

ROLE OF COMMISSURAL CHANNELS OF THE SOMATOSENSORY SYSTEM IN TRANSMITTING FEEDBACK SIGNALS DURING VOLUNTARY MOVEMENT CONTROL

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The cerebral commissures play an important role in the transmission of modality-specific signals from peripheral receptors to the projection areas of the cerebral cortex [2, 3, 5-7, 9, 13]. Evidence of the high functional efficiency of the commissural pathways of the forebrain is given also by the results of behavioral and neurological investigations, which indicate their important role in learning and rehabilitation of functions in patients with lesions of the CNS [4, 12]. In particular, the writers showed previously that commissural projections of the visual and somatosensory systems play an important part in compensatory restoration of complex visual and motor functions after injury to the principal afferent pathways [8, 10]. This suggests a role for interhemispheric communication in the neurophysiological mechanisms of integration and control.

The aim of the present investigation was accordingly to study the effectiveness (in relation to behavioral and electrophysiological parameters) of the commissural pathways in the transmission of somatosensory feedback during control of forelimb movements in cats performing instrumental acts. The principal (classical) afferent pathways of the somatosensory system were interrupted by unilateral division of half of the tegmentum mesencephali, when spino-thalamic, spino-servico-thalamic and spino-reticulo-thalamic tracts and tracts of the posterior column were injured [3, 4]. Under these circumstances control of the forelimb could be effected by somatosensory feedback signals running into the "working" hemisphere along commissural channels of the telencephalon and diencephalon only.

EXPERIMENTAL METHOD

Experiments were carried out on 23 adult cats, divided into five groups: group 1) control, 2) division of the right tegmentum mesencephali; 3) division of the left optic tract and right tegmentum mesencephali, 4) division of the left optic tract and left tegmentum mesencephali, 5) combined division of the left optic tract, right tegmentum mesencephali, and commissures of the tel-, di-, and mesencephalon. Division of the left optic tract enabled direct visual control of the forelimb to be excluded, so that the limb was controlled only by commissural channels of somatosensory feedback in the animals of group 4, and in cats of groups 3 and 5 only by the classical somatosensory feedback channels [3, 4]. The investigation was done in two parts: formation of a conditioned instrumental defensive reflex [11] and electromyography. The cats were trained to strike a white target with their forelimb. Electrodermal stimulation of the anterior surface of the forearm with square pulses of current (40-60 V, 50 Hz, 1 msec) served as negative reinforcement. In the course of an experiment 20 attempts were made. Conditioning began 15-30 days after neurosurgical operations. Electromyography were carried out against the background of a well formed instrumental reflex. Electromyograms (EMG) were recorded from muscles of the anterior surface of the forearm by percutaneous electrodes. Parameters of electrical responses, after amplification, were recorded on a four-channel magnetic recorder (from Brüel and Kjaer), and then reproduced on an automatic ink-writer and analyzed by computer. The significance of the results was analyzed by the use of

