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Cortical Projection of Afferent Impulses from the Distal Colon via the Pelvic Nerve in the Dog

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ABSTRACT. The cortical projection of the colonic afferent impulse in the pelvic nerve was studied in dogs anesthetized with chloralose. After afferent stimulation of the right rectal branches of the pelvic nerve, initial positive waves were evoked on restricted areas of the precuneus, posterior sigmoid, postcruciate, anterior sylvian, anterior ectosylvian, anterior sigmoid, medial frontal and cingulate gyri. The shortest latency of the waves was 12 msec in the first five of these gyri. The threshold intensity of the afferent stimulation for the evoked potentials was one third of that for the reflex discharges of the rectal branch.

Despite the urge to pass a bowel motion, man can control the initiation of defecation. The behavior of dogs in regard to defecation suggests that this is true in this animal also. Therefore, afferent activity from the distal colon apparently projects to the cerebral cortex which then controls the defecation reflex and related behavioral activities. To understand the neuronal mechanisms underlying this cerebral control, we first clarified the cortical areas which receive the colonic afferent activity via the pelvic nerve. Experimental results showing directly the colonic afferent projection have not been reported previously.

METHODS

This study used 23 dogs weighing 6–12 kg. The dogs were anesthetized with intravenous α-chloralose (80–100 mg/kg), then fixed on a stereotaxic headholder. The animals were paralyzed with gallamine triethiodide (1 mg/kg), then artifical respiration was maintained through a tracheal cannula at a rate of 20–25 strokes/min and a tidal volume of 150–250 ml. Arterial blood pressure was monitored through a cannula inserted in the femoral artery. Body temperature was maintained at about 36°C by the light from two 100-watt tungstem lamps. Anesthesia and paralysis were maintained at deep levels with additional doses of α-chloralose and gallamine triethiodide.

Branches of the pelvic nerve innervating the rectum and distal colon were exposed bilaterally by a mid-line incision. The lumbar colonic nerve and the bilateral hypogastric nerves were severed in all dogs. The central cut-ends of the rectal branches of the pelvic nerve were stimulated. One of the branches

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was prepared for recording of the efferent discharges in three dogs. Bipolar electrodes of platinum wire were used for stimulation and recording. The discharges were amplified by an RC coupled amplifier and displayed on an oscilloscope. The output of the amplifier was led to a spike counter in parallel with the oscilloscope. The counted outputs in bins of 100 msec were averaged 100 times on a digital computer. The averaged outputs were recorded by a pen recorder.

The pia surface of both cerebral hemispheres was exposed by a craniectomy. Both the exposed cortical surface and the rectal branches were covered with pools of warmed mineral oil.

Cortical evoked potentials after stimulation of the central cut-ends of the right and left rectal branches, the anal mucosa and the perianal skin were recorded from the pia surface with a unipolar platinum wire electrode of 0.8 mm tip diameter. A differential plate electrode was attached to the exposed skull. The anal mucosa was stimulated with a special electrode and the perianal skin was stimulated with a bipolar needle electrode[1)]. The evoked cortical potentials after such stimulation were amplified with an RC coupled amplifier and averaged 100 times on the digital computer.

Gyral names according to Singer (1962) were used for explanation of the results[2)].

RESULTS

The cortical evoked potentials after afferent stimulation of the rectal branches of the right pelvic nerve were explored systematically according to a 2–5 mm grid on the pia surface. The explorations were performed on the dorsal and lateral surfaces of the left hemisphere and on the medial surface of the right hemisphere. One example of such explorations is shown in Fig. 1A. This exploration was performed on the medial surface of the right hemisphere. Initial positive waves were observed in restricted regions of the precuneus and medial frontal gyri. The cortical areas showing such initial positive waves are summarized in Fig. 1C. The borderlines of these areas were median lines determined optically from 3–6 maps as shown in Fig. 1A. These figures show that the waves occurred in restricted areas in the left anterior sylvian, anterior ectosylvian, anterior sigmoid, posterior sigmoid and postcruciate gyri, and the right medial frontal, precuneus and cingulate gyri. Typical records from focal points in these cortical areas are shown in Fig. 1B. At the focal point, the largest initial positive wave was observed with the shortest latency.

