimb steps were performed and the diagonal limbs became approximately synchronized (see thicker vertical line on the scheme - synchronization of the left hindlimb and right forelimb). This restored the transverse order of limb movements and since then the rhythm difference was progressively reduced to its residual value, which led again to pacing and a new episode of rhythm dissociation. It is worth stressing that the episodes of rhythm dissociation occurred in a similar way independently whether the lesion was of the ventrolateral or dorsolateral type i.e. (1) the lateral order of limb movements always corresponded to the increasing and the successive transverse order to the decreasing of rhythm differences, (2) the episode was usually composed of four forelimb steps and three hindlimb steps and (3) the background difference was similar before and after the episode of rhythm dissociation.

Apart from these similarities in the occurrence of the episodes of rhythm dissociation after both types of lesions, some differences also existed. In cats with ventrolateral lesions the maximum shortening of the step cycle duration in the forelimbs was smaller than in dorsolateral group (about 45 ms i.e. 7-8% of the initial values in the VL group vs. 75-158 ms i.e. 13-17% in the DL group) and the same applied to the lengthening of the hindlimb step cycle duration (84 and 119 ms i.e. 13-17% after VL lesions vs. 112 to 284 ms i.e. 15-31% after DL lesions). This resulted in a smaller maximal difference between the fore- and hindlimb step cycle durations after VL lesions (approximately 200 ms), than after DL lesions (approximately 250 to 450 ms).

The mechanisms controlling the episodes of fore-hindlimb rhythm dissociation are far from being understood. Since the lateral order of limb movements which appears in the first half of such an episode is considered as very unstable from the

