Effects of unilateral somatosensory cortex lesion upon locomotion in dogs

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Abstract. Locomotive limb movements were studied in 6 dogs before and after unilateral (right) primary somatosensory cortex (SI) lesion. Single limb movement parameters as well as interlimb coordination in lesioned dogs differed significantly from the parameters measured before surgery. Both left limbs showed a proprioceptive deficit and were more flexed during normal posture and during locomotion. This resulted in prolonged stance in the left fore and in the right hind legs. The symptoms were greatly pronounced in the left fore limb compared to a slightly impaired left hindlimb. Due to the proprioceptive deficit, the dogs did not have satisfactory control over the position of the distal part of the front limb which caused frequent stumbling and even falling. The symptoms were transient and fully compensated after 3-4 weeks.

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INTRODUCTION

Limb locomotive movement, including single limb and interlimb coordination commands, is provided by spinal and supraspinal circuitry contributing to the so-called central pattern generator (for review see Wetzel and Stuart 1976, Grillner 1981). During normal overground locomotion, the central nervous system appears to have access to a functionally useful input from a range of peripheral receptors in addition to internally generated signals (Gandavia and Burke 1992). Thus, all kinds of sensory inputs which are determined by the external constraints of the locomotion influence both single limb movement parameters and interlimb coordination. These influences can act *via* local as well as long neural loops including the sensory and motor cortex (Angel 1977). Thus, a modulatory role of the cerebral cortex in normal locomotion has been suggested; however, no sufficient experimental data has been presented to support this view. The existing data have shown that even decerebrate animals can walk without a noticeable deficit (Orlovsky 1969, 1972, Wetzel and Stuart 1976, Zomlefer et al. 1984). However, the studies of decorticated animals were routinely performed on a motor driven treadmill which significantly alters locomotive control (Wetzel et al. 1975, Błaszczyk and Loeb 1993). Additionally, many researchers reported a motor deficit in dogs with a SI sensory cortex lesion (Stępień and Stępień 1959, Stępień et al. 1961, Dobrzecka et al. 1964, 1965, Ivanova 1973). The purpose of the presented investigation was to quantify the characteristics of overground locomotion in dogs with a unilateral somatosensory cortex lesion.

METHODS

Subjects and experimental procedure

Six adult mongrel dogs (2-4 years old, 12-17 kg body weight) were trained to walk and run on a stationary experimental platform. The performance of the task was reinforced with food that was offered at both ends of the runway. Aversive stimuli were never used. During these trials, dogs were allowed to move at their own preferred speeds, which ranged from 0.9 to 3.7 m/s. The runway was long enough to accommodate about 10-12 strides from the standing start, but only 8-9 strides of steady state trotting from each trial were taken for analysis. The first and last steps of these regular sequences were discarded because of differences in the duty factor that are known to occur during the acceleration and deceleration phases (Błaszczyk and Dobrzecka 1989, Błaszczyk and Loeb 1993).

The method of two-dimension gait diagrams was used to evaluate interlimb coordination and to measure single limb movement parameters. The detailed account of the recording technique is available elsewhere (Afelt et al. 1983a, Błaszczyk and Dobrzecka 1989). In essence, dogs were moving freely along an 8 m long and 1 m wide metal mesh mate. The ends of the mesh were connected to a low voltage DC power supply so that the voltage drop along the mesh platform was linear. Thus, the platform created an 8 m long ruler which allowed for easy recording of spatial and temporal locomotive limb movement parameters.

Swing stance epochs and the position of particular limb placement were recorded from four limbs simultaneously by means of custom made contact electrodes. The electrodes were fixed to the pad of the third digit of each foot. Foot contact with the mesh, i.e. the stance phase, was recorded as a square pulse the amplitude of which was proportional to the distance along the platform and its width depended on stance duration. Such a sequence of pulses recorded simultaneously for all four legs creates a two-dimensional gait diagram (Fig. 1A). Using such measurements, limb symmetry factors were computed as a ratio of the right limb to the left limb stance durations during successive strides for the fore and hind limbs respectively.

