EXTRASPINAL PATHWAYS IN THE REFLEX INTERACTION OF LARGE AND SMALL INTESTINES

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In the physiological literature and in the clinic, numerous data have been amassed concerning the presence of marked interoceptive effects, not only on neighboring internal organs, but also on distant ones. The mechanism of these effects is still poorly understood. In a number of papers it has been shown that they can be produced within the peripheral divisions of the sympathetic nervous system after destruction of the spinal cord [1, 4, 13, 15, 16, 17, 18, 20, 21, and 22].

In studying the interneuronal connections of the organs of the abdominal cavity, we [10] established that in man and the rabbit the two mesenteric nervous plexuses that innervate the small and large intestine are connected by a short cut by means of the intermesenteric tract. This is located to the left, and partially in front of, the abdominal aorta and is connected with the inferior mesenteric ganglion. These data and experiments on rabbits [6, 9] have shown that, except for monkeys [3], the tract is the most differentiated in these animals, and as was supposed [2], it contains ascending and descending fibers, which allows us to regard it as a complex of interorgan connections, creating the functional interaction between the caudal division of the large intestine and the small intestine that has been demonstrated by a number of authors [8, 11, 12, 14].

In the present investigation we undertook the further study of the significance of the intermesenteric tract in this interaction.

METHOD

The work was carried out on 23 rabbits. In rabbits immobilized by high spinal cord transection, the abdominal cavity was opened. A loop of jejunum was placed in a glass cylinder with no bottom, which was held firmly in an incision in the anterior abdominal wall and filled with Ringer's solution at 38°. The movements of the intestine were recorded on kymograph paper. From the caudal portion of the large intestine, a segment 8-10 cm long was separated with its mesentery. A rubber balloon was inserted into it that could be inflated with air to obtain a pressure of 80-200 mm Hg. During the experiments or ten days previously, the caudal mesenteric ganglion was decentralized by severing all its nervous connections with the marginal sympathetic trunks and the abdominal aortic plexus. The hypogastric nerve, which connects this ganglion with the pelvic nervous plexus, was sectioned at this time, and in some experiments the spinal cord was destroyed below the tenth thoracic segment. Diplacine was used to block synaptic connections in the ganglion. After this the investigation proceeded.

RESULTS

In the initial background, rhythmic contractions of the jejunum occurred at a frequency of 12-18 waves per minute, and slight variations in tone were noted. Upon mechanical stimulation of the caudal portion of the large intestine against a background of intensive movements of the small intestine, inhibition of these movements and a reduction in tone occurred (Fig. 1a); if a segment of small intestine was in a state of comparative rest, mechanical stimulation of the large intestine produced no perceptible changes in the kymograph tracing.

In addition, the intensity of stimulation of the large intestine and the rate of increase of stimulus intensity were important: an intense mechanical stimulus (200 mm Hg instead of 100 mm), or a rapid inflation of the balloon, caused more pronounced inhibition of the peristaltic movements of the small intestine. These changes ordinarily were observed at the moment of stimulation of the large intestine; aftereffects were not seen.

Decentralization of the caudal mesenteric ganglion, either 10 days in advance or at the time of the experiment, resulted in enhancement of the movements of the small intestine: the rhythm of contractions was intensified, the frequency of the waves increased to 20 per minute, and unusual variations in tone appeared. Under

