THE POSITION OF THE VISCERAL AFFERENT PATHWAYS IN THE INTERNAL CAPSULE

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The widespread use of electrophysiological methods has extended our understanding of the physiology of the interoceptor analyzer. New results have been obtained by the method of evoked potentials, which has been used to study the distribution of the visceral pathways in the central nervous system [4, 12, 14, 16, 18, 19, 26].

The cortical projection of visceral sensitivity has been studied in detail. Amassyan [13], Downman [17], Newman [23] and others have investigated the cortical projection of the splanchnic nerve. In each hemisphere they found two projection areas corresponding to somatic sensory areas S_1 and S_2. Our knowledge of the cortical end of the interoceptor analyzer has been greatly extended through the researches of V. N. Chernigovskii [10, 11] and his co-workers. In a series of works K. M. Kullanda [5-9] studied the cortical representation of the pelvic and pudendal nerves. In dogs (and in cats) within the area of cutaneous and muscular sensitivity we found four zones where these nerves were represented (two in each hemisphere). The primary responses to stimulation of these nerves were recorded at certain points of the limbic cortex. Primary responses in the cingulate gyrus were also found on stimulation of the splanchnic nerve [2].

Results obtained by K. M. Kullanda on the primary cortical responses obtained by adequate stimulation of the viscera are interesting [6], and the representation of visceral afferents in the cerebellar cortex has been investigated by the method of evoked potentials [1, 7, 8, 16, 26].

Many studes have been made of visceral representation in the thalamus. A topographical representation of the splanchnic and vagus nerves has been found in the posteroventral thalamic nucleus [12, 21, 24]. R. A. Durinyan [3, 4] studied the thalamic representation of the pelvic nerves. The maximum primary response was found in the lateral part of the posteroventral nucleus. Here the latent period was 5-8 msec, and the amplitude of the positive phase 60-75 μv.

A cursory examination of the literature on the representation of visceral afferents in the central nervous system shows that the use of improved modern methods (stereotaxic technique and recording of primary responses) has made possible great advances in the determination of visceral representation in the central nervous system.

We have found no reference to the localization of the visceral pathways within the internal capsule. The capsule is bordered by the thalamus and caudate nucleus medially and by the lentiform nucleus laterally, and constitutes the chief ascending system of the brain. Here there are concentrated bundles of fibers having a variety of function. The afferent somatic fibers run in the posterior limb of the capsule. Here are found the thalamocortical sensory pathways which take origin in specific thalamic nuclei. Beside them course the visual and auditory projection pathways. The posterior limb includes a large proportion of proprioceptor pathways. This portion of the capsule has therefore a very complex constitution. Besides the sensory pathways, there are also the corticofugal fibers running to form the corticospinal (pyramidal) tracts, as well as the pathways of the extrapyramidal system. It has been shown [25] that the nonspecific pathways of the ascending activating reticular system also run through the internal capsule.

We have now to find whether the internal capsule contains an autonomic projection of visceral origin. The topographical localization of these visceral afferent pathways in the internal capsule is yet to be determined, and we do not know how it is related to the somatic sensory pathways. To answer these problems we have used a stereotaxic technique, and have recorded primary responses evoked by electrical stimulation of the splanchnic nerve.

EXPERIMENTAL METHOD

The work was carried out on 30 cats anesthetized with 50-70 mg/kg intraperitoneal chloralose. The splanchnic nerve was exposed outside the peritoneum, divided, and the central end placed upon a silver electrode. To prevent drying up it was covered with vaseline. It was stimulated by single or paired stimuli of 0.5 msec duration supplied from a IG-1 electronic stimulator. In all experiments simultaneous recordings were made of potentials from the cortex and from different parts of the internal capsule displayed on the screen of a double beam oscillograph. At the start of the experiment we determined the cortical projection of the splanchnic nerve, and subsequently throughout the whole experiment these cortical responses served as controls for investigating the region occupied by the fibers in the internal capsule. When there was no cortical response the experiment was broken off.

