

REPRESENTATION OF THE INTERNAL ORGANS IN THE CEREBRAL CORTEX AND CEREBELLUM OF CATS AND DOGS COMMUNICATION IV. CORTICAL REPRESENTATION OF THE PELVIC AND PUDENDAL NERVES IN DOGS

K. M. Kulanda

Laboratory of General Physiology (Head - Active Member AMN SSSR V. N. Chernigovskii) of the Institute of Normal and Pathological Physiology (Director Active Member AMN SSSR V. N. Chernigovskii), AMN SSSR, Moscow

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In previous communications details were given concerning the representation of the pelvic [4] and pudendal [5] nerves in the cortex of the cerebral hemispheres in cats, and also findings related to the reception of information from the internal organs by the cortex [6].

In the present communication we describe facts obtained from experiments on dogs.

METHOD AND RESULTS

After it had been ascertained, in experiments on cats using the method of recording primary action potentials, that the zones of representation of the pelvic and pudendal nerves are situated within the confines of the specific projection fields of somatic sensation, viz. in the area of representation of afferents from the hind limb, it could be assumed that these zones would be similarly situated in dogs. Experiments carried out on 16 adult animals confirmed this*. It was found that in dogs, the zones of representation of these nerves were bilateral and were present in both fields I and II of general somatic sensation, where they were situated within the area of representation of the hind limb. As in cats, the zones of representation of the two nerves overlapped each other, and their foci of maximum activity (FMA) were situated in continuity with each other, although the size of the area occupied by each FMA was smaller than in cats. The FMA and the adjacent areas of the surface of the cortex did not coincide with the previous description [15, 18] of the cortical zones of representation of the splanchnic nerve.

In dogs, the first zone was situated in the anterior part of the presplenial gyrus. In Fig. 1 we show the results of an experiment in which the zones of cortical representation of the right pelvic nerve were defined. Tracing No. 1 illustrates the primary response in the FMA of zone I of the contralateral hemisphere. The latent period of this reaction was 12.9 millisecc, and the

amplitude (positive phase of the potential) was 100 μ v. Besides the primary response, a series of secondary reactions is shown in Fig. 1 (tracings Nos. 2-10).

In this communication we shall confine ourselves to a very general description. Under light or moderately deep anesthesia, for instance, the secondary reactions were distinguished by their great profusion and variety. Their latent periods exceeded those of the primary reactions, and their extremely variable amplitude could be much greater than the amplitude of the primary response (see Fig. 1, tracing Nos. 1 and 10). Some of them arose in wide areas of the cortex, whereas others, on the contrary, were recorded within the limits of more localized areas, in immediate contact with the zones of specific projection. The secondary reactions were unstable towards anesthesia, and on increasing the depth of the latter they became more uniform, their latent period lengthened sharply and their "resistance" to repeated stimulation, i.e., their ability to develop in response to each individual stimulus, fell considerably. Tracings A and B must also be examined (see Fig. 1). Tracing A shows the primary response recorded in the same experiment in the contralateral zone II, during stimulation of the right pelvic nerve. Tracing B illustrates the action potential recorded in the ipsilateral zone I of the pelvic nerve during stimulation of that nerve. Attention is drawn to the smaller amplitude and longer latent period (14.8 millisecc; 72 μ v) of this ipsilateral response by comparison with the contralateral (see Fig. 1, tracing No. 1).

The second zone of cortical representation of the pelvic and pudendal nerves is situated in dogs in the middle part of the anterior ectosylvian gyrus.

* The method of these experiments is described in detail in Communication I [4].

