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STEPPING MOVEMENTS INDUCED IN CATS BY STIMULATION OF THE DORSOLATERAL FUNICULUS OF THE SPINAL CORD

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KEY WORDS: spinal cord; dorsolateral funiculus; locomotion.

Locomotion can be induced in the mesencephalic cat by stimulating the locomotor region in the brain stem [6, 7, 9, 12]. For spinal stepping generators to be activated under these circumstances, the ventrolateral funiculi must be intact, whereas destruction of the dorsolateral funiculus (DLF) at the C1 level does not prevent the effect [13]. In the turtle, however, swimming movements can be induced by stimulation of DLS [8, 14]. Sherrington observed stepping movements of the ipsilateral hind limb in the decapitated cat in response to stimulation of DLF at the level of spinal cord section [10, 11]. In the curarized, precollicularly decerebrated cat, after division of the spinal cord in the lower thoracic region, stimulation of DLF or of the lateral funiculus at the C3 level induces rhythmic discharges in the nerves to the muscles of the ipsilateral forelimb ("fictitious stepping"). After hemisection of the spinal cord rostrally to the site of stimulation the discharges continued, although they became irregular [15]. DLF and the lateral funiculus in the cat, just as in the turtle, thus contain fibers whose stimulation can activate limb stepping generators. Under these experimental conditions, however, it was impossible to determine whether the generator is activated directly by the stimulated fibers or through propriospinal neurons.

In the present investigation stepping movements of the hind limb were induced by stimulation of DLF in an uncurarized mesencephalic cat. With this technique stimulation of DLF remains effective even after injury to it caudally (at the L1 level) and rostrally (at the C2 level) to the site of stimulation.

EXPERIMENTAL METHOD

After precollicular postmammillary decerebration [6] one or two laminectomies were performed at different levels from C1 to L2. The animal's head was fixed in a stereotaxic apparatus, and the spine was fixed in two places. The cat's limbs were resting on the belt of a treadmill. By means of a manipulator, a tungsten electrode in glass insulation, 50 μ in diameter, was inserted into the dorsolateral funiculus. Monopolar stimulation was carried out with square pulses of negative polarity, 0.4 msec in duration, with a frequency of 60 sec^{-1}, and with a strength of 5-20 μA. Destruction in the region of the effective point was carried out by passing a steady current of 200 μA through the same electrode for 3 min, but if only labeling was required, a current of 10 μA was passed for 2 min. After fixation of the spinal cord in formalin transverse sections were cut to a thickness of 60 μ on a microtome with freezing stage, and after clearing with glycerin, they were photographed.

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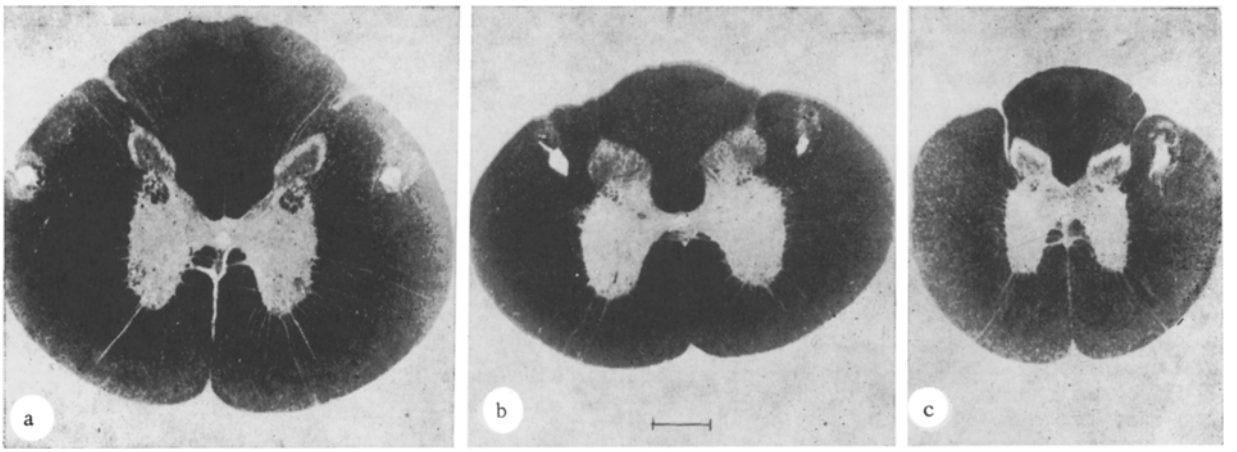

Fig. 1. Effective points in dorsolateral funiculus at levels C2 (a), C1 (b), and L2 (c). Electrolytic tagging at points whose stimulation induced stepping movements of ipsilateral hind limb. Frontal sections. Scale 1 mm.