The latencies of the positive waves in such restricted areas are shown in Fig. 2 as histograms. Fast and late peaks are evident in the histogram of all responses (n = 229, Fig. 2h). Such peaks are obvious in the latency histogram of the right medial frontal gyrus and the left anterior sigmoid gyrus (Fig. 2a and d). Therefore, the positive waves apparently separated at the trough between the fast and late latency groups. The histogram of the right precuneus

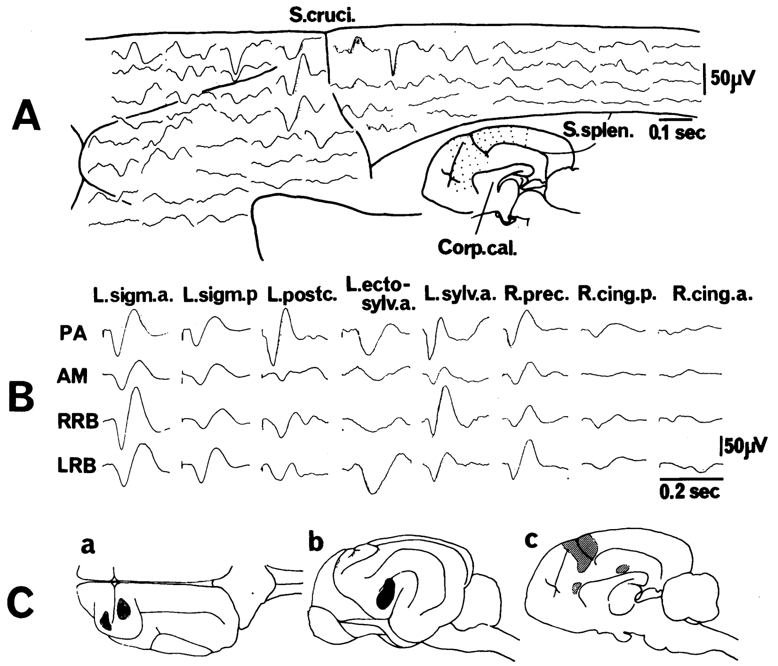

Fig. 1. Cortical evoked potential after afferent stimulation of rectal branches of the pelvic nerve, the anal mucosa and the perianal skin.

A : An example of exploration of the evoked potential in the medial surface of the right hemisphere. The central cut-ends of the right rectal branches were stimulated with pulses of 10 volts intensity, 0.5 msec duration and 0.5 Hz frequency. Evoked potentials were averaged 100 times. Each record is shown on the point where the record was obtained. S. cruci. ; cruciate sulcus. S. splen. ; splenial sulcus. Corp. cal. ; corpus callosum.

B : Examples of evoked potentials recorded from each focal point in the left anterior sigmoid (L. sigm. a.), posterior sigmoid (L. sigm. p.), postcruciate (L. postc.), anterior ectosylvian (L. ectosylv. a.) and anterior sylvian (L. sylv. a.) gyri, and the right precuneus (R. prec.), posterior cingulate (R. cing. p.) and anterior cingulate (R. cing. a.) gyri after afferent stimulation of the perianal skin (PA), the anal mucosa (AM), the right rectal branches (RRB) and the left rectal branches (LRB). These abbreviations are used in the following figures. Evoked potentials were averaged 100 times. In all cases, stimulation was of 10 volts intensity, 0.5 msec duration and 1 Hz frequency.

C : Oblique lined areas show projection areas of the afferent activity of the right rectal branches. a ; dorsal view. b ; lateral view. c ; medial surface.

shows the fast peak only, and the histogram of the anterior and posterior cingulate gyrus shows the late peak only (Fig. 2b and c). The mean latencies of the fast and late groups are shown on each histogram. Significant ($p<0.2$) variations were not recognized among the mean latencies of the fast or the late groups. The shortest latency was 12 msec in the right precuneus, the left posterior sigmoid, postcruciate, anterior sylvian and anterior ectosylvian gyri, 13 msec in the right medial frontal gyrus, 15 msec in the left anterior sigmoid

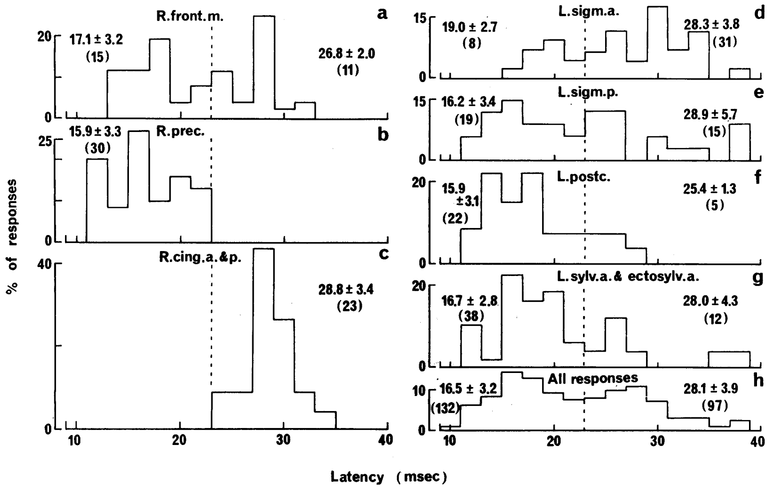

Fig. 2. Latencies of the initial positive waves after afferent stimulation of the right rectal branches.
Latencies of the waves evoked on the areas indicated by the abbreviations are shown as histograms. a ; right medial frontal gyrus (R. front. m.). h ; all responses. Evoked waves are divided into the fast and late groups at 23 msec latency. The mean latency and standard deviation of the fast group are shown on the left side of each histogram together with the number of the responses. Those of the late group responses are shown on the right side.

gyrus, and 24 msec in the right cingulate gyrus.