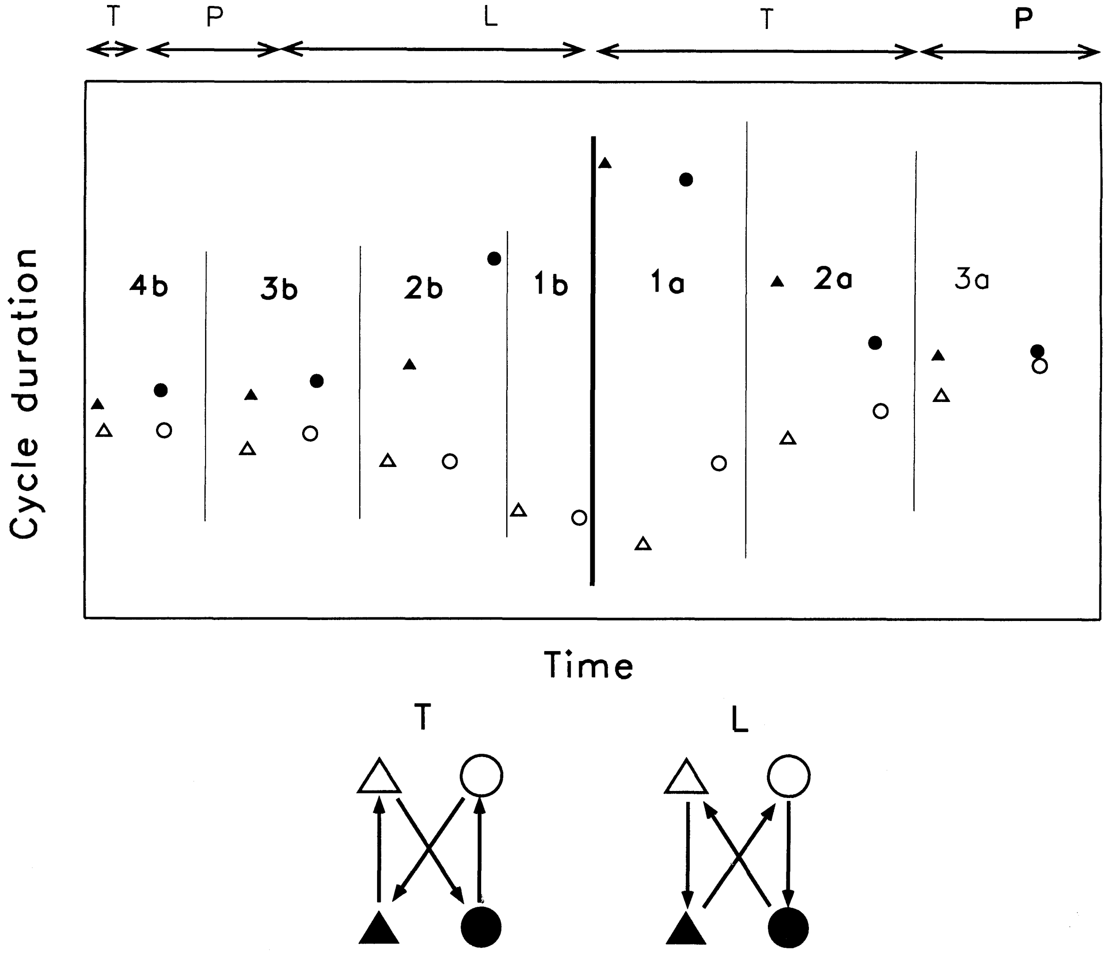

Fig. 5. Schematic representation of an episode of rhythm dissociation. Thin vertical lines divide the sequence into successive steps, which occurred before (numbers denoted by b) and after (numbers denoted by a) the synchronization of the diagonal limbs (thick vertical line). Symbols of particular limbs as in Fig. 2. The transverse (T) and lateral (L) order of movements are illustrated in the diagrams at the bottom. P, pacing.

point of view of quasi-static equilibrium of the body (Gray 1944), it is, therefore, possible that the sudden increase in the rhythm difference might be a definite strategy adopted by the animal in order to reduce a period of stepping with a poor stability: if the residual value of rhythm difference was not increased, the lateral order of movements would last longer. The alternative hypothesis concerning episodes of rhythm dissociation is that they could result from a transient functional disruption between the two girdle generators. The lateral order of movements which appeared in operated animals as a consequence of background rhythm difference has not been described during actual locomotion in the cat. Therefore, it is possible that completely atypical afferent input to the girdle generators associated with the lateral order of movements could result in a functional disruption of coupling between them, whereas the resynchronization of locomotor rhythms was possible only after restoration of the typical, transverse order of movements during the second half of the episode of rhythm dissociation.

Permanent dissociation of fore- and hindlimb rhythms

The last observed pattern of the impairment in the fore-hindlimb coordination, present in cats with the largest lesions, consisted in a permanent difference of the locomotor rhythms in both girdles

(Fig. 6A). These differences were usually independent on the locomotor speed as illustrated in Fig. 6B, in which the regression lines of the fore- and hindlimb step cycle durations on the locomotor speed were parallel, and were due to an increase of the step cycle durations in the hindlimbs and a decrease of the step cycle durations in the forelimbs. It is also worth stressing that the differences between the fore- and hindlimb steps in the case of permanent dissociation of locomotor rhythms were in cats with dorsolateral lesions usually greater (from approximately 350 ms to 450 ms) than in the case of ventrolateral lesions (about 200 ms).

In order to see whether the fore- and hindlimbs steps were completely independent from each other or whether some remnant forms of coordination still did exist, we have analysed the distribution of the onsets of the hindlimb swing in different phases of the forelimb step cycle (Fig. 7). In intact cats (Fig. 7A) the onsets of the swing phase in the hindlimbs occurred exclusively during the swing phase of the diagonal forelimb, whereas after surgery they appeared in all phases of the forelimb step cycle, i.e. during the swing phase of the diagonal as well as of the ipsilateral forelimb (Fig. 7B: phases II and IV) and during both phases of the double support in the forelimbs (Fig. 7B: phases I and III). However, this

