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THE RESPONSES TO STIMULATION OF THE CAUDAL END OF THE LARGE BOWEL IN THE CAT.

By R. C. GARRY.

(*From the Institute of Physiology, the University, Glasgow.*)

Our knowledge of the phenomena of defæcation is derived mainly from work on man. In few other fields of Physiology has clinical observation played so large a part. Unfortunately, the study of clinical material is at the mercy of the capriciousness of disease processes and of accident. Thus systematic investigation in man of the factors controlling the behaviour of the caudal end of the large bowel is well-nigh impossible. On the other hand, observations on lower animals are scanty, due mainly to the absence of a satisfactory mode of stimulation capable of eliciting defæcation responses.

The terminology used here is, in the main, that recommended by Langley and Anderson [1896]. The origin and course of the nervous outflows to the large bowel in the cat are illustrated in a previous paper [Garry, 1933]. In the cat, however, it is not justifiable, as Elliott and Barclay-Smith [1904] point out, to divide the colon into regions corresponding to those of human anatomy. Nevertheless, it is convenient to refer to the cranial and caudal regions of the large bowel and to regard the anal canal as that part encircled by the anal sphincters. The name external anal sphincter should be applied to the entire striped muscle innervated by the pudendal nerves, and the name internal and sphincter confined to the circular aggregation of smooth muscle fibres at the anus. The external anal sphincter overlaps the internal anal sphincter and surrounds the anal glands. The levator ani in man is the homologue of the pelvo-caudal muscles which flex and abduct the tail in the cat.

Previous work.

The influence of the spinal cord on defœcation.

Gowers [1877] experimented on three men, two of whom suffered from a complete transverse lesion of the spinal cord. In these two patients irritation of the rectal mucous membrane or distension of the rectum by a puff of air caused dilatation of the anal canal. Head and Riddoch [1917] and Riddoch [1917] found that in spinal man, after recovery from the long period of spinal shock, distension of the rectum led to defæcation.

Goltz and Freusberg [1874] showed that the large bowel in spinal dogs is able to expel foreign bodies. Sherrington [1900] states that defæcation occurs normally in spinal mammals and that stimulation of the rectal mucous membrane craniad to the anal canal leads to relaxation of the anal sphincters. Apparently, then, defæcation is essentially unaffected by transection of the spinal cord craniad to the lumbar region.

On the other hand, after destruction of or injury to the lumbo-sacral region of the spinal cord, defæcation is affected, although the large bowel is still able to expel its contents. The third patient of Gowers suffered from injury to the dorsal roots of all the sacral nerves and to both roots of the caudal sacral nerves. The circumanal region was insensitive, there was incontinence of fæces and the external anal sphincter was paralysed. In this man, as in the other two men, irritation of the rectum caused dilatation of the anal canal. Goltz and Ewald [1896] claimed that defæcation ultimately became normal in their "cordless" dogs. Bayliss and Starling [1900] with difficulty obtained "descending inhibition" and "ascending excitation" in the decentralized large bowel of dogs. In rabbits similar responses were more easily obtained. It is doubtful, however, if such responses can be regarded as true defæcation responses since Bayliss and Starling deliberately avoided the anal canal because its control is "more intimately connected with the central nervous system." Elliott and Barclay-Smith [1904] observed that excretion of fæces was quite satisfactory, and that irritation of the anal mucous membrane caused extrusion of fæcal pellets in rats, even after destruction of the lumbo-sacral spinal cord. Nevertheless, these authors concluded that decentralization does disturb the normal coordinated activity of the large bowel.

The peripheral nerves concerned with defæcation.

Head [1893], from a study of pain in visceral disease, came to the conclusion that the sensory inflow from the rectum in man passes by the dorsal roots of the second, third and fourth sacral nerves. Langley and Anderson [1895] found that cutting the sacral nerve roots abolished voluntary defæcation in lower animals. Although his primary interest was in the behaviour of the tail, Merzbacher [1902] noted that, after section of the dorsal roots of the sacral and tail nerves, the presence of a foreign body in the rectum led neither to expulsion of that body nor to adoption of a typical somatic defæcation posture.

Barrington [1915], on the other hand, found that cats, with the pelvic and pudendal nerves both cut, still had the desire to defæcate and that fæcal matter did not accumulate in the large bowel. In spite of this fact, Barrington believes that the main afferent pathway for the impulses leading to defæcation lies in the pudendal nerves.

The nature of the stimulus for defæcation.

It is generally accepted that defæcation is elicited by stimulation of the caudal end of the gut. Zimmermann [1909] and Hertz [1911] believe that distension of the rectum is the stimulus in man, and Cannon [1911] states that distension of the caudal end of the large bowel initiates defæcation in lower animals. Garry [1932] elicited defæcation by stimulation of the distal part of the large bowel in decerebrate cats.

