ELECTRICAL REACTIONS OF THE CEREBELLAR CORTEX TO STIMULATION OF THE VISCERAL NERVES AFTER DENERVATION

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Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 54, No. 10,
pp. 3-8, October, 1962
Original article submitted January 2, 1962

The investigation of the electrical reactions of the cerebellar cortex in response to stimulation of the visceral nerves in decerebrate animals is of considerable interest. Exclusion of the higher centers may help to obtain a final solution of the problem of the independent interoceptive pathways for the cerebellum, which is still in doubt. Widen [18], for instance, found that nociceptive impulses from the splanchnic nerve are transmitted to the cerebellar cortex directly via the spinocerebellar tract. Nevertheless, the opinion is also held that the cerebellum receives impulses from the internal organs only via the cerebral hemisphere [8]. To resolve this difference of opinion, it is necessary, therefore, to discover if responses may be formed by the cerebellum to visceral stimulation after exclusion of the cerebral hemispheres.

At the same time, experiments on decerebrate animals may help to clarify the character and degree of the influence of the cerebral hemispheres on the function of the cerebellum and, in particular, on its visceral function. Finally, decerebration allows maximal exposure of the cerebellar field to be obtained, so that the visceral representation in the cerebellum can be studied more fully.

It was Widen who first undertook the investigation of the electrical responses in the cerebellar cortex of decerebrate animals during the study of the representation of the splanchnic nerves. Although he was not especially concerned with the electrographic features of the responses after decerebration, Widen pointed out that in most cases satisfactory results could not be obtained because, in his opinion, the blood supply of the cerebellum had been disturbed. Meanwhile, various writers have described the electrical responses of the cerebellum to exteroceptive and proprioceptive stimulation in decerebrate animals [10, 14, 16 and others].

Our object was to investigate the ability of the cerebellum to respond by electrical reactions to stimulation of various visceral nerves after exclusion of the cerebral hemispheres.

EXPERIMENTAL METHOD

Experiments were carried out on 44 cats. The preliminary operation (isolation of the nerves, trephining of the skull, followed by decerebration) was performed under thiopental-sodium anesthesia.

A cathode-ray oscillograph with a resistance-capacitance amplifier was used to record the cerebellar potentials picked up with unipolar leads. The active electrode was a cotton thread soaked in physiological saline; the indifferent electrode was a tinned brass rod, fixed into the nasal bones.

Stimuli were applied to the central segments of the principal visceral nerves (the splanchnic in the abdomen and the vagus in the neck) and also to the nerve twigs leaving the stomach and intestine. Single "break" pulses of induction current were used as stimuli.

At the beginning of each experiment for control purposes we investigated the electrical reactions of the cerebellum to stimulation of the visceral nerves in animals with an intact nervous system. These animals were then decerebrated at the intercollicular level. Between 20 and 30 min after decerebration the reactions of the cerebellar cortex to stimulation of the same nerves were again tested. Only those experiments in which the general condition of the animals continued to be satisfactory after decerebration were analyzed.

EXPERIMENTAL RESULTS

In response to stimulation of the visceral nerves, obvious electrical reactions may develop in the cerebellar cortex of decerebrate animals. Consequently, the cerebellum, if deprived of its connections with the higher centers, can still react to impulses from the interoceptors. Meanwhile, exclusion of the cerebral hemispheres modifies the ability of the cerebellum to receive interoceptive impulses. In our investigations this showed itself primarily by a change in the excitability of the cerebellar cortex to stimulation of the visceral nerves, as could be judged by changes in the thresholds of stimulation.

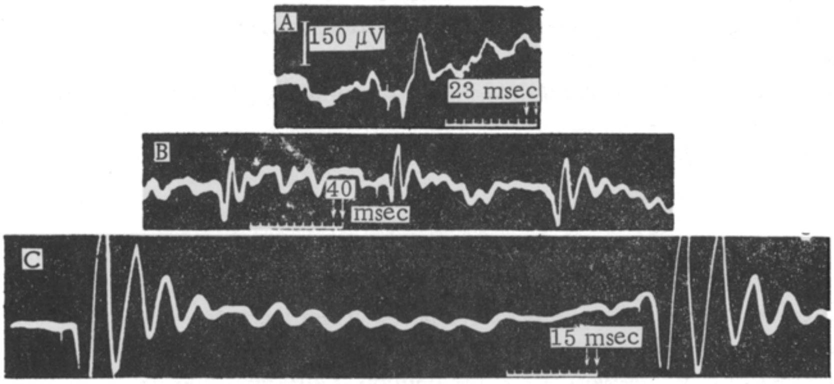

Fig. 1. Electrical reactions of the cerebellar cortex of a cat recorded in the anterior lobe during stimulation of the right splanchnic nerve. A) With the nervous system intact, under thiopental-sodium anesthesia (distance between coils 10 cm); B) 1 h after decerebration (distance between coils 8.5 cm); C) after decerebration, in the inferior folium of the right anterior lobe, at its border with the cerebellar peduncle (coil distance 8.5 cm, voltage of battery 2.6 V).

