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Overground locomotion in intact rats: contact electrode recording

Teresa Górska[1], Henryk Majczyński[1] and Wojciech Zmysłowski[2]

[1]Department of Neurophysiology, Nencki Institute of Experimental Biology, 3 Pasteur St., 02-093 Warsaw, Poland; [2]Institute of Biocybernetics and Biomedical Engineering, 4 Księcia Trojdena St., 02-109 Warsaw, Poland

Technical communication

Abstract. The aim of the experiments was to check the validity of the method of contact electrodes for studying overground locomotion in the rat. The basic indices of locomotion, obtained in 7 intact rats with at least 100 steps recorded in each, were analysed and compared with those described by other authors using different methods of movement recording. It was found that the method of contact electrodes gives reproducible and reliable results and may thus be used in further experiments of rat locomotion after CNS lesions.

Key words: rat, overground locomotion, gait indices, contact electrodes

INTRODUCTION

Overground locomotion in the rat represents an attractive model for studying the effects of CNS lesions on motor behaviour and the effectiveness of various reparative techniques and pharmacological agents to compensate movement disorders. However, despite the extensive use of the rat in the latter type of experiments (e.g. Commissiong and Toffano 1989, Bregman et al. 1993, Iwashita et al. 1994, Cheng et al. 1996, Sławińska and Majczyński 1997 and others) there have been relatively few studies on locomotion in intact rats (Cohen and Gans 1975, Hruska et al. 1979, Yakhnitsa et al. 1985, Clarke and Parker 1986, Westerga and Gramsbergen 1990, Clarke 1991, Clarke and Williams 1994) and besides they analysed different aspects of locomotion. Moreover, these data did not consider inter- and intraanimal variability, since the results from several animals were pooled together. This was, to our mind, mainly due to a lack of a simple but reliable method of locomotor movement recordings, without employing the most often used but time consuming analysis of movements from cinematographic or videotape recordings.

To overcome this difficulty, in the present experiments we applied the method of contact electrodes to study overground locomotion in the rat. This method has been used successfully in our previous experiments in cats and has proved to be a useful tool in describing changes in locomotion after partial spinal lesions (Górska et al. 1993a,b,c, 1996) or some supraspinal structures (Górska et al. 1995).

The present paper deals with basic gait indices such as locomotor speed, step cycle, stance and swing durations and the relationships between these variables. A comparison of our results with the data in the literature shows that in rats the method of contact electrodes may also be successfully used in studies of locomotor behaviour because it provides reliable and reproducible results. Preliminary results have been presented in abstract form (Zmysłowski et al. 1995).

METHODS

Animals and recording procedure

The experiments were performed on 7 intact adult hooded rats of either sex (males: Nos. 1-4, females: Nos. 5-7), weighing 250 to 350 g.

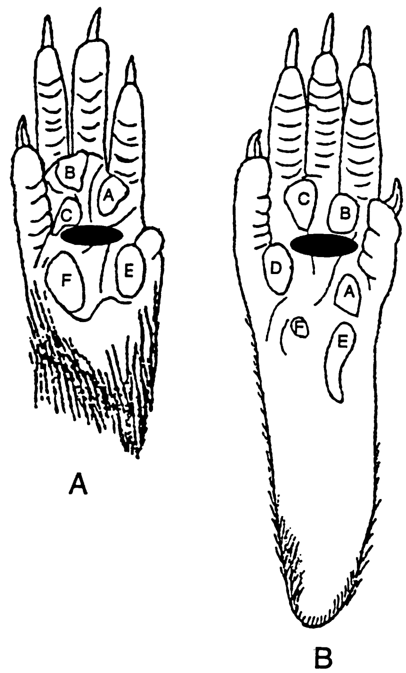

Fig. 1. View of the rat palmar (A) and plantar (B) surface showing the position of the contact electrodes. The letters denoting interdigital pads are taken from Clarke and Williams (1994).

The overground locomotion was tested using a method of contact electrodes adapted for rats, similar to that applied in previous experiments on cats (Afelt and Kasicki 1975, Górska et al. 1993a). Briefly, the animals, fitted with contact electrodes on each paw, moved along a runway (2 m long and 0.12 m wide) covered with an aluminium sheet connected to a 100 mV DC source. The sheet was roughened to avoid slipping. The runway was placed 1.5 m above floor level and had a dark cage on one end in which the animals could shelter themselves. The contact electrodes were spindle-shaped (4 mm long and 3 mm in diameter in the middle) and were made of a thin copper wire wound around a thin (1 mm) rubber band which served to fix the electrodes to the palmar or plantar surface of the paws by tightening the band around the toes of each paw. In the forepaws the electrodes were positioned in the indentation between interdigital pads A-C and the more proximal pads E and F (see Fig. 1A). In the hindlimbs they were placed between the interdigital pads C-B and A, D (see Fig. 1B). Such placement of the electrodes correlated well with the paw zone which makes contact at the start and end of the stance (Clarke and Williams