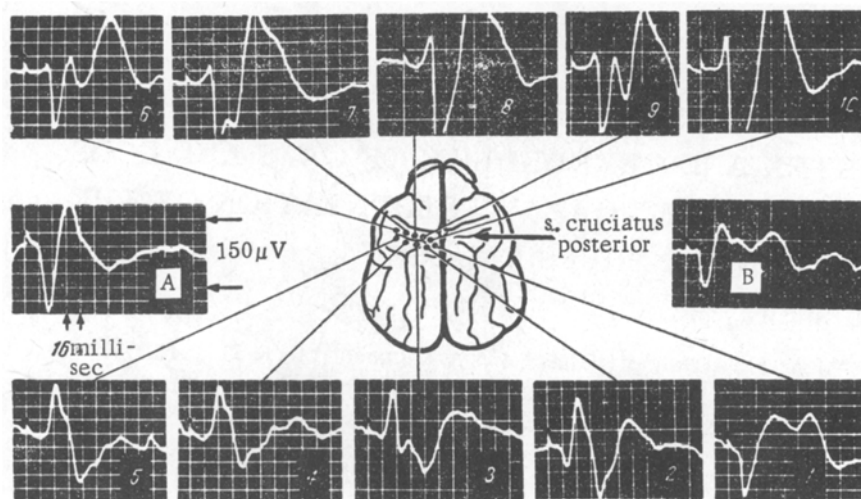


Fig. 1. Representation of the pelvic nerve in the cerebral cortex of a dog. Experiment on January 24, 1957. Anesthesia - chloralose. The right pelvic nerve was stimulated. Amplitude of stimulating impulse - 3.5 v; duration - 0.2 millise. 1) Primary response in contralateral zone I; A) primary response in contralateral zone II; B) primary response - in ipsilateral zone I. The scale of amplification and time were the same for all the tracings (see text).

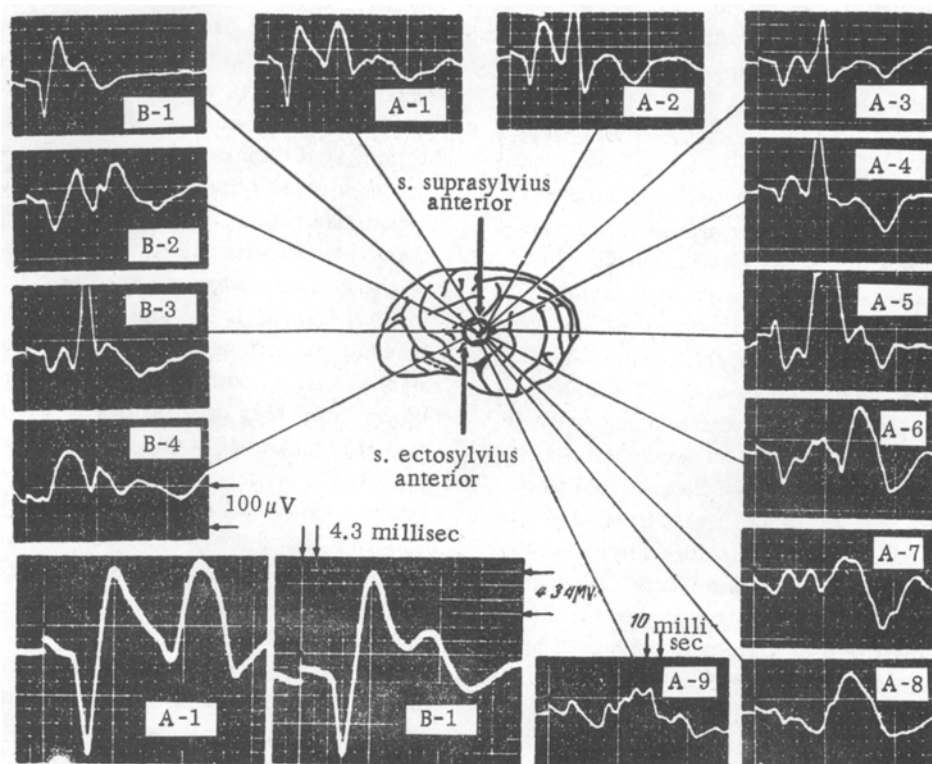


Fig. 2. Comparison between the representation of the pelvic (tracings A, 1-9) and pudendal (tracings B, 1-4) nerves in the contralateral zone II of the cerebral cortex of a dog. Experiment on February 18, 1957. Moderately deep anesthesia with a nembutal-chloralose mixture. Diplacin (a curare-like drug). Artificial respiration. Amplitude of stimulating impulse - 6 v; duration - 0.2 millise. Scale of amplification and time for the enlarged tracings A-1 and B-1 given separately (see B-1), and for all the remaining tracings (see A-9 and B-4).

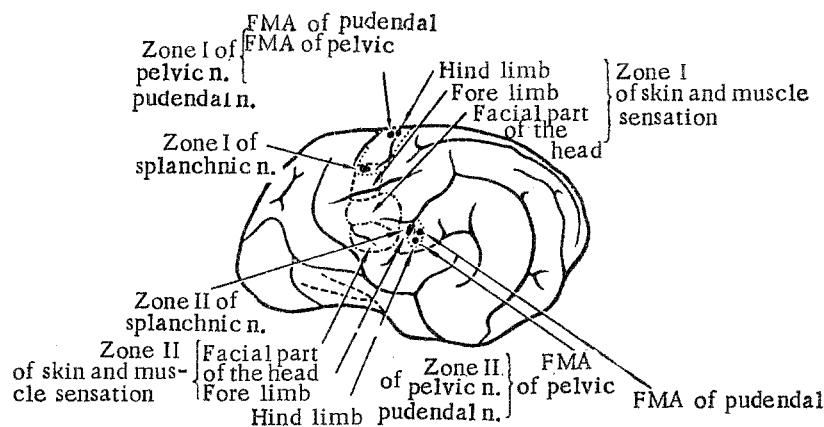


Fig. 3. Diagram of the situation of the zones of representation of the pelvic and pudendal nerves in the cerebral cortex. The black circles designate the foci of maximum activity (FMA), i.e. those areas of the surface of the cortex from which primary potentials with the greatest amplitude and shortest latent period were recorded.

