

CONTROL OF THE EXTERNAL SPHINCTER OF THE ANUS IN THE CAT

BY BEVERLY BISHOP, R. C. GARRY, T. D. M. ROBERTS
AND J. K. TODD

From the Institute of Physiology, Glasgow University

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There is of necessity co-ordination between the activity of the caudal region of the large gut and the behaviour of the sphincters which control the anal canal. There are, however, two sphincters. The internal anal sphincter of smooth muscle receives its motor supply through the hypogastric nerves from the sympathetic outflow and its inhibitory supply through the pelvic nerves from the parasympathetic outflow. The external anal sphincter of striped muscle is controlled by the somatic pudendal nerves. In this case relaxation can only be due to a reduction in frequency of existing motor impulses in the pudendal nerves. Since the two sphincters are superimposed, one upon the other, it is difficult to disentangle the roles played by these two in the control of the anal canal. Garry (1933*a*, 1934) gives diagrams of the anatomical arrangement, with the nerve supply, both in the cat and in man. Floyd & Walls (1953) have an accurate drawing of the actual relationships in man. The nerve supply to the distal portion of the colon and to the anal sphincters of the cat is shown schematically in Fig. 1 of this paper.

Garry (1933*b*) was able to show by mechanical recording in the cat that movement of an object within the distal colon, when the pelvic and pudendal nerves were both intact, led to dilatation of the anal canal. Such dilatation could still be evoked after section of both pudendal nerves had paralysed the external anal sphincter. Thus stimulation of the colon must lead to inhibition of the internal anal sphincter by impulses travelling in the pelvic nerves. But there was no actual proof for inhibition of the external anal sphincter when the colon was stimulated. Such inhibition had to be assumed, otherwise dilatation of the anal canal could not have taken place when the pudendal nerves were intact. This belief that the two sphincters relaxed simultaneously was further supported by the observations of Barrington (1921, 1931) on the reciprocal behaviour of the detrusor muscle of the urinary bladder and the striped

external sphincter of the urethra. A comparison of the behaviour of the colon and its sphincters with that of the urinary bladder and its sphincters is justified by the similarity in origin and in innervation. In the case of the urethra the smooth internal sphincter and the striped external sphincter are separated by some little distance so that their individual behaviour can be separately recorded by mechanical means. Distension of the urinary bladder brings about relaxation of the external urethral sphincter; the paths are in the pelvic nerves from the bladder and in the pudendal nerves to the sphincter. There is a 'centre' in the lumbo-sacral cord since the response can still be obtained after transection of the spinal cord in the lower thoracic region. This is Barrington's fifth micturition reflex.

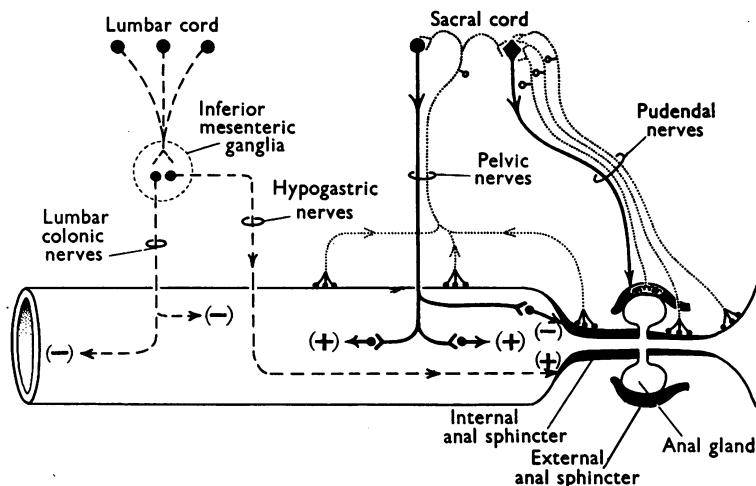


Fig. 1. A schematic representation of the innervation of the distal colon and anal canal in the cat. The lumbar sympathetic outflow inhibits the colon and is motor to the internal anal sphincter. The sacral parasympathetic outflow in the pelvic nerves is motor to the colon and inhibits the internal anal sphincter: ingoing fibres from the tissues surrounding the anal canal and from the wall of the colon run in the pelvic nerves. The pudendal nerves innervate the external anal sphincter: ingoing fibres from the circumanal skin, from the tissues surrounding the anal canal and from spindles in the external anal sphincter run in the pudendal nerves.