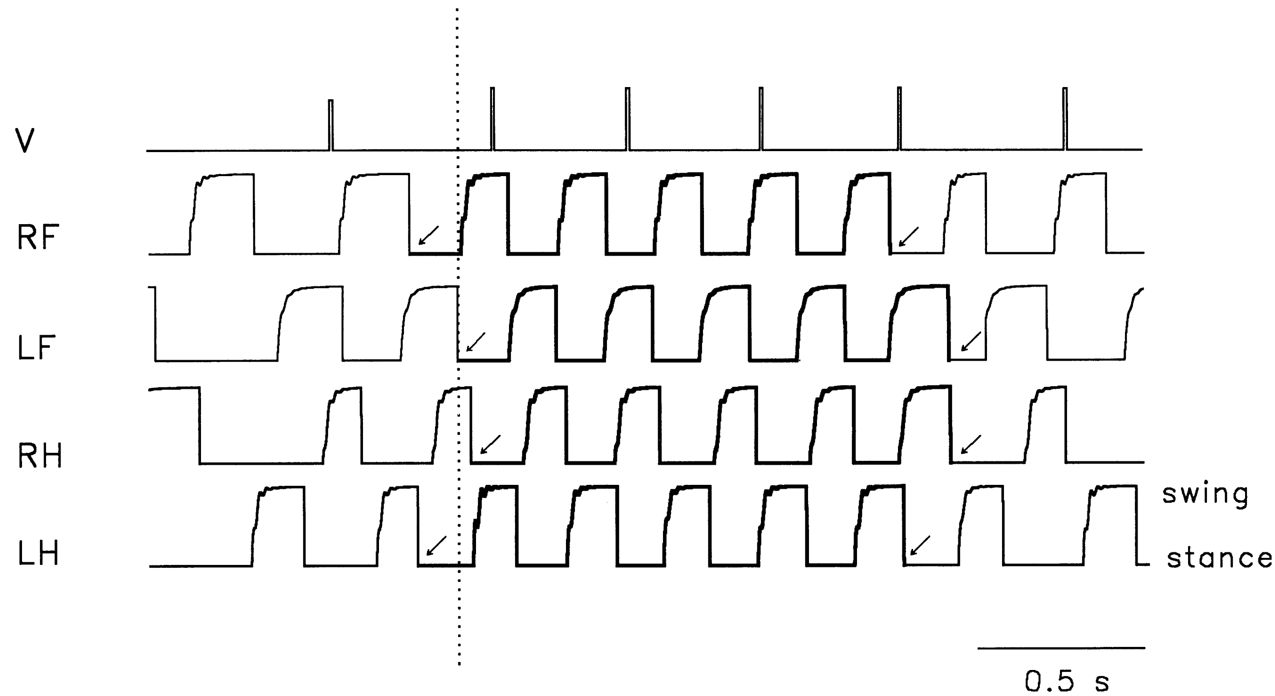

Fig. 2. An example of signals from contact electrodes recorded during one pass along the runway. RF, LF, RH and LH denote right forelimb, left forelimb, right hindlimb and left hindlimb, respectively. V indicates impulses from photocells. For each limb the lower level signals denote the stance phases (circuit closed) and the higher ones the swing phases (circuit opened). The arrows delineate the beginning and the end of the selected sequence of steps to be analyzed. The vertical dotted line is the zero line from which the onsets and offsets of stance phases were measured.

1994). Rats after some period of adaptation tolerated the electrodes relatively well and did not try to remove them even in the forelimbs.

The signals from the electrodes were amplified, digitized at the rate of 200 Hz and stored in a computer memory, as were the signals from photocells, used to measure the locomotor speed. The photocells were mounted every 25 cm along the runway, 3 cm above it. Figure 2 shows an example of the record of a sequence of steps obtained during one pass along the runway.

One experimental session usually consisted of 20 -30 passes along the runway. After each pass the animals rested about one minute in the cage at the end of the runway. The recording sessions were preceded by approximately 2 weeks of training, during which the animals were taught to move along the runway with relatively constant speed and to become accustomed to the electrodes. A bell ring was used to speed up locomotion (Sławińska and Kasicki 1993). Passes in which the animals stopped or suddenly accelerated were discarded from further analysis.

Data analysis

The records from contact electrodes were used to measure the time of the onset and offset of successive stance phases in each limb with respect to an arbitrarily chosen reference point, which was the onset of the left forelimb stance phase in the first step of an analysed sequence (Fig. 2). From each pass, only a sequence of steps (5-12) performed with velocity differing not more than 10% was evaluated. At least 100 step cycles collected from about 20 passes during one experimental session were used for the analysis in each rat. The time measurement errors were estimated to be 5 ms, while the speed measurement errors between two adjacent photocells was 0.01 m/s.

The data analysis included: (1) the locomotor speed, (2) the swing, stance and step durations, and (3) the relationships between these variables.

All the relationships were evaluated by regression (least square method) and correlation analysis. The means were compared with the Student's t test. In all cases $P<0.01$ was considered significant.

