PARTICIPATION OF THE SUBCORTICAL STRUCTURES IN INTERACTION BETWEEN THE HEMISPHERES

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Previous investigations showed that paroxysmal excitation arising at any point of the cerebral hemispheres on application of strychnine to it spreads within a short time to the whole cortex [1]. Since paroxysmal excitation can easily be detected electrophysiologically, the opportunity has been presented for solving some of the problems concerned with the mechanisms and ways of spread of excitation in the central nervous system. The study of these problems is of more than theoretical interest. It must help clinicians to understand many of the unexplained aspects of the pathogenesis of those diseases of the central nervous system which are based on a cortical focus of excitation (trauma, cerebral tumor, epilepsy, etc.).

The authors' experiments were so devised that the spread of excitation from one hemisphere to another through the intra- and intercortical fibers of the cortex was completely prevented (stimulation of the "isolated islet" of cortex, division of the fibers of the corpus callosum). The results of these experiments showed that subcortical structures must play an important role in the transmission of excitation from one hemisphere to the other after division of the corpus callosum [1]. However, the precise localization of these structures is not yet clear.

The object of the present investigation was to determine the levels of the brain stem through which excitation may be transmitted from one hemisphere to the other.

EXPERIMENTAL METHOD

Acute experiments were performed on rabbits anesthetized with urethane (1.0-1.5 g/kg body weight). The rabbit's head was secured in a Horsley—Clark—Dell stereotaxic apparatus. The skin and soft tissues were removed, the cranial bones were partially nibbled away, and the cerebral cortex was exposed for stimulation and for the operative procedures. The electrical activity of the various parts of the cortex and, in some experiments, of the subcortical structures also, was recorded by means of a "Racia" universal electrophysiological apparatus. The electrodes for recording the electrocorticogram were either placed on the exposed surface of the cortex (silver balls) or inserted into the residual portions of the cranial bones (steel needles). The subcortical electrodes were implanted in accordance with the stereotaxic coordinates of Sawyer's atlas [2]. The EEG was recorded by both unipolar and bipolar methods. The cortex was stimulated by pieces of filter paper (1 · 1 mm or 2 · 2 mm) soaked in 1% strychnine solution. The pieces of paper were applied to the parietal region of the cortex of one hemisphere. After the appearance of aproxysmal discharges in the strychninized point and in the remaining parts of both hemispheres of the cortex, the fibers of the corpus callosum were divided. Having verified that after this operation the paroxysmal discharges continued to be transmitted from one hemisphere to the other, the longitudinal division of the brain stem began. The brain stem was divided by a specially made thin scalpel, oriented stereotaxically before the experiment in accordance with the coordinates of Sawyer's atlas. The incision began at the level A_6, thereafter, the scalpel was carried 1 mm posteriorly and downward into the substance of the brain until it met the resistance of the bone at the base of the skull. To minimize bleeding the division of the brain stem was usually not taken as far as the zero sagittal plane, but stopped 1.5-2.0 mm short of it on the right or left side. In this way the brain stem was gradually (1 mm at a time) and completely divided in a longitudinal direction as far as the level of the corpus callosum, and the cerebral hemispheres were completely isolated from each other.

EXPERIMENTAL RESULTS

One or two minutes after application of strychnine characteristic paroxysmal discharges with an amplitude of 1 mV or more appeared at the stimulated point of the cerebral cortex. A few minutes later these discharges became generalized, i.e., they were recorded from different parts of the ipsilateral and contralateral hemispheres

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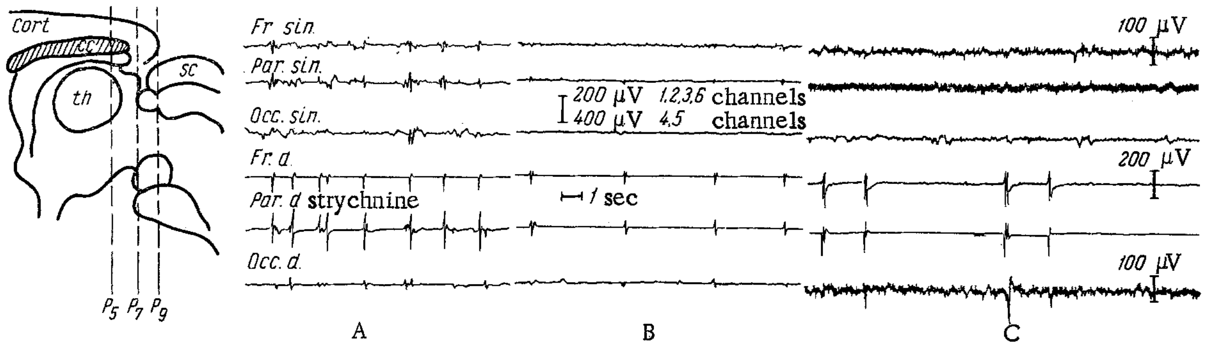

Fig. 1. Changes in generalization of paroxysmal excitation during gradual longitudinal division of the brain stem. A) Corpus callosum divided. Brain stem divided to the level of P_5 (posterior border of the thalamus). Discharges persist in both the strychninized (right) and the contralateral hemisphere; B) division to the level of P_7 (see scheme). A sharp decrease in the amplitude of the paroxysmal discharges, seen especially clearly in the contralateral (left) hemisphere; C) division to the level of P_9 (rostral portions of the mesencephalon). Complete disappearance of generalized paroxysmal discharges in the contralateral hemisphere. Amplification doubled in degree. On the scheme: P_5, P_7, P_9) levels of division. Cort) cerebral cortex; CC) corpus callosum; th) thalamus; SC) superior colliculus.

