J. Physiol. (1959) 146, 438–458

THE EFFECTS OF DISTENSION OF THE BLADDER ON SOMATIC REFLEXES IN THE CAT

By M. H. EVANS* and A. McPHERSON*
From the National Institute for Medical Research, Mill Hill, London, N.W. 7

(*Received* 26 *September* 1958)

Distension of the bladder in man is said to prolong the period of spinal shock that follows transection of the spinal cord (Fulton, 1955), and during the chronic stage of paraplegia bladder distension increases the frequency and severity of flexor spasms of the legs (Riddoch, 1917). Dusser de Barenne & Ward (1937) found that distension of the urinary bladder inhibited the knee jerk of rhesus monkeys or cats anaesthetized with allobarbitone. When the bladder was emptied the knee jerk returned sometimes abruptly and sometimes gradually. They obtained similar effects in monkeys and cats with high spinal transections. Mellanby & Pratt (1940), using decerebrate cats or cats anaesthetized with chloralose, found that isometric contraction of the bladder was usually accompanied by contractions of the diaphragm, muscles of the abdominal wall, shoulder girdle and pelvic girdle. Sometimes these isometric contractions of the bladder did not produce muscular activity, producing instead quiescence of any already existing activity. Chernigovsky (1947) found that distension of the bladder at very high pressures decreased the reflex contractions of the semitendinosus muscle.

Evans & McPherson (1958) found that monosynaptic and polysynaptic reflexes recorded from the ventral spinal roots of anaesthetized or spinal cats were depressed during distension of the bladder. The present investigation is an extension of this work, to determine the extent to which distension of the urinary bladder can bring about alterations in certain specific reflexes and muscle tone in the hind limbs of decerebrate, spinal or anaesthetized cats. Both inhibitory and excitatory actions have been found, the final effect upon the reflexes being dependent upon the type of preparation and on the degree of bladder distension.

* Present address: M.R.C. Institute of Orthopaedics, Royal National Orthopaedic Hospital, Brockley Hill, Stanmore, Middlesex.

METHODS

The experiments were carried out upon adult cats weighing 1·8–6·2 kg. Some cats were anaesthetized with intravenous chloralose (70 mg/kg), but the majority were decerebrated under ether anaesthesia. The brain stem was divided with a spatula through a wide craniotomy, the level varying from precollicular to intercollicular, and the fore-brain was removed. The carotid arteries were occluded during and for a few minutes after decerebration; the vertebral arteries were never compressed. The decerebration was sometimes done before proceeding with the main part of the dissection, but it was found that the preparations were in better condition if the decerebration was done after completing all the dissection under ether (G. L. Brown, personal communication). In some cats the main dissection before decerebration was done under sodium thiopentone (Pentothal, Abbott Laboratories) anaesthesia, but it was found that these preparations were less active than those in which ether was used. To maintain a high blood pressure polyvinyl pyrrolidone (Polyvidone) 3·8% or glucose 5% (w/v) in Locke's solution was infused intravenously about half an hour after decerebrating and the cat was left undisturbed for another half hour. Many of the decerebrate preparations had the spinal cord transected at the thoracic level (T3–T9), either at the time of the main dissection, or some hours later after a period of recording.

In order to distend the bladder and to measure the intravesical pressure the intra-abdominal urethra was cannulated through a mid-line suprapubic incision, a polythene tube being passed up into the bladder, which was then emptied. In the early experiments the polythene catheter was connected to a T-piece, of which one arm was used for filling the bladder with Locke's solution at about 38° C and the other was connected to a mercury manometer. When the bladder was distended rapidly this arrangement measured the pressure in the filling system rather than intravesical pressure. In the later experiments true intravesical pressure records were obtained by using a double-bore polythene catheter. One channel was used for filling or emptying, either by means of a syringe or from a constant-pressure reservoir. The other was connected to a mercury manometer, to record intravesical pressure. The legends to the figures indicate whether the pressure measurements are those in the filling system or true intravesical pressures.

The reflex contractions of hind-limb muscles were recorded on smoked paper, using conventional isometric myography techniques. The reflexes were evoked by stimulating the central cut ends of either the medial or lateral popliteal nerves. Occasionally the whole sciatic nerve was stimulated in order to evoke a crossed extensor reflex. Ipsilateral flexor contractions were recorded from the semitendinosus and tibialis anterior muscles. Crossed extensor contractions were recorded either from the leg at the ankle, with the thigh fixed, or from the freed patellar or gastrocnemius-soleus tendons with the leg and thigh fixed.