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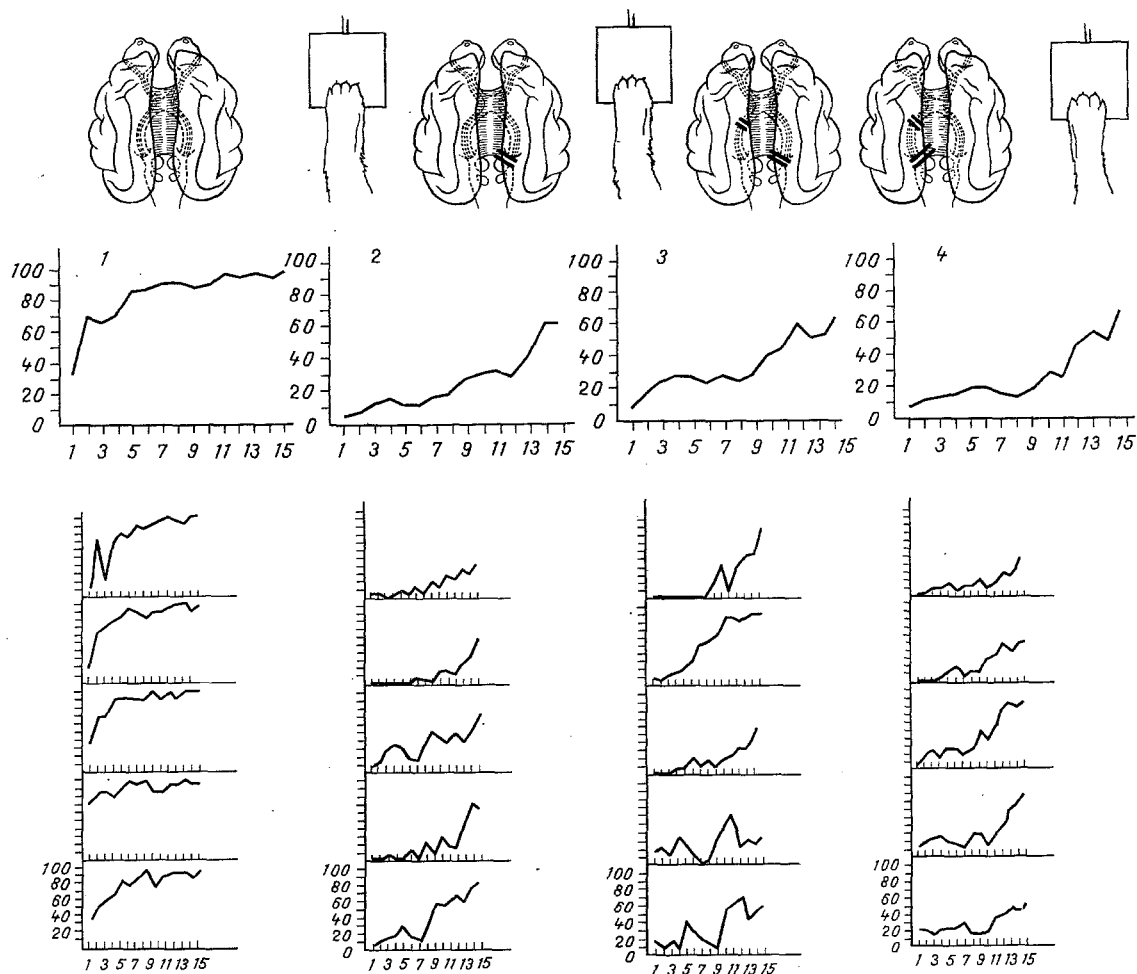


Fig. 1. Time course of formation of conditioned defensive reflex in cats of groups 1-4. Abscissa, day of experiments; ordinate, average percentage of correct responses. Above — averaged learning curves, below — individual curves.

Fisher's angular transformation and Student's test [1]. After the end of the experiments the brain of animals undergoing the operation was examined morphologically.

EXPERIMENTAL RESULTS

The rate of formation of the conditioned instrumental reflex to a limb with only commissural channels of somatosensory feedback (groups 2-4) was about 5 times slower than normally (Fig. 1). In animals of group 5 no conditioned reflex could be formed. The time course of formation of the conditioned instrumental defensive reflex in animals of groups 2-4 did not differ significantly ($P > 0.05$) although the animals of group 2 had an intact visual system, whereas the cats of group 4 were unable to control the movement of the "working" forelimb, deprived of its principal somatosensory projections, visually.