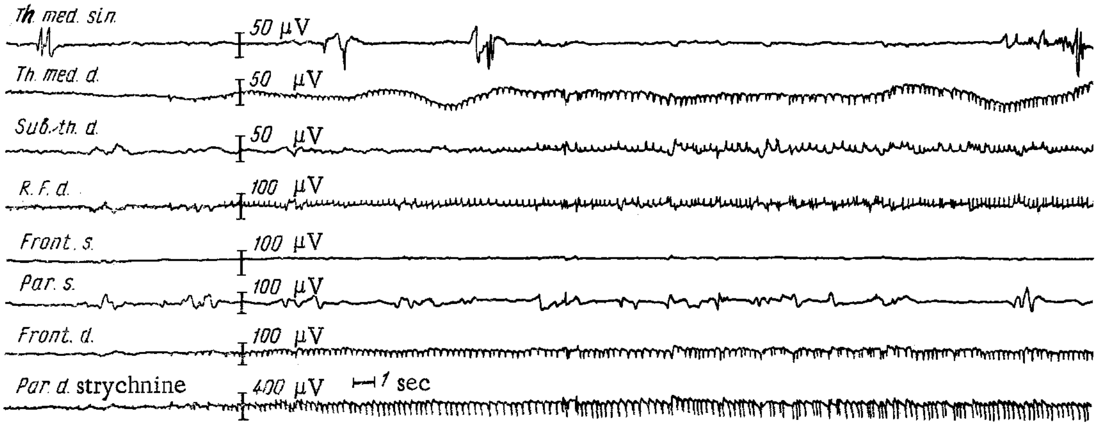

Fig. 2. Appearance of a paroxysmal burst in the strychninized hemisphere. The discharges spread to the subcortical structures only on the same side. No discharges are seen in the contralateral hemisphere and subcortex (brain stem divided to the level of P_9).

(Fig. 1A). Division of the corpus callosum did not significantly alter the character of the generalization, although in many experiments a slight decrease in the amplitude of the generalized discharges could be observed.

The gradual division of the brain stem had no effect on the character of the generalization until the level P_7 (after Sawyer's atlas) was reached, i.e., the level of the caudal portions of the thalamus and subthalamus and the rostral portions of the mesencephalon (Fig. 1B). When the scalpel dividing the brain stem reached P_7 a marked decrease in the strength of the strychnine discharges was observed both at the strychninized point and in the other parts of the cortex of both hemispheres (see Fig. 1C). At this stage the discharges sometimes disappeared completely. After a short time they usually recovered, although their amplitude did not regain its previous value. In some cases strychnine had to be reapplied before the discharges were restored. When division of the brain stem involved the rostral portions of the tectum mesencephali, reaching the posterior colliculi, the paroxysmal discharges in the opposite hemisphere disappeared completely, and could not be detected even by increasing the amplification (Fig. 1C). In some experiments electrical activity of the medial thalamus, the subthalamus, and the reticular formation of the tectum mesencephali was recorded. It was observed in these circumstances that when the longitudinal division of the brain stem reached the level P_9, i.e., it involved the rostral portions of the mesencephalon, both halves of the brain began to work at different rhythms. The paroxysmal discharges disappeared not only in the contralateral hemisphere, but also in the contralateral subcortex, and the discharges on the side of application of strychnine and in the ipsilateral subcortex, on the other hand, were completely preserved. Sometimes the development of a burst of paroxysmal activity was observed at the point of application of strychnine. Before division of the brain stem this burst soon became generalized, but after division of the brain stem it affected only one half of the brain (Fig. 2).

The dysrhythmia in the working of the hemispheres appeared especially clearly when strychnine was applied simultaneously to both hemispheres. The dissociated halves of the brain worked at different rhythms.

The results obtained reveal a unique form of interhemispheric relationships. It is natural to ask what proportion of this form of transmission of excitation from hemisphere to hemisphere takes place at the level of the brain stem. To answer this question, the known mechanisms of interhemispheric coordination must first be compared. The most important of these mechanisms are the links of the corpus callosum. They are responsible for widely different yet discrete forms of connection of the cortex—cortex type, ensuring synchronization of the activity of the cortical levels. In another form of coordination the two hemispheres received generalized excitation from the subcortical structures.

The coordination of the functions of the two hemispheres described in this paper is of a special kind. It is effected on the initiative of the cerebral cortex and it is generalized throughout the cortex. The physiological significance of this form of coordination is evidently that the nongeneralizing, discrete callosal connections between the hemispheres must be strengthened actually in the process of cortical activity by generalized influences from the level of the nonspecific nuclei of the thalamus and the formations of the brain stem. The further elucidation of the physiological importance of this form of connection requires experimental investigation.

When insisting on the decisive role of the synchronizing subcortical apparatuses in the spreading of paroxysmal excitation over the cerebral cortex as a special form of synchronization of the parts of the brain, the authors in no way imply that there is no possibility of the spread of excitation through intra- and intercortical connections. Evidently each of these mechanisms of the complex cortical activity plays a specific part in the integrative activity of the brain as a whole.

LITERATURE CITED

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2. C. H. Sawyer, J. W. Everett, and J. D. Green, J. Comp. Neurol., 101 (1954), p. 801.