RESULTS

Locomotor speed

The mean locomotor speed in individual rats ranged between 25 ± 6 (rat No. 6) and 45 ± 7 cm/s (rat No. 2) (Table I). Out of 7 animals, two (Nos. 3 and 6) were relatively slow (mean speed below 30 cm/s), four (Nos. 1, 4, 5 and 7) moved at moderate speed (mean 30-40 cm/s) and one was fast (No. 2) (mean above 40 cm/s) (Table I). The minimal speed ranged between 10 (No. 3) and 25 cm/s (No. 2), while the maximal between 43 (No. 6) and 78 cm/s (No. 2). The most common range of speed used by the animals was 20-40 cm/s.

Step cycle, stance and swing durations vs. locomotor speed

The mean duration of the step cycle, stance and swing phases in each limb and each rat are shown on Table I. The mean step cycle duration in individual rats ranged between 304 ± 85 (No. 2 RF) and 512 ± 102 ms (No. 6 RF). The minimal and maximal values of step cycle duration ranged between 215 ms (No. 2) and 685 ms (No. 6).

The mean stance phase durations ranged from 135 ± 36 (No. 2 RF) to 337 ± 92 ms (No. 6 RF). The minimal and maximal stance durations were 80 (No. 2) and 405 ms (No. 5), respectively. The mean swing duration ranged between 146 ± 16 (No. 2 LH) and 243 ± 24 ms (No. 1 RH), with the minimal and maximal values being 105 ms (No. 2) and 310 ms (No. 3), respectively.

In all the animals, the step cycle and stance phase durations markedly decreased in each limb as the locomotor speed increased. Smaller changes were observed with regard to the swing phase duration. The relationships between the step, stance and swing durations and the locomotor speed could be fitted best by using the power function: $y = ax^b$. Table II gives the results of the correlation and regression analysis for the left fore- and hindlimb in each rat.

As presented in Table II, the relationships between the step cycle and stance phase duration and the locomotor speed were essentially similar, which shows that the decrease in step cycle duration occurred mainly at the cost of the stance phase. For the step cycle and stance phase the values of log *a* ranged, correspondingly, from 7.60 to 8.51 and from 7.57 to 9.08, of *b* from -0.46 to -0.71 and from -0.58 to -1.04, while *r* ranged from -0.67 to

TABLE I

Mean (±SD) locomotor speed (V) in individual rats and mean (±SD) duration of the step (T_c), stance (T_{st}), and swing (T_{sw}) phase duration in each limb. Denotations of statistically significant differences: ↓ between homolateral limbs (fore- and hindlimb); → between homologous limbs (left and right)

Rat No.	V cm/s	limb	T_c left	T_c right	T_{st} left	T_{st} right	T_{sw} left	T_{sw} right
1	39 ± 9	fore	431 ± 90	428 ± 96	224 ± 76 ↓	242 ± 70 ↓	207 ± 15 ↓	186 ± 24 ↓
		hind	432 ± 93	435 ± 85	187 ± 37	192 ± 60	245 ± 23	243 ± 24
2	45 ± 7	fore	306 ± 52	304 ± 85	141 ± 40 ↓	135 ± 36 ↓	165 ± 18 ↓	169 ± 20 ↓
		hind	308 ± 42	308 ± 52	162 ± 36	157 ± 42	146 ± 16	151 ± 26
3	28 ± 5	fore	454 ± 87	454 ± 91	269 ± 85	→ 246 ± 74	185 ± 21	→ 208 ± 27
		hind	455 ± 94	456 ± 93	266 ± 82	→ 232 ± 63	180 ± 24	→ 224 ± 30
4	32 ± 5	fore	445 ± 69	442 ± 61	234 ± 66	→ 216 ± 48	211 ± 21	→ 226 ± 26
		hind	450 ± 62	447 ± 65	239 ± 46	→ 220 ± 52	211 ± 22	→ 227 ± 22
5	34 ± 5	fore	407 ± 81	404 ± 81	197 ± 65 ↓	→ 220 ± 71	210 ± 20 ↓	→ 184 ± 20
		hind	411 ± 80	399 ± 77	236 ± 64	220 ± 62	175 ± 18	179 ± 25
6	25 ± 6	fore	502 ± 87	512 ± 102	335 ± 78 ↓	337 ± 92 ↓	157 ± 21 ↓	175 ± 29 ↓
		hind	505 ± 93	507 ± 86	301 ± 66	305 ± 60	204 ± 38	202 ± 35
7	36 ± 9	fore	429 ± 93	425 ± 94	218 ± 79	→ 250 ± 78 ↓	211 ± 26	→ 175 ± 24 ↓
		hind	430 ± 96	431 ± 95	210 ± 65	220 ± 69	220 ± 38	211 ± 35

TABLE II

The results of regression and correlation analysis of the relationships between the step (T_C), stance (T_{st}), and swing (T_{sw}) durations in the left fore- and hindlimb and the locomotor speed in individual rats; *r*, coefficient of correlation, *a* and *b*, parameters of function $y = ax^b$, * denotes values not statistically different from zero