The latent period of the EMG of the instrumental movement (time from beginning of exposure of the target to the beginning of the EMG accompanying movements) in animals of groups 1-4 did not differ significantly ($P > 0.05$). In the intact animals it was 2.6 ± 0.6 sec, whereas in the cats of groups 2-4 it was between 2.5 and 3.2 sec. The main differences in the character of EMGs of the normal and commissurotomed animals related to a change in its total duration (the time from beginning of the EMG of the instrumental movement to its end). Animals of groups 2-4 had a significantly ($P < 0.05$) longer duration of the EMG of the instrumental movement of the forelimb, which had only commissural somatosensory channels for transmission of feedback signals, compared with normal and with the opposite side (Fig. 2). The duration of the electromyographic response was 2.4 ± 0.3 sec in cats of group 1, 4.7 ± 0.8 sec in group 2, 4.8 ± 0.9 sec in group 3, and 3.9 ± 0.7 sec in group 4. The duration of the elec-

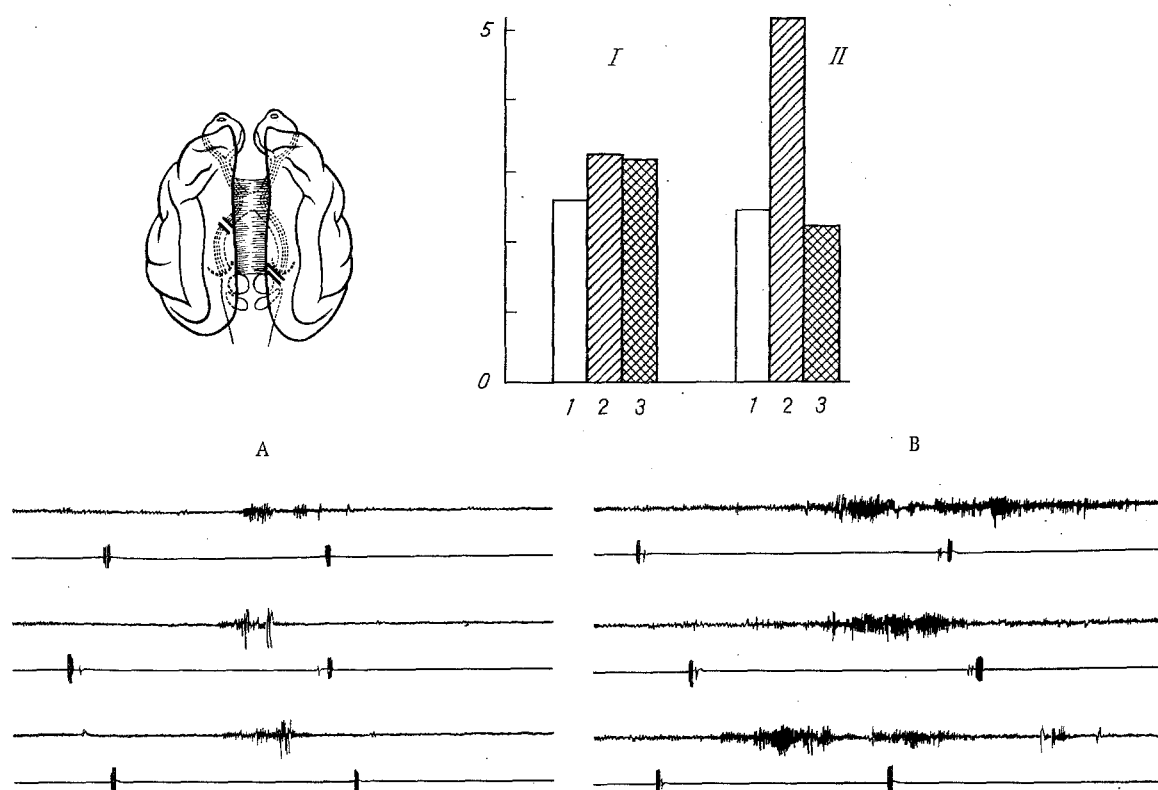


Fig. 2. EMG of instrumental movements recorded in cat in group 3 from "intact" (A) and "deafferented" (B) forelimbs. Top beam shows EMG, bottom shows marker of beginning and end of exposure of target. Top histograms show mean latent period (I) and duration (II) of electromyographic responses. 1) Group 1, 2) group 3: "deafferented" forelimb; 3) group 3; "intact" forelimb. Ordinate, time (in sec).

tromyographic response of the "intact" forelimb in the animals of groups 2 and 4 did not differ significantly from normal.