In Fig. 2 are shown the results of an experiment in which the representation of the two nerves was determined concurrently. The tracings from A-1 to A-9 are the bioelectrical reactions arising in the contralateral zone II in response to stimulation of the central end of the right pelvic nerve with a current of 6 v. The tracings from B-1 to B-4 are the bioelectrical reactions arising in this zone in response to stimulation, of the same intensity, of the central end of the right pudendal nerve. A-1 and B-1 are tracings of the primary responses in the FMA of the corresponding nerves. Tracings A-2 and B-2 were taken after a slight displacement of the electrode from the FMA of one of the nerves towards the FMA of the other nerve. The tracings from A-3 to A-9, B-3, and B-4 were taken within the zone outlined by a circle on the diagram of the brain.

Without dwelling on the analysis of the secondary reactions, we may take note of certain peculiarities of the primary responses. A-1 had a shorter latent period (9.3 millisecc) than B-1 (10.9 millisecc). Although the combined amplitudes of the positive and negative phases of the variations of potential in the two responses were equal, the amplitude of the positive phase in A-1 was greater than in B-1.

This superiority of the activity of the pelvic nerve over the pudendal was characteristic, and we observed it in both zones I and II of their joint representation in the cerebral cortex of dogs.

It has already been mentioned above that each nerve has its independent FMA, but that usually these areas of greatest activity are situated with each other; the experiment described illustrates this. We have mentioned in an earlier paper [4] the influence of the depth of anesthesia on the dimensions of the zones of representation and on the responses recorded therein. All that has been said on this subject in relation to experiments on cats is fully applicable to dogs also. The only difference observed was that, in dogs under deep anesthesia,

the ratio between the area of the two zones to the whole surface area of the cortex was smaller than in cats. This is in agreement with observations [17] showing that in animals at a higher level in the phylogenetic scale, the relative size of the surface of the cortex occupied by the primary projection zones has become smaller on account of the greater development of the "associative" fields. The zones of representation of the nerves which we were investigating are shown in Fig. 3, in which the FMAs are indicated by black circles.

When the results obtained from the experiments on cats and dogs are assessed, the question must be asked—what is the reason for this arrangement of the zones of cortical representation of the visceral nerves, and what is their functional importance?

We consider that the zones of cortical representation of the nerves under study, which are component parts of the internal analyzer, may be regarded as, in the words of I. P. Pavlov, "locations of primary processes," which first receive the signals arriving from the periphery. Immediately afterwards, and parallel with this event, there occurs that cycle of processes which transforms the cortex into "a grandiose complex of positively and negatively excited points, closely and thoroughly intermingled with each other" [10].

These "locations of primary processes" in the cortex are areas within the bounds of which the specific projection systems terminate.† We mean these areas of the

† By specific projection system of an analyzer, we mean the paths conducting excitation from its peripheral end to its cortical end through the smallest number of serially connected neurones.

In contrast to this, by nonspecific projection systems, we mean paths which conduct excitation from the peripheral ends of different analyzers to the territory of the cortex in general through the multineuronal networks of structures in the brainstem.

cortex whenever we speak of "zones of cortical representation" of particular afferent nerves.

Attention is likewise drawn to the localization of the zones of representation of the visceral nerves (including the zones of representation of the splanchnic nerve) within the limits of those areas of the cortex in which are represented afferent nerves carrying impulses from the skin, muscles, joints and tendons (see Fig. 3). This localization is evidently not accidental, but it is the reflection, in the higher divisions of the central nervous system, of the close associations which have long been known to exist between the visceral afferent systems and the skeletal musculature.

In recent decades the problem of somato-visceral relationships has once again attracted the attention of many workers [3, 8, 9, 11, 13, 14]. V. N. Chernigovskii [13], for instance, showed that stimulation of the sinus and depressor nerves affected the locomotor centers of the cortex, facilitating the irradiation of excitation, as a result of which new muscle elements were involved in the contraction. He later [14] found that direct stimulation of the receptor fields of internal organs may also affect the skeletal musculature.