		T_C			T_{st}			T_{sw}		
Rat No.	limb	*r*	log*a*	*b*	*r*	log*a*	b	r	log*a*	b
1	fore	-0.92	8.26	-0.62	-0.90	9.08	-1.04	-0.48	5.98	-0.18
	hind	-0.88	8.22	-0.60	-0.85	8.21	-0.84	-0.73	6.94	-0.40
2	fore	-0.80	8.09	-0.62	-0.79	8.60	-0.96	-0.55	6.22	-0.29
	hind	-0.83	8.24	-0.65	-0.85	8.64	-0.92	-0.53	6.16	-0.31
3	fore	-0.74	7.60	-0.46	-0.74	8.01	-0.75	-0.02*	5.24	-0.01*
	hind	-0.67	7.70	-0.49	-0.70	7.89	-0.72	-0.27	5.74	-0.16
4	fore	-0.79	7.90	-0.53	-0.75	8.59	-0.93	-0.16*	5.69	-0.10
	hind	-0.74	7.75	-0.48	-0.75	7.86	-0.70	-0.43	6.09	-0.22
5	fore	-0.82	8,18	-0.62	-0.78	8.72	-0.99	-0.51	6.24	-0.26
	hind	-0.85	8.51	-0.71	-0.87	8.88	-0.98	-0.54	6.23	-0.31
6	fore	-0.79	8.36	-0.65	-0.77	8.57	-0.83	-0.40	5.77	-0.22
	hind	-0.82	8.37	-0.65	-0.60	7.57	-0.70	-0.71	7.63	-0.57
7	fore	-0.89	8.30	-0.63	-0.87	8.80	-0.97	-0.56	6.26	-0.26
	hind	-0.85	7.97	-0.54	-0.83	7.96	-0.74	-0.70	6.60	-0.35

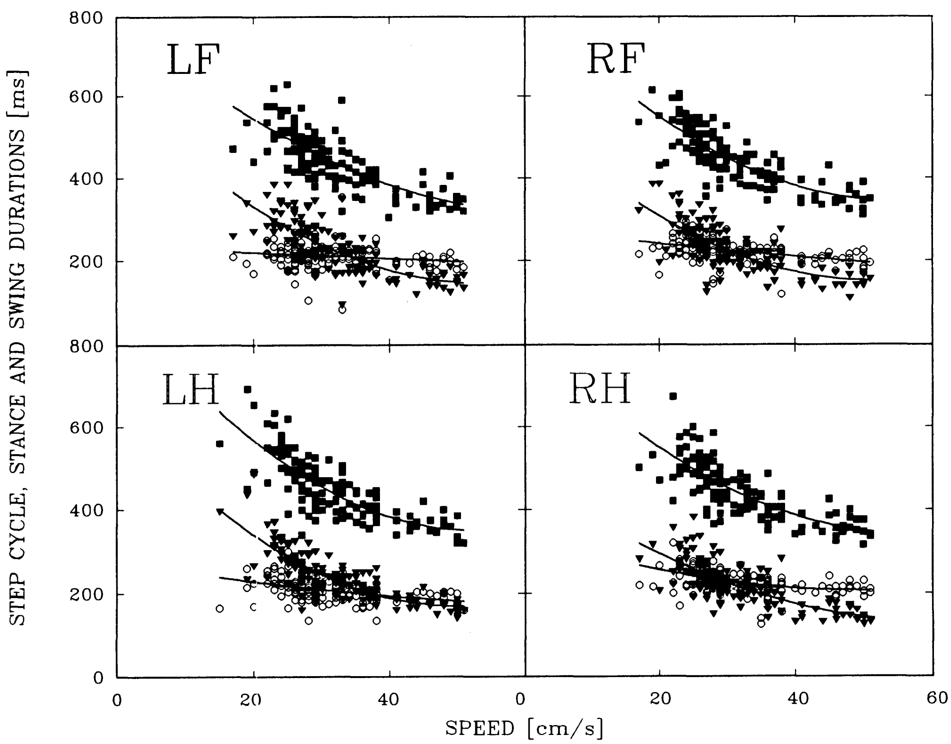

Fig. 3. The relationships between the step (filled rectangles), stance (filled circles) and swing (open circles) durations and the locomotor speed for individual limbs in rat No. 4. For abbreviations of limbs see Fig. 2. The calculated regression lines are shown. For the values of regression and correlation analysis see Table II.

-0.92 and from -0.60 to -0.90. Similar values were obtained for the right limbs (not shown). On the other hand, the swing duration was less dependent on the locomotor speed. In three limbs (Nos. 3 and 4 LF, No. 6 RF) the slopes of regression and the coefficients of correlation were not statistically different from zero (P>0.10), while in the remaining cases log a ranged from 5.74 to 7.63, the values of b from -0.13 to -0.57 and of r from -0.25 to -0.71 (data from left and right limbs taken together). Figure 3 illustrates changes in the step cycle, stance and swing phase durations as a function of the locomotor speed in the left fore- and hindlimb in rat No. 4. It could be seen that at low speed the swing duration was much shorter than the stance, while at higher speeds it was longer. The locomotor velocity at which the stance and swing durations were approximately equal ranged in the majority of animals between 20 and 40 cm/s, but in some animals (Nos. 2 and 6) values of 50 up to 60 cm/s were obtained. The step cycle duration at which the swing and stance phase equalized ranged between 240 and 620 ms.