Similar initial positive waves also occurred on focal points of such restricted areas after stimulation of the perianal skin, the anal mucosa and the left rectal branches as shown in Fig. 1B. The latencies of the positive waves for each focal point were compared in the anterior sigmoid, posterior sigmoid, postcruciate and anterior sylvian gyri of four dogs. Table 1 shows the mean latencies of the positive waves on the four focal points by the afferent stimulation of the right and left rectal branches, the anal mucosa and perianal skin stimulation. There was no significant ($p>0.2$) difference in the mean latencies

TABLE 1. Mean latencies and the standard deviations of the initial positive waves.

Afferent stimulation / Cortical areas	Perianal skin	Anal mucosa	Cont. rectal br.	Ipsi. rectal br.	No. of waves	No. of dogs
Ant. sigm. gyrus	17.9±1.8	23.3±5.5	24.9±3.7	21.3±4.9	4	3
Post. sigm. gyrus	13.5±3.9	24.7±6.2	23.7±5.8	23.4±5.9	6	4
Post. cruci. gyrus	13.1±1.4	22.1±3.2	19.1±5.6	20.6±5.1	4	4
Ant. sylv. gyrus	14.7±3.4	17.2±0.7	19.9±2.9	18.4±2.9	6	4

of the positive waves responding to the stimulation of the rectal branches on the either side and the anal mucosa, but the mean latencies were longer than the mean latencies of the waves elicited by the perianal skin stimulation ($0.01<p<0.2$).

A reflex discharge of the rectal branch was induced by afferent stimulation of the nerve via the pontine defecation reflex center. The threshold intensity of the cortical evoked potential and the reflex discharges during the stimulation of the right rectal branches was evaluated (Fig. 3). The threshold intensity for the cortical evoked potential was about one third of that for the reflex discharges of the left rectal branch.

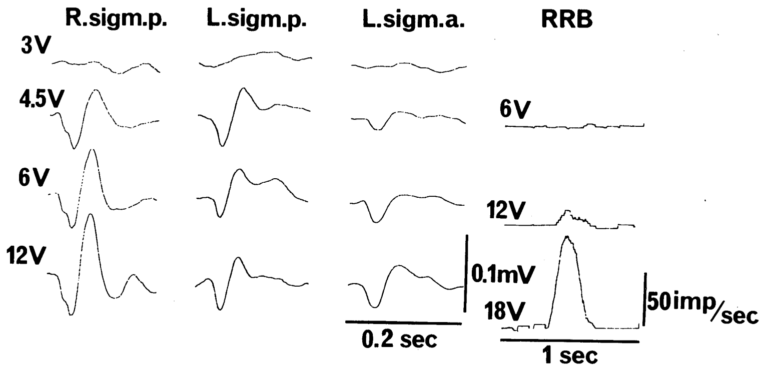

Fig. 3. Threshold intensity of the afferent stimulation of the right rectal branches for cortical evoked potentials and reflex discharges of the left rectal branch.
Left three columns : cortical potentials evoked by the afferent stimulation on the areas indicated by abbreviations. The central cut-ends of the right rectal branches were stimulated with pulses of the intensity indicated on the left side of each row, 0.5 msec duration and 0.5 Hz frequency. Evoked potentials were averaged 100 times. Right column : reflex discharges of the left rectal branch elicited by afferent stimulation of the right rectal branches with 10 train pulses of the intensity indicated on the left side of each record, 5 msec interval, 0.5 msec duration and a repeated frequency of 0.5 Hz. Discharges of the left rectal branch were changed to the frequency histogram of 100 msec bins by a spike counter, then averaged 50 times.

DISCUSSION

Afferent projection from the distal colon to the cerebral cortex has been suggested only by the indirect evidence that the initial positive waves were evoked in some cortical areas after stimulation of the central cut-end of the trunk of the pelvic nerve of cats[3,4,5]. Because afferent fibers from many pelvic viscera should be activated by the stimulation, the colonic afferent areas of the cortex (which receive essentially afferent impulses from the distal colon) could not be demonstrated by these experiments. Therefore, areas responding to the stimulation should be recognized as the pelvic visceral afferent area (the pelvic afferent area). Each of the pelvic afferent areas has been demonstrated in the anterior ectosylvian, anterior marginal, posterior sigmoid, anterior sigmoid, precuneus and orbital gyri of cats. Latencies in the range of 10–26 msec were reported for the evoked potentials in these areas of cats.

