EFFECT OF THE PERIPHERAL VESTIBULAR AFFERENT IMPULSES ON SYNCHRONIZATION OF SLOW CORTICAL RHYTHMS

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This experimental study in animals is the continuation of our previous clinical neurosurgical investigations [2, 3,4], showing that in most patients with a lesion situated in the posterior cranial fossa the EEG shows a considerable increase in the posterior regions of the cortex.

Analysis of the results and comparison between the EEG and the site of the tumor and the results of recordings made from the exposed brain during neurosurgical operations showed that synchronization of this type is observed during compression of the ventrolateral divisions of the caudal portion of the brain stem, namely the superior ventrolateral areas of the medulla and the inferior lateral areas of the pons. It has been observed [3] that the auditory and vestibular nuclei of the VIIth nerve are situated in precisely these divisions of the brain stem. This fact, and also supplementary investigations, including the study of the excitability of the vestibular nuclei, suggested that interruption of the flow of vestibular afferent impulses in the cases under discussion was of fundamental importance for hypersynchronization of the α-rhythm in the cortex. Interruption of the flow of auditory afferent impulses had no appreciable effect.

Apparently this phenomenon of synchronization does not arise directly as a result of the loss of the influence of the vestibular nuclei on the cortex, but indirectly, via the reticular formation at this level, with which these nuclei are connected by numerous collaterals.

This problem is also of interest from the point of view of the few, but contradictory, reports in the literature of the effect of exclusion of the influence of a specific afferent system on the character of the cortical rhythm. For instance, according to Roger, Rossi, and Zirondoli [14], who conducted acute experiments on the "encephale isole" preparation, exclusion of the olfactory, auditory, vestigular, and vagus afferent fibers does not change the electroencephalographic picture characteristically found in the waking state. Synchronization was produced only by deafferentation of the trigeminal nerves. L. A. Novikova [1,6] excluded optic and olfactory afferent impulses in chronic experiments and observed a sharp fall in the amplitude of the electrical potentials in all divisions of the cortex, with slowing of the rhythm and a decrease in the number of fast waves in the curves.

In order to verify our clinical observations and also to ascertain the role of the various links of the vestibular apparatus (the peripheral vestibular apparatus, the vestibular nuclei) and also of the reticular formation in this process, we carried out a series of experiments on animals. In one variant of the experiment, conducted in chronic conditions, the role of the peripheral vestibular afferent system in the synchronization of the cortical rhythm was studied.

EXPERIMENTAL METHOD

Experiments were performed on 14 unanesthetized cats with electrodes permanently implanted in the bone. Potentials were recorded from the anterior and posterior divisions of the optic, parietal, and sensorimotor regions of the cortex, using uni- and bipolar leads. Recordings were made from the intact animal for a period of 1.5-2 weeks, until it became adapted to the conditions and the level of its electrical activity became stabilized. The electrical activity was then recorded after vestibular deafferentation, brought about by exclusion of the labyrinths.