Mono- and polysynaptic reflexes were recorded from the central cut ends of lumbar ventral spinal roots, after stimulation of the central cut ends of the ipsilateral dorsal roots of the same segments. Reflex responses were elicited at rates between 8 and 22 shocks/min, but in order to avoid fatiguing the somatic reflexes greater rates were not used. Intensity modulation of the oscillograph beam (Evans, 1958) was employed in the later experiments to improve the records of monosynaptic action potentials. By recording the intravesical pressure on one beam of the oscilloscope it was possible to determine the intravesical pressures at the precise times of the monosynaptic reflexes. Other details of the electrophysiological techniques have been given in a previous paper (Evans & McPherson, 1958).

RESULTS

Spontaneous bladder activity varied according to the preparation. In acute spinal cats the only activity seen consisted of small bladder contractions, occurring at low resting pressures, which increased the intravesical pressure by less than 10 mm Hg. These small bladder contractions had no detectable effect on the hind-limb reflexes. When such contractions occurred in decerebrate and chloralosed cats they again had no effect on the hind-limb reflexes.

In decerebrate and chloralosed cats in good condition larger spontaneous bladder contractions were seen. These occurred at higher resting pressures and increased the intravesical pressure to peaks of about 80 mm Hg. Their effects upon the hind-limb reflexes were qualitatively similar to the effects of passive distension of the bladder to the same pressure. However, these spontaneous bladder contractions had a quantitatively greater effect on flexor and crossed extensor reflexes and muscle tone than did passive distension of the bladder.

In this series of experiments the relation between the volume of Locke's solution used to distend the bladder and the intravesical pressure which thereby developed was variable. Most of the animals developed intravesical pressures of 30–70 mm Hg when their bladders were distended with 40 ml., but in a few experiments 80–180 ml. was necessary to develop a pressure of 60 mm Hg, and in two experiments pressures of 50 mm Hg were produced by volumes of less than 10 ml. In general, higher intravesical pressures were produced by a given volume of fluid in decerebrate and chloralosed cats than in cats with acute spinal transection. The changes observed in the hind-limb reflexes were correlated with the intravesical pressure, not with the volume of fluid used to distend the bladder. Varying the temperature of the Locke's solution between 25 and 45° C did not alter the effects upon the hind-limb reflexes of distension of the bladder.

The effects of bladder distension on monosynaptic and polysynaptic reflexes recorded from the ventral roots

The typical effect of rapid distension of the bladder was a transient decrease in the amplitude of the monosynaptic reflex, followed at a later stage by an increase in amplitude above the original level. These effects were not obtained in all experiments. They were more regularly obtained in decerebrate cats than in cats anaesthetized with chloralose, and were only occasionally seen in acute spinal cats.

Figure 1 shows monosynaptic reflexes recorded from the 7th lumbar ventral root of a decerebrate cat, following stimulation of the ipsilateral 7th lumbar dorsal root. The width of the lower trace in each photograph is directly proportional to the intravesical pressure. It can be seen that the monosynaptic reflex decreased in size when the intravesical pressure rose. This effect did not persist when the intravesical pressure continued to increase; but the reflex recovered and actually increased above the original level. This was probably a rebound phenomenon which is more clearly shown in Fig. 2, in which the amplitudes of the monosynaptic reflexes and the intravesical pressure are plotted against time. The monosynaptic reflexes were reduced in amplitude at relatively low pressures and they remained decreased for about 10 sec while the pressure was rising to 80 mm Hg (*A*). They then returned to the original level while the intravesical pressure was rising to 120 mm Hg, and then increased above the original level while the bladder was distended at a higher pressure (*B*). A sudden, spontaneous increase in the intravesical pressure, due to a bladder contraction, decreased the size of the coincident monosynaptic reflex considerably; this is seen at *C* in Fig. 2. When the bladder was emptied the monosynaptic reflexes remained above the original level, returning to it about 10 min after emptying.