Lehmann [1913] found that stimulation of the central ends of various somatic nerves led to contraction of the cranial and to relaxation of the caudal part of the large bowel in dogs. The integrity of the pelvic nerves was necessary for such responses. Stimulation of the central ends of visceral nerves supplying the large bowel itself, however, did not cause this "defæcation" response. As a result Lehmann came to the somewhat surprising conclusion that the stimuli initiating the act of defæcation do not act on the large bowel. This conclusion is accepted by Ranson [1921].

Methods.

The preparation of the cats and the operative technique have already been described [Garry, 1933]. The movements of the large bowel and of the anal canal were recorded by two tandem balloons inserted through the anus (Fig. 1). Recording was either by volume changes at a constant pressure in the neighbourhood of 21 cm. water pressure or by pressure changes at a constant volume. Simple distension of the balloons, both

in the large bowel and in the anal canal, rarely elicited responses. On the other hand rotation or a slight to-and-fro movement of the balloons, distended or undistended, almost invariably elicited marked response which had as its obvious purpose expulsion of the stimulating balloon. Such stimulation, although not recognised as normal according to currently accepted views, does enable one to elicit defæcation responses with ease and with certainty and thus to investigate the part played by the various extrinsic factors in defæcation.

The holder for the balloon in the large bowel moved freely within the holder for the balloon in the anal canal. It was thus possible to move one balloon without moving the other balloon. The holder of the

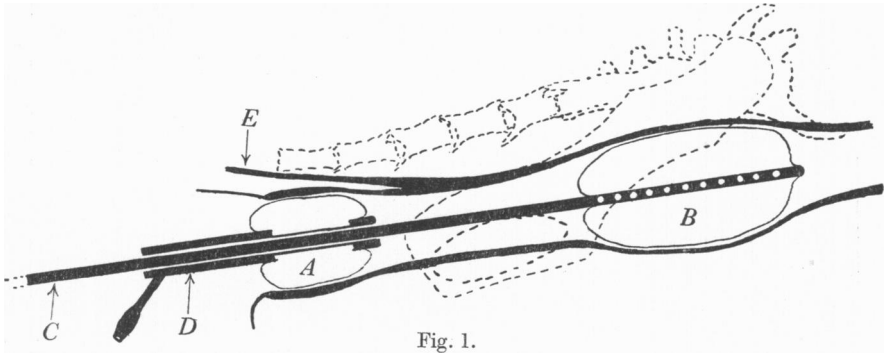

Fig. 1.

The recording balloons. *A*, the balloon in the anal canal; *B*, the balloon in the large bowel; *C*, holder for balloon in the large bowel; *D*, holder for balloon in anal canal; *E*, recto-coccygeus muscle.

stationary balloon was firmly grasped by a clamp attached to the operating table. In this way it was possible to stimulate, and, if the stimulating balloon were distended, to record the local response to the stimulation as well as the response at a distance.

The balloon within the large bowel was 4 cm. long and the balloon within the anal canal 2 cm. long. Usually 4 to 6 cm. separated the cranial end of the balloon in the anal canal from the caudal end of the balloon in the colon.

In several cats the balloon for the large bowel was introduced on a short metal holder through a colostomy in the left flank. The colostomy was close to the ileocolic sphincter. In such cases rubber tubing connected the balloon to the recording system. The responses obtained did not differ from those elicited by the simpler and less objectionable technique, although, due to injury to the peritoneum, it was usually impossible in

cats with a colostomy to produce any response before division of the lumbar outflow.

When necessary curare was given by slow intravenous injection of a 0·05 p.c. suspension.

Results.

(1) *The response of the large bowel to stimulation of the large bowel.*

Movement of the balloon within the large bowel causes contraction of the large bowel. Unless the stimulus is prolonged or vigorous, there is

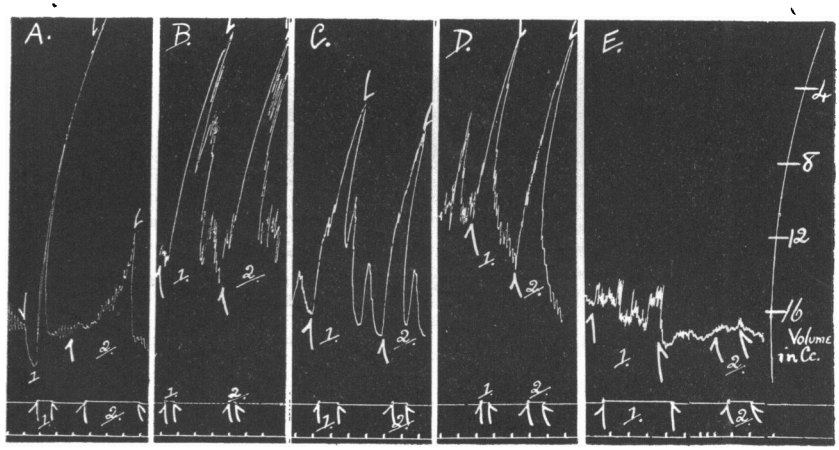

Fig. 2.