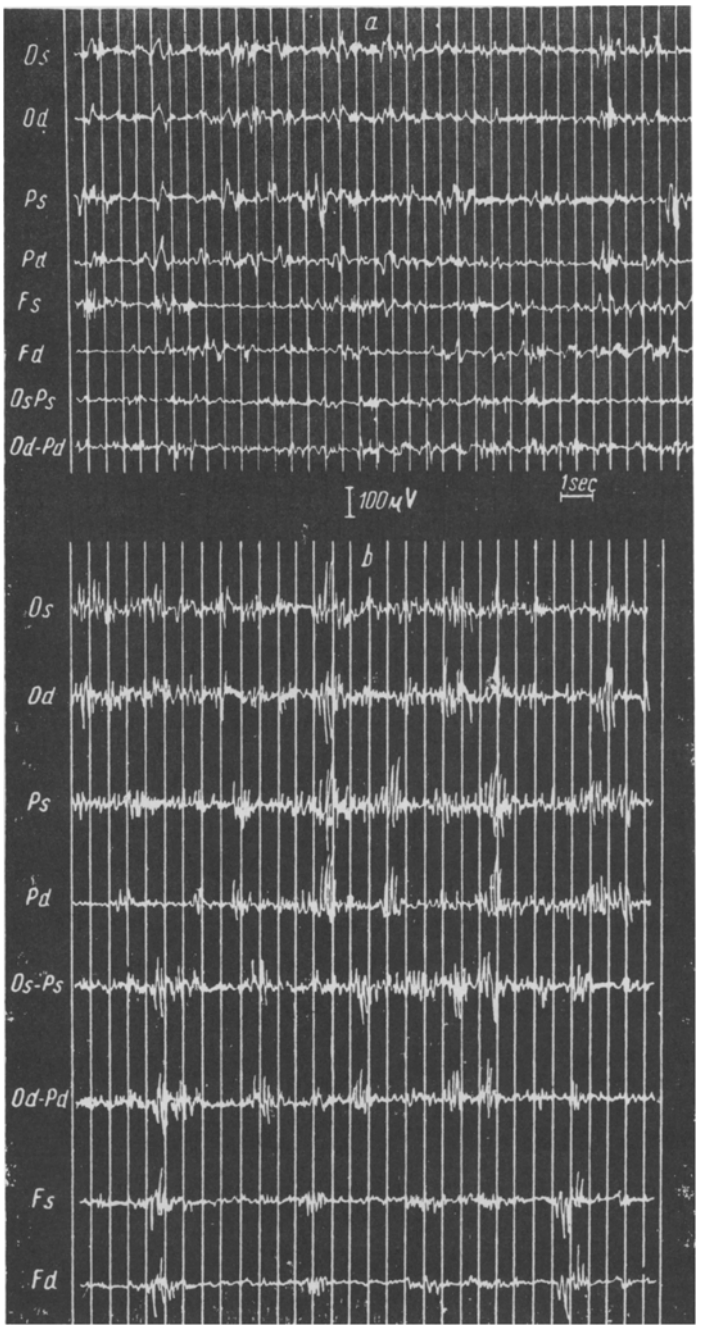

Fig. 1. EEG of a cat before (a) and after (b) one-stage bilateral labyrinthectomy. Os – left occipital lead; Od – right occipital lead; Ps – left parietal lead; Pd – right parietal lead; Fs – left sensorimotor lead; Fd – right sensorimotor lead; OsPs – bipolar left occipito-parietal lead; OdPd – bipolar right occipito-parietal lead.

Systematic recordings were made for an initial period of 3 weeks or 1 month, and thereafter (in some animals up to 6 months and 1.5 years) periodically. The labyrinths were inactivated by injecting 96° alcohol through the bulla into the fenestra rotunda. Labyrinthectomy was performed uni- or bilaterally, the bilateral procedure being carried out in 1 or 2 stages. In the latter case the second stage of the operation was performed 3 weeks or 1 month after the first.