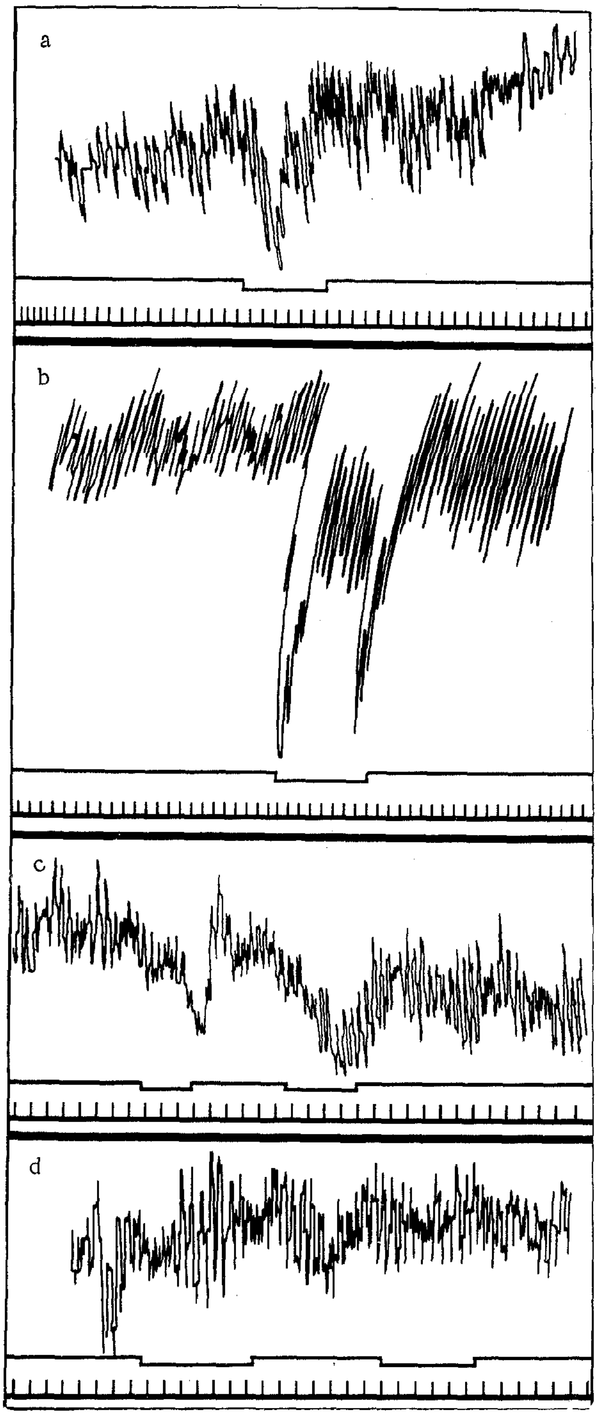

Fig. 1. Changes in interoceptive afferent effects exerted on the small intestine by the caudal portion of the large intestine in the rabbit. a) Initial background (rabbit No. 22, experiment of December 28, 1958); b) after decentralization of caudal mesenteric ganglion (rabbit No. 18, experiment of June 16, 1958); c) after destruction of the spinal cord (rabbit No. 11, experiment of December 27, 1957); d) after section of the intermesenteric tract (rabbit No. 11, experiment of December 27, 1957). Interpretation of curves (from top): movements of small intestine; mechanical stimulation of large intestine; time (5 sec).

these conditions mechanical stimulation of the segment of large intestine continued to inhibit the small intestinal movements, with this effect even being enhanced at times (Fig. 1b), and being observed even after destruction of the spinal cord (Fig. 1c). Sectioning of the intermesenteric tract performed against this background caused a considerable reduction in the inhibition of motor activity of the small intestine, or complete absence of such inhibition (Fig. 1d), and in only two experiments was it as pronounced as in the initial state.

The data obtained confirm the presence of a reflex interconnection, not only between adjacent segments of the gastrointestinal tract [16, 22], but even between such distant segments as the initial portion of the small intestine and the caudal portion of the large intestine. On the basis of the fact that these interorgan interoceptive effects are predominantly of a neuroreflex nature [11, 14, 22], we sought to determine the specific pathways by which they are mediated.

Analysis of the distribution of the interneuronal connections of these organs in the rabbit (Fig. 2) allowed us to suggest three main pathways of afferentation from the portion of the large intestine under investigation: 1) along its intramural nervous plexuses and the arciform connections of the mesenteric nerves accompanying the vascular arcades, in the cranial direction; 2) along the mesenteric nerves to the caudal mesenteric ganglion, and then along its connections with the sympathetic trunks, through the corresponding spinal ganglia into the spinal cord, from which, along pre- and postganglionic neurons within the celiac and cranial mesenteric plexuses, impulses arrive at the small intestine; 3) along the mesenteric nerves to the caudal mesenteric ganglion, and from there along the intermesenteric tract connected with it, directly to the small intestine, within the cranial mesenteric plexus.