Cat: decerebrate; volume record from large bowel at constant pressure of 21 cm. H_2O. Time records in minutes.

A. (1) Collapsed caudal balloon moved to and fro in anal canal. (2) Distended balloon rotated within large bowel.

B. Pudendal nerves and lumbar outflow cut. (1) Collapsed caudal balloon moved to and fro in anal canal. (2) Distended balloon rotated within large bowel.

C. Lumbo-sacral cord isolated. (1) Collapsed caudal balloon moved to and fro in anal canal. (2) Distended balloon rotated within large bowel.

D. Full curarization induced. (1) Collapsed caudal balloon moved to and fro in anal canal. (2) Distended balloon rotated within large bowel.

E. Spinal anæsthesia induced. (1) Distended balloon rotated within large bowel. (2) Collapsed caudal balloon moved to and fro in anal canal.

rarely any sign of participation of the somatic muscles in the response. Such contraction of the large bowel may be elicited in anæsthetized cats (Fig. 4 B), in decerebrate and in decapitate cats (Figs. 2 A(2)), and in cats with isolated lumbo-sacral cord (Fig. 2 C(2)). Full curarization does not affect the response (Fig. 2 D(2)).

The response is more easily elicited and is of greater magnitude after division of the lumbar outflow to the large bowel (Fig. 2 A(2), B(2)).

After section of the pelvic nerves (Fig. 4 D) and after induction of spinal anæsthesia (Fig. 2 E(1)) the large bowel usually fails to respond to stimulation. When the bowel does respond, the contraction is fugitive and difficult to elicit. Abolition of the response during spinal anæsthesia and reappearance of the response after disappearance of the spinal anæsthesia is shown in Fig. 5 B.

Application of 5 p.c. cocaine hydrochloride to the mucous membrane of the large bowel causes contraction of the gut for some time and abolishes all response to stimulation.

(2) *The response of the anal canal to stimulation of the large bowel.*

Movement of the balloon within the large bowel causes relaxation of the anal canal. This occurs in anæsthetized cats (Fig. 4 B), in decerebrate cats (Fig. 3 A(1)), in decapitate cats (Fig. 3 C) and in cats after transection of the cord in the lower thoracic region (Fig. 3 B(1)). Dilatation of the anal canal occurs after division of the pudendal nerves (Fig. 3 A, B). Section of the lumbar outflow facilitates the response (Fig. 3 C). Full curarization does not affect the response (Fig. 3 B(3)).

After induction of spinal anæsthesia (Fig. 3 B(7)) and after section of the pelvic nerves (Fig. 3 A(3)) stimulation of the large bowel is without effect on the anal canal. Application of 5 p.c. cocaine hydrochloride to the mucous membrane of the large bowel abolishes this response.

Two cats, both decerebrate, gave responses out of keeping with the above description. In both apparently complete section of all outflows to the large bowel, combined with spinal anæsthesia, did not abolish dilatation of the anal canal on stimulation of the large bowel craniad to the anal canal.

(3) *The response of the anal canal to stimulation of the anal canal.*

A to-and-fro or rotary movement of the balloon within the anal canal causes relaxation of the anal canal. Such stimulation of the anal canal in uncurarized cats, in marked contrast to stimulation of the large bowel, is usually accompanied by active participation of the somatic muscles in the response. If anything, a to-and-fro movement is more potent than a rotary movement.

The somatic response to the attempt to penetrate the anal canal is contraction of the external anal sphincter and defensive lowering of the tail, but, whenever the canal is entered, somatic expulsive efforts set in.

In lightly anæsthetized preparations the somatic expulsive response consists of elevation of the tail, of contraction of the abdominal muscles, of stretching and then straddling of the hind limbs. Finally, on cessation