It can be concluded from the results of this investigation that the functional effectiveness of the commissural channels of somatosensory feedback is inadequate, as is reflected in an increase in the total duration of the instrumental movement and slowing of formation of the conditioned reflex in animals of groups 2-4. Additional interruption of these channels (group 5) completely prevented the formation of a voluntary movement of this type. Excluding the possibility of direct visual control of the forelimb performing the instrumental movements (group 4) did not significantly affect the EMG.

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MECHANISMS OF INHIBITION OF CARDIAC ACTIVITY BY THE STELLATE GANGLION

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It was shown about 50 years ago that stimulation of the stellate ganglion in experimental animals may not only stimulate, but also inhibit the work of the heart [3, 6-9, 11]. The few attempts which have been made to analyze this inhibitory phenomenon, which is unusual for the sympathetic nervous system, have led to contradictory conclusions. For instance, it has been shown [7] that weak stimulation of the sympathetic nerve in rats between the stellate ganglion and the heart reduced, whereas stronger stimulation increased the heart rate. The workers cited concluded that the sympathetic nerve contains cholinergic fibers which inhibit the work of the heart. However, their conclusion was not based on any special investigations, and in addition, the extent of the inhibitory phenomenon (1.5%) in their experiments was within the limits of spontaneous fluctuations of the heart rate [1]. A more penetrating analysis of the mechanisms of this phenomenon showed [11] that stimulation of certain branches given off by the stellate ganglion in cats does not accelerate, but inhibits the work of the heart. Since the inhibitory effect was blocked by hexamethonium and atropine, the authors cited concluded that it is the result of excitation of intracardiac cholinergic neurons, connected synaptically with sympathetic fibers of the stellate ganglion. According to a third hypothesis [4, 5], the inhibitory phenomenon may involve the participation of acetylcholine (ACh) contained in sympathetic endings, which under ordinary conditions facilitates catecholamine (CA) release. Stimulation of sympathetic nerves after exhaustion of CA by reserpine is accompanied by release of ACh by sympathetic endings and the development of a cholinergic effect in various organs, which is abolished by atropine.

Since no general agreement has yet been reached on the mechanisms of inhibition of cardiac activity during stimulation of the sympathetic nerve, these mechanisms were investigated in the experiments described below.

EXPERIMENTAL METHOD

Experiments were carried out on 49 cats weighing 2-3 kg and 28 dogs weighing 5-10 kg. The blood pressure in the left carotid artery, pressure in the left ventricle, and its first derivative ($\Delta P/\Delta t_{\max}$) were recorded on a "Mingograf-82" apparatus (Siemens-Elema, Sweden) and N327-5 automatic ink writer, UBP2-03 biopotentials amplifiers, and EMT-35 pressure transducers. The catheter for recording the intracardiac pressure was introduced through the right carotid artery. The animals were anesthetized with hexobarbital or urethane and artificial respiration was applied (apparatus of type 297 and AID-3). Thoracotomy was performed, the sternum was divided by a longitudinal incision, and both vagus nerves were dissected in the neck and divided at the level of the larynx. In acute experiments only the right ganglion, but in chronic experiments both stellate ganglia were dissected in the thorax. To obtain access to them the brachiocephalic artery and the cranial vena cava were ligated and divided. The stellate ganglion was found at the base of the 1st and 2nd ribs and its branches were dissected. Individual branches and the body of the ganglion were stimulated. In cats the cardiac branch (caudal cardiac nerve) was stimulated most frequently, whereas in dogs both branches were stimulated in equal proportions. ÉSL-2 and T-2 stimulators were used (7-15-30-45 V; 20-30 Hz; 1-cm sec, duration 20-30 sec). Different parts and structures of the autonomic nervous system were blocked successively in the experiments either surgically (division of the vagus nerves in acute and chronic experiments, in the latter case the right vagosympathetic bundle was divided to produce degeneration 2-4 weeks before the main part of the experiment),

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