PHYSIOLOGY

THE ROLE OF THE CEREBELLUM IN THE PERFORMANCE OF MOTOR ACTIVITY

I. M. Gil'man

Department of Human and Animal Physiology (Director – Prof. A. N. Kabanov),
the V. P. Potemkin Moscow City Pedagogical Institute

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The question of the mechanism involved in the effect of the cerebellum on the course of coordinated movements when the cerebral cortex is intact has not so far been fully clarified, although there are several interesting references to this problem [1, 4-6, 9-11, 13-21].

Our investigations were devoted to the study of the role of the cerebellum in the coordination of movements which arise under the influence of cerebral cortical stimulation.

EXPERIMENTAL METHOD

Experiments were performed on 80 cats. The motor area of the left cerebral hemisphere and the paramedian lobe of the right cerebellar hemisphere were exposed under ether anesthesia. It is known that the latter structure is particularly closely associated with the hind limb areas of the contralateral cerebral hemisphere. The distal ends of two antagonist muscles of the right hind limb – semitendinosus and quadriceps femoris (rectus) – were dissected and connected by a thread to the angular levers of a double myograph. The experiments, conducted under urethane anesthesia, consisted of investigation of the effect of changes in the cerebellum on the motor effect of induction-current stimulation of appropriate points on the cerebral cortex.

The cerebellum was stimulated for 2-7 seconds by direct current (anode or cathode) of subthreshold strength, the diameter of the stimulating electrode being 0.3 mm. The animal was allowed to rest for not less than 7-10 minutes after each stimulation of the cerebellum. Usually the character of the coordination relations between antagonist muscles was determined prior to cerebellar stimulation, during such stimulation, and following it. In a number of experiments cerebellar stimulation was carried out briefly against the background of cerebral stimulation lasting 6-8 seconds: this gave us the opportunity to observe the muscular reaction to cerebral stimulation during the first few seconds without cerebellar stimulation, during the subsequent 2-3 seconds against the background of such stimulation, and finally during the last 2-3 seconds after its termination.

In experiments without general anesthesia, stimulation of the appropriate cortical point usually leads readily to reciprocal reactions in antagonist muscles. Under anesthesia no such constancy of reaction could be observed and simultaneous contraction of both muscles was noted frequently.

EXPERIMENTAL RESULTS

The experiments showed that stimulation of the cerebellum with direct current exerts an influence on the effect of cortical stimulation, and two main types of changes were found to be consistently reproducible in many experiments. The first and more frequently encountered type of change consisted only of enhancement or diminution of the intensity of those muscular reactions which were observed during stimulation of the cerebral cortex (Fig. 1). If, for example, cortical stimulation evoked reciprocal reactions of antagonist muscles, then cerebellar stimulation either increased the reciprocity by increasing the height of contraction of one muscle and the simultaneous enhancement of relaxation in its antagonist, or, conversely, diminished the reciprocity. If, however, cortical stimulation led to the contraction of both muscles, i.e. a unidirectional reaction, then

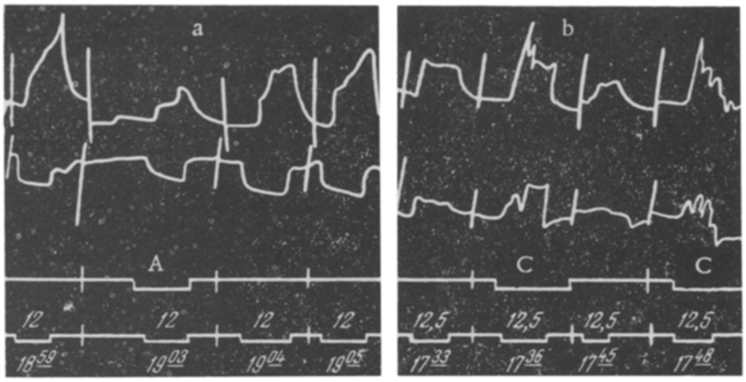

Fig. 1. Change in the intensity of reactions.
a) Diminution of reciprocity (experiment December 4, 1952); b) increase in height of contraction of both muscles (experiment May 13, 1953). Records (from above down): reaction of the quadriceps-muscle reaction of the semitendinosus muscle; marker denoting start and termination of anodic (A) and cathodic (C) direct current stimulation of the cerebellum; marker denoting cerebral cortical stimulation (figures designate the distance between induction coils in centimeters; figures in the last line indicate time).

