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LOCOMOTION IN CATS WITH VENTRAL SPINAL LESIONS: SUPPORT PATTERNS AND DURATION OF SUPPORT PHASES DURING UNRESTRAINED WALKING

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Abstract. The sequences and duration of support phases in the four-legged step cycles performed during unrestrained walking with moderate speed (0.4-1.0 m/s) were analyzed in two groups of cats: intact ones and animals with lesions of the ventral quadrants of the spinal cord at the low thoracic level. Spinal lesions resulted in a much greater variability of support patterns and an increase in the relative durations of the support on two ipsilateral limbs, accompanied by a reduction of support on two diagonal limbs. It is suggested that these changes reflected an impairment of fore-hindlimb coordination, due to an increased phase shift between the onsets of stance phases in the forelimb and in the contralateral hindlimb and may account, at least partly, for the unsteady and ataxic gait described in cats with ventral funicular lesions.

INTRODUCTION

Studies on animal locomotion after spinal lesions have been mainly focused on hindlimb activity in animals with complete spinal transections, tested on a treadmill belt. Under such conditions, low spinal cats did not manifest clearcut changes: the basic parameters of hindlimb movements were preserved, the animals could adjust the step duration to the belt speed and showed both symmetric (walk, trot) and asymmetric (gallop) hindlimb coordination (5, 8, 9, 10, 14).

One important aspect of locomotion is the coordination between movements of the shoulder and the pelvic girdles. This problem has been much less extensively studied. Complete spinal transections at low thoracic level were found to affect the fore-hindlimb coordination, measured by the correlation coefficient, in animals moving on the treadmill (6). Subtotal spinal lesions had a similar effect (7). An uncoupling of fore- and hindlimb movements in overground locomotion has been also described after subtotal spinal lesions sparing small parts of ventral funiculi (1).

In view of the limited knowledge concerning locomotor impairment after partial spinal lesions, in the present paper we have attempted to analyze those changes after lesions of the ventral quadrants of the spinal cord. Lesions of those structures have been found to affect locomotion by rendering the gait highly unstable, paretic and ataxic (1, 7). To describe changes in the gait we have recurred to a method used in the early studies on locomotion (13, 16, 22) based on an analysis of the support sequences and durations of support phases in the four-legged step cycle. It will be shown that this method allowed us to reveal clear-cut differences between locomotion in intact cats and cats with partial spinal lesions.

MATERIAL AND METHODS

The experiments were made on 5 adult intact cats and 4 cats with partial spinal lesions performed at the low thoracic level (Th_{10}-Th_{12}). In the majority of cats, the lesions were bilateral and involved the ventral and ventrolateral funiculi, encroaching upon the ventral parts of the dorsolateral funiculi.

The locomotion was tested by using a slightly modified method developed by Afelt et al. (2, 3). In short, the animals moved along a wire-made stationary platform, 6 m long and 1 m wide, one end of which was connected to a DC source. Cats wore on the middle of the third toe pad of each limb contact electrodes, which allowed to record the stance phases. In each run only sequences of steps of approximately equal velocity were taken into account and for those steps the sequence and durations of particular support phases in each four-legged step cycle were counted. The step cycle always began with the onset of the left forelimb stance phase (13) and included the stance and swing phase of that limb together with the corresponding swing and stance phases of other limbs (cf. Fig. 1*A*). The details of the experimental procedure will be described elsewhere (in preparation).

The results described below are based on an analysis of approximately 450 step cycles collected in 5 intact cats and a similar number of step cycles collected in 4 operated cats, tested 5-6 months after surgery. The locomotor speed spontaneously chosen by intact and operated animals ranged from 0.4 to 1.0 m/s. As this speed corresponds to walk (13, 16, 22), our analysis is confined to this kind of gait exclusively. The mean (± SD) velocity of locomotion in intact and operated cats were 0.70 ±0.11 and 0.68 ±0.12 m/s respectively.

RESULTS

The results obtained in intact and operated cats are compared in Fig. 1. A more detailed description of locomotion in each of these groups is given below.