The possibility that these interoceptive effects were spreading toward the pelvic plexus and out from it, or along the first of the pathways indicated above, was excluded, since the balloon was introduced into a segment of large intestine that was isolated from its proximal and distal portions. In order to interrupt transmission along the second pathway, formed by afferent spinal fibers, an anatomically thorough decentralization of the caudal mesenteric ganglion was carried out under the magnifying glass, and in some experiments, destruction of the spinal cord as well. Under these conditions the most probable pathway for reflex interaction of the isolated fragment of large intestine with the small intestine was the third, the shortest and most direct extraspinal pathway, represented by the intermesenteric tract (12, 14, and 15, Fig. 2).

The fact that after decentralization of the caudal mesenteric ganglion even more intense inhibition of peristalsis was observed in the small intestine, and a reduction of its tone, when the caudal portion of the large intestine was stimulated, apparently indicates that this autonomic ganglion was liberated from inhibitory centrifugal influences from the spinal cord [19, 23, 24]. This type of enhancement of viscerovisceral reflexes was noted by E. I. Sinel'nikov et al. [16] after destruction of the spinal cord. According to M. G. Durmish'yan [4], the spinal cord "imposes," so to speak, definite functional characteristics upon the autonomic ganglia.

Subsequent section of the intermesenteric tract led in most experiments to complete disruption of the reflex connection between the large and small intestine. The same results were obtained with prior decentralization of the ganglion, where, as I. P. Razenkov has shown [13], all the preganglionic effector fibers of spinal origin are found to have degenerated, and the possibility of transmission of stimulation by axon-reflex connections is eliminated. It must be suggested that the transmission of interoceptive influences in our experiments might to some extent be brought about (the two experiments mentioned give evidence of this) along "short pathways," formed by the extremely fine retroperitoneal nerve fibers [7] and vascular nerves which run along the branches of the caudal mesenteric artery to the abdominal aorta and from there to the perivascular plexus of the cranial mesenteric artery.

From histological study of preparations impregnated by the Bielschowsky-Gross method, it was established that after section of the intermesenteric tract a large number of intact fibers remain in its distal portion along with the degenerated ones. In addition, in the ganglia and connections of the celiac and cranial mesenteric plexuses we found many more altered fibers than in the caudal mesenteric ganglion and the plexus surrounding it. Finally, section of the tract results in degeneration of some of the neural elements in the first part of the small intestine and its mesentery, and stimulation of the tract with an induction current produces inhibition of peristalsis of the small intestine [9]. All of this confirms the opinion that predominantly ascending fibers are present in the tract [2, 10, 25]; these fibers, it must be supposed, have a relation to the nerve cells of the ganglion itself or constitute a continuation of those afferent sympathetic connections that enter into the composition of the mesenteric nerves from the caudal portion of the large intestine. These nerves, according to I. F. Ivanov [5], represent the processes of Dogiel's type II