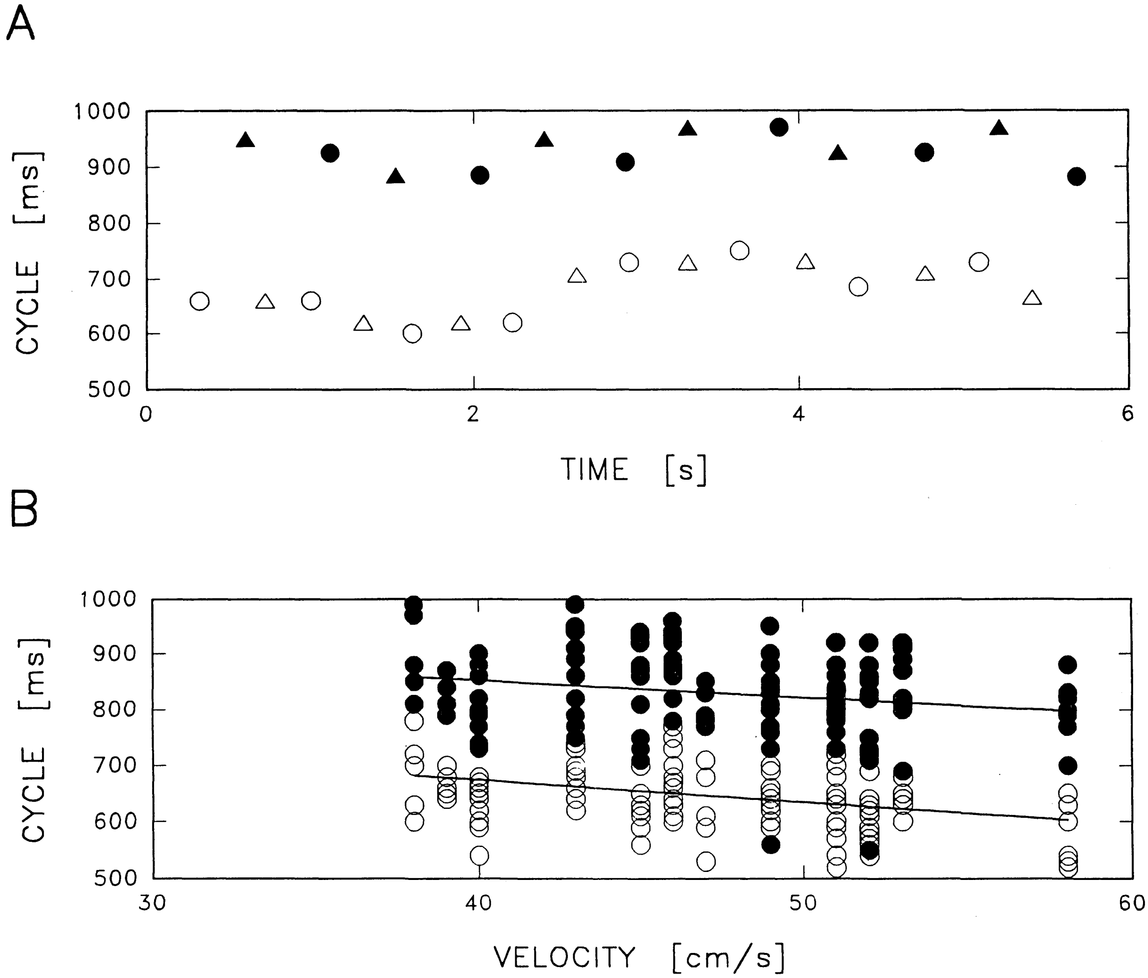

Fig. 6. A, timing of the onsets of stance phases in a sequence with a permanent difference of locomotor rhythms in both girdles. Abscissa, ordinate and symbols of particular limbs as in Fig. 2. B, the relationships between the right forelimb (open circles) and right hindlimb (black circles) step durations (ordinate) and the locomotor speed (abscissa) in a cat (No Op6VL) with a permanent rhythm difference. Note the similarity ($P>0.05$) of the slopes of regression lines in the fore- and hindlimbs. (reproduced from Bem et. al. 1995, Fig. 4 with permission of Springer-Verlag GmbHandCo.KG).