EXPERIMENTAL RESULTS

Stepping Movements of the Ipsilateral Hind Limb. In 62 experiments stimulation of DLF induced stepping movements of the ipsilateral hind limb along the moving belt of the treadmill. The labels were always located in DLF (Fig. 1) although their arrangement was not identical in different animals. Meanwhile displacement of the electrode relative to the given effective point by only 0.2-0.3 mm sharply raised the threshold or made induction of stepping impossible. With an increase in the strength of stimulation the contralateral hind limb in some cases also started stepping movements, and sometimes the forelimbs also joined in. However, by contrast with stimulation of the locomotor region of the brain stem, which as a rule involves the left and right limbs in walking, the effect of stimulation of DLF was usually confined to ipsilateral stepping. By stimulating two points simultaneously (in the left and right DLF) it was easy to obtain coordinated (out of phase) stepping movements of the left and right limbs. The threshold of stimulation (of each point) became lower under these circumstances. Summation could also be observed during combined stimulation of the locomotor point in the midbrain (see below) and in DLF.

For further investigation of stepping induced by stimulation of DLF three series of experiments were carried out. In series I, two effective points were found in one DLF, after which one of them was destroyed. In series II three effective points were found in the same DLF, a distance of 10-12 mm apart, after which the middle one of the three was destroyed. In the experiments of series III, three or four effective points were found in one DLF, after which the outer two were destroyed. Electrolytic destruction of the effective point led to injury of part of the cross section of DLF (Fig. 2). The results of the first two series of experiments will be described together.

Destruction of One of Two or Three Effective Points in the Same DLF. After destruction of the point at the C2-C3 level, the more rostral point usually became ineffective, whereas stimulation caudally to the point of destruction continued to induce stepping (in eight of 10 experiments). Admittedly, if the point was located only 10-12 mm caudally to the level of destruction, the threshold was raised by 1.5 times. Destruction at the C5-T3 level did not prevent elicitation of stepping from L1 (in eight of nine experiments), whereas stimulation of neighboring points gave variable effects. In some experiments the rostral point remained effective whereas stimulation of the caudal point no longer induced stepping, whereas in other experiments the opposite was the case. In some cases, moreover, the threshold of stepping was raised a little.

After destruction of DLF at the T6-T10 level stepping could be induced from point L1 in only four of 11 experiments, whereas destruction at the T13 level made point L1 ineffective. Under these circumstances stimulation rostrally to T13 continued to induce stepping of the hind limb, but admittedly the threshold could be raised to 20-40%. Consequently, the stimulated structures of DLF could not activate the generator of limb stepping movements directly. Their action on it was mediated by certain neurons located rostrally to the site of stimulation, and sending their own axons into the ventral half of the spinal cord.

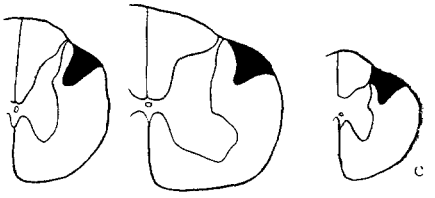

Fig. 2. Destruction in region of middle of three effective points at levels C2 (a), C6 (b), and D13 (c). Different experiments. Drawings made from frontal sections at site of greatest injury. Scale 1 mm.

Stimulation of Two Effective Points in the Same DLF. After destruction of points C2 and L1 stimulation at any level from C3 to T13 continued to induce stepping (two experiments). After destruction of points at levels C5 and L1, stepping could be induced by stimulation at level C6-T13 in four of six experiments, but after destruction at levels T5 and L1, it could be induced in only one of four experiments (by stimulation at the T13 level). Under these circumstances the threshold was doubled. Meanwhile destruction at level L1 alone did not reduce the effectiveness of the more rostral points. This suggests that to activate the stepping generator of the hind limb by stimulation of DLF, propriospinal neurons must be excited over a considerable length of the spinal cord. Stimulation of DLF rostrally to the site of its injury also induced stepping only if DLF was intact over a considerable distance, and it became ineffective if the injury was made at the C2 level. The "ascending" component necessary for stepping is thus propriospinal, and intervention by the brain stem is not essential.