After two-day preliminary training, the locomotion of the dog was recorded and main parameters describing the movement were calculated. Normal overground locomotion was recorded twice a week for 5 weeks.

Surgical procedure

Unilateral cortical lesions were performed in all the dogs studied after five weeks. Ablation of the right sensory cortex (SI) was performed under aseptic conditions under general anaesthesia. On the day of surgery, the animals were sedated with ketamine hydrochloride (10 mg/kg i.m.). The dog was then anaesthetized with minimal dose of barbiturate (Nembutal, 25 mg/kg i.p.). Supplements of intravenous barbiturate were administered throughout surgery as required. The animal was placed on a heating pad to control its body temperature and its head was secured in a head holder. Skin was cut along the midline; m. temporalis was resected along the margin of its aponeurosis and pushed retracted without injury. The skull of the dog was opened and the cerebral tissue was removed by subpial aspiration. The area of the lesion was bordered by gyrus ansatus, coronal sulcus and fissura longitudinalis. Care was taken to avoid a damage of the white matter. The extent of the cortex ablation is shown in Fig. 1. After surgery, the wounds were closed in anatomical layers with silk sutures. The animals were then placed in an incubator to maintain body temperature before being moved to a postoperative treatment room. As a prophylactic measure against infectio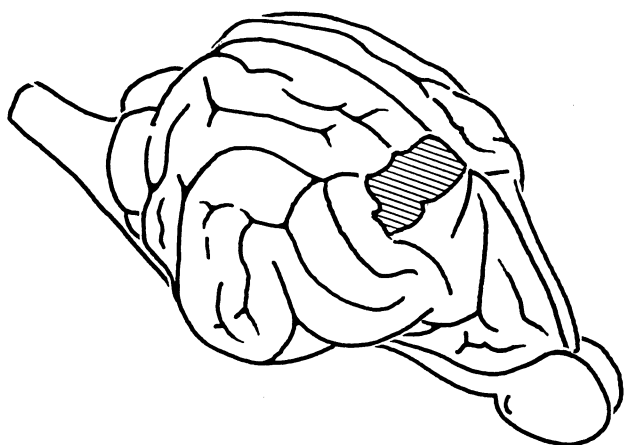n, all animals received gentamicin sulfate (5 mg/kg, i.m.) on the day of surgery and on five consecutive postoperative days.

Statistical analysis of the data

Recordings of limb movements were registered for five weeks, twice a week, beginning on the second day after surgery. The dependent measure was the symmetry factor calculated during constant speed symmetrical locomotion (trot). The individual mean and standard deviation for each trial as well as the mean for all trials were calculated. The effect of the surgery was analysed using a repeated measure ANOVA with two trial factors (2 x 5 x 2, operation x week x leg). Subsequent analysis involved the Duncan test performed for the fore- and hind-limbs separately.

RESULTS

Normal overground locomotion

All six dogs moved with typical walking, trotting and transverse gallop patterns. It was possible to distinguish three characteristic periods of locomotor activity. The first, a period of intensified activity, was only observed during the first 10-30 trials. During this period the dogs galloped at high speeds. Following the initial period of intensified locomotion, velocity of locomotion decreased and became stabilized, so that the animals trotted at an almost constant speed ranging between 1.3 and 3.7 m/s depending upon size of the dog (especially limb length). Finally, during the third period of extinguishing locomotor activity, the tired animals began to slow down and walked for few trials. Therefore, during each experimental session several hundred steps at various velocities were recorded. However, only strides of steady state trotting were taken into account. The limb movement parameters in trotting dogs are shown in Table I.

Effects of SI lesion upon locomotion

All the dogs studied could walk and run as soon as they recovered from the anaesthesia. Typical

Fig. 1. The right hemisphere of the dog brain with indication of the somatosensory cortex lesion.