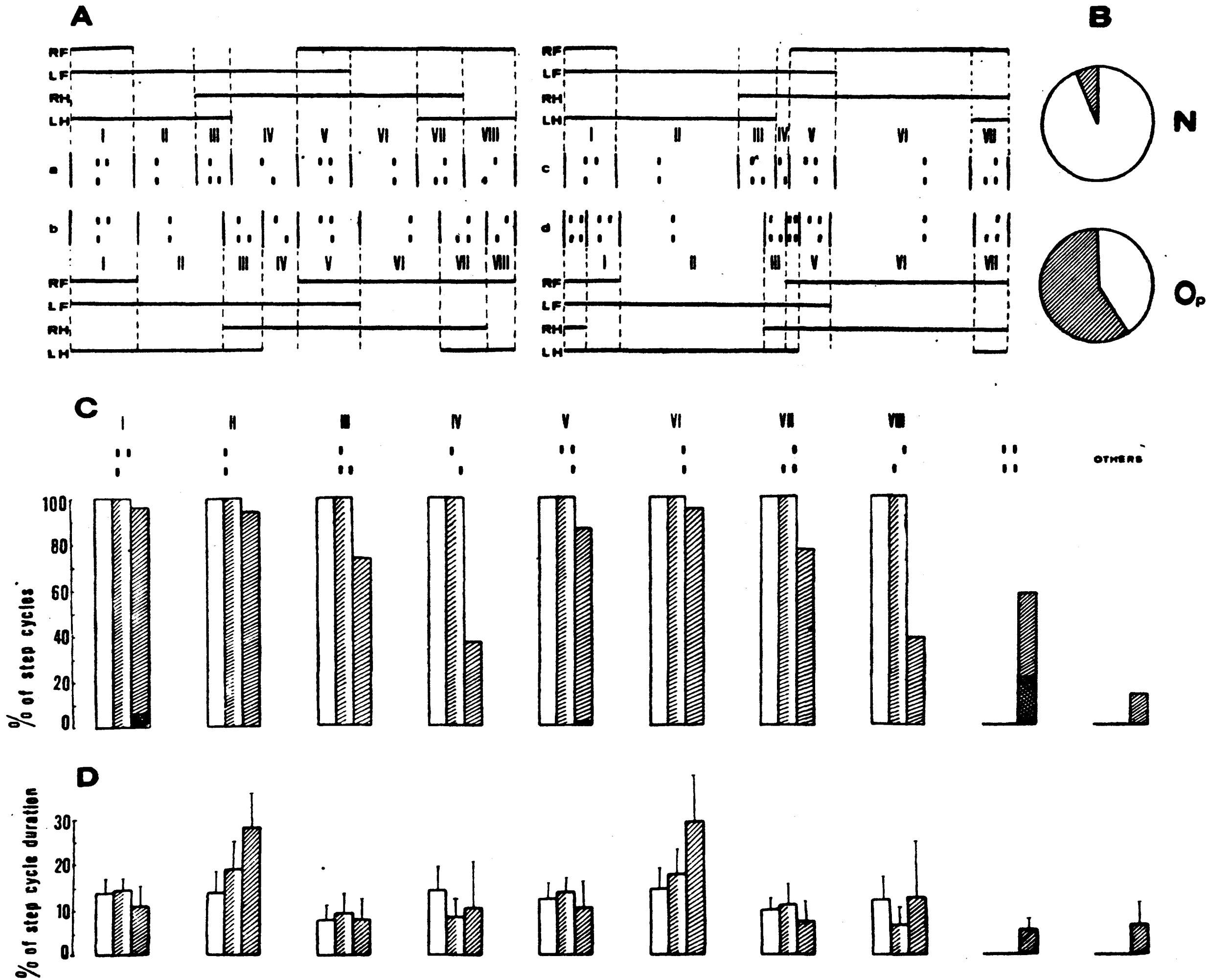
Sequence and duration of support phases in intact cats

Intact cats, when walking, used almost exclusively (mean 94% of step cycles, see Fig. 1*B*) the numerical support formula 3-2-3-2-3-2-3-2, in which the three- and the two-legged support phases alternated (Fig. 1*A*a). The three-legged phases consisted of support on two fore- and one hindlimb and two hind- and one forelimb. In the two-legged phases the animals supported themselves on ipsilateral and on diagonal limbs. This pattern of support corresponded to that described by other authors as *typical* for walk at moderate speed (transverse walk of Muybridge (22) and Howell (16) or normal walk of Gray (13)).