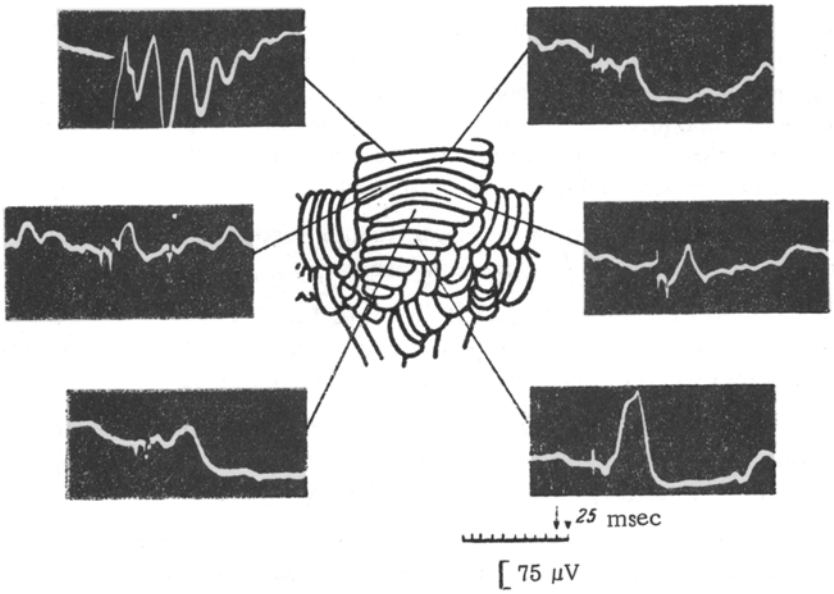

Fig. 2. Electrical reactions of the cerebellum of a cat, recorded at various points of the cerebellar cortex during stimulation of the right splanchnic nerve after decerebration (thiopental-sodium anesthesia with a 210 mg dose) (distance between coils 6.5 cm, voltage of battery 2.6 V).

The changes in the thresholds after denervation varied from one experiment to another. In half the animals the threshold of stimulation was increased; in these cases the lowered excitability could have been associated with disturbance of the blood supply of the cerebellum. The threshold level of stimulation remained unchanged in six cats (21.4%). The remaining experiments, in which the threshold of stimulation was lowered in the animals after decerebration, were of much greater interest. This group also included six cats from the cerebellar cortex of which no responses could be obtained, or they were very weak, when the nervous system was intact, while after denervation stimulation of the same nerves led to the development of adequately clear electrical responses. We consider that the increased excitability of the cerebellum to interoceptive stimuli after exclusion of the cerebral hemispheres may have been due to the constant inhibiting influence of the cortex or other division of the hemispheres on the cerebellum.

The second characteristic feature of the electrical responses of the cerebellar cortex after denervation was a change in their electrographic appearances. In animals with an intact nervous system, and under adequately deep barbiturate anesthesia, the electrical response reaction of the cerebellum to stimulation of the visceral nerves (or the somatic) was as a rule very similar in its time characteristics and form to the primary response, and consisted of a monophasic electrically positive action potential, or a biphasic response with a first positive and a second negative