TABLE I

Limb movement parameters (mean for four limbs) in dogs during overground locomotion. The postsurgery data are shown in brackets

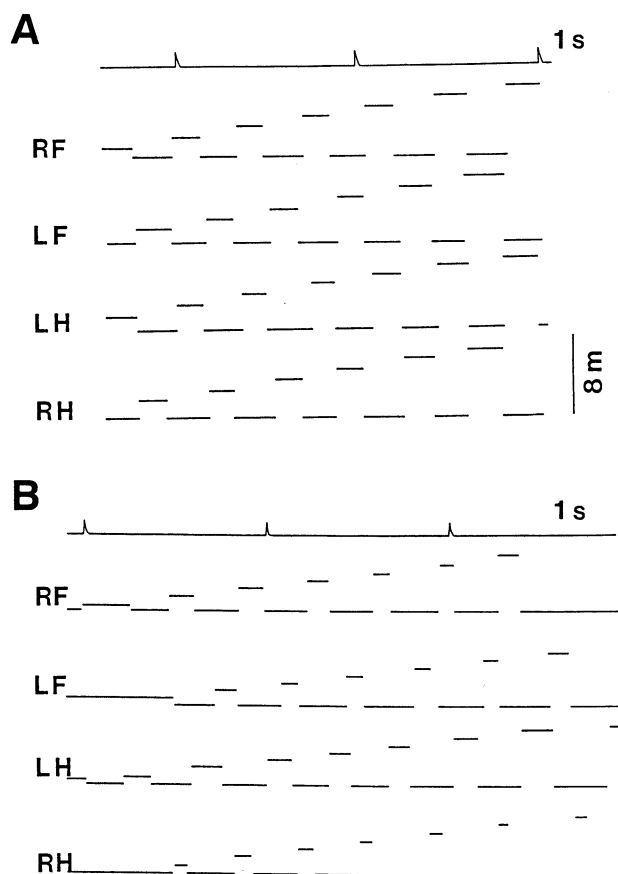| Dog	Velocity range m/s	Number of steps	Stance ms	Swing ms
1	1.7-2.9	640	198±29	261±13
	(1.3-2.4)	(238)	(228±19)	(241±9)
2	1.5-2.1	516	210±23	254±17
	(1.1-1.3)	(68)	(223±11)	(231±9)
3	1.9-2.7	456	176±18	230±8
	(1.5-1.7)	(46)	(196±9)	(236±10)
4	1.4-1.8	394	188±18	253±11
	(1.2-1.4)	(112)	(193±21)	(247±18)
5	1.7-2.7	118	153±13	210±12
	(1.5-1.9)	(96)	(168±15)	(218±16)
6	2.6-3.7	216	161±24	218±14
	(1.8-2.3)	(82)	(176±17)	(230±14)

Fig. 2. A typical 2-D gait diagram of overground trotting in normal dog (A), and 3 days after SI cortex lesion (B). Subsequent traces show the sequences of swing (low level) and stance (high level) phases of the individual limbs: RF, right forelimb; LF, left forelimb; LH, left hindlimb; RH, right hindlimb.

examples of 2-D gait diagrams in the dog before and after lesion are shown in Fig. 2. After unilateral SI sensory cortex lesion, the impairment of locomotion was confined to the contralateral limbs which were both hyperflexed during quiet stance and locomotion, causing body tilt toward this side. While standing, the dogs had a tendency to lean on the wall or on the experimenter's leg. Similarly, during the test, all dogs preferred running while touching the wall with their left body side. The dogs slid on the flat surface, put one leg on the other and crossed limbs very often.