The mean durations of support phases calculated in ms decreased with the increase of locomotor speed, as did the total step duration. However, the relative duration of the support phases, expressed in percent of the total step duration, remained essentially constant within the range of analyzed velocities. Figure 1*D* (left columns) shows that in typical step cycles in intact cats the mean relative duration of the majority of support phases were essentially similar and ranged from 12.2% (phase VIII) to 14.6% (phase IV). Somewhat shorter (by approximately 5%) was the duration in phases consisting of two hindlimb and one forelimb support (phase III and VII).

Sequences and durations of support phases in operated cats

Typical pattern of walking. The above described typical pattern of support during walking, occurred in operated cats in a much smaller percent of step cycles (mean 40%, see Fig. 1*B*). As in intact, cats its occurrence did not depend on the speed of locomotion.


A
B
RF
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I II III IV V VI VII VIII
a
b
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OTHERS
% of step cycles
% of step cycle duration

Fig. 1. Characteristics of support patterns and durations of support phases during unrestrained walking in intact cats and cats with lesions of the ventral quadrants of the spinal cord. A, Examples (a-d) of normalized four-legged step cycles showing different support patterns. In each diagram horizontal lines indicate the stance phase of each limb; abbreviations: R, right; L, left, F; forelimb; H, hindlimb. Ventrical broken lines mark the duration of different support phases, which are schematically represented below (a, c) and above (b, d) the diagrams. Support phases I-VIII are numbered after Gray (13). a, a typical support pattern for walking in an intact cat; b, same support pattern as in a, but in an operated cat; c, d, examples of atypical patterns of support in operated cats; note the absence of one (c) or two (d) diagonal support phases and the presence of additional four-legged support phases (d). B, Percent of step cycles with typical (white) and atypical (hatched) support patterns in normal (N) and operated (Op) cats. C, Percent of step cycles with particular support phases in the typical pattern of support in intact (white) and operated (semi-hatched) cats and in atypical patterns of support in operated cats (hatched). Cross hatched areas indicate the percent of steps in which the same phase of support occurred twice in the same step cycle. D, Mean relative (in % total step cycle) duration of particular support phases in various kinds of step cycles. Denotation as in C. Vertical lines show the standard deviation.

The relative duration of support phases in the typical step cycles were also changed in operated cats (Fig. 1*D*), middle columns. The most conspicuous differences were observed in phases of diagonal and lateral support. The former (phase IV and VIII Fig. 1*D*) were shorter in operated cats than in intact animals by approximately 50%. This was accompanied by a marked increase (about 30%) in the duration of support phases on two ipsilateral limbs (phases II and VI in Fig. 1*D*). Figure 1*A*b shows an example of a step cycle with the typical support formula for walking performed by operated cats.

Atypical patterns of walking. More than half of the step cycles in operated cats (mean 60%, see Fig. 1*B*) had atypical patterns of support, which did not correspond to any patterns of support in walking described in the literature (13, 16, 22, 23). These patterns were diverse, could change from step to step and were often asymmetric. The number of support phases in atypical patterns varied from 4 to 10, although in the majority of step cycles less than 8 support phases were present (mean 6.9 phases/step cycle).

To characterize step cycles with atypical patterns of support, we have calculated the percentage of the steps in which each of the support phases occurred. Fig. 1*C* (right columns) shows that none of the support phases typical for normal walking appeared in 100% of the atypical steps. However, phases occurring at the beginning of each half of the typical step cycle, consisting of support on two fore- and one hindlimb (phases I and V) and on ipsilateral limbs (phases II and VI) occurred more regularly (in 86 to 96% of steps) than the remaining phases. The most reduced were phases of diagonal support (IV and VIII), which were present in 36 and 38% of steps only. Phases of support on two hind- and one forelimb (III and VII) were less reduced and appeared in 72 and 77% of typical steps, respectively.

In step cycles with atypical patterns of support, some support phases, not present in the typical pattern of walking, could also occur. The most frequent was the support on all four limbs, which appeared in 58% of steps (Fig. 1*C*). Other phases as e.g. support on a single fore- or hindlimb or on two fore- or two hindlimbs occurred only occasionally (see Fig. 1*C*). Some support phases could also occur twice in the same step. This happened most frequently with respect to the support on all four limbs (Fig. 1*C*).

