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REFLEXES ELICITED BY VISCERAL STIMULATION IN THE ACUTE SPINAL ANIMAL

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In his description of receptor organs, Sherrington (1906) points out that the surface receptive field presents two divisions. The exteroceptive field, which is co-extensive with the so-called external surface of the animal, and the interoceptive field, its so-called internal surface which is usually alimentary in function. Little is known of the receptor organs of the latter surface. The afferent nerve fibres are, to quote Sherrington, comparatively few as judged by their number in the white rami. 'The poverty of afferent fibres from the interoceptive field is broadly indicated by the fact that we know no wholly afferent nerve trunk in the sympathetic system. The visceral constituent of the spinal ganglion is not present in all segments and is probably, even in those segments in which it is present, numerically the weakest of the three components.'

'The exteroceptive arcs', according to Sherrington, 'appear in most segments less closely connected with the visceral musculature than with skeletal musculature. The interoceptive arcs appear in most segments less closely connected with the skeletal musculature than with the visceral. In physiological parlance a resistance to conduction seems intercalated between the two. But both exteroceptive and interoceptive fields easily influence, through their nervous arcs, the musculature of the blood vascular organs.'

Mackenzie (1930) has described a viscero-motor reflex as one of the phenomena associated with visceral disease. This reflex is described as a contraction of skeletal muscle following visceral stimulation. Lewis (1942) points out that Mackenzie enlisted Sherrington's help, and the latter was able to produce movements of the abdominal wall by stimulating the bile duct or the central end of the superior mesenteric nerve. Subsequent work was done by Miller and his co-workers (1924, 1925*a*, *b*, *c*), who have investigated the reflex in decapitate cats. They found that squeezing the small intestine between finger and thumb, pulling the mesentery and faradizing mesenteric nerves produced contraction of leg and belly muscles with a rise of blood pressure. Lewis & Kellgren (1939) reported, however, that hard pinches of the intestine of decapitate cats did not affect skeletal muscle, whereas pinching the pancreas produced contraction of the abdominal muscles. In each instance a rise of blood pressure was recorded. Lewis & Kellgren also failed to elicit visceromotor reflexes from any of the solid abdominal viscera. They suggested that movements and pain which arise apparently from viscera are in fact the consequence of mesenteric stimulation. It will be remembered that Lennander (1902) had reached a similar conclusion as a result of surgical experience. He demonstrated that in man the solid organs and some of the hollow organs of the abdomen can be cut, burned, crushed or stretched without the subject being conscious of injury. Lennander concluded that the viscera were incapable of initiating pain, and that pain impulses originated only from the parietal peritoneum.

Much of the work on the sensory innervation of the intestine has been aimed at analysis of the mechanism of referred pain. Investigation of changes other than pain, produced by intestinal stimulation, has been neglected. Indeed, the inability of intestinal trauma to cause pain has led to a common belief that the viscera are insensitive to all forms of stimulation.

In this paper are recorded some of the results of intestinal stimulation as seen in the acute spinal animal. Preliminary observations showed that reflexes of intestinal origin could be most easily elicited when the spinal cord was transected in the upper thoracic region. Previous workers have used the decapitate animal, i.e. with cord transected in the upper cervical region. Miller and his colleagues, and Lewis & Kellgren removed the head, as described by Sherrington (1909). McDowall (1942) prefers to turn a decerebrated animal into a spinal animal by occluding the carotid and vertebral arteries. In the majority of cats this results in 15 min. in a spinal preparation in which leg movements result from stretching the intestine, but cutting has no effect. McDowall warns against over-ventilating the preparation, a warning given also by Lewis & Kellgren.

In the following account the reflex activity of three preparations is compared: (1) decerebrate animal with cord transected in upper thoracic region, (2) decapitate animal, (3) decerebrate animal.

METHODS

Cats were used in all experiments, the preliminary transection of the brain stem being made under deep ether anaesthesia. Decerebration was done through a hole in the cranium, the brain being removed anterior to the tentorium cerebelli; bleeding from the brain stump was controlled by tying the common carotid arteries in the neck and applying digital pressure to the vertebral arteries. The spinal cord was cut after removing the lamina of the overlying vertebra; the dura mater was opened and the cord cut across with scissors. For decapitation the carotid arteries were tied in the neck and the spinal cord was exposed by removing the lamina of the axis. The cord was cut intradurally, and the cranial cavity was pithed with a probe passed upwards through the foramen magnum. Positive-pressure ventilation through the tracheal cannula was begun at the time of pithing. All animals were left for 3 hr. to excrete the ether.