Another, and most pronounced symptom of the unilateral somatosensory cortex lesion was the impairment of the distal part of the fore left limb. There was a tendency for the fore foot to 'knuckle under' in stance due to inadequate dorsiflexion of the wrist and digits. The animal did not correct the error when it appeared. Such impairment of the distal part of the fore limb resulted in frequent stumbling (observed as a rapid changes in the stance phase durations, see Fig. 2B) and even falls while walking and running. The effect of the lesion was clearly seen during steady state locomotion when limb movements were rather unperturbed beside that of the exaggerated left side swing phase. The foot contact pattern of the left limbs was characterized by an irregular duration of the stance phase duration as compared to the perfectly regular and unaffected pattern recorded before the SI lesion in the same dog. The unilateral phase shift which remained constant in normal dogs in a wide range of locomotor velocity was changed from step to step due to stumbling and changes in speed. All the symptoms of the lesion
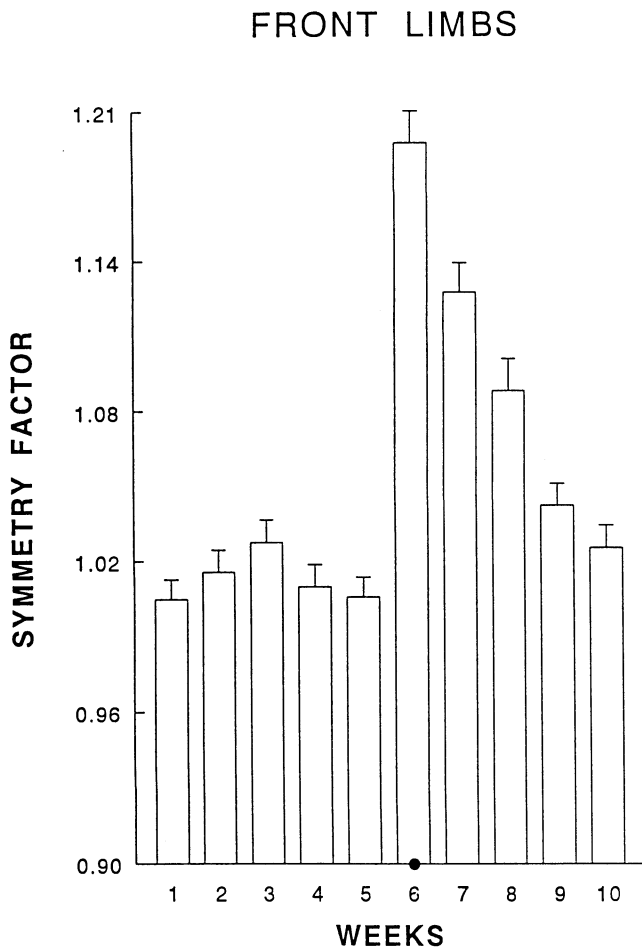
FRONT LIMBS

Fig. 3. Forelimb symmetry factors during symmetrical gaits in dogs with the unilateral somatosensory cortex lesion. The black dot on the x axis marks the first postsurgery week. The error bars represent standard error.
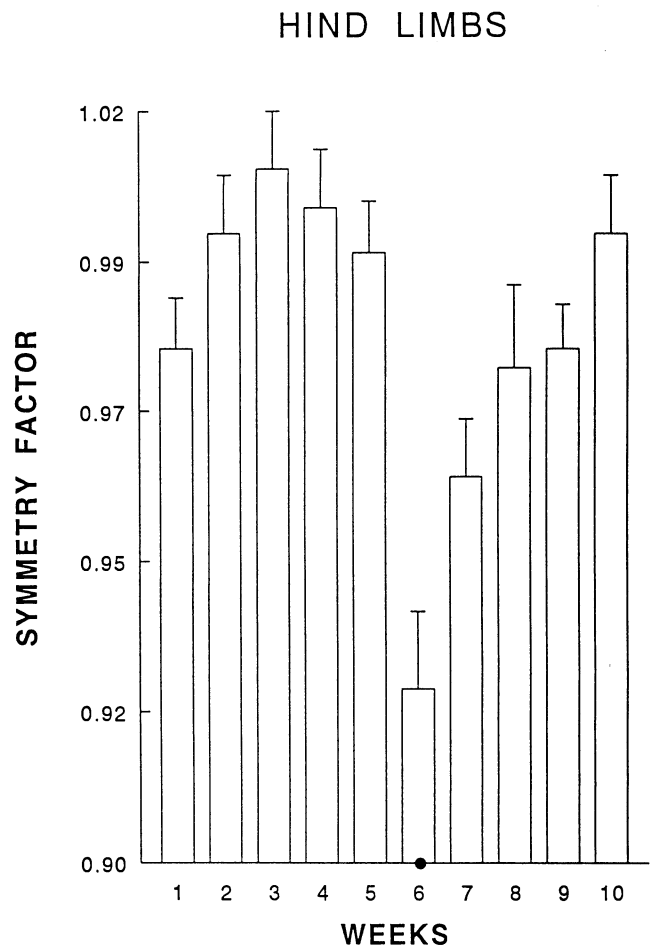
HIND LIMBS

