MOTOR RESPONSES TO ELECTRICAL STIMULATION OF THE TEGMENTUM MESENCEPHALI IN CHRONIC EXPERIMENTS ON CATS

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After destruction of the intralaminar nuclei of the thalamus in cats, electrical stimulation of the dorsal part of the tegmentum mesencephali and inferior colliculi between frontal planes P0.5 and P2.5 evoked the following motor responses: movements of the head (upward, downward, turning to the right and left), rotation, intermittent running with jumps onto a wall, as well as evoked locomotion (walking or running in a straight line or circle). These movements were uncomplicated by any marked effective responses other than dilatation of the pupils. Movements evoked by mesencephalic stimulation are evidently primary and are caused by activation of structures concerned with the control of movement.

Electrical stimulation of the brain usually evokes complex behavioral responses and various movements [4, 5, 8, 13, 14]. In many cases the motor responses to stimulation are secondary in origin following primary changes in the state of nonmotor structures. However, the results of experimental stimulation of the diencephalon [7], the central gray matter and adjacent structures of the rostral part of the mesencephalon [6, 11, 15], and of the inferior colliculi [17] in intact cats demonstrate the possibility of obtaining primary (not indirect) motor responses such as turning the head, flexing the trunk, and rotation. In some cases stimulation evoked elements of nociceptive responses as well as movements [11, 16].

In the investigation described below responses to stimulation of the caudal part of the tegmentum mesencephali were minimized or excluded. This region was investigated because under acute experimental conditions stimulation of the same area of the brain of a mesencephalic cat induced controllable locomotion [1, 2].

EXPERIMENTAL METHOD

Bilateral electrolytic destruction of the centrum medianum and nucleus parafascicularis of the thalamus (points A 6.5, U 2, H 0, +2 and A 7.5, U 2.5, H 0, +2; current 2 mA for 15 sec) and bilateral implantation of electrodes for stimulating the tegmentum mesencephali were carried out in accordance with the stereotaxic coordinates of Horsley and Clarke in 63 cats (weighing 2-3.5 kg (anesthetized with pentobarbital (30 mg/kg body weight, intraperitoneally). Bipolar or multiple steel electrodes with interelectrode distance 1 mm and a diameter of 150 μ (21 animals) or monopolar tungsten electrodes covered with glass and 50 μ in diameter (42 animals) were implanted in a direction rostrally to the tentorium cerebelli (at an angle of 17-18° to the vertical). Penicillin was injected. After the animals' general condition had been restored (not more than 1 week) the experiments began (spontaneous motor activity was depressed in some of the cats). Stimuli were applied for 10-30 sec at intervals of 2-4 min from a stimulator providing dc pulses of an assigned amplitude (duration 0.6-1.0 msec, frequency 60/sec, strength 20-70 μA) and recorded on a cathode-ray oscilloscope. The stimulator was connected to the electrodes with flexible wires which did not interfere with the cat's movements in the empty room (2.5 × 2.5 m). The animal's behavior was recorded on 8-mm motion picture film and also in writing. At the end of the experiment the position of the electrodes in the

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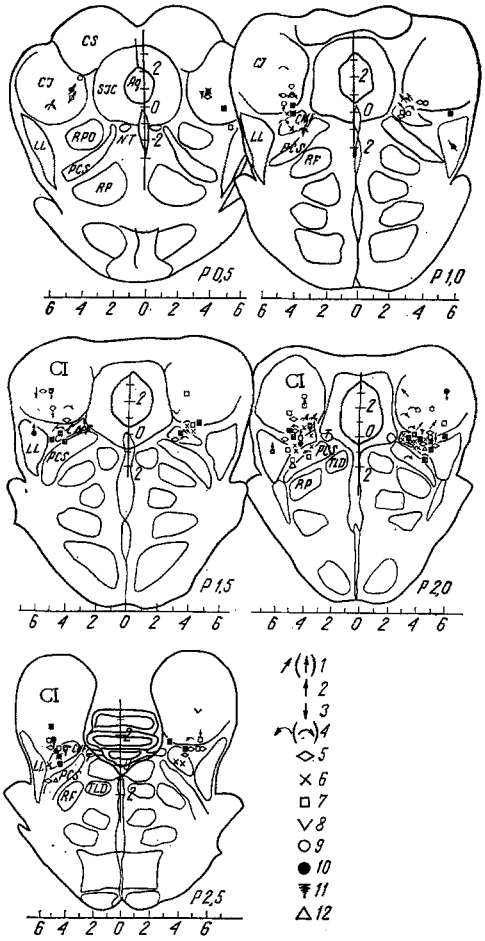

Fig. 1. Location of points in tegmentum mesencephali whose stimulation evokes different motor responses: 1) turning the head; 2) lifting the head and trunk; 3) pressing on the floor; 4) rotation; 5) running with stops; 6) uncomplicated locomotion; 7) jumps on the wall; 8) lifting the forelimb; 9) crying; 10) spasticity; 11) micturition; 12) licking. Drawings of frontal planes P0.5 to P2.5 taken from the atlas [12]. CS) Superior colliculus; CI) inferior colliculus; SGC) central gray matter; Aq) cerebral aqueduct; LL) lateral lemniscus; RPO) oral reticular nucleus of the pons; NT) nucleus of trochlear nerve; PCS(superior cerebellar peduncle; R(mesencephalic reticular formation; CNF) cuneiform nucleus; T) trochlear nerve; TLD) laterodorsal tegmental nucleus.

brain was marked (by passing a current of 0.1-0.2 mA for 15 sec) and the cat was killed by injection of a large dose of pentobarbital. Frontal sections were cut through the mesencephalon and thalamus. The sections and structures in them were identified by reference to atlases [3, 12].