By electromyography it ought now to be possible to record the behaviour of the external anal sphincter without interference from the internal anal sphincter. Beck (1930) did do so; he used a string galvanometer and inserted steel needles through the circumanal skin of dogs, and in one case of man, into the external sphincter. He recorded action potentials from the muscle on dilating the anal canal. Floyd & Walls (1953) studied the behaviour of the external sphincter in normal men by placing surface electrodes on each side of the anus: recording was by an ink-writing oscillograph. During waking hours the external sphincter showed continuous tonic activity. This was augmented

by stimulation of the circumanal skin, by distension of the anal canal, by increase in intra-abdominal pressure; attempts at defaecation inhibited the tone. Kawakami (1954) obtained similar results, also in men, by inserting electrodes through the skin into the muscle. A single motor unit could maintain activity for 10 min or longer.

The present paper deals with some factors reflexly controlling the external sphincter in the cat and the nerve paths involved in this control.

METHODS

The observations were made on decerebrate cats. The external anal sphincter was exposed by a dorso-ventral skin incision, 3-4 cm long and about $1\frac{1}{2}$ cm from the anus on one side. The sphincter, which spreads over the anal gland like a fan, is thereafter best exposed by blunt dissection. Such an exposure gives a convenient pocket to hold a pool of warm liquid paraffin. Spinal anaesthesia of the lumbo-sacral cord, section of the lumbar sympathetic outflow to the gut and division of the pelvic nerves were carried out in the manner previously described (Garry, 1933*a*). The spinal cord was divided under full ether anaesthesia by tying a ligature extradurally round the cord after opening the vertebral canal. Colostomies were made in conventional fashion just caudal to the caecum.

Two very fine unenamelled stainless steel needles, about 3 mm apart, served as electrodes. The tips just penetrated the surface of the external sphincter and were held in position by a light spring. Such electrodes usually picked up the activity of several motor units simultaneously. The potentials were amplified, and displayed on an oscilloscope and recorded by an ink-writing oscillograph.

Balloons were made by tying a condom over a perforated length of a narrow metal tube. Such balloons could be inserted into the colon through the anus or through a colostomy. The balloons were inflated by a bellows: the pressures within the balloon were displayed on a mercury manometer and, by means of a transducer valve, recorded by one of the pens of the ink-writing oscillograph. Soap solution was used to lubricate the balloons. In order to enhance slightly the tonic activity of the external sphincter and to avoid stimulating the circumanal skin and the mucosa of the anal canal during manipulations of the balloon, a narrow brass tube was often placed in the anal canal. The metal holder for the balloon moved freely within the brass tube so that the position of the balloon within the colon could be altered at will.

RESULTS

The 'tone' of the external sphincter

Experiments were made on thirty cats, and, with one exception where the anal glands were pathologically distended and the external sphincter barely visible, a steady tonic discharge could always be obtained from the exposed striped sphincter. This tone showed no signs of waning with time. The steady tonic activity was increased by slight distension of the anal canal. Sharp bursts of activity, visible to the naked eye as twitches, were induced by stroking or pricking the circumanal skin. This is known as the anal reflex in man. Attempts to insert an instrument into the anal canal from without caused strong contraction of the external sphincter, the guarding reflex. Pressure on the abdominal wall also enhanced tonic activity.

Spinal anaesthesia of the lumbo-sacral cord destroyed all tonic activity in

the external sphincter. So did general anaesthesia with ether and full anaesthetic doses of the barbiturates. Section of the pudendal nerves abolished tone in the external sphincter. On the other hand, application of a 5% solution of cocaine HCl to the anal canal and also to the mucous surface of the colon did not impair the tonic activity of the external sphincter.

Inhibition of the tonic discharge

The tonic discharge in the external anal sphincter could be inhibited by inflating the colon with air through a colostomy. This procedure, though free from the objections which may be raised against introducing balloons, did not lend itself to the investigation of the effects of different pressures.

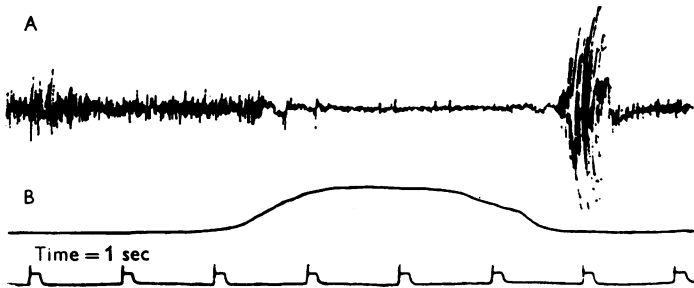


Fig. 2. A, electromyogram of external sphincter of the anus of a decerebrate cat with spinal cord ligated in upper thoracic region. B, pressure in a balloon in the distal colon: maximum pressure 50 mm Hg. Note maintained tonic discharge after spinal ligation; inhibition following distension of colon; rebound after pressure has been released.