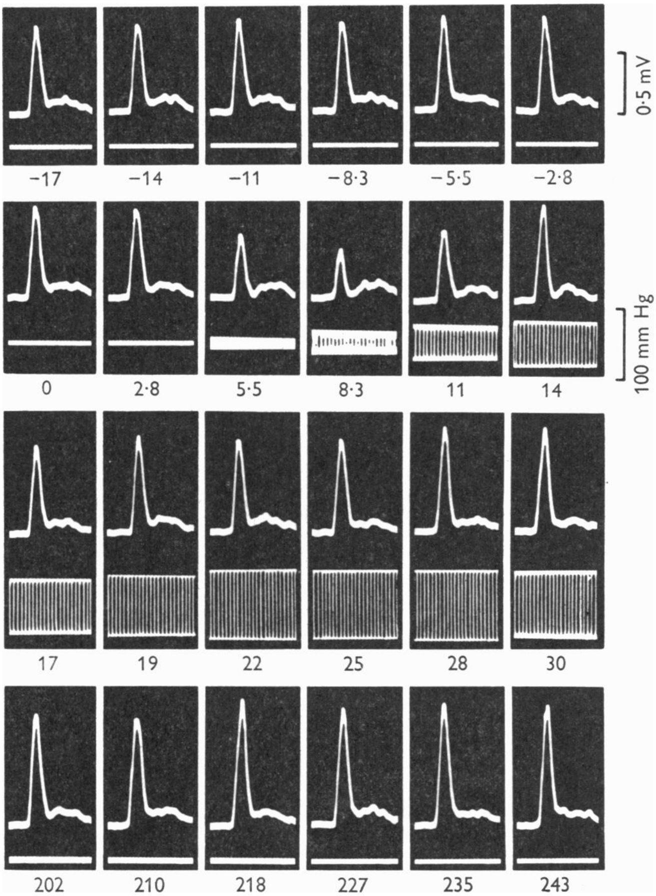

Fig. 1. Monosynaptic with small early polysynaptic reponses recorded from the 7th lumbar ventral root after stimulation of the ipsilateral 7th lumbar dorsal root in a precollicular decerebrate cat. The lower beam records intravesical pressure. Top row, control responses with bladder empty; second and third rows, distension of the bladder with 50 ml. fluid; bottom row, after emptying the bladder. The figures indicate the time in seconds before and after the commencement (0) of distension.

It was frequently seen that when the distended bladder contracted spontaneously the variations in amplitude of the monosynaptic reflexes increased appreciably. This is illustrated in Fig. 3, which shows the amplitudes of the

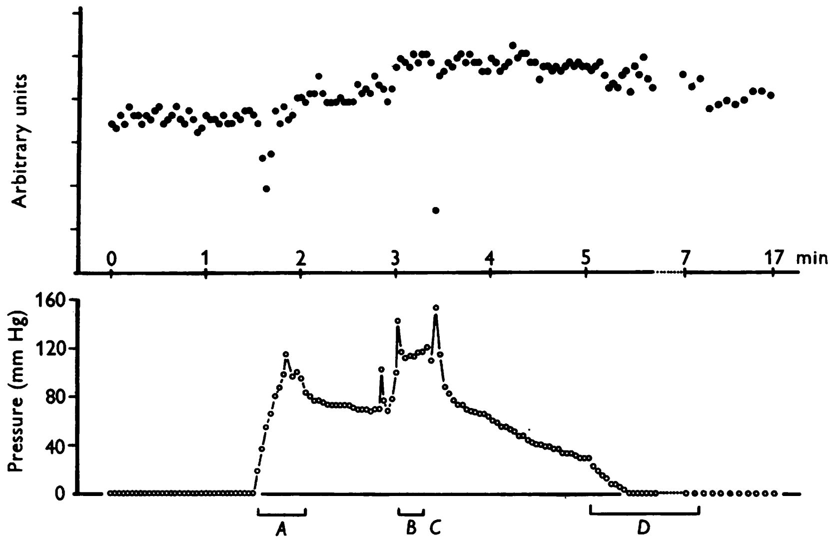

Fig. 2. Same experiment as Fig. 1. Height of monosynaptic reflexes (including those illustrated in Fig. 1) plotted on upper graph and intravesical pressures on lower graph. *A*, 50 ml. fluid into bladder; *B*, additional 20 ml. into bladder; *C*, spontaneous bladder contraction; *D*, withdrawal of 70 ml. from the bladder. Note the compressed time scale for last 11 points.