The potentials evoked in the cortex and capsule were picked up by a unipolar needle electrode while an indifferent electrode was placed in the frontal bone. By a stereotaxic apparatus the deep electrode was introduced below the cortex, the position being defined in terms of the atlas of Jasper and Ajmon-Marsan; in each experiment 100 points were investigated. The deep electrode was moved vertically, laterally, and frontally over a distance of 1 mm. The electrode consisted of a fine needle of stainless steel 0.2 mm in diameter insulated for the whole of its length except for the tip which measured 50-80 μ in diameter. The potentials were recorded by means of a "Zenit" apparatus synchronized with the stimulator, and supplying a delayed sweep scope. At the end of each experiment the last point investigated was destroyed electrolytically, and the position of the electrode was confirmed histologically.

EXPERIMENTAL RESULTS

From the results obtained by Aidar, Geohegan, and Ungewitter [12], McLeod [21] and others on the representation of the splanchnic nerve in the lateral portion of the posteroventral thalamic nucleus we decided to explore the projection of the nerve in the internal capsule in the portion adjacent to this specific thalamic nucleus. In our study of the internal capsule from F_8 to F_{12} (Jasper and Ajmon-Marsan atlas) which corresponds to the region of the posterior nucleus, we found a portion where a primary response was obtained by stimulation of the splanchnic nerve. The characteristic primary responses were maximal in the zone F_{10}, L_9, $V+2+3$. The active part was strictly localized, and when the electrode was shifted 0.5-1 mm the response disappeared (Fig. 1). The primary response was biphasic with the initial excursion positive-going. The latent period was 5-7 msec (Fig. 2b), and the duration of the positive wave was 15-20 msec. The complex consisting of the positive- and negative-going portion had an amplitude of up to 350 μv. The amplitude of the positive phase alone was on average 60-100 μv. Sometimes, immediately after the primary response, there was a secondary oscillation consisting of a slow-positive wave. As the electrode was moved away from the strictly localized focus of the primary response, in the neighboring regions of the internal capsule another response was recorded; it was not a primary response, and consisted of a negative wave having latent period of 20-30 msec (Fig. 2c).

The results we obtained on the characteristic primary responses in this part of the internal capsule correspond to those of other authors who have studied the distribution of primary responses from visceral afferents in the ventral thalamic nucleus. Thus Patton and Amassian [24] stimulated the splanchnic nerve and found a primary response having a latent period of 5-6 msec in the posteroventral thalamic nucleus. The low amplitude of the positive phase (60-100 μv) was probably due to the number of visceral afferents passing through the region of the internal capsule we have studied. Because of the low density of the fibers, when electrodes of 50-80 μ diameter are used it is impossible to demonstrate the activity of all the scattered elements of the intra-central pathways of the splanchnic nerve in this region. The low amplitude of the positive phase of the potential was observed also when records were made of the primary cortical responses, or of the responses in the ventral thalamic nucleus, by stimulation of either the splanchnic nerve [17] or the pelvic nerve [5].

To determine the refractory period of the visceral afferent system within the internal capsule, in a number of experiments the splanchnic nerve was stimulated by a pair of impulses separated by different time intervals (technique of double shock). In this way it was found that the absolute refractory period of the capsular response was by 15-20 msec, which on the average was 10 msec shorter than the cortical refractory period (Fig. 3).

A study of the interaction of the conditioning and test stimuli showed that after the response to the second stimulus had appeared it was usually again suppressed when the interval between the stimuli was extended to 25-45 msec, i.e., the curve of recovery of excitability of the nervous structures conducting the afferent excitation wave was itself biphasic. The response to the second stimulus usually disappeared if its rival coincided with the negative phase of the primary response or with the positive phase of the secondary response (Fig. 3f).

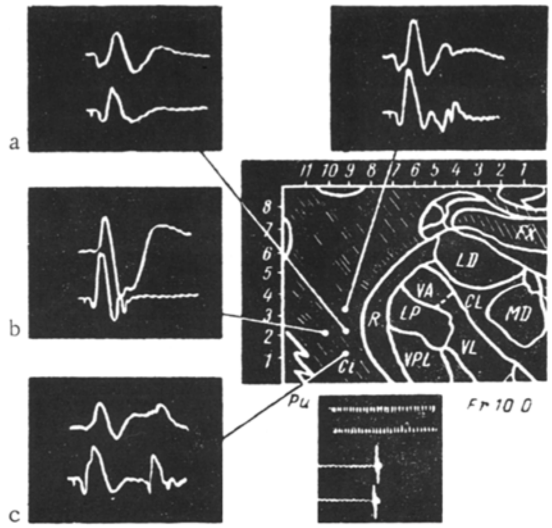

Fig. 1 Topographical localization of the primary responses in the internal capsule on stimulation of the splanchnic nerve. In this and in all succeeding figures: upper curve—evoked potentials in the internal capsule; lower curve—primary response in the second cortical somasensory projection area of the splanchnic nerve. Calibration marks: for magnification 100 μv, for time 100 cycles. Deviation of the trace upwards represents a negative potential.