Relationships between the stance and swing durations and the step cycle duration

The relationships between the stance and swing durations and the step cycle duration could be fitted best by using a linear model: y = ax+b. Figure 4 shows an example of the regression lines relating the stance and swing phases to the step cycle duration obtained in rat No. 4, while the results of the correlation and regression analysis for each limb and each rat are shown in Table III. The slopes of regression lines a for the stance phase ranged between 0.63 and 0.88, while the values of the coefficient of correlation r ranged between 0.86 and 0.97. On the other hand, the slopes for the swing phase duration were more flat, which shows that the swing phase was less dependent on the step cycle duration than the stance phase. The slopes of the regression line a for the swing phase ranged from 0.12 to 0.37 and the values of coefficients of correlation r between 0.25 and 0.88.

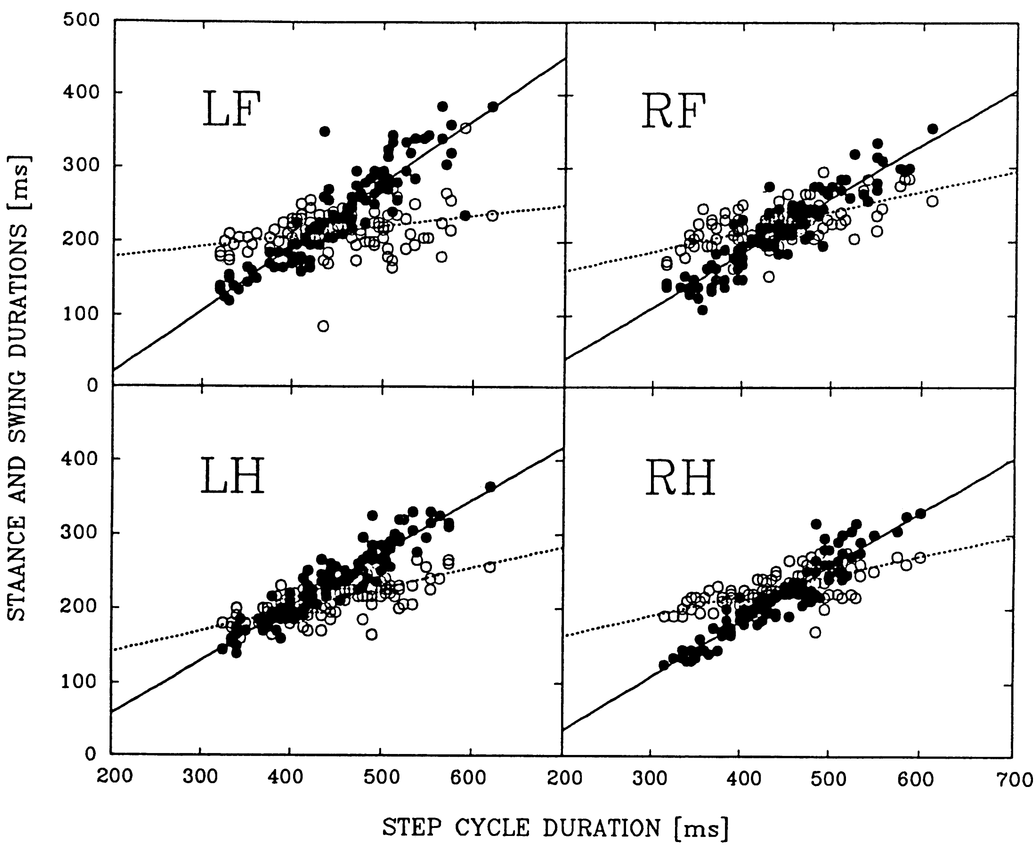

Fig. 4. The relationships between the swing (open circles, dotted line) and stance (filled circles, continuous line) durations and the step cycle duration. Cat No. 4, all four limbs. See Fig. 2 for abbreviations of limbs and Table III for the values of slopes of regression lines and coefficients of correlation.

TABLE III

The results of regression and correlation analysis of the relationships between the stance and swing duration and the step cycle duration in individual rats; *a*, slope of linear regression lines, *r*, coefficient of correlation

		Stance vs. step				Swing vs. step			
		left limbs		right limbs		left limbs		right limbs	
Rat No.	limb	*a*	*r*	*a*	*r*	*a*	*r*	*a*	*r*
1	fore	0.82	0.96	0.71	0.98	0.18	0.25	0.29	0.88
	hind	0.64	0.93	0.67	0.94	0.36	0.69	0.33	0.82
2	fore	0.73	0.68	0.68	0.88	0.27	0.73	0.32	0.63
	hind	0.78	0.71	0.71	0.86	0.22	0.63	0.29	0.68
3	fore	0.87	0.93	0.79	0.93	0.13	0.41	0.21	0.65
	hind	0.82	0.92	0.63	0.87	0.18	0.55	0.37	0.61
4	fore	0.88	0.95	0.70	0.89	0.12	0.39	0.30	0.63
	hind	0.67	0.94	0.72	0.91	0.33	0.67	0.28	0.79
5	fore	0.76	0.91	0.84	0.94	0.24	0.53	0.16	0.58
	hind	0.76	0.94	0.75	0.92	0.24	0.60	0.25	0.64
6	fore	0.84	0.97	0.88	0.95	0.16	0.53	0.12	0.51
	hind	0.74	0.89	0.68	0.95	0.26	0.71	0.32	0.82
7	fore	0.81	0.95	0.80	0.96	0.19	0.64	0.20	0.65
	hind	0.64	0.94	0.68	0.94	0.36	0.82	0.32	0.79