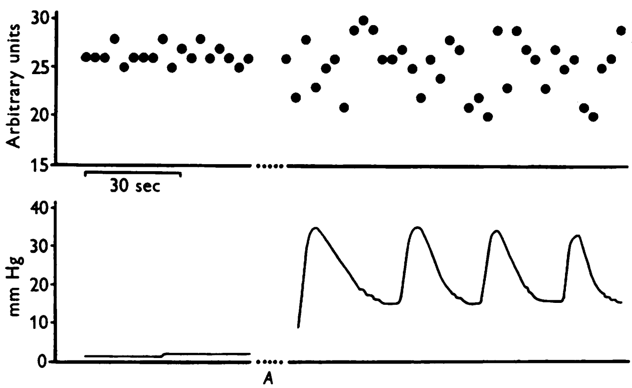

Fig. 3. Monosynaptic responses recorded from 7th lumbar ventral root, following stimulation of ipsilateral 7th lumbar dorsal root in a cat decerebrated under sodium thiopentone, plotted above intravesical pressure, At point *A* the bladder was distended with 30 ml. of fluid and spontaneous contractions occurred.

monosynaptic reflexes and the intravesical pressure. When the bladder was distended with fluid it started to contract, and the monosynaptic reflexes, whose amplitudes had previously varied by 10%, now varied by 20%.

These results suggest that the 'spontaneous' variations in monosynaptic reflexes which have been seen by many workers may have been due to a distended bladder. To obtain monosynaptic reflexes of regular amplitude it is advisable to empty the animal's bladder.

In previous experiments (Evans & McPherson, 1958), on acute spinal cats and cats anaesthetized with chloralose, it was found that polysynaptic reflexes were reduced in amplitude by distension of the bladder and that this reduction mainly affected the longer latency components of the polysynaptic reflexes. The same results have been obtained in decerebrate cats.

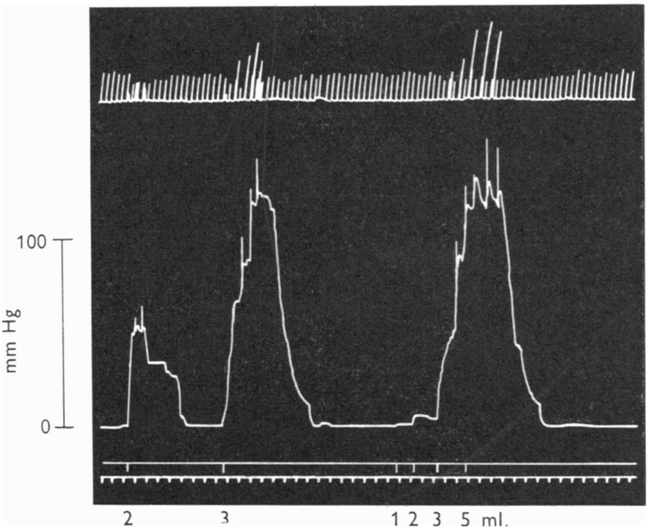

Fig. 4. Upper trace; contractions of the semitendinosus muscle during stimulation of the ipsilateral medial popliteal nerve, in a decerebrate cat. Lower trace; intravesical pressure. The bladder was distended three times, with 2, 3 and 5 ml. fluid respectively, the last distension being performed in steps of 1 or 2 ml. as indicated by the signal marker. Time marker, 30 sec.

In experiments on decerebrate, chloralosed and spinal cats, in which the stimulus evoked both mono- and polysynaptic reflexes in the ventral root, bladder distension sometimes depressed the monosynaptic reflex leaving the early polysynaptic reflex unchanged (Fig. 1), sometimes depressed the late polysynaptic reflex leaving the monosynaptic reflex unchanged, and sometimes depressed both reflexes.