Distension of the colon with a balloon inhibited the tonic discharge (Fig. 2). A soap solution was used to lubricate the balloons. This often seemed to augment the tonic activity in the sphincter and we had the impression that the use of soap made it easier to elicit the inhibitory reflex. A considerable interval may be seen in Fig. 2 to occur between the start of the distension and the onset of inhibition. We failed to establish a relationship between this interval and either the magnitude of the distending pressure or the rate at which the pressure developed. Not infrequently the inhibition was brought to an end by a burst of increased activity in the sphincter. This rebound activity, which is well seen in Fig. 2, was a constant feature in the response after spinal ligation.

Inhibition could always be obtained when the balloon distended the caudal region of the colon, but, in some cats inhibition was also quite marked when the cranial region of the colon was distended. The pressure required to evoke inhibition ranged from 10 to 60 mm of mercury. We were unable to satisfy ourselves that the rate at which pressure developed in the balloon had an influence on the magnitude of the pressure required to induce inhibition.

Distension of the colon, with inhibition of the external sphincter, was by no means always followed by the characteristic general viscerosomatic responses of defaecation. On several occasions complete inhibition was maintained for well over 2 min. Ultimately either activity returned to the sphincter or defaecation set in. During spontaneous defaecation the tone in the external sphincter always disappeared. Towards the end of the act the inhibition frequently alternated with phases of strong contraction of the external anal sphincter. Spontaneous micturition was accompanied by inhibition of the external anal sphincter.

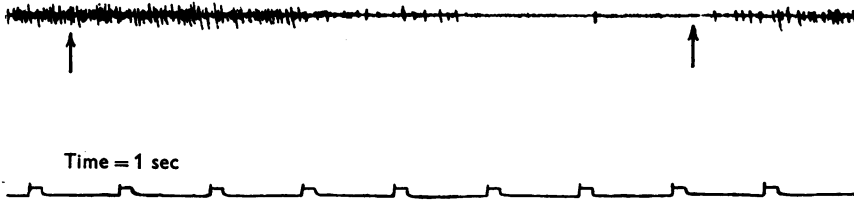


Fig. 3. Electromyogram of external anal sphincter of a decerebrate cat. Between arrows deflated balloon moved to and fro within the colon. Note inhibition of the tonic discharge.

Distension of the colon was not the only effective stimulus for eliciting inhibition. To-and-fro movement, or rotation, of the undistended balloon within the colon led to inhibition of the external sphincter (Fig. 3). Movement within the anal canal also caused inhibition of the external sphincter. Simple distension of the anal canal, on the other hand, produced an increase in the tone of the external anal sphincter. It was more difficult to show the effect of the movement, since, unless this was gentle, it was apt to displace the electrodes resting on the external sphincter.

The nervous paths

Isolation of the lumbo-sacral region of the spinal cord by ligation at or above L2 did not impair the tonic activity of the external sphincter, nor its reflex inhibition (Fig. 2). If spinal shock were present it could only have been of short duration. Ether anaesthesia was used during exposure and ligation of the spinal cord. By the time the anaesthetic had worn off, as indicated by the return of the knee jerk, distension of the colon produced inhibition of the external sphincter as before.

Injection of a 1% solution of procaine HCl intrathecally between the last lumbar and first sacral vertebrae abolished the tonic activity in the external sphincter as long as the spinal anaesthesia lasted. This confirms the view that the tonic activity is reflex in nature. When the tonic discharge was re-established it was again possible to elicit the inhibitory response by distension of the colon (Fig. 4).