The basic sequence of support phases characteristic for the typical pattern was preserved in the majority of atypical step cycles, with some of the phases lacking. Fig. 1*A*c illustrates a step cycle, in which phases I-VII appeared in the proper sequence, but the last phase (phase VIII) was absent. The additional four-legged support phase occurred, in general, either at the beginning of the step cycle, before phase I, or in the middle of it replacing the diagonal support phase (phase IV) (Fig. 1*A*d).

The relative duration of support phases in atypical step cycles were also changed in comparison with steps with the typical pattern of support in operated cats (Fig. 1*D*, right-hand columns). The most conspicuous differences concerned the ipsilateral support phases (II and VI). Both these phases were additionally increased, so that their sum amounted to 60% of the total step duration, i.e. twice as much as in normal animals and 50% more than in steps with the typical pattern of support in operated cats.

The relationship between the extent of spinal lesions and the changes in locomotion in individual cats will be reported elsewhere (in preparation).

DISCUSSION

The mechanism of the above described locomotor disturbances after ventral spinal lesions require further studies. Nevertheless, our results strongly suggest that the main reason of the observed changes in locomotion was the impairment of fore-hindlimb coordination, i.e. an increase in the phase shift between the onsets of stance phases of the forelimb and of the diagonal hindlimb.

Inspection of Fig. 1*A* shows that in operated animals (b-d) the onsets of right hindlimb stance phases were more delayed with respect to the onsets of the left forelimb stance phases than in intact animals (Fig. 1*Aa*) and a similar delay occurred between the onsets of the right forelimb and left hindlimb stance phases. As a result, the relative durations of the ipsilateral support phases (phase II and VI) increased in operated animals. The reduction of the diagonal support phases (IV and VIII) in operated animals were also a mere consequence of this increased phase shift, because the onsets of the hindlimb swing phases were also delayed. This resulted in a shortening (Fig. 1*Ab*) or complete disappearance (Fig. 1*Ac*, *d*) of the diagonal support phases. On the other hand, the relative duration of other phases in the step cycle were much less changed in operated cats, because they were determined by the intervals between the onsets of the stance and swing phases in both forelimbs (phase I and V) or in both hindlimbs (phase III and VII), which remained essentially unaltered in operated cats.

The above changes altered the gait in our cats into a more "pacing-like" type, i.e. a form of gait characterized by synchronous movements of ipsilateral limbs (13). Pacing is seldom observed in intact animals except for some longlimbed cursors, such as camels and giraffes (13).

On the mechanical grounds the lateral support appears to be an extremely unstable pattern (12, 13). Its increase, therefore, even up to 60% of the total step duration observed in the present experiments might have been an important factor contributing to gait unstability after ventral spinal lesions, as manifested by poor balance of the body, marked oscillatory movements of the lower trunk and overabduction of the hindlimbs (1).

The impaired fore-hind limb coordination observed in our operated cats might have been primarily due to the weaker influence exerted by the shoulder girdle on the pelvic girdle, of vice versa, caused by the destruction of long propriospinal pathways connnecting the brachial and lumbar enlargements. These pathways, both ascending and descending, run in the ventral and ventrolateral funiculi and possess both crossed and uncrossed fiber systems (11, 18, 19, 21). However, the contribution of supraspinal structures in the control of limb coordination in locomotion cannot be excluded, since these structures exert influence on long propriospinal systems and the spinal circuitry (4, 17, 23). Pacing episodes in walking have also been observed in high spinal cats (15, 20), in which the propriospinal pathways were not damaged. The possibility of a quantitative assessment of impairment the fore-hindlimb coordination described in the present paper should help in understanding which structures and pathways play a major role in this process.

