PHYSIOLOGY

REPRESENTATION OF INTERNAL ORGANS IN THE CEREBRAL CORTEX AND CEREBELLUM OF CATS AND DOGS

COMMUNICATION 2: PRIMARY BIOELECTRIC REACTIONS OF THE CEREBRAL CORTEX TO STIMULATION OF INTERNAL ORGANS

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It was shown in previous communications [1, 2] that the pelvic nerve in cats and dogs was represented in the cerebral cortex with definite localization. In cats one zone is situated on g. cruciatus, another on g. ectosylvius ant., both zones being bilateral (Fig. 2, scheme 1). Primary responses appear in these zones on both hemispheres on stimulation of the pelvic nerve with single shocks.

Similar reactions in corresponding areas of the cortex may be detected on electric stimulation of other afferent nerves from internal organs, such as the vagus and splanchnic (Amassian, Dell et al).

There is now no doubt concerning the possibility of primary bioelectric reaction occurring in the cerebral cortex in response to stimulation of any afferent nerve. At the same time, the question of primary responses to adequate stimulation of the peripheral terminations of analysors has not been sufficiently investigated. So far it has proved possible to obtain cortical primary responses to adequate stimulation of the retina, the organ of Corti and cutaneous receptors [4].

Almost nothing has so far been discovered about the possibility of obtaining primary responses to visceral stimulation. Thus the present author found only one reference in the literature, in the work of V. Amassian, to a bioelectric reaction, which he considered as a primary response, recorded from the contralateral zone of cortical representation of the splanchnic nerve on stimulation of intestinal mesentery in the cat with a brief single mechanical stimulus [5].

No data with reference to other viscera were available.

In the course of mapping the zones of cortical representation of various internal organs we have found that mechanical stimulation of the bladder, rectum and uterus gives rise to primary responses in the cerebral cortex of cats and dogs; these are recorded from zones in which primary responses to stimulation of the pelvic nerve were recorded [1]. In that communication certain characteristics of the responses to stimulation of internal organs were also given.

Subsequently T. E. Orlova [3] reported that when air was insufflated into the bile ducts in dogs it was possible, in part of the experiments, to detect a "local" reaction in the premotor cortical zone which proceeded in accordance with the "primary effect" type of reaction.

The obvious inadequacy of data concerning this question led to this more detailed investigation.

EXPERIMENTAL

Short experiments under nembutal or chloralose anesthesia were performed on 48 cats and 6 dogs; in these experiments the appearance of primary responses in definite cortical zones following stimulation of the bladder, uterus, rectum, stomach and pericardium was studied. Several organs were subjected to stimulation in one and the same experiment. The bladder, rectum and stomach were stimulated by inflation of a fine rubber balloon inserted in their lumen; the uterus and pericardium were stimulated by pulling on silk ligatures attached to them or by touching with a sharp-pointed glass rod.

On stimulation of the bladder the maximal pressure in the balloon, recorded by a kymograph, was equal to 50 mm of mercury. In order to avoid artefacts which arise whenever the distended organ comes into contact with the abdominal wall or the surface of the skin, the bladder was withdrawn from the widely opened abdominal cavity and suspended by ligatures from an insulated stand, while the edges of the incision were widely separated by means of silk ligatures. In addition to the inserted balloon, a cannula was tied into the floor of the bladder which connected its cavity with two recording devices by means of a system filled with warm physiologic solution. The first of the recording devices registered the periodic contractions of the bladder on a kymograph, while the second recorded the same on a cine-film simultaneously with a recording of bioelectric processes (Fig. 1 and 2).