Inter- and intraanimal variability

To assess the interanimal variability we have compared (from the regression lines shown in Table II) the durations of the step cycle, stance and swing phases which occurred or would occur in different animals at speed of 20 and 50 cm/s. For v = 20 cm/s the differences between the minimal and maximal step duration were 129 ms (step range: 494-623 ms), while for the stance and swing phases 220 and 185 ms, respectively (stance range: 218-438 ms; swing range: 166-351 ms). For v = 50 cm/s these differences for the step cycle were 73 ms (step range 287-360 ms) and about 90 ms for the stance and swing phases (stance range 111-204; swing range 134-223 ms). This corresponds to the data obtained in cats walking on a treadmill (Halbertsma 1983, Vilensky and Patrick 1984) or overground (Górska et al. 1993a).

The interlimb differences in the same animal were limited to the stance and swing phases, and the differences in the mean step cycle duration were not statistically significant in all the animals (Table I). The maximal mean difference in the step cycle duration amounted to 12 ± 23 ms (No. 5 LH-RH)

In the majority of rats the mean durations of the stance phases, and hence the swing phases, differed significantly (by 18 to 50 ms) either between homologous or homolateral limbs (cf. Table I) The maximal mean difference was 55 ± 16 ms (rat No. 1 LH-RF, Table I).

To see whether this interlimb variability was not due to the method of recording, i.e., differences in the placement of the electrodes in individual limbs at the beginning of the experiment or some displacement during the experiment, we have also analysed the relationships between the durations of the step cycles and of the stance phases in pairs of homologous and homolateral limbs, as well as the relationships between the differences in the step cycle and in the stance durations between these pairs of limbs and the step cycle duration of the corresponding limb.

In each rat, the step cycle durations in the homologous and homolateral pair of limbs were strongly correlated with $r \geq 0.85$ and the slopes of the corresponding regression lines ranging between 0.82 and 1.01. The stance durations in the pairs of homologous and homolateral limbs were also strongly correlated, similarly to the step cycle durations, with $r \geq 0.83$ and the slopes of the regression lines ranging between 0.83 and 1.11. In addition, both the differences in the step cycles and in the stance phases were not correlated, or only weakly, with the step cycle duration of the corresponding limb (r for the step ranged between 0.06, P=0.67 and 0.37, P<0.01; for the stance between 0.01, P=0.91 and 0.48, P<0.01). Figure 5 shows relationships between these variables in rat No. 3, in which the correlation coefficients were the greatest. It could be seen that the differences in the step cycles as well as in the stance phase durations did not exceed 100 ms. All this suggests that the interlimb variability was due to an inherent feature of locomotion in a given rat, rather than to an asymmetrical position of the electrodes on both limbs. This is corroborated by the results of our control experiments in which we found that the difference in the measurements between the usual placement of the electrodes in the hindlimb compared to their placement on the tip of the third toe was about 20 ms. Since the differences observed by us in the stance and swing phases were usually greater than 20 ms they could not be attributed to the method employed.

DISCUSSION

The overall picture of intact rat locomotion obtained in the present study is in general similar to that described by other authors who used the methods of video or cinematographic records (e.g. Cohen and Gans 1975, Hruska et al. 1979, Westerga and Gramsbergen 1990, Clarke 1991, Molinari and Petrosini 1993, Clarke and Wiliams 1994), EMG analysis (i.e. Cohen and Gans 1975) or other methods (Clarke and Parker 1986). A detailed comparison is, however, difficult due to the fact that various authors analysed different indices of gait and range of speed.

A decrease of step and stance phase with an increase of locomotor speed, best described by the function logy = A+Blogx was found by Hruska et al. (1979), who analysed a relatively small (ca 60) sample of steps obtained in 19 untrained rats, moving freely in a walkway with speed ranging from 20 to 80 cm/s. A curvilinear model regarding the step cycle and the stance phase was also described by Westerga and Gramsbergen (1990), who