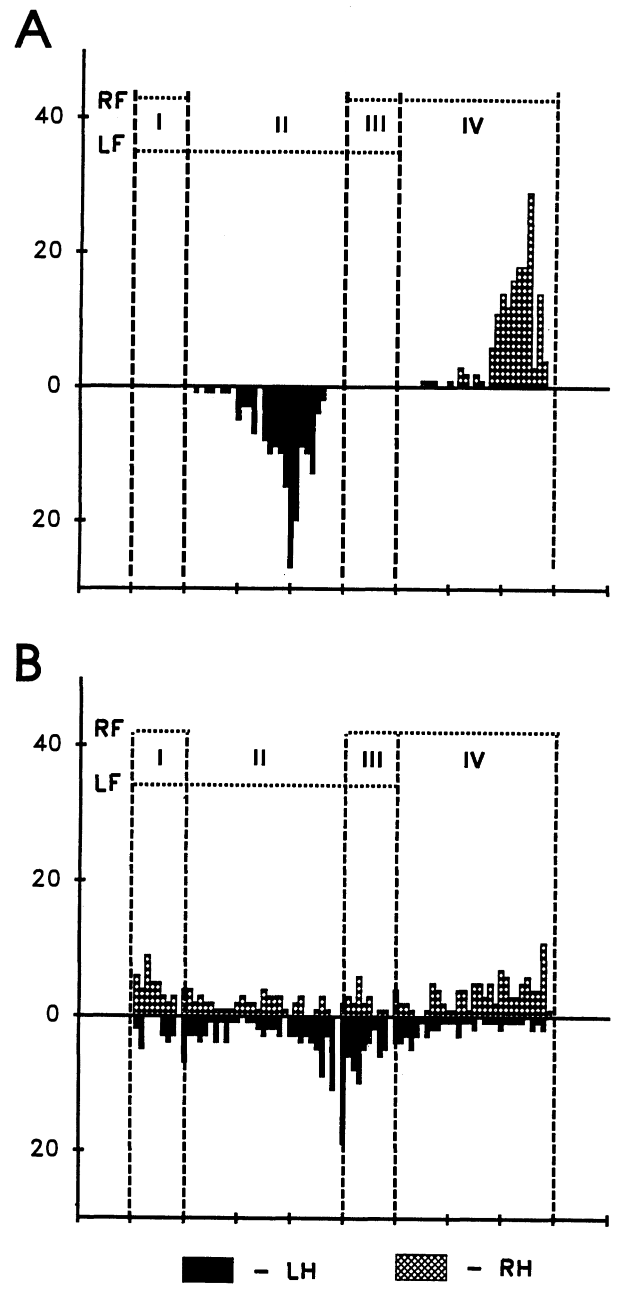

Fig. 7. Distributions of the onsets of the hindlimb swings (ordinates) in different phases (I-IV) of the forelimb step cycle (abscissae) in an intact cat (A) and the same cat (No 104 VL) after surgery (B) stepping with a permanent rhythm difference in the fore- and hindlimbs. Dotted lines in Fig. 7A and B correspond to forelimb stance phases. Note that in Fig. 7B the LH was lifted off in the transverse (RF, LH, LF) order in phases II and III, while in phases I and IV in the lateral order (LF, LH, RF). Correspondingly, the RH was lifted off in the transverse (LF, RH, RF) order in phases IV and I, while in phases II and III in the lateral order (RF, RH, LF). (Reproduced from Bem et al. 1995, Fig. 5 with permission of Springer-Verlag GmbHandCo.KG).

distribution was not entirely uniform and the onset of the swing of a given hindlimb occurred more frequently in those phases of the forelimb step cycle which corresponded to the transverse order of movements (Fig. 7B: phases II and III for LH and phases I and IV for RH) than in those corresponding to the lateral order (Fig. 7B: phases I and IV for LH and II and III for RH). These results indicate that even during locomotion with permanent rhythm dissociation some of the movements in both girdles were not independent of each other and thus suggest some remnants forms of fore-hindlimb coordination. It should be noticed, however, that the prevalence of the transverse over the lateral order of the onsets of swing phases in cats with permanent rhythm difference was slightly greater in the ventrolateral than in the dorsolateral group (approximately 60-70% of the total number of steps in the VL group vs. 50-60% in the DL group). Moreover, the distribution of the onsets of the hindlimb swing phases were also slightly different in these two groups of operated cats (mainly phase IV and I for RH and II and III for LH in cats with VL lesions vs. phase I for RH and III for LH in cats with DL lesions).