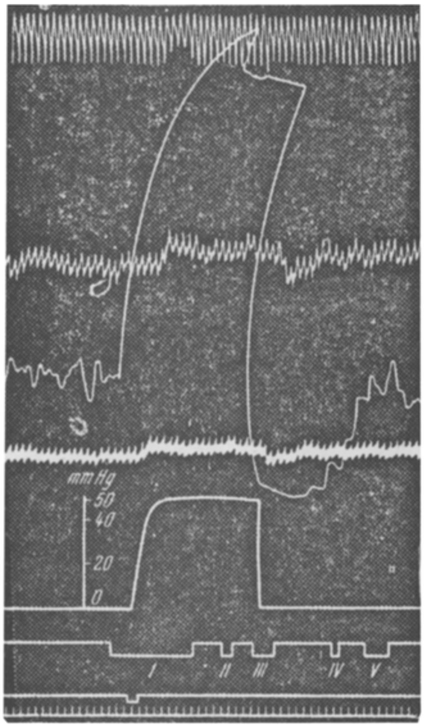

Figure 1. Stimulation of the bladder by inflation of an inserted rubber balloon. Cat. Chloralose anesthesia of medium depth. Records from above down: 1) respiration; 2) arterial pressure shown by mercury manometer; 3) pressure within the bladder shown by tonometer; 4) arterial pressure shown by tonometer; 5) pressure in rubber balloon shown by mercury manometer; 6) moments of recording the oscillograms given in Fig. 2, A, B, C, D, E; 7) beginning of stimulation; 8) time marker (5 seconds).

One of the small branches of the pelvic nerve was dissected and its peripheral end placed on a pair of silver recording electrodes with an inter-electrode distance of 5 mm. The electrodes were mounted on a small block of Plexiglas which was attached to the surface of the bladder; this diminished the difficulties usually attendant on displacement of the nerve on the electrodes with changes in the volume of the organ. These electrodes recorded afferent impulses arising in the pelvic nerve on distention of the bladder walls. During the whole experiment measures were taken to protect the surface of the bladder from drying and cooling.

In order to exclude possible reflex contraction of muscles the animals were immobilized in a number of experiments by intravenous administration of "diplacin" (0.5 ml 2% solution per 1 kg body weight). The monopolar method of recording cerebral biopotentials has been described in detail in a previous communication.

The frequency characteristic of the amplifier was linear within the limits from 10 to 500 cps during the recording of afferent impulses and from 5 to 300 cps during the recording of cortical biopotentials.

RESULTS

All the experiments gave, in general, similar results, viz: stimulation of mechanoreceptors of the organs mentioned led to the appearance of primary responses in the cerebral cortex which, in the case of the bladder, rectum and uterus, were recorded both from the first and second zones of cortical representation of the pelvic nerve. Stimulation of the stomach and pericardium evoked the appearance of primary responses in the first and second regions of general somatic sensation [2] in zones adjacent to the cortical projections of the pelvic and splanchnic nerves. Results of one of these experiments are presented in Figs. 1 and 2.

Comparison of the kymogram with the oscillograms indicates that the moment of distention of the bladder walls is accompanied by the appearance of afferent impulses in the pelvic nerve and of bioelectric reaction in the cerebral cortex (Fig. 1, 1; Fig. 2, A) in the first zone of cortical representation of the pelvic nerve (Fig. 2, scheme 2, C). The question arises as to whether it is possible to regard this bioelectric reaction of the cortex as a primary response to the stimulation of the bladder mechanoreceptors. One of the main signs of a primary response is its latent period. When the pelvic or splanchnic nerve is stimulated by single electric stimulus the length of the latent period usually fluctuates between 6 and 12 milliseconds, whereas in the cortical reaction under consideration the latent period is 30 milliseconds. This difference in the length of the latent periods becomes explicable when it is taken into account that primary responses, obtained on adequate stimulation of receptors, have a longer latent period. For example, the latent period of the primary response to electric stimulation of the optic nerve equals 2.3 milliseconds, while on adequate stimulation of the retina (by illumination of the eye) it fluctuates between 17 and 25 milliseconds [6]. This can be explained by the time required to excite the receptors in the latter case. However, if orientation is based not on the mechanical marker of the beginning of stimulation with its degree of inertia, but on the appearance of afferent impulses as a signal of the beginning of stimulation (such impulses show that some of the receptors have already been excited) even then the value of the latent period exceeds the time necessary for the impulses to reach the cerebral cortex. All this leads to the hypothesis that in order for primary cortical reaction to occur in response to stimulation of internal organ receptors it is necessary that a certain threshold quantity of afferent impulses reach the sensory nuclei of the thalamus. The afferent impulses cause a gradual growth of excitation in the thalamic neurons culminating in a discharge into the cellular layers of the cortex, this latter event being accompanied by the appearance of the primary reaction.

