THE NERVOUS CONTROL OF THE CAUDAL REGION OF THE LARGE BOWEL IN THE CAT.

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To find the influence of a nervous outflow on an organ in the body one may either cut the nerve, with subsequent stimulation of the cut ends, or one may simply divide the nerve. In the former case the response of the organ is to nerve impulses set up by an abnormal stimulus which may elicit impulses in quantity and in quality different from the normal, while in the latter case, after the disturbances due to trauma have subsided, the response exhibited by the viscus is due to the absence of normal impulses.

The latter method has found little favour in the past. Barrington [1915], however, used just such a method, often in acute preparations, to elucidate the normal nervous control of the urinary bladder. The close developmental and physiological connection between the large bowel and the urinary bladder suggests that a similar method may be successful in investigating the normal nervous control of the large bowel.

NOMENCLATURE.

Because of present uncertainty about the constitution and function of the nervous outflows to the large bowel the purely morphological terms "lumbar" and "sacral" are used in preference to "sympathetic" and "parasympathetic" respectively. The names applied to the subdivisions of the outflows are those recommended by Langley and Anderson [1896]. The lumbar outflow arises from the second, third, fourth and sometimes fifth lumbar nerves. The fibres pass without interruption through the sympathetic chains and run as four or five strands on either side to the inferior mesenteric ganglia. These strands are the spinal rami of the inferior mesenteric ganglia. The inferior mesenteric ganglia, usually four in number, form a ring round the inferior mesenteric artery about $l\frac{1}{2}$ cm. from the origin of the artery from the agont. The majority of the fibres of the lumbar outflow form synapses in these ganglia. From the ganglia arise the lumbar colonic nerves which accompany the inferior mesenteric artery to the colon. There also arise from the inferior mesenteric ganglia the hypogastric nerves which run caudad to join the pelvic plexus.

The sacral outflow consists of the pelvic nerves which usually arise from the second and third sacral nerves. The pelvic nerves divide after a short course into a cranial and caudal branch on each of which there is a conspicuous ganglion. From the caudal ganglion arise four or more branches which run dorsad to the colon as the sacral colonic nerves. The fibres of the sacral outflow have synapses close to the bowel itself.

Fig. 1, drawn from the description by Langley and Anderson [1896], illustrates diagrammatically the outflows to the large bowel.



Fig. 1. Diagram of the outflows to the large bowel in the cat. A, spinal rami to the inferior mesenteric ganglia; B, lumbar colonic nerves; C, inferior mesenteric artery; D, inferior mesenteric ganglia; E, pelvic nerve; F, pelvic plexus; G, hypogastric nerve; H, sacral colonic nerves; I, pudendal nerve.

PREVIOUS WORK.

Bayliss and Starling [1900] and Elliott and Barclay-Smith [1904] found that the colon was always inactive after opening the peritoneum. Pithing the lumbo-sacral cord or dividing the nervous outflows to the large bowel led to activity of the gut. Lehmann [1913] noted increased colonic movement in dogs after division of the spinal rami to the inferior mesenteric ganglia. Markowitz and Campbell [1927] showed that spinal anæsthesia in dogs removes inhibition of the small intestine produced by intense peritoneal irritation, and in one of their five cases they thought that the movements of the colon were also augmented. Learmonth and Markowitz [1930] found that division of the lumbar colonic nerves in dogs increased colonic activity. This increase in activity was apparently greater when the pelvic nerves were intact. In these experiments, unfortunately, the peritoneum had been opened before section of the lumbar colonic nerves. Rankin and Learmonth [1930] recommend division of the inferior mesenteric (lumbar colonic) nerves and of the presacral (hypogastric) nerves in man for the relief of megacolon.

Kuré [1931] and his fellow workers, however, cut the rami communicantes to the lumbar sympathetic chain on both sides in four dogs. The caudal part of the small intestine and the large intestine relaxed. Application of nicotine solution to the ganglia of the lumbar sympathetic chain on both sides in four dogs led to contraction of the large intestine and of the distal part of the small intestine. These results are supposed to be due to the presence of "spinal parasympathetic" fibres in the lumbar outflow. These fibres have no synapses, as have the true "sympathetic" fibres, in the lateral ganglia. In addition, stimulation of the lumbar sympathetic chain gave motor responses from the colon both in cats and in dogs with or without the use of nicotine.

