THALAMIC REPRESENTATION OF THE VISCERAL AFFERENT SYSTEM

COMMUNICATION I. REPRESENTATION OF THE SPLANCHNIC NERVE IN THE POSTEROVENTRAL THALAMIC NUCLEUS OF THE CAT

R. A. Durinyan

Laboratory of General Physiology (Head, Academician B. N. Chernigovskii)
Institute of Normal and Pathological Physiology (Director, Active Member AMN SSSR V. V. Parin) AMN SSSR Moscow
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For more than half a century the study of the central representation of the afferent systems was confined mainly to the extroceptive and somatic systems.

Even the first anatomical studies [11] gave some information on the somatotopical distribution of the afferent systems within the posteroventral thalamic nucleus. Recently, special morphological investigations have been made on the cat [4].

Progress on this problem began after Horsley and Clarke [13] had described their stereotactic method.

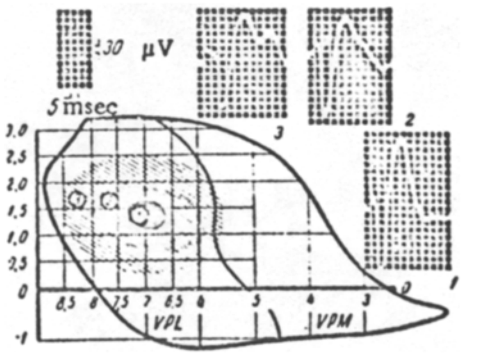

Fig. 1. Organization of the area of representation of the splanchnic nerve in the posteroventral nucleus (n. ventralis posterior) of the contralateral thalamus of the cat. 1) Focus of maximal activity, and maximum potential recorded at this focus; 2) zone of primary responses, and potential recorded in this zone; 3) zone of secondary responses, and potential recorded in this zone. Frontal plane 9.

The most important results on the representation of the somatic afferent systems was obtained by Mountcastle and Henneman [18], and by others, by recording the primary electrical responses in the posteroventral nucleus [7, 12]. The nucleus consists of two halves, medial and lateral, and is the principal relay station in which the pathways of the medial lemniscus terminates. It is the origin pathway of the 3rd neurone which forms the thalamocortical projection onto the specific cortical areas of the cerebral hemispheres.

Immediately after the studies referred to above, others were published concerning the representation of the visceral afferent systems in the same nucleus [1, 9]. First Patton and Amassian [6, 19] showed that the rapidly conducting type A fibers of the splanchnic nerve are interrupted in the outer part of the nucleus, but their topographical representation was not investigated. Similar work was done by other authors [5, 9, 10]. We must note particularly the work of McLeod [16, 17]. He obtained valuable results on the representation of the splanchnic nerve in the posteroventral nucleus, which, however, in many respects contradicted previous findings. According to him, the latent period of the response to electrical stimulation of the nerve had an average value of 12.2 mseconds, which was very much greater than the latent period of the primary response initiated by fibers of the Aβ type originating in the splanchnic nerve, even for the cerebral cortex [6, 19]. In addition, McLeod failed to give an account of the precise topography of the splanchnic nerve representation within the nucleus.

We here report the results of a neurophysiological analysis of the representation of the splanchnic nerve in the posteroventral thalamic nucleus.

METHOD

Acute experiments were carried out under nembutal-chloralose anesthesia (25-30 mg/kg nembutal, 40-50 mg/kg chloralose) on cats weighing 3-3.5 kg. The depth of anesthesia was increased until the so-called spontaneous electrical activity was completely suppressed. To eliminate reflex muscular contractions, the relaxants ditilene and listenone were used in conjunction with artificial respiration.

