STEPPING MOVEMENTS OF THE FORELIMBS AND THE SCHIFF–SHERRINGTON PHENOMENON

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The precollicular cat, in which the ventral edge of the section through the brain stem passes between the mammillary bodies and the point of exit of the roots of the third pair of cranial nerves, does not perform stepping movements either spontaneously or on the moving belt of a treadmill, but locomotion can be induced in such an animal by stimulation of the "locomotor" region of the mesencephalon [3, 4]. After a more caudal transection of the brain stem, so that the ventral edge passes through the anterior boundary of the pons, locomotion can no longer be evoked even by stimulation of the mesencephalon. In both preparations, however, after division of the spinal cord in the lower thoracic region, when extensor rigidity of the forelimbs is increased (the Schiff–Sherrington phenomenon), stepping movements of the forelimbs can be obtained on the moving belt of the treadmill and without stimulation of the mesencephalon.

Division of the spinal cord in the lower thoracic region is accompanied by an increase of decerebrate rigidity and of certain reflexes of the extensor muscles of the forelimbs (the Schiff–Sherrington phenomenon) [13, 14]. The rigidity of the forelimbs is not relaxed after deafferentation of the lumbo-sacral region of the spinal cord [12]. Consequently, the facilitation is due to removal of the ascending tonic inhibitory effects of the propriospinal neurons and not of the ascending afferent flow. Facilitation of some reflexes of the forelimb muscles is observed, it will be noted, after postbrachial transection of the spinal cord even in the decapitated cat [14]. This means that tonic inhibitory ascending effects on rostral segments of the spinal cord can be transmitted not only through the brain stem, but also along propriospinal pathways. Even reflexes of the upper lumbar segments in the spinal cat are facilitated after transection at the level L5-L6 [7].

In the present investigation acute experiments were carried out on mesencephalic cats, which cannot perform stepping movements either spontaneously or on the moving belt of a treadmill [4, 9]. Deafferentation of the hind limbs likewise does not make such a preparation able to walk along the moving belt of a treadmill; this is possible only during stimulation of the mesencephalic locomotor area (MLA) [2]. However, as will be described below, after division of the spinal cord in the lower thoracic region the forelimbs of the mesencephalic cat can perform stepping movements along the moving belt of a treadmill even without stimulation of MLA.

EXPERIMENTAL METHOD

After tracheotomy and ligation of the common carotid arteries of 19 cats under ether anesthesia, precollicular decerebration was carried out so that the ventral border of the section passed caudally to the mammillary bodies but rostrally to or through the point of exit of the roots of the third pair of cranial nerves (Fig. 1, Section II). The spinal cord was divided at the level of vertebrae T10-11. In six experiments additional transection of the brain stem was carried out under repeated ether anesthesia so that the ventral border of the section passed caudally to the roots of the third pair of nerves (Fig. 1, section between levels III and IV).

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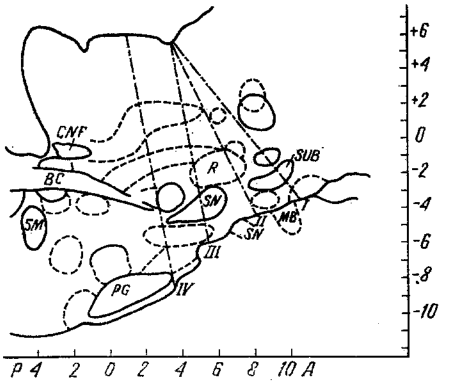

Fig. 1. Scheme of section through brain stem (after [5]): BC) brachium conjunctivum; CNF – nucleus cuneiformis; MB) mammillary bodies; 5M) trigeminal motor nucleus; PG) pontine gray matter; R) nucleus ruber; SN) substantia nigra; SUB) subthalamic nucleus. Structures surrounded by continuous line are in the parasagittal plane passing through the mesencephalic locomotor area (4 mm laterally to the medium plane). Structures surrounded by a broken line are situated medially.

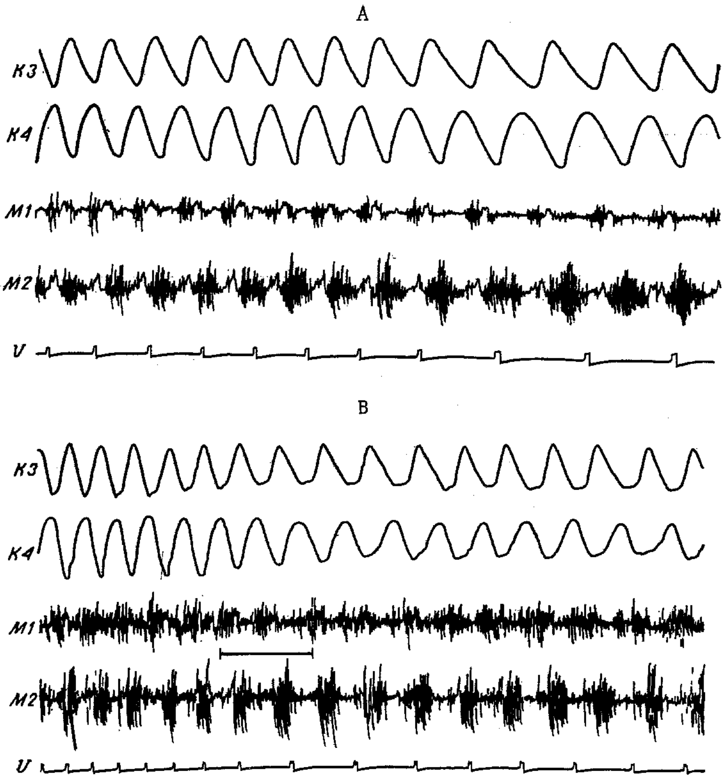

Fig. 2. "Liberation" of locomotion of forelimbs after transection of spinal cord in the lower thoracic region: A) plane of transection of brain stem passed through rostral border of superior colliculi and third pair of nerves; B) same preparation but with more caudal transection of brain stem – through middle of superior colliculi and beginning of pons; K3 and K4) longitudinal displacements of left and right hind limbs, upward deflection of curve corresponds to transfer, downward to support; V) velocity of movement of treadmill belt, distance between marks corresponds to 0.5 m; M1 and M2) EMGs of left clavobrachialis and triceps brachii mucles. Time marker 1 sec.