Division of both pelvic nerves by Elliott [1906] apparently did not lead to gross atony of the colon in cats because faeces did not accumulate in the large bowel. Barrington [1915] observed dilatation of the large bowel in cats after cutting the dorsal roots of the sacral nerves. A damson and Aird [1932] found that section of the pelvic nerves in cats led, after an interval of several weeks, to megacolon.

METHODS.

The cats were decerebrated under ether anæsthesia and no observations were carried out for at least 1 hour after decerebration. In a few cases decapitation or anæsthesia with one of the barbituric derivatives was substituted for decerebration. Faecal matter was removed from the large bowel after decerebration by means of a soap and water enema. The animals received a meal of porridge and milk on the morning of the day of the experiment some 2 hours before anæsthetization.

The behaviour of the large bowel was recorded by a thin rubber balloon of large diameter inserted through the anus. The balloon holder, 22 cm. long, was a thin copper tube with numerous perforations in the terminal 4 cm. where the balloon was attached. The copper tube was marked off in cm. so that the position of the balloon within the gut could be gauged. Usually the caudal end of the balloon lay from 4 to 6 cm. craniad to the anal canal. The balloon holder was firmly grasped by a clamp attached to the operating table.

Volume recording at a constant pressure of 21 cm. water was used. The tonicity of the gut was estimated by recording the volume of fluid accepted by the balloon in the gut at constant pressure. The rhythmical behaviour of the gut appeared on the record after release of the pressure. Several consistent records were obtained before interfering with the nervous outflows to the gut.

The lumbar outflow was approached extraperitoneally through a left flank incision. The hypogastric nerves were cut without opening the peritoneum, but the peritoneum had to be opened in order to divide the spinal rami to the inferior mesenteric ganglia and also to cut the lumbar colonic nerves. The pelvic nerves were exposed and cut extraperitoneally by incisions along the inguinal canals.

The lumbo-sacral cord was isolated by tying the spinal cord in the lower thoracic region. Full ether anæsthesia was used and ample time allowed for disappearance of the ether before continuing the observations. Such cord section is craniad to the roots of origin of the lumbar and sacral outflows in cats.

Spinal anæsthesia was induced by intrathecal injection of 1 to 2 c.c. of a 1 p.c. "Novocain" solution craniad or caudad to the last lumbar spinous process. As tested by the knee jerk, anæsthetization of the cord lasted for from 30 to 60 minutes.

RESULTS.

(1) The effect of division of the lumbar outflow. When the lumbar outflow is intact the large bowel is inactive. Section of the entire lumbar outflow leads to increase in tone and in rhythmical activity (Fig. 3, C, 1, 2). Section of the spinal rami to the inferior mesenteric ganglia alone causes a slight increase in tone and the appearance of rhythmical contraction. Subsequent section of the lumbar colonic nerves and of the hypogastric nerves leads to marked increase both in tone and in rhythmicity (Fig. 2, B). Division of the hypogastric nerves alone has little effect, but section of the lumbar colonic nerves, even when the hypogastric nerves are intact, leads to this marked increase in gut activity (Fig. 2, A, C, 1, 2, 3). Such results occur after isolation of the lumbo-sacral cord and the integrity of the pelvic nerves seems to make little difference to the result.

(2) The effect of division of the sacral outflow. In five cats the sacral nerve roots or the pelvic nerves themselves were cut and the animals allowed to recover. These animals experienced difficulty in emptying the large bowel and post-mortem the colon was dilated.