The abdomen was opened by a diagonal incision in the abdominal wall, running forwards and downwards from the renal area towards the mid-line and exposing the parietal peritoneum. Blood was not allowed to enter the peritoneal cavity, care being taken that all bleeding had ceased before the peritoneum was cut with scissors. It was possible, through a 2 in. incision, to produce any part of the intestine and the organs of the same side. To keep the environment of the exposed viscera as constant as possible, the trunk of the animal was submerged in a deep bath of Locke's Ringer solution (Bain, 1938) maintained at 38–39° C.

Movements of the hindlimbs were recorded by attaching the foot directly to an isometric myograph with a weak spring, by means of a wire stirrup strapped to the foot with adhesive tape. In other experiments the movements of a single muscle, e.g. gastrocnemius, was recorded isometrically in the usual way. In the majority of experiments the movements were observed by eye. Blood pressure was recorded with a mercury manometer from the central end of a divided carotid artery, using saturated sodium bicarbonate solution as an anticoagulant in the recording system.

RESULTS

Decerebration with chordotomy. In these experiments the spinal cord was divided between the eighth cervical and first thoracic roots, and the animal was decerebrated immediately afterwards.

This preparation had the characters of a decerebrate animal in the head and forequarters but of a spinal animal in the trunk and hindquarters. Breathing was maintained by the diaphragm. The hindlegs had good tone, and the muscle jerks were strong and sensitive. Handling or squeezing the paws caused flexion with crossed extension, the movement usually being a rhythmic stepping or a shaking-off. Tickling the hairs of the scrotum or labia produced flexion of the hind limbs, often with a superposed rhythmic walking movement. Gently squeezing the parts sometimes produced flexion, but usually strong extension, of the legs, with superposed stepping movements. The muscles of the abdominal wall were very sensitive to stretching, a gentle tap on the surface producing a sharp twitch of the underlying muscles.

Stimulation of the abdominal viscera caused movement of the hindlimbs; contraction of the belly muscles and rise of carotid blood pressure (Fig. 1). These responses followed, for example, pinching the small or large intestine with forceps, or gently squeezing a short length of bowel between finger and thumb. The responses of the limbs had many patterns. Some animals abducted the limbs and flexed them on the belly, others extended the limbs strongly downwards and backwards, while some first flexed the legs and then extended them. Most commonly initial extension was followed by, and merged into, rhythmic alternating flexion and extension which resembled walking or trotting. It was noted that the pattern of response to squeezing the external genitalia usually forecast the pattern of response to visceral stimulation, if the latter elicited movements.

The visceral stimulation produced also a rise of blood pressure. The rise was usually small, of the order of 20–40 mm., but rises of 80 mm. have been recorded (Fig. 2). A dissociation between the leg and vascular responses was sometimes seen, when animals which had lost the leg response still gave good blood-pressure responses. This disappearance of certain of the reflexes will be referred to again later.

Decapitation. These animals were prepared by pithing the cranium in the way described previously. They were kept alive by positive-pressure ventilation of the lungs for the rest of the experiment. During the subsequent 3 hr. these preparations showed progressively increasing activity of the limb. The muscles had good tone, and the muscle jerks were brisk and sensitive in all limbs. In the hindlimbs the flexion and crossed extension reflexes were strong and sensitive. Flexion reflexes were present in the forelimbs but were less strong and less sensitive. A scratch reflex was easily elicited from a large saddle-shaped area of the back of the neck and trunk.

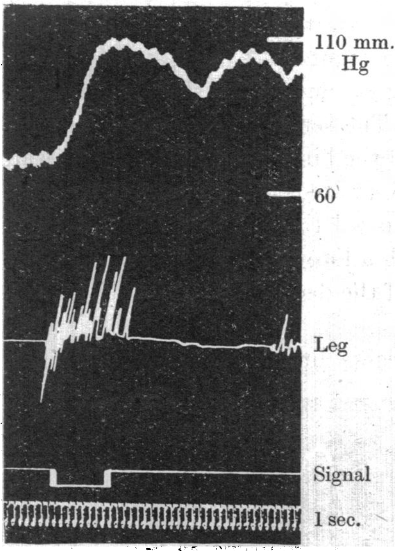

Fig. 1.

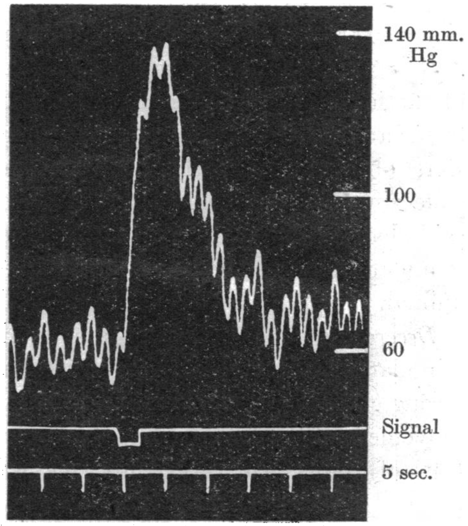

Fig. 2.