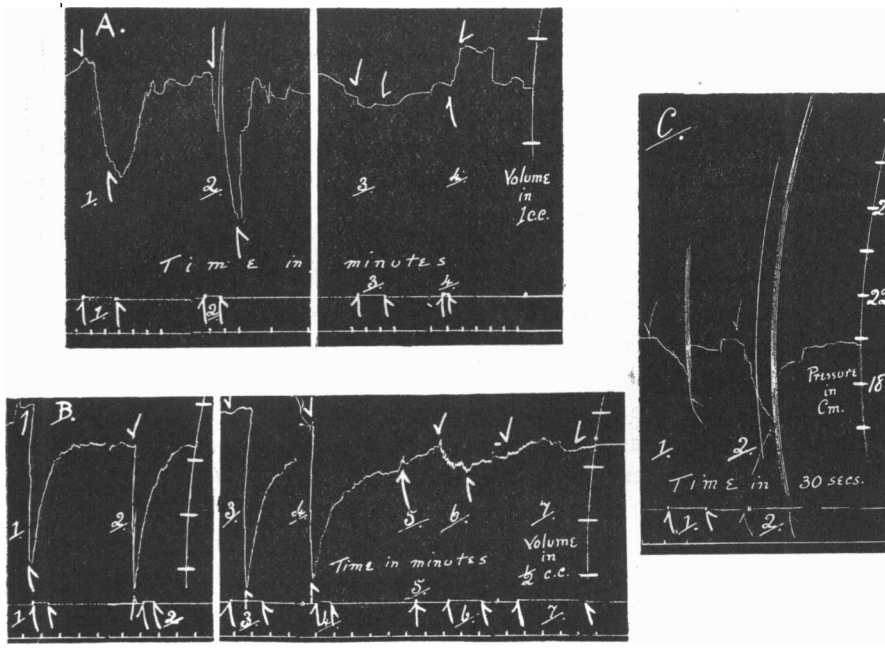

Fig. 3.

A. Cat: decerebrate; lumbar outflow cut; pudendal nerves cut; volume record from anal canal at constant pressure of 21 cm. H_2O. (1) Balloon within large bowel rotated. (2) Balloon within anal canal rotated. (3) Pelvic nerves cut. Balloon within large bowel rotated. (4) Pelvic nerves cut. Balloon within anal canal rotated.

B. Cat: decerebrate; pudendal nerves cut; lumbar outflow cut; lumbo-sacral cord isolated; volume record from anal canal at constant pressure of 21 cm. H_2O. (1) Balloon moved to and fro within large bowel. (2) Balloon rotated within anal canal. (3) Full curarization induced. Balloon moved to and fro within large bowel. (4) Balloon rotated within anal canal. (5) Spinal anæsthesia induced. (6) Balloon rotated within anal canal. (7) Balloon moved to and fro within large bowel.

C. Cat: decapitate; pressure record from anal canal at constant volume. (1) Balloon within large bowel rotated. (2) Lumbar outflow cut. Balloon within large bowel rotated.

of the stimulus, twitching in the external anal sphincter and in the pelvocaudal muscles sets in. In decapitate preparations the somatic response is less marked and less purposeful, but twitching in the external

anal sphincter is most obvious. Indeed, as Ott [1879] showed, rhythmical twitching in the external anal sphincter is a striking phenomenon in cats with transection of the spinal cord.

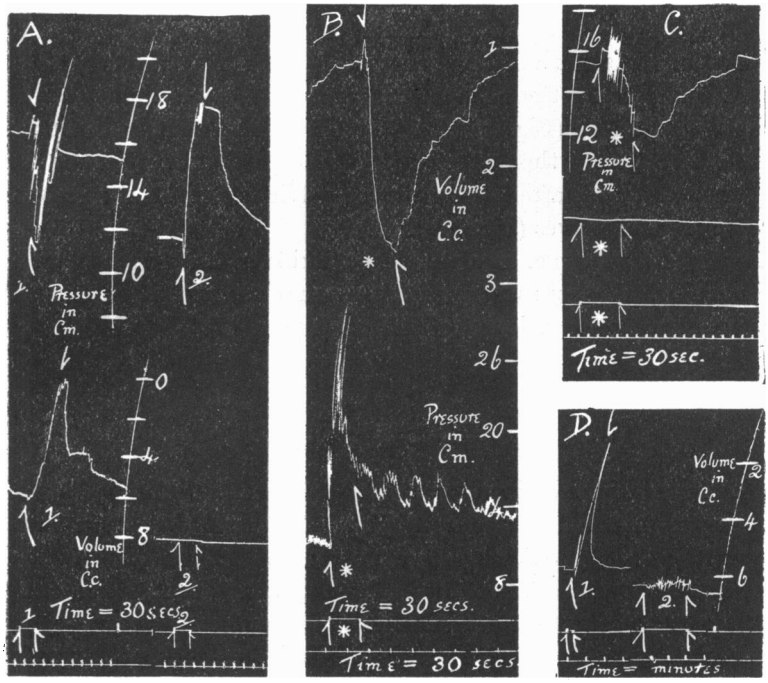

Fig. 4.

A. Cat: anæsthesia Dial Liq. Compound—"Ciba"—0·5 c.c./kg.; upper pressure record from anal canal at constant volume; lower volume record from large bowel at constant pressure of 18 cm. H_2O. (1) Balloon in anal canal rotated. (2) 5 p.c. cocaine HCl applied to mucous membrane of anal canal. Balloon in anal canal rotated.

B. Cat: Na amytal anæsthesia—50 mg./kg.—upper volume record from anal canal at constant pressure of 33 cm. H_2O; lower pressure record from large bowel at constant volume. * = Balloon in large bowel rotated.

C. Cat: decerebrate; pelvic nerves cut; upper pressure record from anal canal at constant volume; lower volume record from large bowel at constant pressure of 20 cm. H_2O. * = Balloon within anal canal rotated.