In essence this is similar to electric stimulation of sensory nerves: weak single stimuli produce excitation in the nerve but do not evoke a primary response in the cortex.

These views find a certain analogy in A. L. Roitbak's [4] interpretation of the causes of the increase in amplitude of the positive potential of the primary response on increased peripheral stimulation. Thus, the long latent period of the bioelectric reaction under consideration in the present work cannot be considered as an obstacle to interpreting it as a primary response. Nor is it contradicted by its other characteristics. The somewhat increased duration of its phases can be explained by nonsynchrony of afferent impulses. In those cases where stimulation is associated with a more powerful and synchronous burst of afferent impulses the duration of the phases of the primary response approaches that of responses to nerve stimulation (Fig. 2, F). Primary reactions to stimulation of internal organs, similarly to primary responses to nerve stimulation, are localized. Thus, when the bladder is stimulated they arise in the zones of pelvic nerve representation (Fig. 2, A record at point C, scheme 2) and do not appear in other regions of the cortex. In cortical areas at a distance from the zones of pelvic nerve representation a generalized reaction is observed, expressed by changes in the basic rhythm of bioelectric activity. In the experience of the present author this is reflected in some depression of the basic rhythm. Analogous picture is observed on stimulation of the rectum (Fig. 3). In some cases, however, stimulation of internal organs led to primary responses which had a fairly brief latent period (12-13 milliseconds) following the appearance of afferent impulses (Fig. 2, G). Evidently this occurs in those cases where the excitation of the corresponding thalamic sensory nuclei neurons is such that the brief burst of afferent impulses suffices to produce their discharge into the cellular structures of the cortex.

Such a state of thalamic neurons can be determined by a continuous inflow of afferent impulses from other visceral receptive fields.

If it is supposed that thalamic neurons are capable of summating stimuli ascending from the viscera along afferent pathways and of discharging periodically into the cortex then the bioelectric complexes arising in the cerebral cortex in response to continuing stimulation (Fig. 1, II, Fig. 2, B) may be regarded as individual primary responses following each other in a way in which they would have arisen in the case of rhythmic stimulation of receptors or afferent nerves.