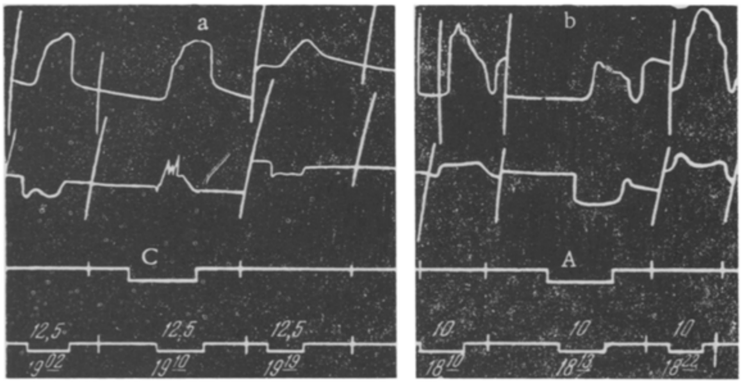

Fig. 2. Change in coordination relations to reverse ones.
a) Transition from reciprocal reaction to contraction of both muscles;
b) appearance of reciprocal reaction instead of contraction of both muscles. Records the same as in Fig. 1.

cerebellar stimulation led to simultaneous change in the intensity of their contraction, which was either enhanced or diminished.

The second type of change manifested itself in a fundamental rearrangement of coordination relations and establishment of new muscle interrelationships – the reverse of those which had been obtained as the result of cerebral cortical stimulation without cerebellar stimulation (Fig. 2). Thus, in cases of initial reciprocal reaction, simultaneous contraction of both muscles took place, since one of them, instead of relaxing, began to show a definite contraction reaction. In cases of contraction of both muscles, cerebellar stimulation was followed by relaxation of one of them while the other continued to contract, i.e. reciprocal relationships came to the fore. In those experiments in which cerebellar stimulation was briefly superimposed on prolonged cortical stimulation, the change in coordination relations occurred during that interval of time when the cerebellum was subjected to the action of direct current, the initial coordination relations becoming re-established on termination of cerebellar stimulation.

An intermediate group of changes evoked by cerebellar stimulation consisted either of altered intensity in the reaction of one of the muscles with its antagonist's reaction remaining unchanged, or of diminution in the reaction of one and simultaneous enhancement of the reaction in the other (Fig. 3). In other words, the direction of coordination relations was not altered completely, but only a tendency to changes in coordination relations to the reverse ones made its appearance. These intermediate changes can be regarded as transitional -- forming a link between both the described types of change, since as a rule they precede the transition, observed in a number of experiments, from one type of cerebellar stimulation effect to the other. Such transition is evidently explained by a change in the functional state of the corresponding nerve centers under the influence of anesthesia or other factors associated with the experiment.

Reference to the results of cerebellar stimulation with induction current of suprathreshold strength in our own experiments and those of R. S. Mnukhina [3, 4], as well as those of Tilney and Pike [20] who extirpated the cerebellum, leads A. M. Aleksanian [1] to regard the change in coordination relations to opposite ones resulting from cerebellar effect as disturbance of the "correct functional interrelations of reflex arcs."

In our experiments the cerebellum was subjected to relatively mild influences affecting its functional state, and consequently the manifestation of its participation in the coordination of motor reactions.

Nonetheless even such mild influences not only produced changes in the intensity of motor reactions, but also reversed coordination relations, which A. M. Aleksanian regards as a disturbance of the normal cerebellar function.

However, if some changes in muscular reactions are taken to be a manifestation of the normal activity of nervous centers other changes which often occur in the same experiments and under the same conditions can hardly be regarded as a distortion of such activity.

Our experiments suggest that under normal conditions the cerebellum also not only imparts greater precision to motor reactions, "not only moderates or enhances" them, but can, under the influence of signals reaching it, even alter the established coordination relations to opposite ones without distorting but only increasing the precision of the body's motor activity.