D. Cat: decerebrate; volume record from large bowel at constant pressure of 21 cm. H_2O. (1) Rotation of balloon within large bowel. (2) Pelvic nerves cut. Rotation of balloon within large bowel.

When the cord is cut in the lower thoracic region, the somatic response consists of flexion of the caudal limbs onto the abdomen and of contraction of the abdominal muscles. The tail is not elevated.

The essential local dilatation of the anal canal may be obtained in anæsthetized cats, in decerebrate cats, in decapitate cats and in cats with isolated lumbo-sacral cord (Fig. 3 A(2), B(2); Fig. 4 A(1)).

The response is independent of the integrity of the pudendal nerves (Fig. 3 A, B), is enhanced by division of the lumbar outflow and full curarization does not affect the response (Fig. 3 B(4)).

After division of the pelvic nerves (Fig. 3 A(4)), and after induction of spinal anæsthesia (Fig. 3 B(6)), stimulation of the anal canal does not lead to dilatation of the anal canal. Infrequently dilatation of the anal canal was obtained, after section of the pelvic nerves, in the presence of intact pudendal nerves (Fig. 4 C).

Application of 5 p.c. cocaine hydrochloride to the mucous membrane of the anal canal causes sustained dilatation of the canal, and stimulation may now lead to constriction of the canal (Fig. 4 A(2)).

(4) *The response of the large bowel to stimulation of the anal canal.*

Movement of the balloon in the anal canal leads to contraction of the large bowel in anæsthetized cats (Fig. 4 A(1)), in decerebrate and in decapitate cats (Fig. 5 A) and in cats after transection of the cord in the lower thoracic region (Fig. 2 C(1)). Shortly after decapitation, and less often after decerebration, stimulation of the anal canal frequently leads to relaxation of the large bowel (Fig. 5 D). Very vigorous stimulation may superimpose contraction on this initial relaxation. Such a relaxation response invariably gives place, later in the experiment, to contraction, while division of the lumbar outflow immediately converts the relaxation into contraction. Such relaxation has not been obtained in the presence of an intact lumbar outflow after division of the pelvic nerves, but in one cat, with both outflows intact, stimulation of the anal canal, after induction of spinal anæsthesia, led to relaxation of the large bowel.

The usual motor response is not affected by division of the pudendal nerves (Fig. 2), is facilitated and augmented by section of the lumbar outflow (Fig. 5 A(1, 2)) and occurs during full curarization (Fig. 2 D(1)).

After induction of spinal anæsthesia (Fig. 2 E(2)), and after cutting the pelvic nerves (Fig. 5 A(4)) stimulation of the anal canal is without effect on the large bowel.

If the pelvic nerves are cut and the pudendal nerves are intact, movement of the balloon within the anal canal may cause undoubted hardening of the abdominal muscles and some attempt at adoption of a defæcation

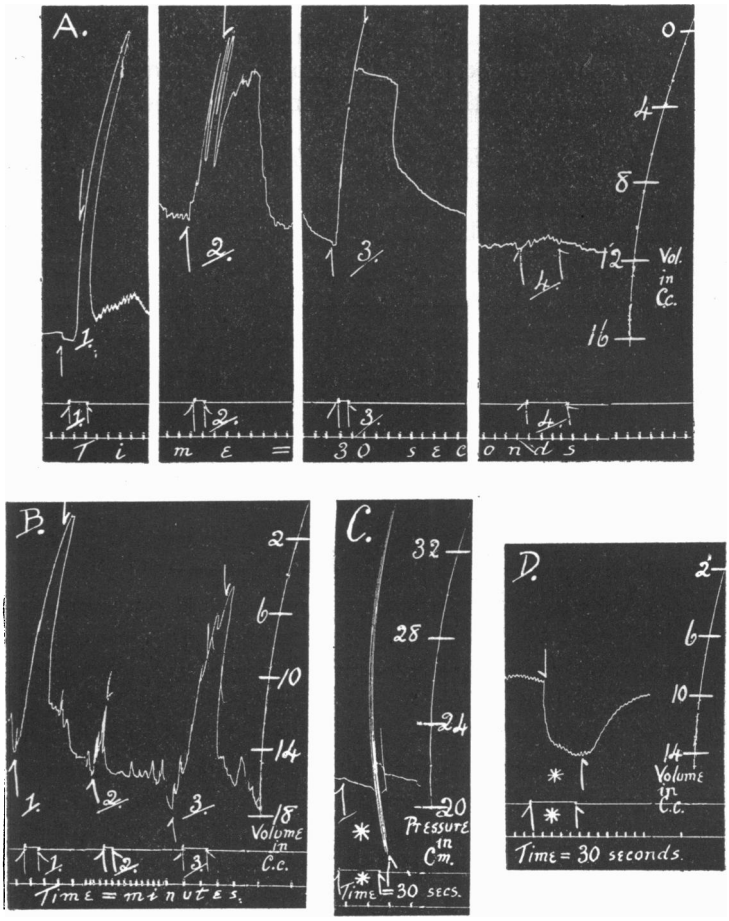

Fig. 5.