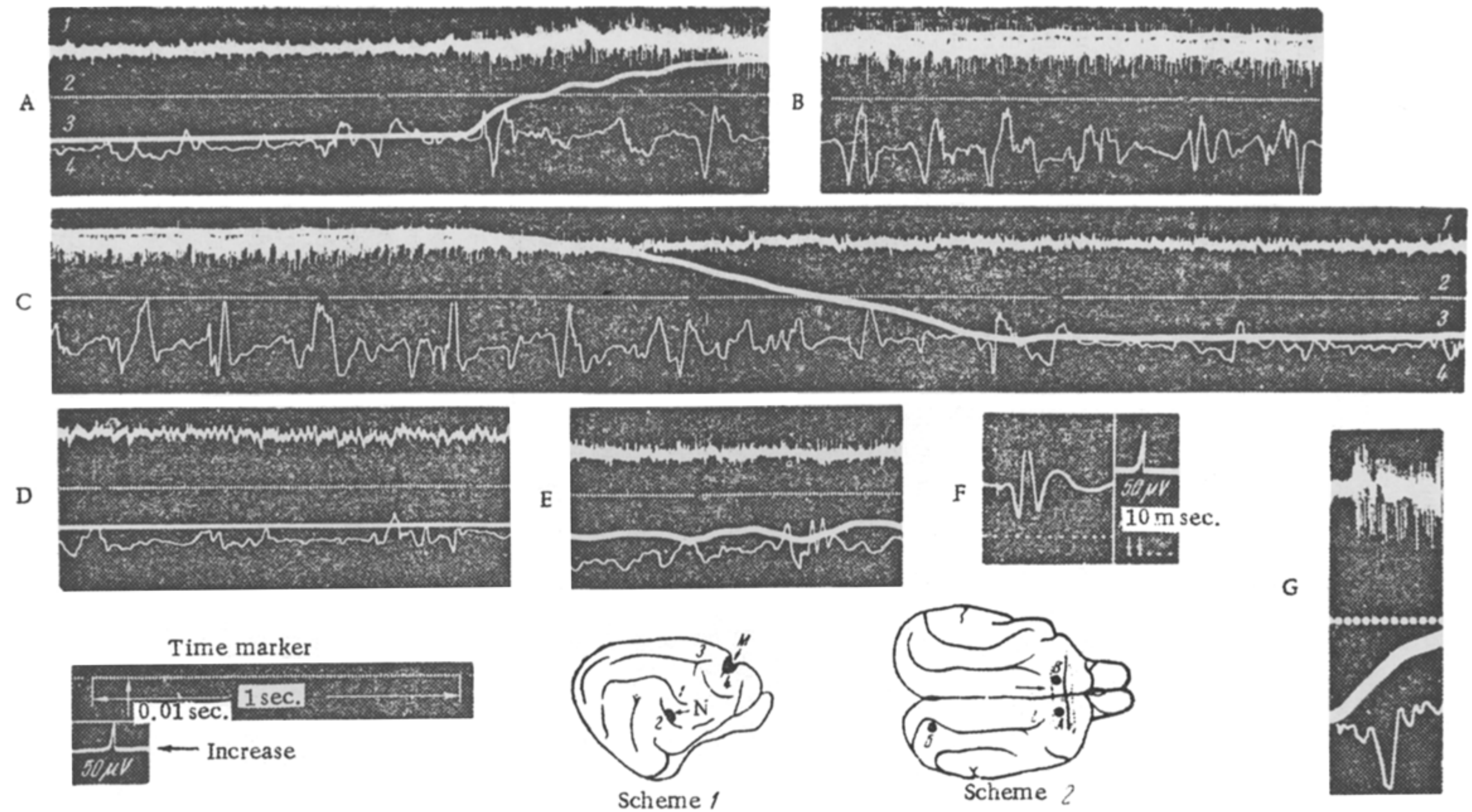

Figure 2. Appearance of primary responses in the cerebral cortex of cat on stimulation of the bladder by inflation of an inserted rubber balloon. Records in all oscillograms from above down: 1) afferent impulses in n. pelvicus; 2) time marker (1 second and 0.01 second); 3) changes in pressure within the bladder; 4) cerebral cortical biopotentials. Scheme 1: M – first and N – second zones of cortical respresentation of n. pelvicus; 1) s. suprasylvius ant.; 2) s. ectosylvius ant.; 3) s. ansatus; 4) s. cruciatus. Scheme 2: 1) s. cruciatus; 2) s. ansatus; F) primary cortical response to stimulation of n. pelvicus by a single shock; G) primary response in the first zone of pelvic nerve representation on stimulation of the bladder possessing a short latent period (12 milliseconds) following the appearance of afferent impulses.