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REFERENCES

1. AFELT Z. 1974. Functional significance of ventral descending tracts of spinal cord in the cat. Acta Neurobiol. Exp. 9: 393-407.
2. AFELT Z., BŁASZCZYK J. and DOBRZECKA C. 1983. Stepping frequency and stride length in animal locomotion: a new method of investigation. Acta Neurobiol. Exp. 43: 227-233.
3. AFELT Z. and KASICKI S. 1975. Limb coordinations during locomotion in cats and dogs. Acta Neurobiol. Exp. 34: 369-378.
4. BALDISSERA F., HULTBORN H. and ILLERT M. 1981. Integration of spinal neuronal systems. *In* V. B. Brooks (ed.), Handbook of Physiology, Chapter 12, The nervous system II. Am. Physiol. Soc., Bethesda, p. 509-595.
5. BUDAKOWA N. N. 1973. Stepping movements in the spinal cat due to DOPA administration (in Russian) Fiziol. Zh. SSSR. 59: 1190-1198.
6. EIDELBERG E., STORY J. L., MEYER B. L. and NYSTEL, J. 1980. Stepping by chronic cats. Exp. Brain Res. 40: 241-246.
7. EIDELBERG E., STORY J. L., WALDEN J. G. and MEYER B. L. 1981. Anatomical correlates of return of locomotor functions after partial spinal cord lesions in cats. Exp. Brain Res. 42: 81-88.

8. FORSSBERG H. and GRILLNER S. 1973. The locomotion in the acute spinal cat injected with clonidine i.v. Brain Res. 50: 184-186.
9. FORSSBERG H., GRILLNER S. and HALBERTSMA J. 1980. The locomotion of the low spinal cat. I. Coordination within a hindlimb. Acta Physiol. Scand. 108: 269-281.
10. FORSSBERG H., GRILLNER S., HALBERTSMA J. and ROSSIGNOL S. 1980. The locomotion in the low spinal cats. II. Interlimb coordination. Acta Physiol. Scand. 108: 283-295.
11. GIOVANELLI B. M. and KUYPERS H. G. J. M. 1969. Propriospinal fibers interconnecting the spinal enlargements in the cat. Brain Res. 14: 321-330.
12. GRAY J. 1944. Studies on the mechanics of tetradod skeleton. J. Exp. Biol. 20: 88-116.
13. GRAY J. 1968. Animal locomotion. Weidenfeld and Nicolson, London. 479p.
14. GRILLNER S. 1973. Locomotion in the spinal cat. *In* R. B. Stein, K. G. Pearson, R. S. Smith and J. B. Redford (ed.). Control of posture and locomotion. Plenum Press, New York, p. 515-535.
15. HALBERTSMA J. M., MILLER S. and van der MECHE F. G. A. 1976. Basic programs for the phasing of flexion and extension movements of the limbs during locomotion. *In* R. M. Herman, S. Grillner, P. S. G. Stein and D. G. Stuart (ed.). Neural control of locomotion. Plenum Press, New York, p. 489-517.
16. HOWELL A. B. 1944. Speed in animals. University of Chicago Press, Chicago, 247 p.
17. JANKOWSKA E., LUNDBERG A. and STUART D. 1973. Propriospinal control of last order interneurones of spinal reflex pathways in the cat. Brain Res. 53: 227-231.
18. MILLER S., REITSMA D. J. and van der MECHE F. G. A. 1973. Functional organization of long ascending propriospinal pathways linking lumbosacral and cervical segments in the cat. Brain Res. 62: 169-188.
19. MILLER S. and van der BURG J. 1973. The function of long propriospinal pathways in the coordination of quadrupedal stepping in the cat. *In* R. B. Stein, K. G. Pearson, R. S. Smith and J. B. Redford (ed.). Control of posture and locomotion. Plenum Press, New York, p. 561-577.
20. MILLER S., van der BURG J. and van der MECHE F. G. A. 1975. Locomotion in cats: basic programs of movement. Brain Res. 91: 239-253.
21. MOLENAAR I. and KUYPERS H. G. J. M. 1978. Cells of origin of propriospinal fibers and of fibers ascending to supraspinal levels. A HRP study in cat and rhesus monkey. Brain Res. 152: 429-450.
22. MUYBRIDGE E. 1957. Animal in motion. Dover Pub., New York 74p., 183P1.
23. STUART D. G., WITHEY T. P., WETZEL M. C. and GOSLOW, G. E. 1973. Time constrains for interlimb coordination in cat during unrestrained locomotion. *In* R. B. Stein, K. G. Pearson, R. S. Smith, J. B. Redford (ed.). Control of posture and locomotion. Plenum Press, New York, p. 537-560.

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