A. Cat: decerebrate; volume record from large bowel at constant pressure of 20 cm. H_2O. (1) Balloon within anal canal moved to and fro. (2) Lumbar outflow cut. Stimulus applied as before. (3) Pelvic nerves exposed. Stimulus applied as before. (4) Pelvic nerves cut. Stimulus applied as before.

B. Cat: decerebrate; lumbar outflow cut; lumbo-sacral cord isolated; volume record from large bowel *via* colostomy at constant pressure of 21 cm. H_2O. (1) Balloon in large bowel moved to and fro. (2) Spinal anæsthesia induced. Stimulus applied as before. (3) 90 min. later. Stimulus applied as before.

C. Cat: decapitate; lumbar outflow cut; anal canal deprived of visceral innervation by gut section; pressure record at constant volume from anal canal. * = Balloon within cranial segment of gut rotated.

D. Cat: decerebrate; volume record from large bowel at constant pressure of 23 cm. H_2O. * = 60 min. after decerebration balloon within anal canal rotated.

posture. Such responses have never been vigorous and have had no marked influence on the balloon in the large bowel.

Application of 5 p.c. cocaine hydrochloride to the mucous membrane of the anal canal abolishes the response from the large bowel (Fig. 4 A (2)).

The effect of division of the large bowel on the responses.

Unfortunately it is not possible to cut the large bowel and to leave intact the innervation to both the cranial and caudal segments of the gut produced by the division. It is possible, however, so to cut the large bowel that the cranial segment retains the lumbar and sacral visceral outflows, while the caudal segment, deprived of its visceral innervation, yet retains the somatic nerve supply by the pudendal nerves to the external anal sphincter and to the circumanal region. To do this the gut must be cut just caudad to the peritoneal reflection, with the result that the caudal segment, including the anal canal, is very short.

Such division of the large bowel, which necessitates splitting the symphysis pubis, may be carried out by section between ligatures, in which case the balloon for the cranial segment must be introduced through a colostomy, or the bowel may be tied on to a short length of flanged glass tubing of bore sufficiently wide to allow free movement for the holder of the balloon in the cranial segment. The latter method is simpler, preserves the integrity of the peritoneal cavity, and the continuity of the muscular tissues of the gut wall and of the visceral nerves running on the surface of the gut is effectively interrupted by the ligature. Two experiments were carried out by the former, four by the latter method.

After such division the response of the large bowel to stimulation of the large bowel was unaffected. Stimulation of the large bowel craniad to the point of section, on the other hand, no longer produced unequivocal dilatation of the anal canal, although, so long as the pudendal nerves were intact, such stimulation still led to post-stimulation twitching in the external anal sphincter (Fig. 5 C).

Even when the pudendal nerves were intact, stimulation of the anal canal led in no case to relaxation of the anal sphincters, and in only two of the six cats did contraction of the large bowel result. So long as the pudendal nerves were intact stimulation of the anal canal led to some response from the abdominal muscles.

In two cats the colon was divided between ligatures just caudad to the inferior mesenteric artery. In these cases the cranial segment of the large bowel received only the lumbar outflow by the lumbar colonic

nerves, while the caudal segment received the sacral outflow and the hypogastric nerves. The recording balloon for the cranial segment was passed into the gut through a colostomy close to the ileo-cæcal sphincter. The caudal segment responded to stimulation in normal fashion, but no effect was transmitted to the cranial segment. Stimulation of the cranial segment produced no response locally and was without influence on the caudal segment.

Discussion and conclusions.

The nature of the stimulus for defæcation.

Even if it be conceded, in spite of Lehmann's work [1913], that the afferent impulses eliciting defæcation arise locally in the caudal part of the gut, there are difficulties in accepting the method employed in the present series of experiments as representative of a normal mode of eliciting defæcation.

Zimmermann [1909], experimenting on himself, found that the rectal mucous membrane 10 to 12 cm. craniad to the anus is insensitive to touch, to moderate variation in temperature and to electrical stimulation. Nevertheless, when the rod used to test for tactile sensation caught on a fold of mucous membrane, an unpleasant dragging sensation was produced. As the anal canal was approached, temperature sensation appeared and stimulation with an electrical current was felt. Distension of the rectum by means of a balloon at a pressure of 20 mm. Hg produced a desire to defæcate. Variations of 2 to 3 mm. Hg pressure could be detected.

Hertz [1911] also found that the rectal mucous membrane in man is insensitive to tactile, to painful and to thermal stimuli, while the mucous membrane of the anal canal is sensitive to thermal stimuli and to friction. Distension of the rectum gives rise to the sensation of fullness associated with the desire to defæcate. The closer to the anal canal, the greater the length of the distending balloon and the more rapid the distension, the less the pressure necessary to evoke the sensation.