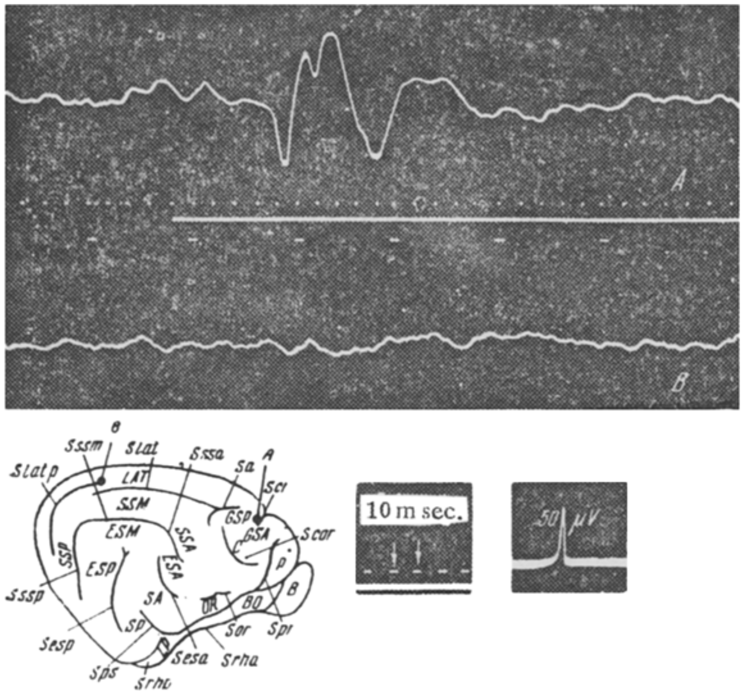

Figure 3. Appearance of primary response in the first zone of cortical representation of the pelvic nerve (A) on stimulation of the rectum and its absence from other cortical areas (B). Cat. Nembutal anesthesia of considerable depth. Animal immobilized by intravenous administration of "diplacin" (artificial respiration). Below at left surface map of the cat's brain with recording electrode positions marked A and B. Continuous line in the center of the oscillogram marks the beginning of inflation of rubber balloon in rectum. Maximal pressure of air in balloon equalled 40 mm of mercury.

The proposed hypothesis is not contradicted by changes in configuration of the primary complexes (Fig. 2, B and C).

The pattern of changes in the configuration of primary responses observed by A. I. Roitbak [4] on rhythmic electric stimulation of cutaneous receptors and rhythmic stimulation of the sciatic nerve appears to resemble the pattern described here. We observed similar results on rhythmic stimulation of the pelvic and splanchnic nerves.

Further analysis of the data obtained draws attention to the fact that the appearance of primary complexes in the cortex continues for some time after cessation of stimulation of the bladder (Fig. 1, III, Fig. 2, C).

Evidently the excitation of thalamic neurons under the influence of afferent impulses persists for some time following their termination and thus determines the periodic, gradually weakening, discharges into the cortex. The possibility is not excluded that this excitation is maintained by afferent stimuli arriving from other organs as well.

Afferent impulses in the pelvic nerve appear anew when the relaxation of the bladder wall (Fig. 1, IV, Fig. 2, D) is replaced by its tension, i.e, at the moment of restoration of its rhythmic contractions. Their appearance is accompanied by primary complexes in the cortex (Fig. 1, V, Fig. 2, E). This may indicate that the normal activity of internal organs (for example contraction of the rectum or stomach, stretching of the bladder wall) is capable of eliciting primary responses in the cerebral cortex.

It is quite probable that the periodic bursts of slow potentials of large amplitude observed in the premotor cortical area and in the second general somatic sensory area, which arise without any preliminary experimental stimulation, are primary complexes determined by the activity of internal organs.

The primary responses which arise in the cortical areas mentioned above on stimulation of the uterus, stomach and pericardium are similar to those which arise in response to stimulation of the bladder or rectum and there is thus no need for a special description of them.

SUMMARY

Experiments on cats and dogs have shown that stimulation of the urinary bladder, colon and uterus elicits a primary reaction in the I and II zones of cortical representation of the pelvic nerve. Stimulation of the stomach and pericardium elicits primary reactions in the I and II areas of general sensitivity, bordering the area of representation of the pelvic and splanchnic nerves. If the afferent impulses of the pelvic nerve during dilatation of the urinary bladder are compared with the cortical potentials one might suppose that summation of excitations takes place in the thalamic neurons, while the bursts of slow potentials and great amplitude, registered during prolonged stimulation of the bladder, might be regarded as a series of primary complexes, originating in the IV cortical layer after thalamic discharges.

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