The mechanisms by which these remnant forms of coordination occur requires further investigations, but it is possible that the mechanical coupling between the girdles *via* the trunk was responsible for this remnant form of coordination, by exerting a pulling or pushing action from one girdle to another, which in turn resulted in a change of the position of the body with relation to the limb being in contact with the ground. The deflection of the limb backward may be especially important for coordination, because it promotes the onset of the swing phase of this limb (Shik and Orlovsky 1965, Grillner and Rossignol 1978). It is also possible that the trunk muscles might transmit information between the girdles *via* some reflex pathways which could influence the girdle generators.

Comparison of the effects of ventrolateral and dorsolateral lesions on the fore-hindlimb coordination

The last point to be discussed is the comparison between the effects of the ventrolateral and dorsolateral lesions on the occurrence of the described three forms of impairment of the fore-hindlimb coordination. As stressed above, all the lesions performed, except those essentially restricted to the dorsal columns, elicited an impairment of the fore--hindlimb coordination and the degree of this impairment within each group, was in general correlated with the extent of the lesion. However, destruction of the lateral funiculi seemed to result in a greater impairment of the fore-hindlimb coordination than lesions of other parts of the spinal white matter. For example, the percentage of sequences with equal rhythm of the fore- and hindlimb movements was smaller in DL cats Nos 107 and 119 with lesions of the dorsal columns and about two thirds of the lateral funiculi than in VL cats Nos Op1 and Op4 with lesions sparing both (Op1) or either one dorsal quadrant (Op4) (cf. Fig. 1), although in the latter cat the extent of lesion was definitely greater than in cats Nos 107 and 119. These results suggest that the dorsolateral funiculi play an important role in the preservation of the equality of rhythms in both girdles. The importance of propriospinal pathways interconnecting the lumbar and brachial enlargements running in the dorsolateral funiculi was stressed by Gernandt and Shinamura (1961). Moreover, the so called "stepping strip" running in the dorsolateral funiculus could be also involved in the control of locomotor rhythms, since its stimulation evokes movements of the ipsilateral hindlimb (Kazennikov et al. 1983, Gelfand et al. 1988).

More extensive lesions in both groups of animals elicited episodes of fore-hindlimb rhythm dissociation or a permanent dissociation of these rhythms, depending on the extent of the lesions (see, however, cats No 123 and 122 from the DL group). This latter form of impairment occurred in DL cats with much smaller lesion, than in VL cats (cf. Fig. 1: DL cats Nos 121 and 123 and VL cats Nos Op6, 104 and 105), which would support the hypothesis that the destruction of the lateral funiculi play a crucial role in an impairment of the fore-hindlimb coordination. To what extent these changes were due to destruction of long propriospinal pathways connecting the brachial and lumbar enlargements or to long ascending and descending spinal pathways which run in these parts of the spinal cord cannot be solved at this moment , since long propriospinal tracts are intermingled at the level of the spinal cord with other tracts (Giovaneli and Kuypers 1969, Miller and van der Burg 1973, Miller et al. 1973, Molenaar and Kuypers 1978, English et al. 1985 and others). In addition, other long ascending and descending spinal pathways contribute to the control of interlimb coordination, since they exert influences on long propriospinal systems and spinal circuitry (e.g. Jankowska et al. 1973) and offer plenty of opportunities for peripheral signals to be conveyed back to the spinal cord through supraspinal loops. Such an analysis would require another experimental approach in which lesions of the spinal cord would be followed by lesions of supraspinal structures being the source and/or target of long descending and ascending spinal pathways, as well the use of various pharmacological agents (see Barbeau and Rossignol 1991) in order to see to what extent the impairment of the fore-hindlimb coordination depends on the hindlimb deficits resulting from spinal lesions.

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