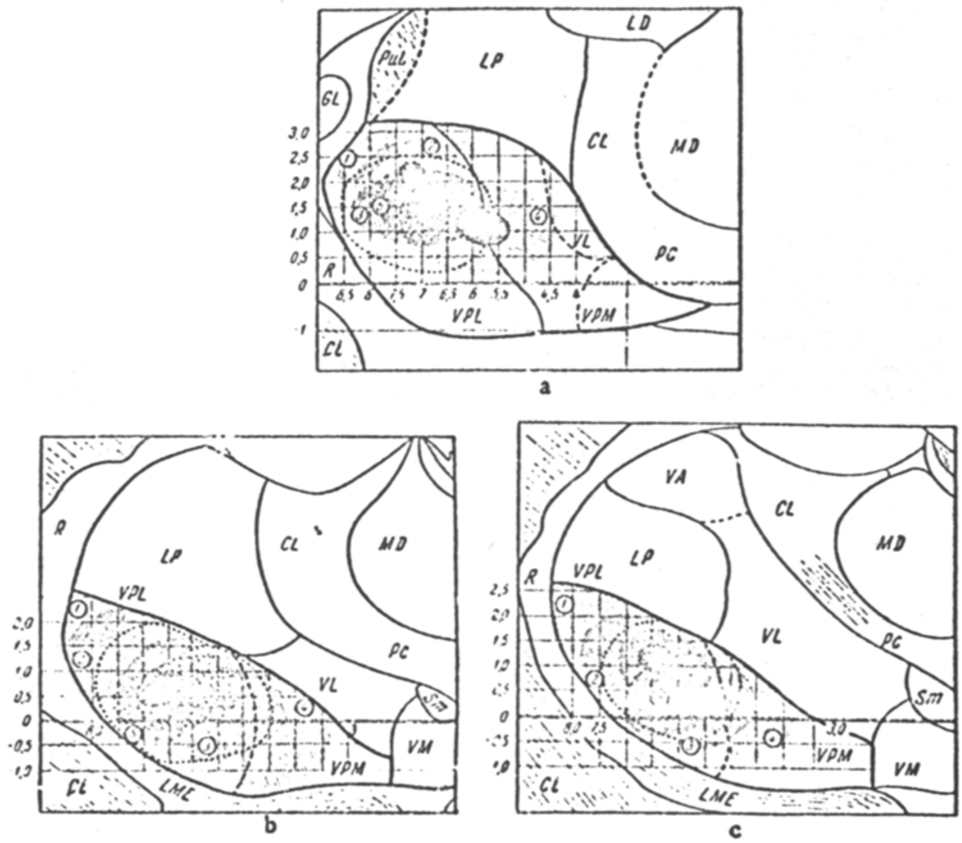

Fig. 2. Somatotopical relationships of the areas of representation of the splanchnic nerve within the posteroventral thalamic nucleus of the cat (of the opposite side). Areas of representation: 1) tail and sacral region; 2) hindlimb; 3) trunk; 4) forelimb; 5) splanchnic nerve. Black circles indicate the FMA in the areas of representation of the hind- and forelimbs and the splanchnic nerve; dotted line indicates zone of secondary response for the splanchnic nerve; a) frontal plane 0; b) frontal plane 9.5; c) frontal plane 10.

The animals were fixed in a stereotactic apparatus [2]. The hemisphere was widely exposed, the dura mater was removed, and the surface of the brain was irrigated by Ringer-Locke at 38°, and at the same time it was warmed by means of a special reflector. The body temperature was maintained at 38° by means of an automatic heater. During the whole of the experiment an intravenous drip of Ringer-Locke or of diluted cat blood was maintained.

Single condenser discharges of duration 200 μseconds were used to stimulate the central ends of the following nerves on the side opposite to that of the hemisphere investigated: splanchnic, sciatic, and intercostal nerves, and the lumbar and brachial plexuses.

The potentials were picked up from a unipolar electrode. The indifferent electrode was placed in the frontal sinus, where there was no electrical activity. The pick-up electrode consisted of a steel needle with a shaft 200 μ thick which was insulated with bakelite except for the tip which had a diameter of 20 μ. The electrode was introduced by the stereotactic manipulator through the cerebral hemisphere, and positioned in terms of the co-ordinates from an atlas [14]. The potentials were taken to a resistance-capacity coupled amplifier incorporating a balanced circuit, and after amplification they were displayed on a cathode-ray rube and photographed. The amplifier was linear from 5 to 500 cycles.