Fig. 1. Record of leg movements and blood-pressure changes on pinching the jejunum. Decerebrate cat with spinal cord transected between C_8 and T_1 roots. B.P. from carotid artery. Movements of left leg recorded by attaching foot to isometric lever.

Fig. 2. Rise of carotid blood pressure on pinching ileum. Decerebrate cat, spinal cord cut between C_8 and T_1 roots.

The liveliness of the reflexes elicited from the skin and of the muscle jerks contrasts with the weak leg movements which followed visceral stimulation. Stimulating the small or large intestine produced no, or but weak, movements of the hindlimbs. To produce these weak responses it was necessary to stimulate the bowel by drastic means, e.g. by pinching with forceps sufficiently hard to rupture the muscle, or by squeezing 1 or 2 in. of the bowel hard between finger and thumb. Movements could be easily elicited, however, by stimulating other organs. Pinching a small piece of the pancreas, squeezing an ovary, and pulling the intestinal mesentery were effective. Stimulating the intestine caused a rise of blood pressure, of the order of 30 mm., this rise of pressure occurring even if there were no limb movements.

The difference in reactivity between the decapitated and the decerebrated-chordotomized preparation suggested an investigation of a decapitated animal with chordotomy. Decapitation, after section of the spinal cord between the eighth cervical and first thoracic roots, gave a preparation in which artificial ventilation was necessary, and at the same time the lower spinal cord was removed from the influence of the cervical segments.

Reflexes elicited by stimulation of sensory endings in the skin and muscles of the hindlimbs were strong and sensitive. The scratch reflex was absent or feeble and slow to appear. Good responses of the hindlegs and abdominal wall were obtained when the intestine was stimulated by pinching or gently squeezing. Rises of blood pressure also followed the stimulation. It can be said that the reactivity of the decapitate-chordotomized animals to visceral stimulation may be equal to the reactivity of the decerebrated-chordotomized animal.

Decerebration. The decerebrate animal reacts little, if at all, to visceral stimulation. Decerebrate cats which had strong extensor hypertonus did not show movement of the limbs or palpable alteration of tonus when the intestine was pinched. Rises of blood pressure have been recorded (Fig. 3), but even this response was absent in some preparations. The insensitivity was not confined to the small and large intestine; stimulating the pancreas and mesentery was also ineffective.

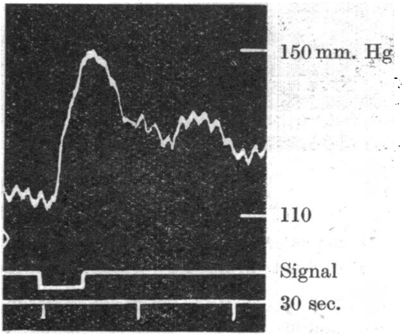

Fig. 3. Rise of carotid blood pressure on pinching jejunum of decerebrate cat.

The absence of response was not due to a failure to stimulate visceral nerves. Pinching the duodenum and pancreas produced contraction of the panniculus carnosus muscle, as described by Ashkenaz (1937), demonstrating that impulses were entering the spinal cord.

In the decerebrate animal the legs are held rigid by the muscular hypertonus, and it may be that the absence of limb movements is due to a splinting action of the contracted muscles. This would not account, however, for the absence of vascular responses in these preparations. That some other mechanism is involved is suggested also by the behaviour of a cat, with the brain stem cut between the superior and inferior colliculi, in which the limbs had low tone and the flexor responses of the hindlegs and the scratch reflex were present; even in this animal, visceral stimulation had no effect. In this experiment it was clear that the limbs could move as part of a reflex from the skin, but not from the viscera.

Comparison of the preparations. The decerebrated-chordotomized animal is a convenient and sensitive preparation for the examination of the reflexes associated with visceral afferent impulses. The viscero-motor and viscero-vascular reflexes are readily elicited by stimulating the intestine and other viscera. Generally the decapitate animal is not as sensitive to intestinal stimulation as the former preparation. Not only does stimulation produce smaller movements of the legs, but stronger stimuli are required to produce them; this animal is, however, sensitive to mesenteric stimulation and pinching the pancreas. On the other hand, the decapitated-chordotomized animal is comparable in sensitivity to the decerebrated-chordotomized animal, but has the disadvantage that artificial ventilation is needed. The decerebrate animal gives no limb movements on intestinal stimulation, and blood-pressure changes may be absent.