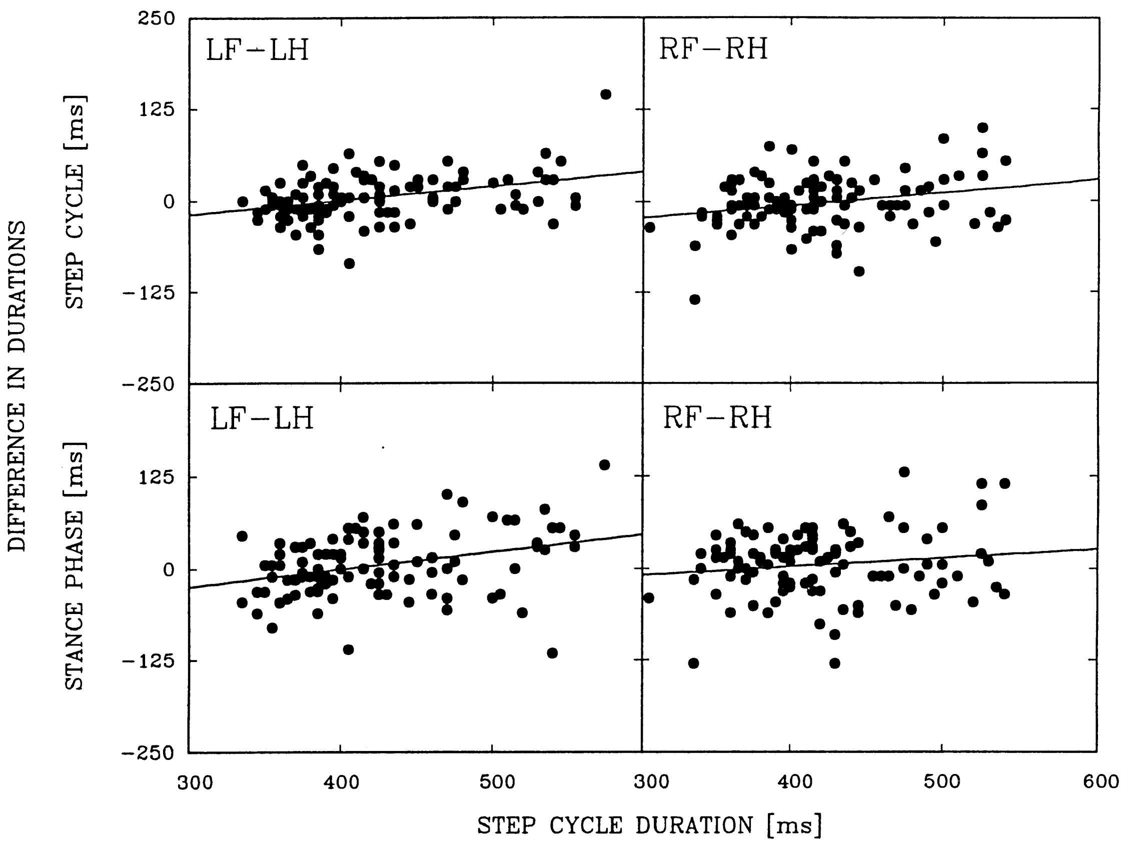

Fig. 5. The relationships between the differences in the step cycle duration (upper two graphs) and in the stance phase duration (lower two graphs) in homolateral limbs and the step cycle duration in the corresponding (LF or RF) forelimb. Rat No. 3. Abbreviations as in Fig. 2.

studied the development of free walking in 10- to 20-day-old pups. In the oldest rats, walking at a speed of 9-24 cm/s, the relationships between the duration of the step cycle and of the stance phase and the locomotor velocity were similar and were best fitted with the power function. The correlation coefficient increased with age and in the oldest pups was -0.94 for the stance phase and -0.96 for the step. This shows that, in spite of age and the speed differences, not only was the type of relationships similar as in our experiments, but also its strength, since the *r* values in the present experiments ranged from -0.67 to -0.92 for the step and -0.60 to -0.90 for the stance. Furthermore, Yaknitsa et al. (1985) found that during stepping movements in restrained intact rats the changes in duration of the cycle were due mainly (by 90%) to the duration of the stance phase.

The relationships between the swing phase and the speed of locomotion are more controversial in the literature. The swing duration in the experiments of Hruska et al. (1979) did not change across the analysed speed (20-80 cm/s). The average swing time ranged in various limbs from 121 to 138 ms. These results were not confirmed by Clarke (1991), who found in a much greater sample of steps ($n = 416$) gathered in 40 animals walking at velocities between 10.6 and 41.7 cm/s, that the swing phase contributed to the step adjustment. This contribution depended on the velocity of locomotion and was much greater for shorter steps (600-200 ms) than for longer (1,000-600 ms) ones. However, the results of Westerga and Gramsbergen (1990) were similar to ours. In their experiments on pups, the swing phase duration decreased across ages with increasing speed, although much less than the stance. Other authors who studied the quantitative aspects of rat locomotion limited themselves to describing changes in the stride frequency with increased speed (Heglund et al. 1974, Cohen and Gans 1975, Clarke and Parker 1986). These parameters were positively correlated and described using a linear model.