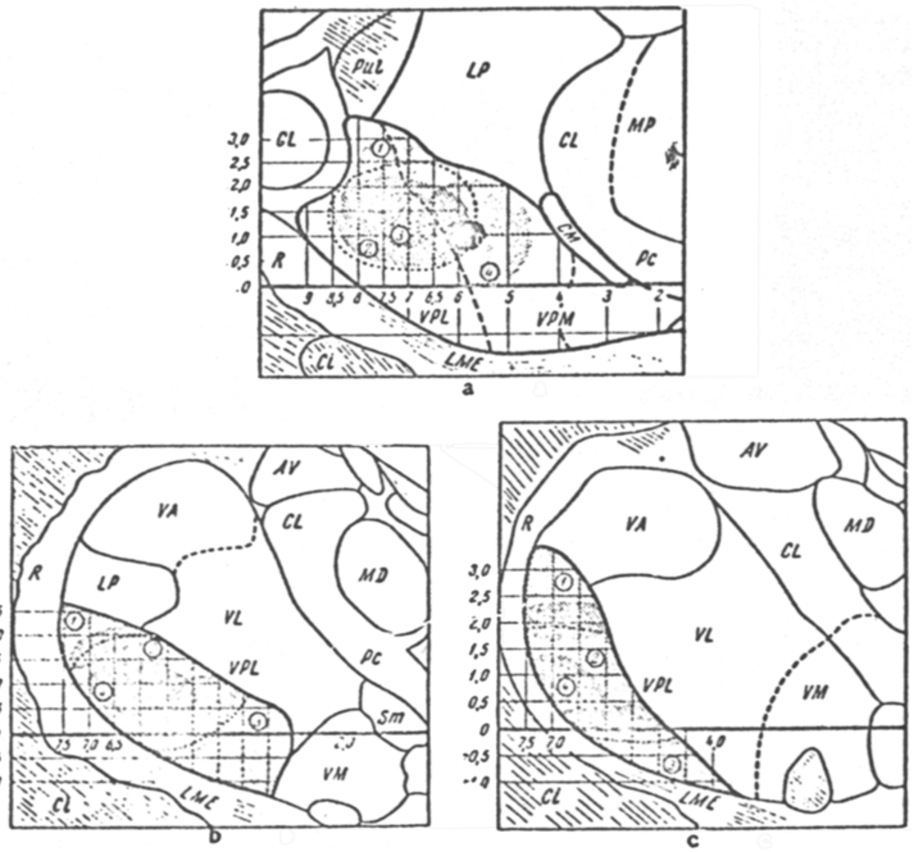

Fig. 3. Same as Fig. 2. The FMA for the splanchnic nerve is absent. The zones of the primary and secondary responses are shown by the dotted line; a) frontal plane 8.5; zones of representation: 1) hindlimb; 2) trunk; 3) splanchnic nerve; 4) forelimb; black circle – FMA for the forelimb; b) frontal plane 10.5; c) frontal plane 11; areas of representation (in b and c); 1) tail and sacral region; 2) hindlimb; 3) trunk; 4) splanchnic nerve.

After the experiment the brain was vitally perfused with Ringer-Locke, and then with 5% formol; blocks were then cut with frontal section by means of the manipulator, they were removed and fixed in 10% formol. Serial frontal sections 50 μ thick were then cut on a freezing microtome, and stained in hematoxylin eosin or in thionine [15]. The area of representation in the nucleus was then determined by superimposition of the sections.

RESULTS

In the cat the posteroventral thalamic nucleus lies in the ventrolateral region and antero-posteriorly it lies between frontal planes 8.5 and 11. Its sagittal extent varies between 2 and 9 mm.

Even in the first experiments it was found that the splanchnic nerve is not represented in the medial portions of the nucleus. For this reason, chief attention was then paid to the lateral path of the nucleus (n. ventralis posterolateralis) between 5 and 9 mm. When exploring horizontally it was found that the part of the nucleus most closely related to the splanchnic nerve lay above the Horsley-Clarke horizontal datum line.

By exploring each 50 μ of nucleus vertically in the frontal and sagittal planes described (at 0.5 mm intervals), we were able to find the most electrically active parts, where the potentials picked up had a minimum latency and maximum amplitude.

It was shown that in the area represented there were 3 belts, with a gradual transition between them. In the central zone, or somewhat to one side of it there was a focus of maximal activity (FMA), where the most characteristic primary responses having a latency of 4.5-5 mseconds and an amplitude of the positive phase of 300 μv were recorded (Fig. 1, 1). Beyond this lay a belt which might be called the zone of primary responses (ZPR), where responses were recorded at a latent period of 5-6 mseconds, and an amplitude which was 20-50 μv less than at the FMA (Fig. 1, 2). Finally there was a belt which occupied a comparatively large area, and which may be referred to as the zone of secondary responses (ZSR). Here were recorded potentials having a latency of 8-12 mseconds, and an amplitude of 70-100 μv less than at the FMA (Fig. 1, 3). Several points should be noted. The potential at the FMA usually consisted of a biphasic oscillation, usually without secondary waves. The duration of the positive phase varied between 12 and 20 mseconds. This wave appeared to be made up of an afferent discharge from the lemniscal terminations in the thalamic neurones. It was recorded most consistently, and was least susceptible to outside influences such as the depth of anesthesia, condition of the preparation, and strength of stimulus. It could be picked up from various parts of the represented area, and it always had more or less the same configuration, although there were of course variations in latency and amplitude.