In all the spinal preparations there was a striking difference between the state of the reflexes elicited by stimulation of the skin and skeletal muscle, and those elicited from the viscera. The former showed a high degree of recovery in the 3 hr. elapsing after chordotomy. The flexor, crossed extensor, stretch and other reflex responses obtained on stimulating the external genitalia were strong and sensitive. In contrast, animals with such lively somatic reflexes might have no, or but poor, viscero-motor reflexes. This was the usual condition of the decapitated animal, but might obtain in the other preparations also. It must be emphasized that the state of the somatic reflex arcs is not an index of the state of the visceral arcs. An animal which gives good demonstrations of the somatic reflexes may, or may not, exhibit viscero-motor reflexes. The state of the visceral arcs can be estimated only by stimulating the afferent neurones of the arcs themselves.

The non-reactivity of the decapitate animal may be partly due to the artificial ventilation. Ventilating with 5% CO_2 in air was accompanied by a small increase in the amplitude of the limb movements, suggesting that hypocapnia is in part responsible for the state of the reflex arcs. The difference between the decapitated and the decapitated-chordotomized animals suggests that in the decapitated animal the cervical segments suppress the activity of lower segments of the cord. Severing the cervical region from the lower regions is accompanied by a stronger and more sensitive reflex movement. The influence of the level of transection is shown also, by the condition of the scratch reflex in various preparations. In the decapitate animal the reflex was strong and easily elicited within 3 hr. On the other hand, when the spinal cord was sectioned in the upper dorsal region there was practically no recovery of the reflex within the same time. In some way severing the cord at this level releases the viscero-motor reflexes but retards the recovery of the scratch reflex.

Relation between limb movements and blood-pressure changes. The blood-pressure changes are not passive effects dependent upon the limb movements. Blood-pressure rises may be observed in the absence of any visible movement of skeletal muscles. This is a common finding in cats in which the viscero-motor arcs are depressed, e.g. decapitates. Again, vigorous active movements of the legs did not influence the blood pressure. This was shown by those preparations in which squeezing the scrotum or labia provoked vigorous movements of the legs without change of blood pressure, whereas pinching the small intestine produced no limb movement with a rise of blood pressure. Finally, pressure rises were observed in preparations in which curarine chloride (Burroughs Wellcome) was injected intravenously in doses sufficient to paralyse respiration and abolish all visible reflex movements of the hindlimbs.

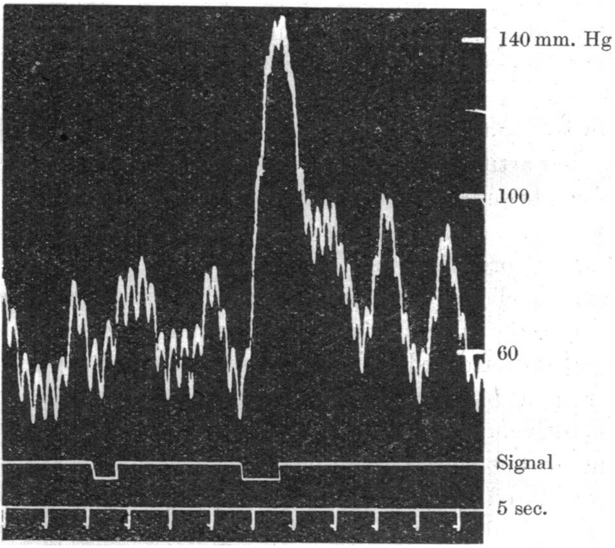

Fig. 4. Record of carotid blood pressure in decerebrate cat with spinal cord transected at C_8/T_1. Squeezing scrotal sac, excluding testis, at first signal, evoked vigorous flexion-extension movements of the hindlegs without significant change of blood pressure. Pinching ileum, at second signal, evoked a weak extension at the ankle joint with rise of blood pressure.

The pressure change was accompanied by a pallor of the intestine. This pallor appeared as the blood pressure was rising and disappeared as the pressure fell. Not only was the stimulated loop of intestine involved, but the pallor extended throughout the small intestine and into the upper one-third of the large intestine, including the caecum. This vaso-constriction is clearly an active process and is probably responsible for the major part of the change of blood pressure.

General influences. The sensitivity of the decerebrated-chordotomized preparations to visceral stimulation varied considerably from animal to animal, and even in the same animal from time to time. The majority gave good movements to gentle stimulation of the intestine, but a few did not respond, or gave only the smallest movement of the foot, to the hardest possible squeeze of the intestine between finger and thumb. No reason for this variation can be given. The impression was gained that blood loss and prolonging the time of ether inhalation would tend to give non-reactive preparations; sometimes, however, apparently similar operative procedures would give dissimilar preparations.