In acute preparations, when the lumbar outflow is intact, division of the pelvic nerves may lead to further relaxation of the large bowel (Fig. 3, A, 2, 3). Such relaxation is rarely marked but, when the lumbar outflow has previously been cut, and the gut in consequence in a state







- Series A. Cat: decerebrate; pudendal nerves cut. 1. Pressure released at 21 cm. H₂().
 2. Lumbar colonic nerves cut; pressure released as before.
 3. Hypogastric nerves cut; pressure released as before.
- Series B. Cat: decerebrate; pudendal nerves cut; lumbo-sacral cord isolated; pelvic nerves cut. 1. Pressure released at 21 cm. H₂O. 2. Spinal rami to inferior mesenteric ganglia cut; pressure released as before. 3. Lumbar colonic and hypogastric nerves cut; pressure released as before.
- Series C. Cat: decerebrate; pudendal nerves cut. 1. Pressure released at 21 cm. H₂O.
 2. Hypogastric nerves cut; pressure released as before. 3. Lumbar colonic nerves cut; pressure released as before. 4. Pelvic nerves cut; pressure released as before.

of high tone and activity, section of the pelvic nerves then produces an unequivocal fall in tone and possibly some decrease in the rate of rhythmical contraction (Fig. 2, C, 3, 4). After the division of the pelvic nerves the decrease in resistance to passage of the recording balloon craniad



Fig. 3.

- Series A. Cat: decerebrate. 1. Pressure released at 21 cm. H₂O. 2. Pudendal nerves cut; pressure released as before. 3. Pelvic nerves cut; pressure released as before.
- Series B. Cat: decerebrate; lumbar outflow cut; lumbo-sacral cord isolated. 1. Pressure released at 21 cm. H₂O. 2. Pelvic nerves exposed; pressure released as before. 3. Pelvic nerves cut 3 hours after cord transection; pressure released as before.
- Series C. Cat: decerebrate; pudendal nerves cut. 1. Pressure released at 21 cm. H₂O.
 2. Lumbar outflow cut; pressure released as before. 3. Cord tied in lower thoracic region; pressure released as before.

along the gut may be very obvious. The fall in tone of the gut is certainly not due to the operative interference necessary to expose the pelvic nerves.

Shortly after isolation of the lumbo-sacral cord, division of the pelvic nerves, although the lumbar outflow be cut, is usually without effect. Cutting the pelvic nerves several hours after transection of the cord may, however, give some indication of relaxation of the large bowel (Fig. 3, B).



Fig. 4.

- Series A. Cat: Na amytal anæsthesia-55 mg./kg.-pudendal nerves cut: pelvic nerves cut. 1. Pressure released at 21 cm. H₂O. 2. Cord tied in lower thoracic region; pressure released as before.
- Series B. Cat: Na amytal anæsthesia-56 mg./kg. 1. Pressure released at 21 cm. H₂O.
 2. 1 c.c. 1 p.c. "Novocain" injected intrathecally; pressure released as before 10 min. after injection. 3. Pressure released as before 60 min. after injection.

(3) The effect of isolation of the lumbo-sacral cord. When the lumbar outflow is intact and the pelvic nerves divided, isolation of the lumbo-sacral cord causes no significant alteration in the large bowel; there is certainly no contraction (Fig. 4, A). When, however, the lumbar outflow is cut and the sacral outflow intact, transection of the spinal cord leads to obvious relaxation of the large bowel (Fig. 3, C, 2, 3). Even when both outflows are intact, isolation of the lumbo-sacral cord may cause slight relaxation of the large bowel.

(4) The effect of spinal anæsthesia. When both outflows to the large bowel are intact, spinal anæsthesia invariably leads to increased activity of the gut. The result is similar after division of the sacral outflow and after isolation of the lumbo-sacral cord.

If the lumbar outflow be cut and the sacral outflow left intact, spinal anæsthesia leads to relaxation of the gut, very apparent before section of the cord but slight after isolation of the lumbo-sacral cord. The possibility that spinal anæsthesia indirectly affects the volume of fluid accepted by the gut by causing flaccidity of the abdominal and pelvocaudal muscles throws some doubt on such observations, although, after division of both outflows to the large bowel, spinal anæsthesia does not have any obvious effect on the record from the gut.

The effect of spinal anæsthesia on the large bowel of an anæsthetized cat with both outflows intact is shown in Fig. 4, B.

When both outflows to the gut are intact, or when only the lumbar outflow is intact, division of the pudendal nerves, in practically every case, leads to slight but definite increase in the activity of the large bowel (Fig. 3, A, 1, 2).