The negative phase of the potential developed immediately after the positive phase and lasted for more than 20 mseconds. This wave was more variable, and less resistant to other influences, and had various configurations in the different zones of the area of representation. With deeper anesthesia the amplitude of the negative phase was reduced, and might fall to the datum line, as was observed when the preparation deteriorated. Apparently this phase results from a potential generated by the thalamic neurones themselves in response to an afferent impulse.

In the ZPR, and more so in the ZSR, the potentials were less constant in shape. Typically there were secondary oscillations which continued directly after the negative phase (see Fig. 1).

K. M. Kullanda [3] showed that in the cerebral cortex the FMA's for the different nerves do not coincide, and that the zones overlap in the area of primary responses. Similar relationships were observed also in the areas of representation of the nucleus which we studied, as is shown in Fig. 2. The greatest overlap was found for the secondary responses, but in the drawings shown, we have indicated only the areas of secondary responses for the splanchnic nerve. It can be seen that the ZSR of the splanchnic nerve extends into the area of representation of the sacral region, the trunk, and fore- and hindlimbs.

There is also a wide overlap of the ZPR. As a rule, the zone of representation of the splanchnic nerve lies in the zone representing the trunk, and extends on to the zone of the hind and forelimbs. The FMA's of the splanchnic and intercostal nerves [8, 9, 10] coincide, but those of the remaining nerves are separated (see Fig. 2). The FMA of the splanchnic nerve lies between the frontal planes 9 and 10, and the zones of the primary and the secondary responses are found on the other planes (Fig. 3).

Consequently the representation of the splanchnic nerve occupies a certain volume within which the focus is confined, and the electrical responses develop over a wider area. Therefore, when talking of the zonal representation of the nerve, we must remember that we mean the zone of primary responses with a FMA.

Frequent stimuli applied to the somatic nerves indicated may block the potential normally elicited by stimulation of the splanchnic nerve. Potentials induced by splanchnic stimulation are still more easily blocked if a pair of stimuli are applied, the first to a somatic nerve and the second to the splanchnic nerve after an interval of 10-20 mseconds. This effect of occlusion is manifested very distinctly on stimulation of the intercostal nerves, and affords yet one more proof of the close neuronal association of the representations of the trunk and splanchnic nerve.

The convergence of the somatic and visceral afferents on to the same neurones, as instanced by the intercostal and splanchnic nerves, appears to represent the morphological and physiological basis for the widespread interaction of visceral and somatic functions at thalamic level.

SUMMARY

Experiments were performed on cats under nembutal-chloralose anesthesia treated with muscle relaxants. The animals were fixed in a stereotactic apparatus, and the central ends of the splanchnic, sciatic, lumbar, intercostal nerves and brachial plexus were excited by a single stimulus. Tactile stimuli were applied to the sacrolumbar, thoracic, and abdominal areas. Unipolar leads were used. The pickup electrode had a point 10-20 μ thick, and was introduced by a stereotactic instrument. The results of the experiment were controlled histologically. In each zone of representation of the splanchnic nerve there are three girdles which overlap. At the center of the zone there is a

focus of maximal activity (FMA) where the primary response has a latency of 4.5-5.0 mseconds and an amplitude of the positive phase of up to 300 μv. Around the focus, the responses had a latency of 5-6 mseconds, and an amplitude 20-50 μv below that at the FMA. The secondary responses were recorded, and found to have a latency of 8-12 mseconds, and an amplitude 70-100 μv less than that at the FMA. The area of representation of the splanchnic nerve (FMA) was located in the n. ventralis posterolateralis between frontal planes 9 and 10 over the zero line, and occupied the median portion of the nucleus. It coincided with the area of representation of the body and trunk, and penetrated into the zones of the fore- and hindlimbs. Such overlap of the zones evidently represents the morphological and physiological basis for the widespread interaction of visceral and somatic function at the thalamic level.

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