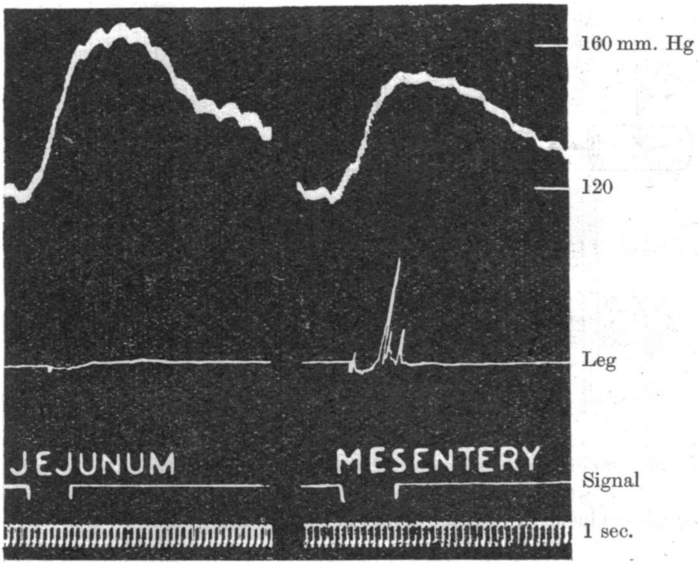

Fig. 5. Record of carotid blood pressure and movements of hindleg of a decerebrated-chordotomized cat, showing results of deterioration of preparation. Leg movement obtained on rubbing jejunal mesentery, but not on pinching jejunum. Rise of blood pressure in both instances.

The different preparations may be grouped according to their reactions to various stimuli. (1) The best preparations responded to non-traumatizing stimuli of the small or large intestine with leg movements and rise of blood pressure. (2) In the next group, the leg movements were deteriorating. Strong stimulation of the intestine produced no movements or but weak movements of the legs, but a rise of blood pressure was recorded; stimulating the mesentery or the pancreas produced vigorous leg movements and rise of blood pressure (Fig. 5). (3) In this group, intestinal stimulation severe enough to rupture the muscle layers did not elicit leg or vascular responses, but both responses were still obtained from the mesentery and pancreas. (4) The worst preparations were insensitive to stimulation of intestine, mesentery or pancreas, but did give leg movements and a rise of blood pressure on faradizing or pinching the central end of a cut splanchnic nerve.

The reactivity of an animal varied during the experimental period. When the belly was first opened some animals were relatively insensitive to intestinal stimulation, but improved if left for an hour; the majority of animals were as sensitive when the belly was opened as at any subsequent time. Repeated stimulation of the intestine, with the same strength of stimulus, at intervals of 5 to 10 min., produced leg movements and blood-pressure responses which varied in size. Occasionally a stimulus might fail entirely to produce responses, but the next stimulus might be effective. The lack of constancy in the response makes difficult any quantitative study involving successive stimulations of the gut. Prolonged experimentation, e.g. frequently eliciting viscero-motor reflexes for an hour, was often accompanied by deterioration of the responses even to extinction. Handling the intestine was another way of causing a rapid deterioration of the reflex responses, while exposing the splanchnic nerve by the retroperitoneal approach caused such profound and prolonged depression that the effects of section of the nerve could not be investigated in an acute experiment.

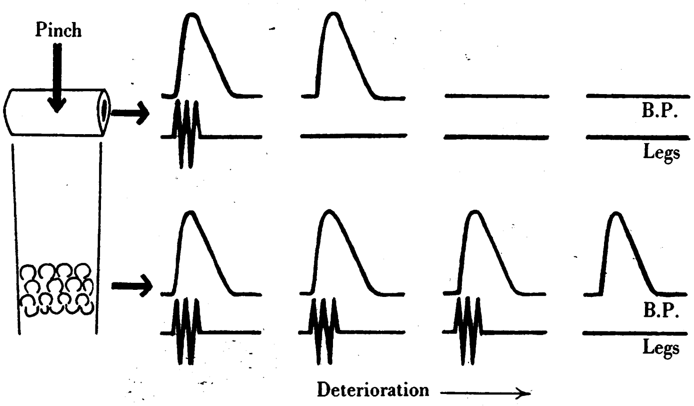

Fig. 6. Diagram representing the sequence of disappearance of the vascular and skeletal muscle responses to stimulation of the intestine and pancreas by pinching. This deterioration may be the result of such influences as bodily trauma, or handling the viscera. The different patterns of responses may also be the consequence of transecting the central nervous system at different levels.