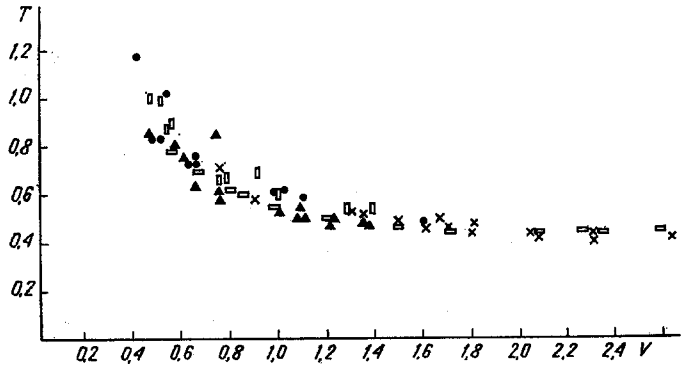

Fig. 3. Duration of stepping cycle (in sec) plotted against velocity of movement of treadmill belt (in m · sec). Postmammillary decerebration. Different symbols represent different walking sessions.

The cat's head was fixed in a stereotaxic holder. The trunk was suspended so that the limbs rested on the belt of a treadmill. The experiment began 2 h after the end of anesthesia. The rectal temperature was maintained at 37-37.5°C. The electromyograms (EMGs) of the flexors and extensors of the elbow were recorded from bipolar wire electrodes sutured into the muscles simultaneously with the longitudinal displacements of the forelimbs (using potentiometric transducers) on an electroencephalograph [3, 4].

EXPERIMENTAL RESULTS

As the mesencephalic cat with its spinal cord divided recovered from the anesthetic, it developed severe rigidity of the forelimbs. When the limbs, straightened and stretched forward, were shifted backward by the moving belt of the treadmill, alternating stepping movements began. In some preparations stepping did not arise until 4 h after the operation. These movements were stable and could last as long as 90-100 sec. Once it had ceased, stepping could be renewed if the limbs were left rigid by moving any one of them forward. After the end of a long period of stepping movements the tone of the extensors decreased and locomotion could no longer be induced in the cat. In that case a rest of 2-3 min was required before rigidity could be restored.

Electrical activity of the flexors and extensors of the elbow occurred at the same phases of the stepping cycle as during walking evoked by electrical stimulation of MLA (Fig. 2A). The duration of the stepping cycle depended on the speed of movement of the treadmill belt (Fig. 3). The faster the belt moved, the shorter the cycle, just as during locomotion induced by stimulation of MLA [3].

In five experiments the spinal cord was divided 3-4 h after decerebration, it having been ascertained that stepping could not be induced by the moving belt. After transection of the spinal cord, as the animal recovered from the anesthetic, rigidity of the forelimbs increased and movement of the belt began to induce stepping. From 40 to 50 min after transection of the spinal cord these stepping movements were unstable and they ceased after 10-15 sec. Gradually the stepping became more prolonged, and 1.5 h after transection of the spinal cord its duration could exceed 1 min.

As the animal recovered from the anesthetic and after the additional, more caudal, transection of the brain stem the stepping movements along the moving belt also were gradually restored (Fig. 2B). The most caudal transection of the brain stem after which locomotion of the cat's forelimbs could still be obtained along the moving belt of the treadmill corresponded to level IV in Fig. 1. In cats with transection of the brain stem at the anterior border of the pons (Fig. 1, Section III) and lower, but with the spinal cord intact, walking along the moving belt could not be induced even by stimulation of MLA [4]. Walking along the moving belt without stimulation of MLA or of the dorsal roots could be obtained only in the premamillary preparation with a much more rostral transection (Fig. 1, Section I) [1, 3]. Periods of spontaneous motor activity also were observed in the premammillary cats [9].

Besides releasing the rigidity and the reflexes of the forelimbs, transection of the spinal cord in the lower thoracid region thus also facilitated the resumption of stepping movements of the forelimbs. Two points of view may be held on the relationship between these three components of the liberation phenomenon developing in the mesencephalic cat after transection of the spinal cord. They all may be presumed to be due to the liberation of a single common mechanism, but it is quite possible that facilitation of the mechanism responsible for the increase in rigidity and of the reflexes of the forelimbs is primary, for this is an essential (but not the only) condition enabling stepping movements to be evoked. If stepping movements are produced by the method used in this investigation, it is in fact necessary for the limbs to be straight.

The liberation of rigidity and the reflexes, at least in part, is due to abolition of propriospinal tonic inhibitory influences [7, 14]. The facilitation of the stepping movements presumably also was due to some extent to this mechanism. Moreover, the possibility cannot be ruled out that inhibitory propriospinal influences are not all destined for the rostral regions. The lumbo-sacral region of the spinal cord may perhaps produce tonic inhibition of activity of the stepping program itself, and for that reason in acute experiments on spinal cats it must be liberated by a corresponding descending flow [2, 11] or by administration of adrenomimetics [1, 6, 8, 10, 15].

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