Distension of the large bowel is supposed to act upon sense organs in the muscles of the gut wall. The inadequacy of distension as a stimulus in the present series of experiments is striking. This may be due to the acuteness of the experiments and consequent shock to the nervous system. Under such conditions a gross stimulus such as movement within the gut, with inevitable dragging on the wall of the viscus, may be necessary to reach the threshold for the reflex.

Nevertheless, there is some evidence that sensitive tissues are placed nearer the lumen of the gut than the muscle coats. The disappearance of all response on cocainizing the mucous membrane is suggestive. The cocaine, of course, may penetrate and affect sensory endings deep to the mucous membrane. Again the rectal tenesmus which occurs in severe diarrhœa, when there is practically no material in the gut apart from a small quantity of thin ichorous fluid, is difficult to explain if distension is the sole stimulus.

While distension is an adequate stimulus for peristalsis in the small intestine [Trendelenburg, 1917], it is doubtful if this applies in the same degree to the large intestine [Alvarez, 1929]. Cannon [1912] also comes to the conclusion that the cause of true peristalsis in the caudal region of the large bowel must be sought for in a stimulus other than pure distension, and he suggests that movement of firm fæcal masses may supply this stimulus.

It may be, then, that the mucous membrane of the large bowel, although insensitive to localized contact, is yet sensitive to gross movement such as that produced by the passage of firm fæcal masses into the caudal region of the gut. Such a conception would explain most effectively the transitory nature of the "call to defæcation" in man.

There is less difficulty in accepting movement within the anal canal as a normal stimulus. Such a conception is in keeping with the experimental work on man. In addition, Barrington [1921] used movement of a catheter or of fluid within the urethra to elicit micturition responses in the cat. Such susceptibility of the mucous membrane of the anal canal to a frictional stimulus, however, is obviously designed to maintain a defæcation effort already in progress rather than to initiate such an effort.

The response of the large bowel to stimulation of the large bowel.

This response is largely dependent on the lumbo-sacral region of the cord. Nevertheless, the gut seems to retain some degree of autonomy; possibly in preparations surviving destruction of the lumbo-sacral cord this autonomous power is enhanced, or, probably more correctly, regains much of its primitive independence.

The lumbar outflow is inhibitory and both afferent and efferent pathways are in the pelvic nerves.

The response of the urinary bladder to distension likewise depends on the integrity of the pelvic nerves, but this response, far from showing indications of autonomy, depends on a micturition centre in the mid-brain [Barrington, 1928]. However, the presence of a centre for the

large bowel in the lumbo-sacral cord is in keeping with the results of Head and Riddoch [1917] and of Riddoch [1917] in spinal man. In such patients the evacuation of the gut, and also of the bladder, seems to be complete.

The response of the anal canal to stimulation of the large bowel.

This response is also largely dependent on the integrity of the pelvic nerves and of the lumbo-sacral cord, and the lumbar outflow exerts an inhibitory influence.

It is difficult to determine the part played by the pudendal nerves and by the striped anal sphincter. Dilatation of the anal canal occurs in all cases after division of the pudendal nerves, while indication of participation of the pudendal nerves in the response is shown by the post-stimulation anal twitching which is present on stimulation of the large bowel after gut section. Unfortunately, to eliminate participation of the internal anal sphincter without gut section necessitates division of the pelvic nerves and destruction of the afferent pathway for the response; failure to show relaxation of the external sphincter after gut section may be due to difficulties of recording in such cases. Ott [1879], however, has shown that inhibitory impulses reach the external anal sphincter from a centre in the brain, so that it is possible that normal relaxation of the external anal sphincter in defæcation can occur only in intact animals. Nevertheless, Barrington [1921, 1928] finds that dilatation of the urethra, as a result of distension of the bladder, depends on a centre in the lumbo-sacral cord, the afferent pathway being in the pelvic nerves and the efferent pathway in the pudendal nerves.

The response of the anal canal to stimulation of the anal canal.

This response also, so far as the internal anal sphincter is concerned, is dependent on the lumbo-sacral cord alone and on the integrity of the pelvic nerves. The lumbar outflow again tends to inhibit the response.

The dilatation obtained after section of the pelvic nerves in decerebrate cats is not a constant response. Probably the relaxation of the external anal sphincter under such conditions is part of a general somatic response which certainly can be elicited, although imperfectly, by stimulation of the anal canal after division of the pelvic nerves. Barrington [1921] finds that the reflex relaxation of the urethra, which occurs on passage of fluid through the urethra, is controlled by a centre in the lumbo-sacral cord, and has both afferent and efferent channels in the pudendal nerves.