Destruction of the lumbar sympathetic outflow was carried out as completely as possible by section of the spinal rami to the inferior mesenteric ganglia, by avulsion of the ganglia themselves, by stripping the periarterial nerves off the inferior mesenteric artery and by section of the hypogastric

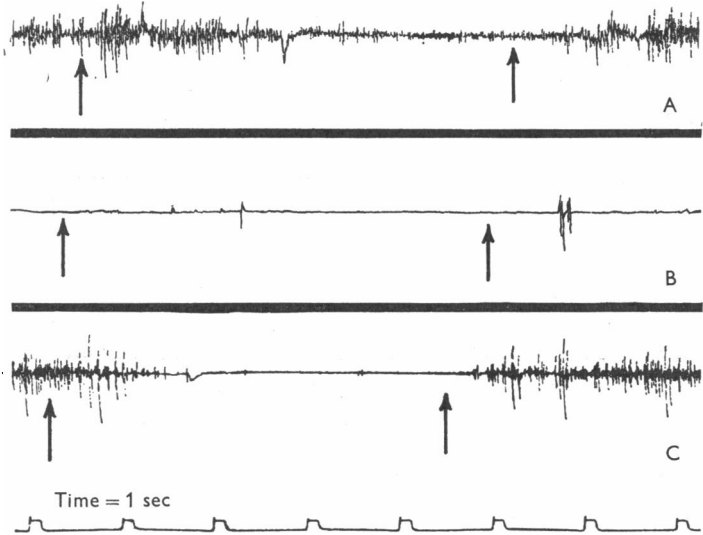


Fig. 4. Electromyograms of the external sphincter of the anus of a decerebrate cat. Between the arrows in each record the distal colon was distended with a balloon. A, before spinal anaesthesia, balloon pressure 20 mm Hg; B, during spinal anaesthesia, balloon pressure 60 mm Hg; C, after spinal anaesthesia had worn off, balloon pressure 40 mm Hg. Note that tonic activity is abolished as long as spinal anaesthesia lasted. With the return of tonic discharge the inhibitory reflex to colon distension could again be elicited.

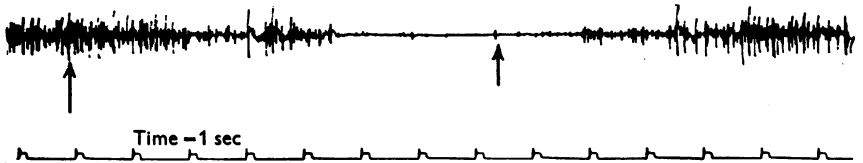


Fig. 5. Electromyogram of external anal sphincter of a decerebrate cat after division of the lumbar sympathetic outflow. Between the arrows the colon was distended with a balloon inflated to a maximum pressure of 60 mm Hg.

nerves. There was no obvious change in the tonic activity of the external sphincter; distension of the colon still produced inhibition (Fig. 5) sometimes more easily than before sympathectomy.

After division of the pelvic nerves the resting tonic activity of the external sphincter, far from being impaired, was actually enhanced. But distension of the colon no longer induced inhibition of the sphincter (Fig. 6). In one cat

in which only a small twig of one pelvic nerve remained uncut, distension of the colon still produced inhibition.

After application of a 5% solution of cocaine HCl to the mucous surface of the colon no inhibition of the external sphincter could be obtained either by distension of the colon or by movement of the balloon within the colon (Fig. 7). During the period in which the cocaine prevented the distension of the colon from eliciting inhibition it was observed that complete inhibition of the discharge in the sphincter still occurred as an accompaniment to spontaneous micturition.



Fig. 6. Electromyogram of external anal sphincter of a decerebrate cat. Between the arrows the pressure in the balloon in the distal colon was raised. A, balloon pressure 20 mm Hg; B, after division of the pelvic nerves, balloon pressure 80 mm Hg; inhibitory response no longer obtained.



Fig. 7. Electromyogram of external anal sphincter of a decerebrate cat 10 min after application of a 5% solution of cocaine HCl to the mucous membrane of the distal colon. Between the arrows the colon was distended with a balloon inflated to a maximum pressure of 100 mm Hg; the inhibitory response to colon distension is no longer elicited.

After section of the lumbar sympathetic outflow and of the pelvic nerves attempts were made to inhibit the external anal sphincter by moving an object within the anal canal. Such movement inevitably disturbed the sphincter and the electrodes mechanically. However, when a thin brass rod with serrations was rotated or moved to and fro within the anal canal slight inhibition of the external sphincter could be seen in spite of the mechanical disturbance.