In contrast to these works, the central cut-ends of rectal branches of the pelvic nerve were selectively stimulated in this work; therefore, cortical areas responding to this stimulation should be recognized as the colonic afferent area. Three of the colonic afferent areas of dogs (one in the precuneus, one in the anterior sigmoid gyrus and one which stretched over both the posterior sigmoid and postcruciate gyri) coincided well with pelvic afferent areas in the corresponding gyri of cats. The following differences, however, exist between the colonic afferent areas of dogs and the pelvic afferent areas of cats. 1. Pelvic afferent areas were reported in the anterior marginal and orbital gyri of cats; however, potential changes could not be evoked on the exposed surfaces of these gyri in dogs. This may be due to different forms of the cortical gyri and sulci in the two species. The cortical areas of dogs corresponding to the pelvic afferent areas in the marginal and orbital gyri of cats are hidden in the deep lateral and presylvian fissures, respectively[6]; therefore the potentials evoked in these areas of the dog may be undetectable by electrodes on the exposed brain surface. 2. The colonic afferent area of dogs corresponding to the pelvic afferent area in the anterior ectosylvian gyrus of cats situated on the position is shifted posterolaterally, and therefore has expanded to the anterior sylvian gyrus. This difference cannot be explained. 3. Each colonic afferent area in frontal, anterior cingulate and posterior cingulate gyri was demonstrated in this work; however, corresponding pelvic afferent areas have not been reported in cats because the cortical evoked potential has not been explored in these areas.

Pinto Hamuy et al.[7] (1956) described somatic afferent areas I (SI) and II (SII) in dogs. The colonic afferent areas in the precuneus and in the ectosylvian gyri are in SI and SII respectively, and correspond to the parts which received somatic afferents from the body part innervated by the sacral spinal nerves. Therefore, these colonic afferent areas may be concerned with the sensation of the distal colon. The colonic afferent area which stretched over both the posterior sigmoid and postcruciate gyri corresponds to the SI area that received afferent impulses from the abdominal wall. It has been reported that this area in SI of cats receives visceral afferent impulses via the vagal[8], splanchnic[9] and pudendal[10] nerves, as well as the somatic afferents of the abdominal wall. Slimp and Towe[10] (1980) showed that the afferent impulses of the pudendal nerve projected mainly to the wide-field neurons in this area of cats; therefore, they assumed that the wide-field neuron acts as a modulator of efficiency of the synaptic transmission between afferent fibers mediating the abdominal wall sensation and the small-field neurons, which may be directly concerned with modality perception and topognosis of the abdominal wall. In this view, is expected the colonic afferents are thought to project on to the wide-field neurons and modify the sensation of the abdominal wall.

The colonic afferent area in the medial frontal gyrus corresponds to the motor area of the muscles innervated by the sacral spinal nerves[11]. Therefore, it was suggested that the area is concerned with the motivation aspect of the colonic afferent activity. The colonic afferent area in the anterior sigmoid gyrus is in the motor area for the anterior abdomen[12]. The wide-field neurons have been found in the motor area of the cat; therefore fibers mediating colonic afferent activity for this area may synapse with the neurons and act as a modulator of the pyramidal cells innervating the abdominal muscles[13].

The cingulate gyrus is generally known as a part of the limbic system which is closely concerned with instinctive behavior and, thus, the activity of the autonomic nervous system. The colonic areas in this gyrus may be concerned with behavioral and autonomic activity related to defecation.

As shown in Fig. 2, the initial positive waves evoked by afferent stimulation of the rectal branches should be divided into the fast and late groups by their latencies. The mean latencies of the fast group waves did not significantly differ from the colonic afferent areas. The same relationships were also observed among the mean latencies of the late group waves. This suggests that afferent activities from the colon project to these colonic areas through two main pathways, one of which has a conduction velocity higher than the other.

The reflex activity of the rectal branch elicited by the afferent stimulation of the contralateral rectal branches usually has a long latency[14] as shown in Fig. 3. It has been clearly shown that the reflex activity with the long latency occurs through the pontine defecation reflex center existing in the pontine reticular formation[15,16,17]. When the reflex is elicited by rectal distention, the reflex discharges of the rectal branches cause a propulsive contraction of the distal colon[14,17]. The threshold intensity of the afferent stimulation for the cortical evoked potentials was one third of that for the reflex activity (Fig. 3). Moreover, the mean latency of the fast group of waves of the cortex is shorter than that of the responding discharges of units of the pontine defecation reflex center[17,18]. This suggests the possibility that activity of the pontine defecation reflex center is controlled by the cortical colonic areas which are first activated by afferent impulses from the distal colon through the afferent pathway faster than that to the pontine defecation reflex center.

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