The comparison of the step, stance and swing durations obtained in our experiments with the data of other authors present difficulties due to the different ranges of speed analysed by various authors. However, data obtained for the step cycle duration in our experiments do not seem to vary much from the data in the literature. At a locomotor speed of v = 20 cm/s, Heglund et al. (1974) reported a step cycle duration of 664 ms (1.6 Hz) and Hruska et al. (1975) of approximately 500 ms (data calculated from his Fig. 3), while in our experiments we obtained values of 494 to 623 ms. At speed close to 50 cm/s the reported step duration was approximately 300 ms (Heglund et al. 1974, Clarke and Parker 1986), 350 ms (Hruska et al. 1979) and 370 ms (Cohen and Gans 1975), while we obtained values between 287 and 360 ms. For the stance and swing duration the only possible comparison is with the pooled data calculated from Hruska et al. (1979) experiments (cf. his Fig. 3). At v = 20 cm/s the stance phase lasted approximately 350-400 ms, while in our experiments it lasted 218-438 ms. At v = 50 cm/s the stance phase lasted approximately 200 ms, while in our experiments it ranged from 111 to 204 ms. The swing duration in the experiments of Hruska et al. (1979) did not depend on the locomotor speed and lasted ca 130 ms, while in our experiments it decreased from 166-346 ms at v = 20 cm/s to 134-223 at v = 50 cm/s (data calculated from the regression lines). It is also worth mentioning that, according to Hruska et al. (1979), the stance and swing durations became equal at speed of ca 80 cm/s, while in our experiments it occurred mainly at speeds ranging from 20-40 cm/s. Similar to ours results were, however, the data obtained by Westerga and Gramsbergen (1990) who found that the swing and stance phases in pups 20 days old became equal at the speed of 0.24 m/s, i.e. step cycles corresponding to ca 400 ms.

Our results concerning the linear relationships between the duration of the stance and swing phases with the step cycle are similar to those reported in cats moving on a treadmill (Halbertsma 1983) or overground (Górska et al. 1993a), in which the slopes of the regression lines for the stance phase were also steeper than for the swing. In decerebrate rats, a linearity between the duration of the extensor and flexor EMG bursts and the step cycle duration was found by Nicolopoulos-Stournaras and Iles (1984). The correlation was weak for flexor muscles and stronger for extensor muscles (slope of linear regression 0.16 and 0.53, respectively). Similar results were obtained by Goudard et al. (1992) and Bem et al. (1993) in acute thalamic cats. The coefficient of correlation for the duration of extensor muscle bursts and the step cycle duration in spontaneous locomotor movement and in fictive locomotion, elicited by stimulation of the lateral hypothalamic area, ranged from 0.97 to 0.99, while that for the flexor muscle bursts between 0.16 and 0.68 depending on the type of preparation and the muscle examined. In our experiments on intact rats there was a large difference between the slopes of regression lines for the relationships of the stance and swing phase durations and the step cycle duration (slopes for the stance 0.63 to 0.88;

for the swing 0.12 to 0.37) whereas the coefficient of correlation did show much smaller differences (r for the stance 0.86-0.97; for the swing 0.25 to 0.88; cf. Table III).

Comparison of the data obtained in individual animals in the present study points to interanimal and interlimb differences in the way they locomote. Both the durations of the step cycles performed at similar speed by different animals as well as the swing and stance duration in different limbs in the same animal were not equal. Since the experimental data obtained in rats by various authors on different animals were usually pooled together, no comparison of the extent of inter- and intraanimal variability in rat locomotion can be made. However, our results are consistent with the data obtained in cats moving on a treadmill (Halbertsma 1983, Vilensky and Patrick 1984) or overground (Górska et al. 1993a). In our previous experiments on cats (Górska et al. 1993a) the interanimal variability of the step cycle durations was approximately 100 ms in overground locomotion (speed 0.65 m/s) and similar data could be deduced for the same speed from Halbertsma's (1983) data for cats walking on a treadmill. In the study of Vilensky and Patrick (1984) on cats moving on a treadmill, the stride duration performed by different animals at the same speed could vary up to 80 ms and similar differences were observed between the maximum and minimum stride durations in the same animal moving at the same speed on the treadmill. The same authors reported that the intratrial differences between the swing and stance duration in different steps may vary up to 70-80 ms. This is consistent with our data in which differences in the step and stance phase duration in individual animals spanned 100 ms (cf. Fig. 5). As far as the interlimb differences are concerned, in our previous study (Górska et al. 1993a) we often observed differences of 30-50 ms between the mean stance or swing duration in various limbs in cats. In the present experiments on rats, the mean interlimb differences in the stance and swing phases ranged varied up to 55 ms. These differences could not be due to a different placement of the electrodes in particular limbs, because there was no or only weak correlation between the interlimb differences in the duration of the stance phase and the step cycle. Moreover, the strength of correlation between the stance durations in different limbs shows that, even if the electrodes created differences between the individual limb stance durations, these differences were too small to manifest themselves as an additional measurement error. The similarity of the strength of correlations between the stance durations with correlations between the step cycle durations shows additionally that the electrode placement did not create any remarkable errors.

The resemblance of the overall picture of locomotion obtained in the present experiments in rats to other tetrapods (Grillner 1975), as well as to the results of other authors who studied locomotion in rats with other methods, warrants the conclusion that contact electrode recording is a reliable method that in the future may be used in studies of rat locomotion after central nervous system lesions. Moreover, this method is simple and noninvasive and enables the collection of large sets of data in individual animals, which can be automatically processed.

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