Fig. 4. Hindlimb symmetry factors during symmetrical gaits in dogs before and after the unilateral somatosensory cortex lesion. The black dot on the x axis marks first postsurgery week. The error bars represent standard error.

differed in the fore limb and the hind limb. The symmetry factors before and after surgery were statistically different $(F_{1,10}=23.3, P<0.001)$. The step cycle structure (duty factor) of both left limbs were changed in a different way. Whereas in the left fore limb we observed a decrease of stance phase duration with simultaneous lengthening of the swing phase as compared with the right forelimb (Fig. 3), the effect seen in the hind limbs was opposite in character, i.e. there was an increase of stance phase duration (mean increase 16.3 ± 0.6 ms) during the first postsurgery week with shortening of the swing phase and hind limb movement amplitude (Fig. 4). The interaction (leg x surgery factors) was highly

significant, $F_{1,10} = 96.8, P<0.001$. The changes in the stance and swing phase durations were interdependent; thus, the step cycle of all limbs remained similar.

All the symptoms were transient and dependent upon the postsurgery period (significant leg x week interaction $F_{4,40} =30.91, P<0.01$). However, locomotive parameters of the animals were not readily distinguishable from normal dogs after 4-5 weeks. The Duncan test performed for the fore- and hindlimbs separately established statistically significant differences for front leg symmetry factors during four consecutive postsurgery weeks. In contrast, changes in the hind limb were less pronounced and

TABLE II

Results of the Duncan test for the forelimb symmetry factors. The tabled values represent the level of significance of the difference between symmetry factors in a particular week of study listed above and to the left (NS, not significant)

	Week								
Week	2	3	4	5	6	7	8	9	10
1	NS	NS	NS	NS	0.001	0.001	0.01	0.05	NS
2		NS	NS	NS	0.001	0.001	0.01	NS	NS
3					0.001	0.001	0.05	NS	NS
4					0001	0.001	0.01	0.01	NS
5					0.001	0.001	0.01	0.05	0.001
6						0.01	0.001	0.001	0.001
7							0.05	0.001	0.001
8								0.05	0.01
9									NS

TABLE III

Results of the Duncan test for the hindlimb symmetry factors. The tabled values represent the level of significance of the difference between symmetry factors in a particular week of study listed above and to the left (NS, not significant)

	Week								
Week	2	3	4	5	6	7	8	9	10
1	NS	0.05	NS	NS	0.01	NS	NS	NS	NS
2		NS	NS	NS	0.01	0.05	NS	NS	NS
3			NS	NS	0.001	0.01	0.05	0.05	NS
4				NS	0.001	0.01	0.05	NS	NS
5					0.001	0.01	NS	NS	NS
6						0.01	0.001	0.001	0.001
7							NS	NS	0.01
8								NS	NS
9									NS

recovered earlier to the base line. The results of the Duncan test are shown in Tables II and III. However, impairment in the control of the distal part of the left fore limb was occasionally observed in exhausted animals even six months after surgery.