The presence of a definite functional connection between somatic and visceral structures was also suggested by the experiments of M. R. Mogendovich [9], who showed that stimulation of internal organs may change the chronaxie of the skeletal musculature.

That there is a very close connection between the somatic and visceral afferent system was also shown by the findings of Amassian [15, 16], that the zones of representation of the splanchnic nerve coincided with the zones of representation of skin and muscle sensation in the corresponding areas of the body. These experiments shed light on the activity of the mechanisms by means of which a close association is achieved between somatic and vegetative functions, and it is, moreover, evident that such mechanisms are situated not only in the cerebral cortex but also at other levels of the central nervous system. Everyday practice provides many examples in which the activity of the internal organs is bound up in the closest manner with the activity of the skeletal musculature. It will suffice to recall the acts of vomiting, parturition, micturition, and defecation, and the tension of the abdominal muscles arising immediately after an acute lesion affecting certain internal organs. It is well known, however, that the phenomena observed in the coordinating activity of the systems mentioned above require the direct participation of cortical mechanisms in by no means every case. In S. I. Frankshtein's experiments [12], for instance, mechanical compression of the urinary bladder, or distension of the organ from within, led to inhibition of the extensor rigidity of the hind limbs of a decerebrate cat, i.e., had a direct effect on the skeletal musculature. It is obvious that such an interrelationship did not require the participation of the cerebral cortex.

On the other hand, the facts discovered by E. A. Airapet'yants, N. Vasilevskaya, and A. Perel'man [1], who succeeded in transforming stimulation of the mucous membrane of the intestine into the conditioned signal of a defensive reaction, cannot be explained without accepting the direct participation of cortical mechanisms. We believe that it is this purpose which is served by the zones of representation of afferent nerves which have been found in the cortex.

In other words, if we accept E. A. Asratyan's [2] point of view, the zones of cortical representation of the sensory nerves may be regarded as the functional and morphological basis of the cortical representation of the unconditioned reflex.

The fact that the zones of representation of the nerves which we studied, like the zone of representation of the splanchnic nerve, are situated in that part of the cortex in which are represented the afferent systems of the corresponding somatic structures, is evidently a reflection of the segmental principle of the innervation of the internal organs.

The coincidence between the zones of cortical representation of the visceral and somatic sensory nerves provides the basis for a new approach to the mechanism of production of hyperalgesia in diseases of the internal organs. It is obvious that the existence of Zakhar'in-Head zones may be explained not only by an axon reflex, or a reflex effected at the spinal cord level, but more probably by the fact that afferent impulses from the affected organ reach the same cortical zones (and even the same cortical cells) as impulses from the skin, muscles, joints, and tendons. The correctness of such a hypothesis is further confirmed by the fact that hyperalgesia is often manifested in the muscles, bones, and other structures, as well as in the skin.

It has previously been mentioned that stimulation of any visceral receptor field can lead to the appearance of both primary and secondary reactions in the cerebral cortex. This does not mean, however, that all impulses arising in the internal organs must inevitably reach the cerebral cortex and be incorporated in the sphere of perception and consciousness. We have obtained results which testify to the fact that impulses reaching the central nervous system from somatic structures are capable of completely blocking conduction in the afferent pathways leading from the internal organs [7]. If, for example, soon after a series of stimuli applied to the sciatic nerve, stimulation is transferred to the pelvic nerve, no primary responses can be found in the zone of its cortical representation; they are completely abolished by the previous stimulation of the somatic nerve. Does not this phenomenon explain the well known fact that we call signals arriving from internal organs sensations only when they reach a considerable intensity? That is, they announce either injury to the corresponding visceral structures, or a functional state which is such as to require urgent interference of a voluntary character.

As an example of this, we may cite the signals reaching the central nervous system from the urinary bladder which we are unable to detect, of which we remain unaware, until they become so intensive that no muscular movements are capable of preventing the passage of impulses to the higher divisions of the nervous system. With such a functional state of the organ, the necessity for voluntary interference is obvious.

Such are the general outlines of the functional importance of the zones of cortical representation of the visceral nerves.

SUMMARY

By recording primary responses, 2 zones of representation of the afferent fibers of the pelvic and pudendal nerves were found in the cortex of each cerebral hemisphere in dogs. The zones are bilateral, with their localization in fields I and II of the general somatic sensation, within the area of representation of the hind limb. The zones of representation of the pelvic and pudendal nerves overlap each other. However, each nerve has its own focus of maximal activity (FMA) which does not coincide with the FMA of another nerve.

In dogs, zone I of the cortical representation of the nerves under study is located on the anterior part of the presplenial gyrus and zone II on the medial portion of the anterior ectosylvian gyrus.

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*Original Russian pagination. See C.B. translation.