Bilateral destruction of effective points in DLF at levels from C2 to L1 did not prevent induction of walking movements of the hind limbs by stimulation of the brain-stem locomotor region. Walking was preserved in 12 of 14 experiments during stimulation of the mesencephalic locomotor region (Horsley–Clarke coordinates: P2, L4, H0) in both experiments also when the locomotor point was stimulated in the medulla (P14, L4, H9).

Destruction of DLF did not affect the effects of stimulation of the stepping point in the contralateral DLF. If the point remained effective after destruction in the ipsilateral DLF, additional symmetrical destruction of the contralateral DLF likewise did not prevent induction of stepping.

The locomotor strip in the bulbar locomotor region, i.e., the formation whose stimulation induces walking, is located laterally to a column of cells sending axons into this strip [4, 5]. It can therefore be postulated that the locomotor strip in DLF is the formation to which the cell column homologous to the bulbar column corresponds in the gray matter of the spinal cord. Evidence in support of this hypothesis is given by the fact that at levels C2-C3 there are neurons which give synaptic responses to stimulation of the brain-stem locomotor region [1, 3], and destruction of the gray matter for a distance of 5-6 mm at this level makes induction of walking by stimulation of the brain-stem locomotor region impossible, despite preservation of the lateral and ventral funiculi [2].

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ROLE OF THE CORPUS CALLOSUM IN PAIRED ACTIVITY OF THE RESPIRATORY CENTER

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KEY WORDS: respiratory center; respiratory muscles; callosotomy; asymmetry.

An interesting aspect of the study of the structural and functional organization and regulation of activity of the respiratory center (RC) is the study of its behavior as a paired formation. Close axon-dendritic interaction has been demonstrated between respiratory neurons (RN) of the ventral and dorsal respiratory groups of the right and left halves of the medulla [12-15] and connections have been found between the nuclei of the medial zone and respiratory nuclei of the lateral zone [9], which must play a definite role in the functional unification of the two halves of RC as a single mechanism. At the same time it has been shown that an essential role in paired activity of RC is played by suprabulbar structures [4, 5, 10], including the cerebral commissures [4, 6].

The aim of the present investigation was to study the role of the corpus callosum in the mechanisms of integration of activity of the two halves of RC.

EXPERIMENTAL METHOD

In acute experiments on 63 cats weighing 2.3-3.5 kg anesthetized with pentobarbital (40 mg/kg, intraperitoneally) responses of RN of symmetrical nuclei of the right and left halves of RC and changes in the electromyograms (EMG) of the external intercostal muscles on both sides of the chest induced by successive stimulation of the right and left posterior sigmoid and marginal gyri, were studied before and after callosotomy. Unit activity of RN was derived extracellularly by glass microelectrodes (diameter of tip 3-10 μ), filled with 3 M KCl solution, in the region of the nuclei of the tractus solitarius, nucleus ambiguus, and nucleus retroambigualis, alternately on the right and left sides, and was recorded by means of a UBP1-02 amplifier and S1-18 oscilloscope with FOR-2 photo-optical recorder. EMG of the right and left respiratory muscles (RM) was recorded simultaneously by needle bipolar electrodes, using a UBP2-02 amplifier, S1-33 oscilloscope, and FOR-2 recorder. The cerebral cortex was stimulated through silver bipolar electrodes with interelectrode distance of 1.5 mm by a pulsed current (10-20 V, 50-100 Hz). The corpus callosum was divided with a scalpel and completeness of division was verified morphologically. Activity of RN was analyzed by the method in [8]. During analysis of the EMG the duration of the volleys and intervolley intervals and the frequency and amplitude of oscillations in the volley were determined. The results were subjected to statistical analysis by the direct difference method [7].

EXPERIMENTAL RESULTS

Stimulation of the posterior sigmoid and marginal gyri both before and after callosotomy induced responses in the overwhelming majority of RN tested in both halves of RC, which were manifested mainly as inhibition of activity, and also as various changes in components of the EMG of RM on the right and left sides of the chest.

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