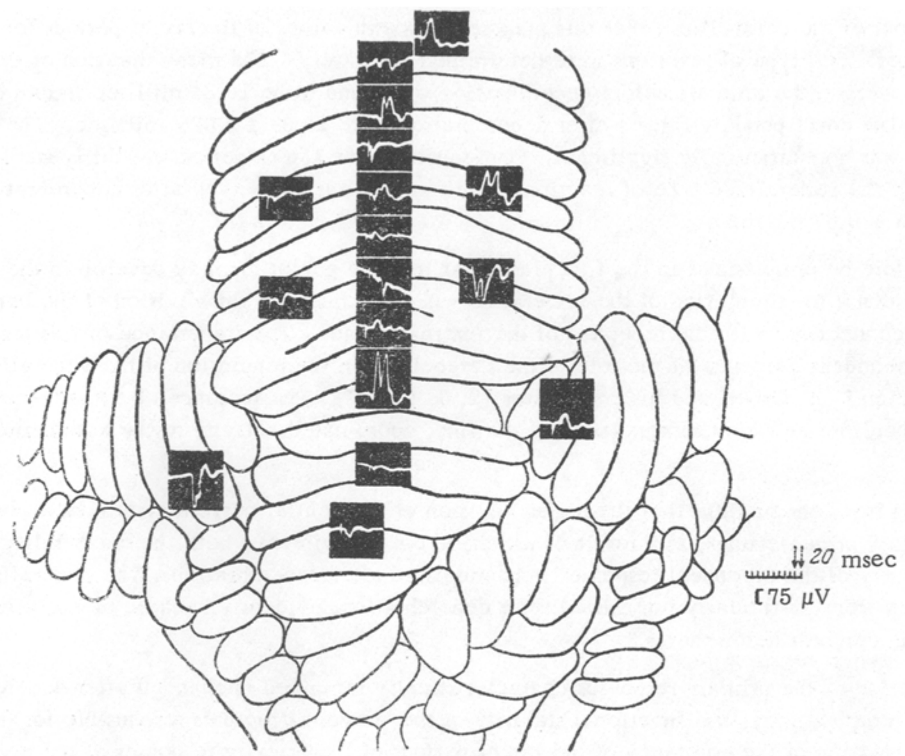

Fig. 3. Scheme of the distribution of the reactions at different points of the cerebellar cortex during stimulation of the right vagus nerve after decerebration (distance between coils 12 cm, voltage of battery 2.6 V).

phase [1, 5, 9, 18]. The distinguishing feature of the cerebellar responses of the decerebrate animals to stimulation of the visceral nerves must be considered to be electrical reactions in the form of slow waves, single or in groups, which could be recorded either independently or in conjunction with the primary effects. The electrical response to stimulation of the splanchnic nerve, recorded from the cortex of the anterior lobe of the cerebellum of a cat anesthetized with thiopental sodium in a dose of 70 mg/kg body weight, is shown in Fig. 1, A. It consists of a biphasic action potential; the first, electrically positive, phase with an amplitude of about 100 μV and duration of 14 millisec can be seen. The second shallow negative phase is represented by a slow, high-voltage wave with an amplitude of 180 μV and duration 55 millisec. In Fig. 1, B are recorded the responses under the same conditions of recording leads and stimulation one hour after decerebration. The response reactions consist of groups of volleys of slow waves, over 100 μV in amplitude. The duration of individual waves is about 50 millisec. In the same experiment (Fig. 1, C) responses were recorded from other areas of the anterior lobe, in which slow high-voltage waves were grouped in long series of gradually diminishing oscillations.

In some experiments, in addition to volleys of slow waves, reactions of the primary response type were fairly prominent after decerebration. During control stimulation of the nerves, before transection of the brain stem, no reactions could be detected in the cerebellar cortex. Nevertheless, after decerebration, in response to stimulation of the splanchnic nerve electrical effects were observed in various leads; these varied in form, consisting of a primary response, either alone or followed by a secondary reaction, made up of single or multiple slow waves (Fig. 2). If the stimuli were repeated, a change in the character of the responses could be observed.

In the decerebrate animals, responses to stimulation of the visceral nerves could be recorded from a wide area of the surface of the cerebellum. Two zones were found to possess maximal activity: the first zone corresponded to a simple lobule with the adjacent regions of the vermis and anterior lobe, i.e., to the region which we detected earlier in the animals with an intact nervous system; the second zone included the two superior foliae of the anterior lobe (Fig. 3). After decerebration, primary responses could be recorded most frequently in the zones of maximal activity. Electrical responses in the form of volleys of slow waves were observed both in foci of maximal activity and in other parts of the cerebellum. They therefore characterized the generalized type of cerebellar response.

It was interesting to discover to what degree decerebration could affect the duration of the latent periods of the response reactions of the cerebellum. For this purpose the mean values of the latent periods for the primary responses and the generalized type of reactions were determined separately. The mean duration of the latent period of the primary responses in the animals before decerebration was found to be 10.84 millisec (mean square deviation ± 0.465 millisec). The corresponding figures after decerebration were 11.39 ± 0.625 millisec. The difference between these values was not statistically significant. Consequently, the latent period was fairly stable in its length. The latent period of the generalized type of reactions which were clearly observed after decerebration was longer and measured 17.28 ± 0.67 millisec.