DISCUSSION

One of the major problems solved during overground locomotion is the maintaining of dynamic stability in the face of continuous changes in support conditions. For the external observer, this adaptive process is based upon adjustments of the limb support phase to changing environmental conditions. During unperturbed symmetrical gaits (walk, trot, pace) the two limbs of front and rear girdle perform exactly the same movement. That movement is described by the symmetry factor equal to 1. In our study, all the dogs trot before surgery with a symmetry factors close to 1 (see week 1-5 in Figs. 3 and 4). Small deviation of the symmetry factor from unity was due to limited accuracy of the applied measurement method. The error of the stance phase duration measurement did not exceed 5% in our study.

Locomotion in dogs observed after unilateral sensorimotor cortex lesion differed significantly from locomotion of normal animals. Generally, the dogs moved more slowly and, therefore, a direct comparison of the stance phase durations was not possible. This limb movement parameter depends in a nonlinear fashion upon the velocity of locomotion (Afelt at al. 1983b, Błaszczyk and Dobrzecka 1989). Thus, the symmetry factor was the most convenient parameter for evaluating the effects of the lesion.

The consistent result of this study was the transient change in the limb movement parameters following surgery. A possible explanation for the retained accuracy of the locomotor limb performance following somatosensory cortex ablation is that the nervous system gradually adapts to the altered cortical inputs. Multi-level control and control redundancy of the central pattern generator results in fast compensation of a single input impairment.

It also seems interesting that the changes were differently manifested in the fore and hind limbs. This might result from different representation of the fore and hind limb in the sensory cortex in the dog (Pinto-Hamuy et al. 1956, Górska 1974). The

major supraspinal structures that control the spinal cord have a discrete somatotopic organization on which an orderly arrangement of peripheral inputs is mapped. In the motor cortex, there is a clear relation between the muscles controlled by local aggregates of neurones and the sites in the periphery which provide sensory input to these neurones. The major sensory input arise from somatosensory cortical area. There is an ordered topographic representation of the contralateral body surface along a mediolateral strip of the cortex termed the primary somatic projection area or SI. The SI area receives sensory information from muscles, skin and joint receptors. This area is involved in the kinaesthetic sense of limb position (for review see Angel 1977, Gandavia and Burke 1992).

The distorted figurine of the body surface is projected onto the cortical surface. The distortion in the cortical area of this representation depends upon the use and sensitivity of the peripheral part, not on its absolute size. This provides a remarkable enlargement of the sensory area for the forepaw (Angel 1977). Such cortical organization might explain the significant deficit in the forelimb control as a whole, and its distal part in particular, as observed in our experiment. In contrast, the locomotor deficit in the hindlimb was not pronounced so clearly, possibly accounting for the hindlimb projection to SI area which is not strictly contralateral and more complex compared to those of the front leg (Angel and Lemon 1975). Thus, we would attribute the changes in locomotive movement, differently pronounced in both left limbs, to the different anatomical organization of the fore and hind limb cortical representations.

The locomotor limb movement deficit was almost completely compensated after 3-4 weeks in the hindlimbs and after 4-5 weeks in the forelimbs. The transient effects of the unilateral SI area lesions may result from a functional reorganization of the connection between SI and ipsilateral SII sensory cortex and interhemispheric connections running via corpus callosum (Armand and Kably 1993). Barth et al. (1990) showed that in case of such a lesion the homotopic contralateral cortex may take over the function of the damaged area. The latter connections, however, are absent between both SI and SII in the projection area of the distal body parts (Ebner and Myers 1965).

The changes in the symmetry factors as observed in our experiment could be also explain in terms of locomotor neural control mechanisms. Command controlling muscle activities during locomotion arise as a result of the integration of central and peripheral inputs at the spinal cord level. The diagonal coupling is widely accepted as the basic element of the spinal control of locomotiom (Schomburg et al. 1986). Thus the deficits produced by the somatosensory cortex lesion in the left forelimb would be readily transfered to the diagonal right hindlimb. This might also explain why changes in stance duration of the left fore and hind limbs were opposite.

In conclusion, our experiment supports the hypothesis that SI somatosensory cortex is involved in the adjustment and tuning of limb movement parameters. This cortical control allows on-line adaptation of locomotive limb parameters to the variability of internal and external movement constraints.

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