DISCUSSION

The external sphincter is composed of 'red', sarcoplasm-rich, striped, muscle fibres of small diameter, 50μ as compared with 75μ in the biceps femoris in the cat. These are the histological features in skeletal muscle which are attributed to the maintenance of prolonged tonic contraction. The electromyographic findings conform to what one would expect from this type of muscle, a steady discharge was observed in the absence of deliberate stimulatory procedures. The discharge ceased on cutting the pudendal nerves. We have, however, no precise information about the genesis of this tone; it is well marked after section of both parasympathetic and sympathetic outflows to the distal portion of the gut and after isolation of the lumbo-sacral region of the cord. Identification of the source of the ingoing impulses concerned in this reflex tonic activity, if reflex in origin it be, will be difficult since many such ingoing impulses no doubt travel in the pudendal nerves which also carry the outgoing axons to the sphincter itself. No attempts have yet been made to cut the dorsal roots for technical reasons. One could object that in our series nociceptive impulses from the trauma at the skin incision and from the exposed tissues generated a tonic activity or that the soap solution used to lubricate the balloons might have sufficient stimulating effect to account for the sustained discharges which we observed. The continuous resting activity has, however, been observed repeatedly with minimal trauma and without the use of soap. Additional trauma had no sustained effect on the discharge. Furthermore, Floyd & Walls (1953), using surface electrodes, also saw this continuous tone in man without surgical interference.

There is obviously a reflex 'centre' for the external sphincter of the anus in the lumbo-sacral region of the spinal cord since the maintained tone and its modification by reflexes can be demonstrated after the spinal cord has been ligated as low as L2. Higher 'centres' and the existence of 'voluntary' control are not excluded. The persisting idea that the external sphincter is independent of the central nervous system and is controlled in some fashion or other by peripheral ganglia of the autonomic system receives no support from our findings.

Both distension of the colon and movement within the colon elicited inhibition of the external sphincter. Garry (1933*b*) rather doubted the effectiveness of simple distension as the prime stimulus for the reflexes of defaecation. He used a water manometer and did not employ adequate pressure. The pressures in the present series, 10–60 mm mercury, are probably not excessive since Goligher & Hughes (1951) and Nathan & Smith (1953) had to use pressures ranging from 40 to 150 mm of mercury in the rectum in man to evoke the desire to defaecate. It is commonly said that this desire in man is fugitive. In our cats the inhibition could be maintained continuously for well over 2 min

at the end of which either the discharge recommenced or defaecation movements set in. Movement within the anal canal was also an effective stimulus for inhibition of the external sphincter as one would expect from the previous observations of Garry (1933*b*) and of Barrington (1921) on micturition. It should be noted that simple distension of the anal canal, as opposed to movement over the mucosa, elicited an increase in the tonic activity of the sphincter.

Inhibition of the external sphincter was always obtained by distension of the caudal region of the colon. Frequently, however, such inhibition could be obtained by distension of the colon as far cranial as the caecum. In man, according to Goligher & Hughes (1951), the desire to defaecate is aroused when distension takes place in the caudal portion alone of the colon, whereas distension of the cranial regions causes colic. It may be that the whole of the colon of the cat, a carnivorous creature, corresponds functionally to the more caudal portions of the large intestine in man.

Since distension of the colon failed to evoke inhibition of the external sphincter when the pelvic nerves were cut and the sympathetic supply was intact, the ingoing fibres for this inhibitory reflex must lie in the pelvic nerves. This inhibitory reflex is the one whose existence Garry (1933*b*) suspected but was unable to establish with the purely mechanical techniques then at his disposal. This viscerosomatic reflex corresponds to Barrington's fifth micturition reflex: 'a spinal reflex evoked by distending the bladder, effecting a relaxation of the urethra and having its afferent path in the pelvic and its efferent in the pudic (pudendal) nerves'.

Section of the pelvic nerves invariably augmented the resting tonic activity of the external sphincter. This suggests that, even when the colon is not distended, there are ingoing impulses in the pelvic nerves exerting a continual inhibitory influence on the local spinal 'centre' responsible for tone in the external sphincter.

On the other hand, when the pelvic nerves were intact, section of the lumbar sympathetic outflow frequently allowed the inhibitory reflex to be elicited with greater ease. The following three possible mechanisms have been considered in relation to this effect. There may be sympathetic afferents which have a facilitatory effect on the motor discharge to the sphincter, so that when the colon is distended with both autonomic nerves intact the pelvic and sympathetic act in opposition, with the pelvic effect predominating. If this were true, distension of the colon with the pelvic nerves cut should produce an augmentation of the tone in the external sphincter. This did not occur (Fig. 6). Alternatively, the sympathetic supply may effect the stimulus-response relationship of those sense organs whose afferents, running in the pelvic nerves, are responsible for the inhibitory reflex. No information is available on this point.

Again, the augmented activity of the gut, due to removal of sympathetic

inhibitory impulses, may make it easier for the mechanical deformations to stimulate the sensory endings of the pelvic afferents. In the light of our present ignorance this is regarded as the likeliest explanation.