When an animal was deteriorating, it passed progressively through the stages described above (Fig. 6). Leg responses to intestinal pinching became more difficult to elicit, and were then lost; at this stage the stimulus still elicited vascular responses. Subsequently all the responses from the intestine were absent even on crushing the muscle layers, but leg and vascular responses could be evoked from the pancreas. With further deterioration the leg and then the vascular responses were lost. By now, pinching the splanchnic nerves produced poor limb movements and but small pressure changes. All this deterioration was unaccompanied by any apparent change in the general limb reflexes; flexion, crossed extension and stretch reflexes retained their sensitivity and briskness.

The depression of the viscero-motor reflex arcs was not related to the way in which the spinal cord was cut. The decapitate animal, prepared by pithing the head, was comparable in its properties to the spinal animal prepared by the method of McDowall (1942). Cutting the cord by tying a thread tightly round the spinal dura mater, thereby conserving the normal cerebro-spinal fluid surround, did not produce unusually sensitive preparations of the decerebrated-chordotomized type.

The depression was not due to impulses from the skin and muscles which were cut when the belly wall was incised. Infiltrating these tissues with a 1% solution of procaine, so that pinching the wound edge did not cause contraction of adjacent muscle, did not alter the reactivity of the preparations.

As stated above, the pattern of the leg movements varied from animal to animal. In some the dominant movement might be flexion, in another extension, and in the majority a rhythmic stepping was superposed upon this movement. It was found also that the pattern of the movement might vary unpredictably during an experiment, an animal which previously gave flexion movements now giving extension movements, or vice versa. Miller & Waud (1925*c*) suggested that irritation at the cut surface of the spinal cord was the cause of this variation, and claimed that faradizing this area caused reversal of the movement. This claim was not substantiated in our experiments. A pledget of cotton-wool soaked in 0·9% sodium chloride solution was placed on the cut end of the thoracic spinal cord and used as one electrode for faradizing the cord face, a large pad of cotton-wool soaked in 0·9% sodium chloride solution forming an indifferent electrode. Faradic current did not cause reversal of the direction of movement of the viscero-motor reflex. The only change seen was a reduction of amplitude of the movement when the stimulation was strong enough to cause the legs to be held rigid in extension.

Sensory field of the reflexes. This field is very large. It includes not only the intestine but also the peritoneum and nearly all of the organs of the abdomen. Limb movements and blood-pressure responses have been elicited by stimulating all regions of the small and large intestine by pinching. Pinching the pancreas, ovaries, uterine horns, spleen and body of the stomach at the greater curvature was effective, and also pulling on the intestinal mesentery, ovaries and splenic ligaments. Pinching or faradizing the nerves running in the intestinal mesentery, and the central end of a cut splanchnic nerve as it crosses the crus of the diaphragm, also elicited responses.

Rubbing the mesentery lightly with a dry wool pellet, and rubbing the surface of the parietal peritoneum lining the abdominal wall, produced leg movements and blood-pressure changes. It was noted that in some animals, however, the parietal peritoneal stimulation was ineffective, whereas the mesentery was still sensitive.

Repetition of visceral stimuli. If the reflex movements of the limbs were elicited by repeated stimulation, the response diminished in size and was ultimately lost. This decay was seen if the interval between the stimuli was short, of the order of 5–20 sec., and generally only three to five responses were obtained. If the preparation was left for 5 min. the responses reappeared and showed the same decay as before, if again elicited repeatedly. This feature of the reflex was seen both with pinching the intestine or with faradizing the mesenteric nerves.

The results of repeated stimulation included a loss of response from immediately adjacent lengths of intestine, but not from more distant loops of gut. Thus, with repeated pinching of the intestine in two places about half an inch apart leg movements disappeared. Pinching the intermediate piece of intestine, although it was previously unstimulated, was now without effect. On the other hand, pinching a neighbouring loop of the intestine was still effective. Similar local loss of sensitivity was seen when the mesenteric nerves were stimulated directly. Repeated electrical stimulation of a nerve resulted in diminishing leg movements, and ultimate loss of response; stimulation of a neighbouring nerve, however, still elicited responses. It may be remarked at this juncture that the intestine often showed a patchy sensitivity to stimulation, severe crushing of one loop being ineffective, whereas gentle pinching of a neighbouring loop was effective. Sometimes the insensitive regions were quite short, of the order of 2–3 cm.

It is not possible to state where the change in the reflex arcs took place in these experiments, although it can be inferred that the spinal motor neurone itself was not affected. The observations could be explained by either a change in the spinal connector-neurone path or by an altered state of the afferent pathways themselves between the intestine and spinal cord. It is conceivable that repeated stimulation of visceral afferent fibres results directly or reflexly in a reduction of their excitability or conductivity. To settle the question, some more direct approach to the problem is needed. At present the situation may be best summed up in the words of Sherrington (1906): 'The interoceptive arcs appear in most segments less closely connected with the skeletal musculature than with the visceral.'