The constriction of the anal canal produced by stimulation after cocainizing the mucous membrane may be the normal contraction response of the circumanal tissues during an attempt to penetrate the anal canal. Such contraction is probably due to stimulation of subcutaneous receptors protected from the cocaine, while the submucous receptors, stimulation of which produces relaxation of the anal canal, are anæsthetized.

The response of the large bowel to stimulation of the anal canal.

The efferent pathway for this response is in the pelvic nerves. After division of the pudendal nerves the response persists so that the pelvic nerves also serve as an afferent path. Probably, however, the pudendal nerves, too, transmit centripetal impulses capable of eliciting contraction of the large bowel, just as afferent impulses from the urethra along the pudendal nerves elicit contraction of the bladder [Barrington, 1921]. The centre controlling this second micturition reflex is situated in the mid-brain, while the centre for the corresponding gut response is in the lumbo-sacral cord. This finding for the gut is in keeping with the results of most workers who find apparently normal defæcation in spinal mammals [Sherrington, 1900].

The influence of the lumbar outflow is once more inhibitory.

Barrington [1921] has shown that stimulation of the urethra causes contraction of the urinary bladder through a reflex arc passing by the hypogastric nerves and a centre in the lumbo-sacral cord. A corresponding response does not appear in the gut. Probably this is due to the fact that part of the bladder musculature in the cat receives a motor nerve supply from the lumbar outflow [Elliott, 1906]. This state of affairs, so far as is known, does not hold in the case of the large bowel.

The nervous connections for the relaxation of the large bowel which frequently occurs on stimulation of the anal canal shortly after decapitation and less frequently after decerebration are obscure. Possibly this is the usual response to noxious stimuli unmasked by temporary depression of the more sensitive expulsive responses. On the other hand the response may be of the nature of a Sokownin reflex through the inferior mesenteric ganglia.

The responses in general.

At the caudal end of the alimentary tract the central nervous system no longer exerts merely a general diffuse influence on the gut, but takes an active part in reception of stimuli from and in emission of impulses

to the gut. This more intimate relationship of the spinal cord to the gut seems to be confined to the sacral outflow, the lumbar outflow exerting the usual "sympathetic" restraining influence on the translation of bowel contents. However, the gut seems not to have wholly surrendered its independence because stimulation of the large bowel is still able, after destruction of the lumbo-sacral cord, to cause contraction of the large bowel and dilatation of the anal canal. In this way it is possible to explain the findings of Gowers [1877] in the patient with injury to the sacral roots, of Goltz and Ewald [1896] in their cordless dogs, of Bayliss and Starling [1900], of Elliott and Barclay-Smith [1904] and of Barrington [1915].

The pathways in the pudendal nerves seem to be much less important in the defæcation responses than in the micturition reflexes. Probably the pudendal nerves do play a part in defæcation, but the difficulties in the way of satisfactory demonstration of this fact are great. On the other hand, it is possible that Barrington's technique recorded mainly the responses of the external sphincter urethræ innervated by the pudendal nerves, so that the full rôle of the pelvic nerves in micturition escaped notice.

The somatic defæcation responses, which are most elaborate, seem to depend on centres craniad to the lumbo-sacral cord, and probably for their full expression, craniad to the spinal cord itself.

Summary.

The behaviour of the caudal end of the gut is recorded by two tandem balloons usually inserted through the anus. Movement of the balloons themselves within the large bowel or within the anal canal elicits co-ordinated expulsive efforts from the gut and from the somatic musculature. Simple distension of the balloons within the gut or within the anal canal is not an adequate stimulus in acute experiments. The responses persist after complete curarization of the somatic musculature, and application of cocaine to the mucous membrane of the large bowel and of the anal canal abolishes all response.

The visceral responses persist after transection of the spinal cord in the lower thoracic region and depend mainly on the integrity of the pelvic nerves. The lumbar outflow exerts an inhibitory influence on all the responses.

Four main responses are present: (1) Stimulation of the caudal end of the large bowel causes contraction of the large bowel: (2) Relaxation of the anal canal. Both these responses may appear infrequently after

complete decentralization of the gut. (3) Stimulation of the anal canal causes dilatation of the anal canal. This dilatation is due mainly to relaxation of the internal anal sphincter. When the pudendal nerves are intact, it is probable that the external anal sphincter participates in the response. (4) Stimulation of the anal canal causes contraction of the large bowel. The main afferent pathway is in the pelvic nerves, but the pudendal nerves probably also convey centripetal impulses for this response.

Shortly after interference with the cerebro-spinal axis, stimulation of the anal canal causes relaxation of the large bowel. The pathways for this response are obscure. The findings are discussed and compared with the corresponding responses of the urinary tract.

I am deeply indebted to Prof. Cathcart for constant encouragement.

The initial cost of the animals was defrayed by a grant from the Carnegie Trust for the Universities of Scotland, and the cost of feeding the animals was borne by the D. C. Andrew fund of the Institute of Physiology, Glasgow University.

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