The tone of the external sphincter is inhibited by movement within the anal canal both before and after the pelvic nerves have been cut. This suggests that ingoing impulses in the pudendal nerves may reflexly decrease the number of impulses passing out in the pudendal nerves to the external sphincter. Garry (1933*b*) was satisfied that such a reflex exists, although he could not demonstrate it on every occasion. Barrington (1921) describes a corresponding fourth micturition reflex in which the flow of urine along the urethra caused inhibition of the external urethral sphincter after section of the pelvic nerves. Garry (1933*b*) showed that movement within the anal canal brought about relaxation of the internal anal sphincter after section of the pudendal nerves. Therefore some centripetal impulses must run from the anal canal in the pelvic nerves. In the intact cat, then, movement within the anal canal probably evokes centripetal impulses in both the pelvic and the pudendal nerves. We have not studied the pathways involved in that inhibition of anal sphincter discharge which accompanies spontaneous micturition.

There is possibly something to be said for numbering the individual component reflexes of defaecation in a manner similar to that used by Barrington for the reflexes of micturition. Such numbering, however, is apt to obscure the normal co-ordinated sequence of events. Probably a truer physiological picture is given by a description which recognizes just two stages. In stage one, distension of the colon and movement within the colon send impulses along the pelvic nerves to the lumbo-sacral region of the spinal cord which acts as a 'centre'. Then motor impulses to the colon and inhibitory impulses to the internal anal sphincter pass out by the pelvic nerves. The external sphincter relaxes, owing to inhibition of its motor centre. In stage two, movement occurs within the anal canal. During this stage, the ingoing impulses run in the pelvic and in the pudendal nerves. The 'centre' is again in the lumbo-sacral cord. Outgoing motor impulses pass, by the pelvic nerves, to the colon to maintain contraction. Continuing inhibitory impulses in the pelvic nerves maintain the relaxation of the internal anal sphincter and the relaxation of the external sphincter persists since the impulses in the pudendal nerves are still in abeyance. At the close of this second stage the inhibition of the external sphincter is interrupted at intervals by phases of strong contraction.

There is little that can be said about the nature, the detailed location and the characteristics of the receptors concerned in defaecation. Receptors essential for faecal continence in conscious human beings may lie in the mucous membrane or in the muscular wall of the rectum (Gaston, 1948*a*, Goligher, 1951; Goligher & Hughes, 1951). But these are not necessarily the receptors concerned in the reflexes of defaecation. Histology alone is of little

assistance in sorting out the physiological functions of the various receptors. Nerve endings have been found in the mucosa and in the muscular wall of the rectum of human foetuses and of the distal colon of kittens (Sotelo, 1954-55), but the functional significance of these remains to be elucidated.

We now know however that the receptors for the inhibitory reflex lie not far from the colonic mucosa and send their afferents in the pelvic nerves, since this inhibitory reflex disappears shortly after the application of cocaine to the mucosa and is absent if the pelvic nerves are cut.

SUMMARY

1. Electromyographic records were made of the activity of the exposed external sphincter of the anus in decerebrate cats.

2. The external sphincter shows tonic activity which persists after transection of the spinal cord in the lower thoracic region, after section of the sympathetic outflow to the colon, after division of the pelvic nerves or after local anaesthetization of the colonic mucosa.

3. The tonic activity of the external sphincter is augmented by tactile stimuli to the circumanal region, by simple distension of the anal canal, by pressure on the abdomen or by division of the pelvic nerves. The activity ceases when the pudendal nerves are cut, during spinal anaesthesia of the lumbo-sacral region of the cord and during general anaesthesia.

4. The tonic activity of the external sphincter is inhibited by distension of the colon, by movement within the colon and by movement within the anal canal. Inhibition was also frequently observed to accompany spontaneous micturition.

5. These inhibitory responses persist after transection of the spinal cord in the lower thoracic region. The inhibition produced by distension after spinal section is followed by a short 'rebound' phase of enhanced activity.

6. The inhibition of the external sphincter in response to distension of the colon is destroyed by section of the pelvic nerves or by anaesthetization of the mucous membrane of the colon: so that some of the receptors for this inhibitory reflex must lie not far from the colonic mucosa and must send their afferents in the pelvic nerves.

7. The inhibition of the external sphincter produced by movement within the anal canal persists even after division of the pelvic nerves: presumably, then, the ingoing and outgoing paths in this case are both in the pudendal nerves.

8. The sympathetic outflow to the colon appears to take no direct part in these inhibitory responses.

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