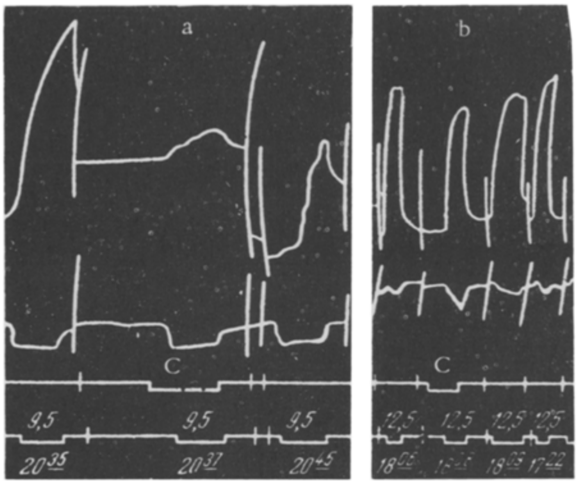

Fig. 3. Intermediate group of changes.
a) Change in the intensity of contraction of the quadriceps muscle with unchanged degree of relaxation in the semitendinosus muscle (experiment October 27, 1952); b) diminution of contraction of the quadriceps muscle and enhancement of the relaxation of the semitendinosus muscle (experiment December 23, 1952). Records the same as in Fig. 1.

During cerebellar stimulation changes in coordination relations occurred mostly by means of changes in the reaction of the extensor muscles, whereas the reaction of the flexors often remained unchanged, or, if it did change, the change was considerably less intense; this entirely agrees with literature data [7, 8, 12]. If, however, cerebellar stimulation evoked a fundamental change in coordination relations, then, in our experiments, this occurred exclusively as the result of sharp changes in flexor reactions, with only slight changes in the height of contraction of the extensor. Furthermore, even the sharpest changes in the extensor reactions did not lead to a fundamental rearrangement of coordination relations in a single experiment.

Demonstration of the role of flexor reactions in our experiments, unlike the data of other investigators, is explained by the fact that usually the effect of the cerebellum on the motor system is studied in the absence of the cerebral hemispheres or on decerebrate animals, i.e. in the presence of only the brain stem and spinal mechanisms with which is associated extensor activity which is inhibited under normal conditions by the higher divisions of the brain. Our experiments were performed on animals with intact nervous systems, a study being made of the effect of the cerebellum on coordination relations arising on cerebral cortical stimulation.

The sharp changes in coordination relations at the expense of the flexor observed by us suggest that the cerebellum not only inhibits innate extensor reactions but also enhances flexor reactions particularly characteristic for voluntary movements. This explains the difference discovered on comparison of our experimental data with the data of A. A. Guminskii [2]. The experimental conditions in both cases are fairly similar. However, the effect of cerebellar stimulation on coordination relations was studied by A. A. Guminskii on decerebrate animals and with peripheral stimulation, whereas we worked with animals with an entirely preserved nervous system, and used stimulation of the cerebral cortex. The effects of stimulation in the two cases proved to be different. Unlike the results of our experiments, A. A. Guminskii's stimulation of the vermis and the cerebellar hemispheres produced no changes in the character of coordination relations in any of his experiments.

It would appear that when the direct interrelationship between the cerebral cortex and the cerebellum is preserved, the consistent influence of the latter on coordination relations is more complex than that which can take place in decorticate animals.

It may be supposed that under normal conditions the cerebellum not only enhances or moderates the intensity of muscular reactions but also can change the established coordination relations to opposite ones, making for greater precision of the motor reaction. In the majority of cases changes in coordination relations occurred at the expense of changes in the extensor's reaction. If, however, cerebellar stimulation evoked fundamental changes in coordination relations, these occurred at the expense of the flexor's reactions.

It seems that the cerebellum not only inhibits innate extensor reactions but also enhances flexor reactions which are particularly characteristic for voluntary movements.

SUMMARY

The author stimulated the paramedian cerebellar lobe in cats by direct current (anode or cathode). He observed 2 types of reactions of antagonist muscles to the stimulation of the corresponding motor area of the cerebral hemispheres: 1) a change in the intensity of the coordinating relations mainly due to the extensor, or 2) establishment of new antagonistic relations, mainly as a result of the altered reactions of the flexor. There was also a conversion from one type of change to another. The cerebellum intensifies the flexor reactions characteristic of voluntary movements by depressing extension.

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