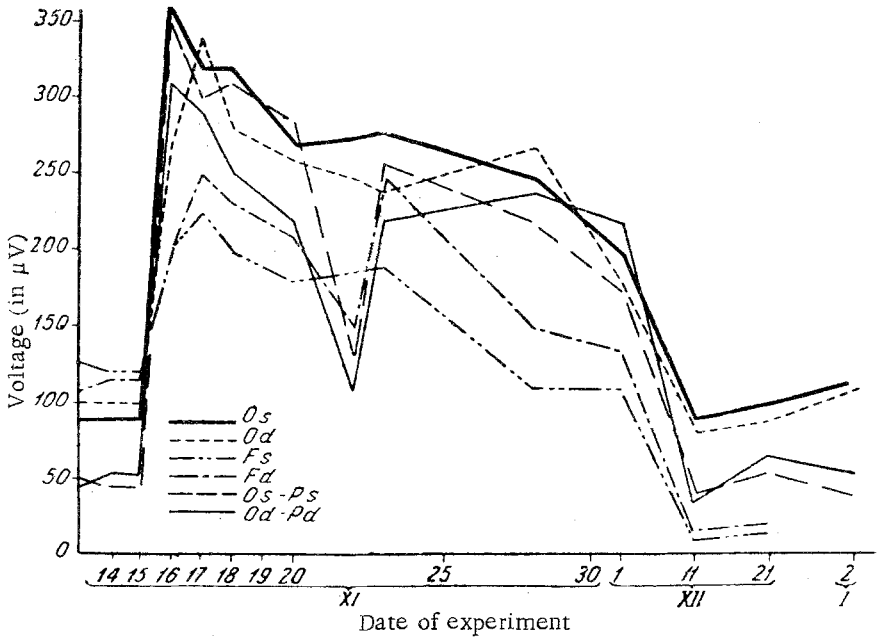

Fig. 2. Trend of the changes in the amplitude of the synchronized rhythms appearing after bilateral vestibular deafferentation in a cat. Labyrinthectomy on November 15. Legend as in Fig. 1.

EXPERIMENTAL RESULTS

In 7 of 9 animals total one-stage bilateral vestibular deafferentation caused very severe changes in the EEG. During the first 3-5 days (and sometimes longer) after the operation a considerable jump in the amplitude of the waves was observed. It will be clear from Fig. 1 that the EEG characteristic of normal cats in a resting state was sharply modified after labyrinthectomy. The bursts of spikes increased in amplitude to, for example, 300-350 μV compared with the initial 50-100-120 μV. Hence, before going on to mention changes in the actual character of the EEG, in some animals the amplitude increased to 2-3 times, in others to 5 times, and in individual cases to 7 times the initial level. These changes were more marked in the posterior divisions of the cortex, although the amplitude of the waves was also increased in the anterior divisions. For example, in cat No. 7, initially the maximal amplitude of the waves in the occipital regions was 60 μV, and in the anterior regions 105 μV; after bilateral labyrinthectomy the maximal amplitude of the waves in the occipital regions was 360 μV, and in the anterior regions 230-340 μV.

This high level of the amplitude of the waves was maintained for several days, after which it fell gradually, to return to the initial level after 3 weeks or a month. In the posterior divisions of the cortex this was more clearly defined, while in the anterior divisions the amplitude was actually observed to fall below its initial level—to 15-20 μV.

The trend of the changes described above is shown in Fig. 2. The degree of synchronization after deafferentation apparently depends to some extent on the initial level of synchronization. For instance, in 2 of the 9 animals subjected to one-stage bilateral deafferentation, the initial amplitude of the waves was fairly high (200 μV or more). For this reason the recording of a significant degree of synchronization in these animals (up to 300 μV or more) after labyrinthectomy in fact demonstrated a small increase in the amplitude of the waves (about 50%) over their initial values. Recordings of the electrical activity during the months following the operation sometimes revealed waves of smaller amplitude than on the initial curves, but with closely related frequency characteristics. In most cases the amplitudes were not less than the initial values. In 3 animals, however, the waves remained more highly synchronized than the initial waves for a long period of time.

The high-amplitude, synchronized rhythms described above were recorded in animals in a tranquil, or rather in a drowsy state, which was a constant feature lasting for a definite period of time after the operation. Any external stimulus, evoking an orienting reaction, naturally led to an arousal reaction, i.e., to the appearance of desynchronization phenomena on the EEG. The drowsy state of the labyrinthectomized cats often passed into a deep sleep. This