Anatomy of the reflex arcs. The evidence of other workers shows that the splanchnic nerves form a great afferent pathway from the intestine. The vagus nerves are not parts of the reflex arcs involved. Sectioning the vagus-sympathetic trunks in the neck leaves the reflexes intact; the only effect is a heightening of the blood-pressure responses, presumably because of loss of the last remaining pathway for effective compensatory adjustments.

Mediation of the limb and vascular reflexes by thoracic-lumbar-sacral segments of the cord, with all connexions with the upper brain stem severed, shows that the reflex arcs are completed within the cord. The efferent paths carry vaso-constrictor impulses to the vessels of the intestine, presumably via the splanchnic nerves, and motor impulses to the muscles moving the lower limbs and belly wall via lumbar and sacral nerves. It is appreciated that the adrenal glands may have some responsibility for the vascular responses, and the mechanism and anatomy of the response requires fuller investigation.

DISCUSSION

It is clear that impulses from the abdominal viscera can influence skeletal as well as vascular musculature. In appropriate preparations mechanical stimulation of the intestine elicits the viscero-motor and the viscero-visceral reflexes together, and the presence of the reflexes in the animal with the cord cut in the upper thoracic region shows that the arcs are completed within the spinal cord below that level. The reflexes are obtained not only from the intestine, but also from the intestinal mesentery, the pancreas and other abdominal organs. Other investigators have shown that the splanchnic nerves form the way-in for impulses from the majority of the abdominal viscera, and the elicitation of the reflexes by stimulating the bared mesenteric and splanchnic nerves suggests that these are the afferent pathways of the specific arcs which have been studied. The vascular reflexes are not dependent upon the vagus nerves; if anything, dividing the nerves heightens the blood-pressure changes, presumably by destruction of reflex buffer mechanisms.

The skeletal muscle responses consist of movements of the hindlegs and contraction of the abdominal muscles. The leg movements vary considerably in their pattern, and, for example, may even change from flexion to extension in the same animal during the experiment. The finding of Miller & Waud (1925*c*), that this is due to irritation at the cut face of the spinal cord, was not confirmed in the experiments, but no other explanation can be offered. The vascular response consisted of a rise of general arterial pressure, which was accompanied by vaso-constriction of a wide area of the intestine. Sherrington (1906) pointed out that conduction is more easily depressed through long arcs in the spinal cord than through short arcs. This is borne out by these experiments. The skeletal muscle responses disappeared before the vascular responses, so that a preparation might show only a blood-pressure response to intestinal stimulation, with no leg or abdominal movements. This dissociation of the arcs depended not only upon certain general influences but also upon the level of transection of the brain stem. The decerebrate animal, with the brain stem transected at the intercollicular level, is characterized by its lack of reaction to stimulation of any of the viscera; rise of blood pressure was the exception rather than the rule. When the level of transection is below the medulla, reflex responses are obtained on visceral stimulation. Transection in the upper cervical regions gives a preparation in which the viscero-motor reflexes are usually weak in execution, and elicited only by strong stimulation of the intestine; the responses may be absent when the abdomen is first opened, as found by Lewis & Kellgren (1939). Transection in the upper thoracic segments gives a preparation in which the viscero-motor reflexes are stronger and can be elicited by gentle stimulation of the intestine. In both spinal preparations pinching the intestine caused a rise of blood pressure, and pinching the pancreas or stimulating the mesentery produced both leg and blood-pressure responses. One explanation of the variations in the conductivity of the spinal arcs in the preparations would be an active suppression of the reflexes by higher levels of the neuraxis. It must be remembered, however, that the nervous system is very sensitive to changes in its blood supply, and there is no information about the nutrition of the spinal arcs in the various preparations. On the other hand, it would be expected that altered nutrition would affect all reflex arcs in the cord, and it is found that the state of the reflexes elicited by visceral stimuli is not related to the state of the reflexes elicited by skin stimulation, although the same final common path is involved in each case.

At present the decerebrated-chordotomized animal, with the cord cut in the upper thoracic region, seems to be the most suitable preparation for investigating the viscero-motor and allied reflexes in the acute experiment. Not only does the preparation maintain its own respiration, but the intestine is more sensitive and the reflexes are stronger. It must be admitted, however, that in any preparation the reflexes are very sensitive to any deleterious influence such as excessive trauma or haemorrhage. Also the level of sensitivity of the reflexes varies unpredictably, which makes it impossible to obtain a constant response for any length of time and limits the scope of experiments.