DISCUSSION AND CONCLUSIONS.

The lumbar outflow exerts a constant inhibitory influence on the large bowel, and this inhibition is apparently more powerful than the motor tone passing by the sacral outflow. If the peritoneal cavity be opened beforehand, such powerful inhibition is understandable, and division of any part of the lumbar outflow can give no true indication of the normal impulses passing along the lumbar outflow. In the present series, however, the integrity of the peritoneal cavity was jealously guarded before division of the lumbar outflow. It may be that the marked inhibition is due to the recent operative interference in acute preparations. On the other hand, the motor influence through the sacral outflow may be intermittent, as the work of Hertz and Newton [1913] on the gastrocolic reflex suggests. Such intermittent activity, however powerful, simple nerve section cannot be expected to detect.

A constant motor influence of the sacral outflow, however, may be detected by previous division of the lumbar outflow, but this does not seem to be powerful in acute experiments, and, even in survival experiments, division of the sacral outflow apparently does not lead to rapid or gross atony of the large bowel. It is possible that the dilatation of the large bowel observed by Barrington [1915] and by Adamson and Aird [1932], after interference with the sacral outflow, is due to distension of the gut as the result of the absence of the normal expulsive responses which depend so largely on the integrity of the pelvic nerves [Garry, 1932].

The central inhibitory tone for the large bowel seems to be confined to the lumbo-sacral cord. In this the colon differs from the urinary bladder where part of the inhibition in the lumbar outflow arises craniad to the lumbar cord [Barrington, 1915]. It is difficult to decide if the inhibitory influence of the inferior mesenteric ganglia is a normal phenomenon or not. Barrington [1915] also found that the inferior mesenteric ganglia act as an extraspinal centre of inhibition for the bladder. Division of the spinal rami to the inferior mesenteric ganglia alone certainly never causes such marked increase in colonic activity as division of the lumbar colonic nerves. This may be due to failure to cut all the spinal rami to the inferior mesenteric ganglia, but it is possible that the inhibitory influence exerted by such an extraspinal centre is the result of the local interference at the time of section of the spinal rami. The marked increase in gut activity following spinal anæsthesia, in effect division of the spinal rami without local interference, suggests that the inhibitory powers of the inferior mesenteric ganglia are acquired in response to an abnormal situation. Distal to the inferior mesenteric ganglia the inhibitory impulses follow the lumbar colonic nerves almost exclusively. The persistence of the inhibition after division of the hypogastric nerves is not due to switching of impulses, normally passing down the hypogastric nerves, to the lumbar colonic nerves, because initial division of the lumbar colonic nerves leads to an increase in bowel activity little, if at all, augmented by subsequent section of the hypogastric nerves. Stimulation of the peripheral ends of the cut hypogastric nerves causes obvious inhibition of the colon which shows the danger of drawing conclusions from the results of nerve stimulation alone.

The motor influence through the sacral outflow arises mainly craniad to the lumbo-sacral cord. There is some slight evidence, even in acute preparations, for a secondary motor centre in the isolated lumbo-sacral cord. Such conclusions are similar to those of Barrington [1915] for the urinary bladder.

The slight increase in activity of the large bowel after division of the pudendal nerves may be due to removal of afferent impulses in the pudendal nerves set up by irritation of the anal canal. Such impulses, like other afferent impulses, may tend to cause inhibition of the gut.

SUMMARY.

The behaviour of the caudal end of the large bowel in cats is recorded by means of a balloon introduced through the anus.

In acute decerebrate cats the gut is invariably inactive. This inactivity is due to inhibitory impulses, arising locally in the lumbo-sacral cord, passing out to the large bowel by way of the spinal rami to the inferior mesenteric ganglia and then by the lumbar colonic nerves. The hypogastric nerves do not normally transmit such impulses to the gut. After section of the spinal rami the inferior mesenteric ganglia still exert an inhibitory influence on the large bowel. The motor influence exerted by the sacral outflow is not strong and arises mainly craniad to the lumbo-sacral cord. There is some evidence for a subsidiary motor centre in the isolated lumbo-sacral cord.

Division of the pudendal nerves causes a slight increase in the activity of the large bowel.

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