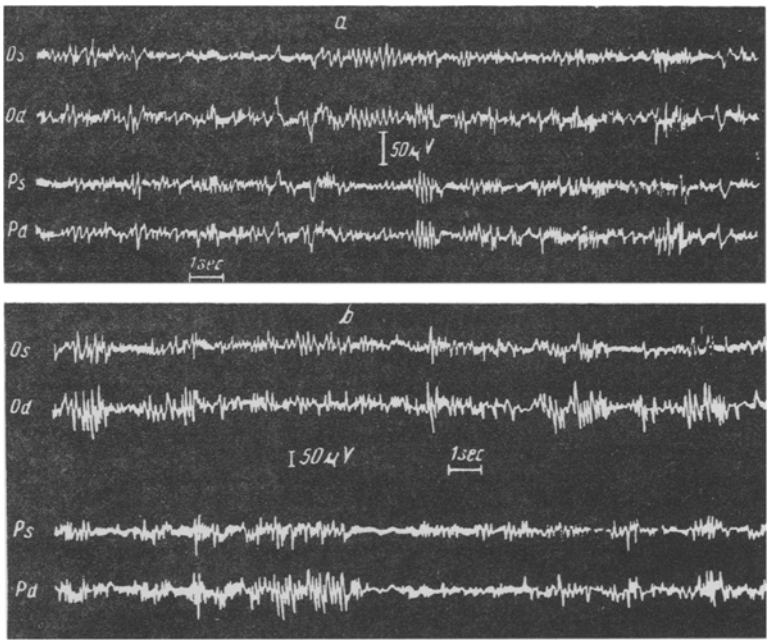

Fig. 3. EEG of a cat before (a) and after (b) unilateral labyrinthectomy. Legend as in Fig. 1.

was accompanied by disappearance not only of the high-amplitude synchronized spikes, but also of the slow waves characteristic of deeper sleep, from the EEG and their replacement by low-amplitude, fast waves (17-20/sec). Desynchronization was in fact observed. Forced awakening of the animals led to the restoration of the synchronized rhythms, and during deep sleep these were again replaced by desynchronization. Similar changes in the EEG have been reported in intact, unanesthetized cats [13]. It has been suggested that desynchronization in these cases is the expression of a deeper stage of sleep than synchronization. It may be that the "zero state" previously described by several writers [5,10] is an expression of the same desynchronization with displaced fast, low-amplitude waves as a result of weak amplification.

After unilateral vestibular deafferentation (5 animals) in every case asymmetry of amplitude was observed between the hemispheres, more especially in the posterior divisions of the cortex, but with a less stable and less marked synchronization of the waves than after bilateral deafferentation. Sometimes, against a background of asymmetry and of existing synchronization of the waves in one hemisphere, a still greater increase in the amplitude of the spikes was observed in this hemisphere, followed by their generalization into the other hemisphere. At this time spikes were recorded synchronously in both hemispheres, although the asymmetry remained obvious (Fig. 3). Exclusion of the second labyrinth in these animals (3 weeks to 1 month later) led to a still more marked hypersynchrony than after the first stage of the operation. No precise relationship between sides (hemisphere and labyrinth) could be discerned.

This variant of the investigations thus confirmed our hypothesis concerning the considerably influence of vestibular deafferentation on synchronization of the cortical rhythm. The suggestion may also be made that the vestibular afferent impulses are particularly important in the maintenance of the waking state in the desynchronization phenomena.

Comparison between our findings and those described in the literature [1,6,14], according to which the exclusion of other afferent systems (optic, olfactory, auditory, etc.) does not cause similar changes to those described in the EEG, suggests that this phenomenon of synchronization does not appear after any form of deafferentation, although the activating effect in the form of desynchronization of cortical activity may result from any afferent stimulus. The exclusion of the vestibular impulses possibly plays a particularly important part in the mechanism of synchronization on account of the exceptional wealth of its connections with the reticular formation. Several investigators have shown that the vestibulo-reticular projections occupy a large area of the brain stem, including the uppermost part of the medulla, the pons, and, possibly, the midbrain [9,11,15,16]. This does not clash with the fact established by some workers [8,12] that vestibular stimulation proved more effective than trigeminal, optic, and auditory stimulation in evoking a

generalized electrographic arousal reaction. Another factor to be considered is the large number of direct connections between the vestibular nuclei and other formations of the central nervous system – the cerebellum, the autonomic nuclei, and the spinal cord.

In our opinion the area discovered by Morruzzi and co-workers [7] in the caudal portion of the brain stem, which they associate with the mechanism of synchronization, and the area of decisive importance to the maintenance of the waking state (desynchronization), are also related to the vestibular system. The important factor here is that anatomically the superior vestibular nucleus of Bekhterev, the nucleus giving rise to ascending tracts, is situated at this precise level above and below which the sections were made. Section at a level above the nuclei must naturally lead to the interruption of the arrival of vestibular impulses in the cortex and must bring about the synchronization of cortical activity. Division below the nuclei does not interrupt their activity, and may even cause irritation. Synchronization therefore does not arise and the EEG shows desynchronization. This hypothesis requires experimental verification.

The electrophysiological expression of the compensatory phenomena coincides in time with the compensation of the disturbed motor functions.

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