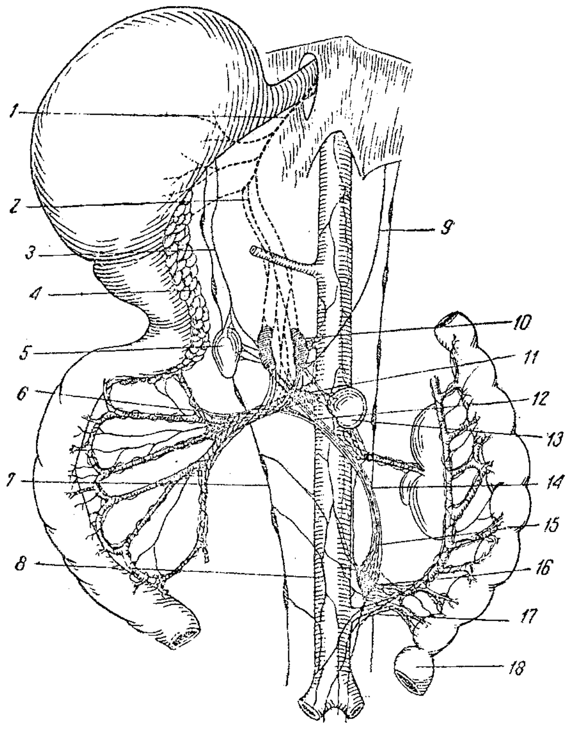

Fig. 2. Interneuronal connections of the caudal portion of the large intestine and the first portion of the small intestine in the rabbit. Semischematic drawing from preparation. 1) Posterior trunk of the vagi; 2) caudal rami of the posterior trunk; 3) right splanchnic nerve; 4) pancreas; 5) right adrenal; 6) cranial mesenteric plexus; 7) sympathetic trunk; 8) abdominal aorta; 9) left splanchnic nerve; 10) left celiac ganglion; 11) cranial mesenteric ganglion; 12) cranial portion of the intermesenteric tract; 13) left adrenal; 14) intermediate portion of the intermesenteric tract; 15) caudal portion of the intermesenteric tract; 16) caudal mesenteric ganglion; 17) caudal mesenteric plexus; 18) caudal portion of the large intestine.

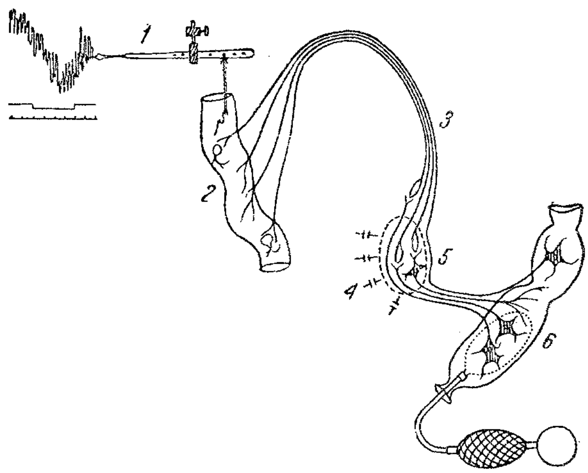

Fig. 3. Diagram of possible interneuronal connections mediating transmission of interoceptive afferent influences from the caudal portion of the large intestine to the small intestine in the rabbit, along the intermesenteric nerve tract. 1) recording of small intestinal movements with an Engelmann lever; 2) loop of jejunum; 3) intermesenteric tract; 4) sites of section of central connections of the ganglion; 5) caudal mesenteric ganglion; 6) caudal portion of the large intestine with balloon inserted into it; sensory cells are dark, motor cells are light.

receptor cells and can be traced to the prevertebral ganglia. According to Kuntz [22], fibers of intestinal origin enter into synaptic connections with motoneurons of the caudal mesenteric ganglion. In addition, it is known [13, 17] that this ganglion also contains sensory cells.

Experiments with blocking of the caudal mesenteric ganglion with diplacine showed that the observed viscerovisceral influences are not completely eliminated. This indicates that some of the afferent intestinal fibers penetrate into the tract without interruption in the ganglion. Finally, the fact that in a number of experiments, the observed reflex remained even after extirpation of the ganglion is explained by the presence of nerve trunks, readily distinguishable in total preparations stained with methylene blue, that enter into the tract from the mesentery without passing through the ganglion. All these possible afferent interneuronal connections are represented in Fig. 3.

The data obtained show that the intermesenteric tract is one of the main autonomic extramedullary pathways along which interoceptive afferent influences from the caudal portion of the large intestine spread to the first portion of the small intestine.

SUMMARY

In rabbits the transmission of inhibitory interoceptive effects from the caudal portion of the large intestine to the first portion of the small intestine takes place mainly along the intermesenteric nerve tract, following decentralization of the caudal mesenteric ganglion. When this nerve tract is divided, in most experiments, no viscerovisceral reflex effects are observed.

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