In any preparation, deterioration is shown by a loss of responses to intestinal stimulation, although stimulating the pancreas or mesentery is still effective. With further deterioration, stimulating the pancreas or mesentery ceases to be effective, and to obtain responses one must stimulate the splanchnic nerve directly. Thus, a preparation which gives leg responses on pinching the intestine and pancreas may change into one giving no leg movements on pinching the intestine, but giving leg movements on pinching the pancreas; on every occasion blood-pressure rises may be recorded. It is clear, therefore, that the absence of leg movements on pinching the intestine does not signify the anatomical absence of a certain type of innervation of the intestine. This point is stressed because Lewis, as a result of his experimental findings, considered that the intestine lacks a functional type of nerve fibre which is present in the mesentery and pancreas. The similarity of response on pinching the intestine, mesentery and pancreas in suitable preparations suggests that the intestine, mesentery and pancreas are supplied by afferent fibres whose impulses can have the same functional significance within the central nervous system. What does differ between the innervations of the viscera is the stability of the spinal reflex in face of certain general influences or the action of higher levels of the nervous system.

Lewis (1942) has recently suggested that the sensory fields of the body could conveniently be grouped into a superficial and a deep field, the latter including skeletal muscles and also the mesentery with its contained pancreas. Each of the fields is supplied by systems of nerve fibres which carry impulses producing a sensation of pain on arrival in the central nervous system. The intestine was excluded from the deep field because of the apparent absence of the afferent limb of the viscero-motor arc, Lewis considering that this was further evidence of lack of a pain-producing afferent innervation of this organ. There is evidence, however, that animal experiments do not substantiate the latter claim, the presence or absence of viscero-motor reflexes on pinching the intestine depending upon the method of preparation of the animal. If the older division of the sensory fields by Sherrington were to be discarded, it is clear that the intestine is not entirely lacking in afferent innervation and would need to be included in the deep field of Lewis.

It is appreciated that in the acute experiment the spinal reflex arcs are in a condition of spinal shock. It is difficult to assess the effect of this shock upon the reflexes which have been studied. The changes in the strength and sensitivity of the reflexes may be an expression of alterations in the degree of the shock, and it is also possible that some other factor may be acting on the synapse or conducting fibre. In any case, it is probable that the condition of the spinal neurones would lower the conductivity of all the spinal arcs, and the ready dissociation of the responses may, in great measure, be due to this.

SUMMARY

1. Reflex movements of the hindlegs and rises of blood pressure have been recorded after visceral stimulation, particularly after pinching the intestine. The reflex arcs are complete within the spinal cord.
2. The reflexes are strongest and most easily elicited in the decerebrate animal with the spinal cord cut in the upper thoracic level.
3. The reflexes are weaker, and movements may be absent, upon intestinal stimulation in the decapitate animal.
4. Movements are absent, but blood-pressure changes have been recorded, on pinching the intestine of the decerebrate animal.
5. The viscero-motor reflexes may be lost while the viscero-vascular reflex remains. This indicates changes in the spinal cord.

6. When intestinal stimuli are ineffective, powerful reflex responses follow stimulation of the mesentery and pancreas.

7. Changes in conductivity in the visceral reflex arcs occur without changes in the somatic reflex arcs.

REFERENCES

Ashkenaz, D. M. (1937). *Amer. J. Physiol.* **120**, 587.

Bain, W. A. (1938). *Schafer's Experimental Physiology*, 6th ed. London: Longmans, Green and Co.

Lennander, K. G. (1902). *Mitt. Grenzgeb. Med. Chir.* **10**, 38. Trans. by A. E. Barker (1903). London.

Lewis, T. (1942). *Pain.* New York: Macmillan Co.

Lewis, T. & Kellgren, J. H. (1939). *Clin. Sci.* **4**, 47.

McDowall, R. J. S. (1942). *J. Physiol.* **101**, 6*P*.

Mackenzie, J. (1930). *Symptoms and their Interpretation*, 4th ed. London: Shaw and Sons, Ltd.

Miller, F. R. & Simpson, H. M. (1924). *Trans. Roy. Soc. Can.* Sec. 5, **18**, 147.

Miller, F. R. & Simpson, H. M. (1925*a*). *Amer. J. Physiol.* **72**, 231.

Miller, F. R. & Waud, R. A. (1925*b*). *Amer. J. Physiol.* **73**, 329.

Miller, F. R. & Waud, R. A. (1925*c*). *Trans. Roy. Soc. Can.* Sec. 5, **19**, 91.

Sherrington, C. S. (1906). *The Integrative Action of the Nervous System.* New York: Scribners.

Sherrington, C. S. (1909). *J. Physiol.* **38**, 375.