It must therefore be emphasized in the first place that induced potentials may develop in the cerebellum after decerebration in response to stimulation of the visceral nerves; consequently, this division of the nervous system possesses independent connections with the receptors of the internal organs. The importance of this fact must be assessed in the light of the abundant evidence of the role of the cerebellum in the regulation of the vegetative functions adduced by Academician L A. Orbeli and his co-workers [2, 3, 4, 6, 7]. The presence of a "back-coupling" from the internal organs is therefore an essential condition of the fine, coordinated activity of the autonomic centers of the cerebellum.

It also follows from our findings that the higher division of the central nervous system have some effect on the cerebellum (inhibitory or depressing), as a result of which, in our experiments, both the excitability to visceral impulses and the intensity of the electrical responses were modified after decerebration. The generalized responses of the cerebellar cortex were particularly intensified after decerebration, evidently because of exclusion of the inhibiting influences of the cerebral hemispheres.

The latent period of the primary responses characteristically remained unchanged after decerebration. This fact pointed to the morphological and functional stability of the nervous structures responsible for the primary response. This interpretation of the constancy of the latent periods of the primary responses of the cerebral cortex is supported by various writers [11, 15, 17, and others]. The primary response reflects the arrival of impulses along the direct, specific pathway. The formation of the generalized responses involves the participation of pathways represented by elements of the nonspecific nervous system; this accounts for the variability of their forms and time characteristics and the absence of well-defined localization.

In the decerebrate animals foci of maximal activity could be detected in the cerebellum in relation to interoceptive impulses, which coincided with those detected in animals with an intact nervous system in response to stimulation of visceral nerve trunks [1, 5]. According to some writers [11, 13, 14], it is impossible to obtain a somatotopic distribution of responses in the cerebellar cortex of decerebrate animals in relation to exteroceptive impulses. It should be remembered that these investigations were conducted on decerebrate, unanesthetized animals; we, on the other hand, used decerebration in combination with barbiturate anesthesia.

SUMMARY

Thiopental-sodium anesthetized cats were decerebrated at the intercollicular level. Stimulation of the central portions of the vagus and splanchnic nerves and their branches led to the appearance of a response in the cerebellar cortex. In some ways these responses differed in decerebrated animals from those recorded in animals with an intact nervous system. Stimulation thresholds could change both in the direction of rise and decrease. A tendency to the

development of reactions of generalized type was intensified, this being represented by a series of slow waves, which appeared spontaneously or accompanied the primary response. There was preponderant distribution of responses in the L. simplex with adjacent areas, L. anterior and the vermis, and the first two lobules of L. anterior. A conclusion was drawn on the presence of independent routes of interception of the cerebellum, as well as on the constant effect of the higher lying centers on this CNS portion.

LITERATURE CITED

1. N. V. Bratus', Fiziol. Zh. SSSR, 2, 179 (1960).
2. L. G. Voronin and A. M. Zimkina, Fiziol. Zh. SSSR 21, 5-6, 743 (1936).
3. P. M. Kaplan, Fiziol Zh. SSSR 25, 3, 315 (1938).
4. A. I. Karamyan, Evolution of the Functions of the Cerebellum and the Cerebral Hemispheres [in Russian] (Leningrad, 1956).
5. K. M. Kullanda, Doklady Akad. Nauk SSSR 124, 6, 1367 (1960).
6. V. É. Maevskii, Fiziol. Zh. SSSR 28, 2-3, 247 (1940).
7. L. A. Orbeli, Uspekhi Sovr. Biol. 13, 2, 207 (1940).
8. E. K. Sepp, History of the Development of the Nervous System of the Vertebrates [in Russian] (Moscow, 1959).
9. V. N. Chernigovskii, The Interoceptors [in Russian] (Moscow, 1960).
10. E. D. Adrian, Brain, 1943, v. 66, p. 289.
11. V. E. Amassian, Cited by A. Morillo.
12. V. Bonnet and F. Bremer, J. Physiol. (Lond.), 1951, v. 114, p. 54P.
13. C. M. Combs, J. Neurophysiol.,1954, v. 17, p. 123.
14. R. S. Dow, J. Neurophysiol., 1939, v. 2, p. 543.
15. H. H. Jasper, In: Brain Mechanisms Consciousness, (Paris, 1954), p. 374.
16. A. Morillo, Electroenceph. clin. Neurophys., 1961, v. 13, pp. 9-17.
17. V. B. Mountcastle and M. R. Covian, Ass. Res. nerv. Dis. Proc. 1952, v. 30, p. 339.
18. L. Widen, Acta physiol. scand. 1955, v. 33, Suppl. 117.
19. O. Larsell, Arch. Neurol Psychiat. 1937, v. 38, p. 580.

All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.