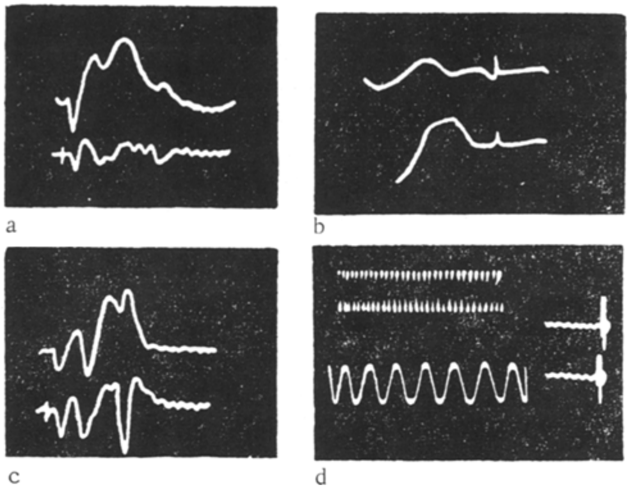

Fig. 2. Experiment of 16/11/1961. a) Primary response in the internal capsule and cortex in response to stimulation of the splanchnic nerve; b) same potentials shown on a rapid sweep. Latent period of potential in internal capsule 6 msec, in cortex 12 msec; c) immediately after the primary response in both the internal capsule and cortex a secondary response is recorded; d) calibration mark 100 μv, time calibration 100 cycles.

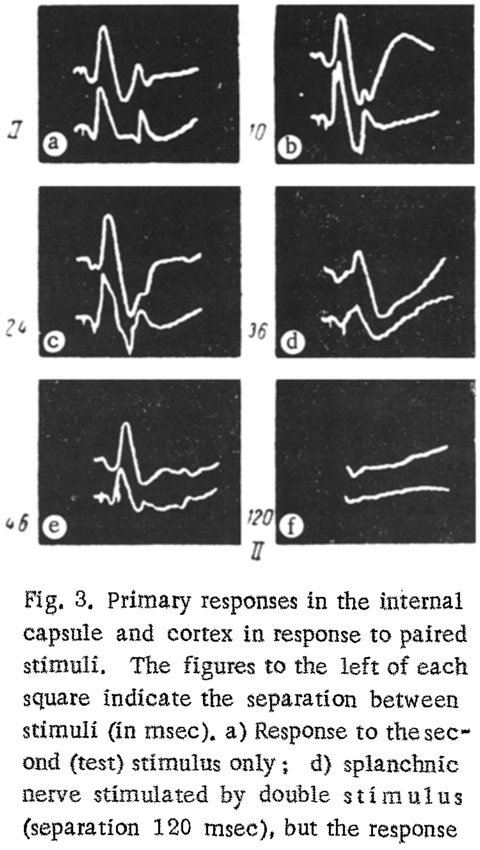

Fig. 3. Primary responses in the internal capsule and cortex in response to paired stimuli. The figures to the left of each square indicate the separation between stimuli (in msec). a) Response to the second (test) stimulus only; d) splanchnic nerve stimulated by double stimulus (separation 120 msec), but the response only to the second stimulus of the pair is recorded (sweep triggered by second stimulus).

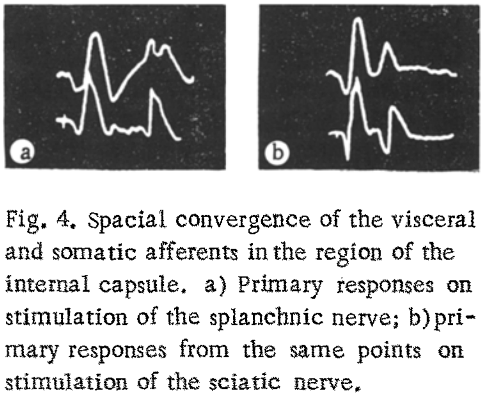

Fig. 4. Spacial convergence of the visceral and somatic afferents in the region of the internal capsule. a) Primary responses on stimulation of the splanchnic nerve; b) primary responses from the same points on stimulation of the sciatic nerve.