EXPERIMENTAL RESULTS

In a preliminary series of experiments (not described in this paper), in which electrolysis of the intralaminar nuclei of the thalamus was not carried out, stimulation of the tegmentum in intact cats was found to evoke severe nociceptive responses. In subsequent experiments those thalamic structures whose injury sharply reduced the reactivity of the cats to stimulation of the dental nerve and to electrical stimulation of the limbs applied through the metal floor of the chamber were therefore coagulated [9, 10]. For the same reason, the use of semimicroelectrodes was adopted. The localization of stimulation achievable by this method (using currents of 20-70 μA) also helped to reduce the nociceptive overlay.

Motor responses arising to stimulation of the dorsal part of the tegmentum mesencephali and inferior colliculi between frontal planes P0.5 and P2.5 (Fig. 1) were investigated.

Stimulation in the ventral and central parts of the inferior colliculus and also in the region of the dorsal nuclei of the lateral lemniscus evoked turning of the head to the side away from the stimulus or toward the stimulus (in the horizontal plane) in 17 and 2 cases, respectively. Turning of the head evoked by tegmental stimulation was usually accompanied by flection of the whole trunk toward the same side (for example, head to the left, trunk flexed with convexity to the right), so that the cat apparently "chased its tail."

In 5 cats stimulation of the inferior colliculi led to elevation of the head, straightening of the forelimbs, and raising the anterior part of the trunk. In 6 cases during stimulation in the center of the inferior colliculus the cats pressed against the floor, dipped their heads, and flexed their forelimbs. Stimulation of 13 points lying chiefly in the tegmentum evoked contralateral rotation, and stimulation of 8 points evoked ipsilateral rotation with a clearly defined threshold (20–50 μA) and latent period of 5–7 sec, for subthreshold stimulation evoked only turning of the head. With strengthening of the current the intensity of rotation increased and the latency of the response decreased. Rotation continued throughout the period of stimulation and stopped immediately after its end.

Stimulation in the region of the tegmentum mesencephali in 19 cases evoked running from place to place, during which the animal was excited, but the actual running observed was chaotic in style with frequent changes of direction. In 20 cases after a short latent period (4–8 sec) the cat began to run around the room and sometimes to jump on the wall; these movements continued throughout the period of stimulation and ceased immediately after its end. Sometimes during stops (while stimulation continued) the cat hid in the corner or pressed against the wall. This behavior was often accompanied by a cry, by dilatation of the pupils, and by micturition.

However, stimulation of other points (19 cases) evoked only jumping upward or onto the wall, unaccompanied by running.

Stimulation of 19 points lying in the region of the cuneiform nucleus (13 of them in plane P2) caused the animal to walk or run about the room, usually along the walls. In 3 cases the animal ran in a circle with radius 0.5–1 m, which is not the same as rotation. The motor response had a threshold of between 10–15 and 40–60 μA and a latency of 3–8 sec. With an increase in the amplitude of the stimuli the latent period was reduced and the running speed increased. The movement was not accompanied by a cry, by jumping onto the wall, or by micturition, but dilatation of the pupils was always observed.

Stimulation of the tegmentum and inferior colliculi in 9 cases evoked spastic contraction of the limb muscles or flection of the forelimb on the side of the stimulus. Sometimes spastic walking with stiff limbs was observed.

Analysis of the histological sections showed that elements of an effective response (crying, micturition, jumping on the wall) occurred only in those cats (38 animals) in which the foci of destruction of the thalamus were small in size or not precisely localized. In those 25 cases in which destruction of the intralaminar nuclei of the thalamus was sufficiently complete, turning of the head, rotation, walking in a straight line, or running, uncomplicated by other responses than dilatation of the pupils, were observed.

These results confirm the view [6, 7, 15] that movements evoked by mesencephalic stimulation are primary responses to it and not secondary to a primary factor of complex behavior (as, for example, during the evoked attack of a cat on a rat [5]). The evidence in support of this conclusion is, first, that the region whose stimulation evoked uncomplicated locomotion under chronic experimental conditions is the same as that whose stimulation evokes locomotion in mesencephalic cats [1]. Second, evoked movements of the animals during chronic experiments are not directed at the performance of any particular goal and can be obtained at different moments of the animal's natural behavior unaccompanied by any significant effective responses.

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