In a study of the interaction of the somatovisceral projection systems it has been shown [15] that the somatic and visceral representations appear to overlap both in the cortex and thalamus. We too found that there was a convergence of the pathways in the internal capsule. In the regions where the primary response to splanchnic stimulation was maximal it could always be evoked by following up with stimulation of a somatic nerve (in this case the sciatic) (Fig. 4).

The results we obtained show that within the internal capsule the projection of the visceral and afferent systems is found in the region of the somatic sensory fibers. Damage to these visceral conducting pathways of the capsule may possibly be responsible for certain symptoms observed clinically in cases of capsular hemiplegia; here visceral disturbances are found after the insult has occurred. The overlap of somatic and visceral sensitivity indicates a convergence of the signals of different modalities below capsular level. From the phenomena of inhibition and occlusion occurring during interaction of visceral and somatic afferent systems Amassian [15] showed that the interaction of these two sensory systems occurs chiefly at thalamic level. The effect has been studied in detail by McLeod [21] by intracellular microelectrode recordings of the potentials of thalamic neurones of the posterolateral ventral nucleus. Occlusion has been shown to result from convergence of the same neurones of the specific thalamic delay of both somatic and visceral afferent impulses. This convergence may to some extent explain the phenomenon of referred pain in visceral disorders.

Many conjectures can be made as to the nature of the positive and negative excursions of the response we have found in the internal capsule. According to Marshall [22] the positive phase indicates that the potential is picked up from fibers damaged by the electrode. If that is so it is difficult to explain the occurrence of the negative phase. From the theory of volume conduction [20], the positive phase is to be interpreted as the summation of synchronized spike discharges running along thalamocortical axons towards the pick-up electrode. Excitation of fibers in the neighborhood of the electrode causes the negative component of the evoked potential.

It would appear that the biphasic potential we have recorded in the internal capsule close to the thalamic nucleus represents a potential of synaptic region. Then the positive phase would represent activity at the terminations of the lemniscal axons. It is known [22] that a positive wave which is picked up from the region of the posteroventral lateral thalamic nucleus and which is regarded as a summation of spikes from lemniscal axons is very short, has a short refractory period, and decreases very little when the interval between the stimuli is made as short as 5 msec. However the positive phase which we have recorded in this part of the internal capsule has a greater duration and a longer refractory period; this indicates a genetic connection with postsynaptic activity of thalamic neurones, which brings about a spike discharge in the thalamocortical neurones whose total effect we have recorded as a positive excursion occurring as the spikes approach the pick-up electrode.

From our investigations we may draw the following conclusions.

When the splanchnic nerve was stimulated, a primary response consisting of a positive and negative excursion having a latent period of 5-7 msec was recorded from the posterior limb of the internal capsule (somatosensory zone). The duration of the positive phase was 15-20 msec. The absolute refractory period of the primary response was less than that of the cortical potentials, and had a mean value of 20 msec. The site of maximum activity was in the region F_{10}, L_9, and $V+2+3$ (atlas of Jasper and Ajmon-Marsan). In the region of the projection of the splanchnic nerve in the internal capsule we found convergence of sensory impulses of visceral and somatic origin which confirmed the presence of a close interrelationship of somatic and visceral afferent systems below capsular level.

SUMMARY

Topographic localization of the splanchnic nerve afferents in the internal capsule was studied in cats under chloralose anesthesia by the method of induced potentials. Primary responses of maximal amplitude were led off from the area in which the posterior femoral region is represented and which corresponds to the F_{10}, L_9 and $V+2$ and $+3$ coordinates of the stereotaxic atlas of Jasper and Ajmon-Marsan. This region of the internal capsule overlaps the area where somatic sensibility is represented, so that it may be called an afferent zone of somato-visceral sensitivity.

The capsular potential was investigated in the projections of the visceral afferents; we also studied restoration of excitation in this region of the internal capsule containing visceral afferent fibers.

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