The effects of bladder distension upon the tone and reflex activity of hind-limb muscles recorded myographically

Distension of the bladder produced changes in the tone and reflex activity of hind-limb flexor and extensor muscles. In addition, in decerebrate and chloralosed cats (but not in acute spinal cats) it produced spontaneous movements of the whole body. This effect was only seen when the bladder was distended at pressures higher than about 50 mm Hg. The cats sighed and gasped and the trunk and limb muscles contracted irregularly. The experiment illustrated in Fig. 4 is from a decerebrate cat with a small hypertonic bladder. The injection of 2–3 ml. of fluid raised the intravesical pressure to more than 50 mm Hg. At this high pressure, spontaneous contractions of the semitendinosus muscle were interposed between its reflex contractions. The contractions of the trunk muscles, which were accompanied by sighs and gasps, can be seen as peaks on the intravesical pressure record. In spite of the generalized 'spontaneous' contractions the treading movements of the fore limbs which are often seen in decerebrate cats were abolished by distension of the bladder at pressures greater than about 20 mm Hg.

Decerebrate cats

In decerebrate cats the effects on the hind-limb muscle tone and reflexes were dependent upon the intravesical pressure; opposite effects were seen at low and high pressures. The critical pressure at which this reversal occurred was not well defined but it varied between about 15 and 30 mm Hg. Where the terms 'low' and 'high' pressure are used in this paper they refer to intravesical pressures below and above this critical pressure. In addition, experiments were performed using intravesical pressures above 50 mm Hg and these pressures are referred to as 'very high pressure'.

Flexor reflexes. At low intravesical pressures the flexor reflexes were either not affected or were increased in amplitude. Fig. 5 illustrates an experiment in which this increase occurred. The centre tracing shows contractions of the tibialis anterior muscle evoked by stimulation of the ipsilateral medial popliteal nerve. When the bladder was distended the reflex increased in amplitude at an intravesical pressure of about 10 mm Hg, and further increased at the beginning of each spontaneous bladder contraction.

At high intravesical pressures of 20–50 mm Hg the flexor reflexes were reduced in amplitude, often with a slight loss of tone. Figure 6 (i) is a record of the reflex contractions of the semitendinosus muscle evoked by stimulation of the lateral popliteal nerve. Approximately 1 min after connecting the bladder catheter to a reservoir 38 cm above the level of the bladder the reflex decreased in amplitude, with a slight fall in muscle tone. Upon emptying the bladder, the reflex contractions returned slowly, taking $5\frac{1}{2}$ min to regain their original amplitude. There was no appreciable difference in the behaviour of the reflex when the bladder was distended under conditions of either constant pressure or constant volume. This is illustrated in the right-hand portion of Fig. 6 (i). Other flexor muscles of the hind limb, e.g. tibialis anterior, showed a similar decrease in their reflex contractions at high intravesical pressure.

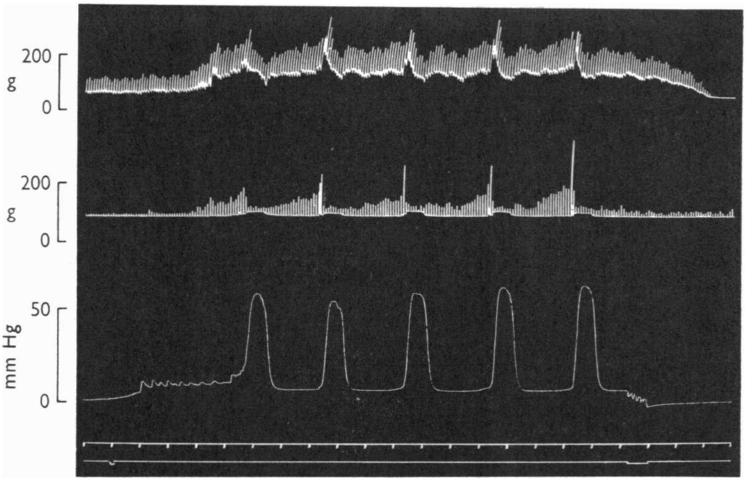

Fig. 5. Upper trace; reflex contractions of crossed extensor, recorded from left gastrocnemius-soleus tendon following stimulation of the right medial popliteal nerve in a precollicular decerebrate cat. Middle trace, flexor reflex contractions of the right tibialis anterior muscle. Lower trace, intravesical pressure (mm Hg). At the first signal mark one channel of the bladder catheter was connected to a reservoir of Locke's solution, which was run in slowly, while the true intravesical pressure was recorded through the other channel of the catheter; at the second signal mark the reservoir was disconnected and 45 ml. fluid was emptied from the bladder. Time marker, 1 min.

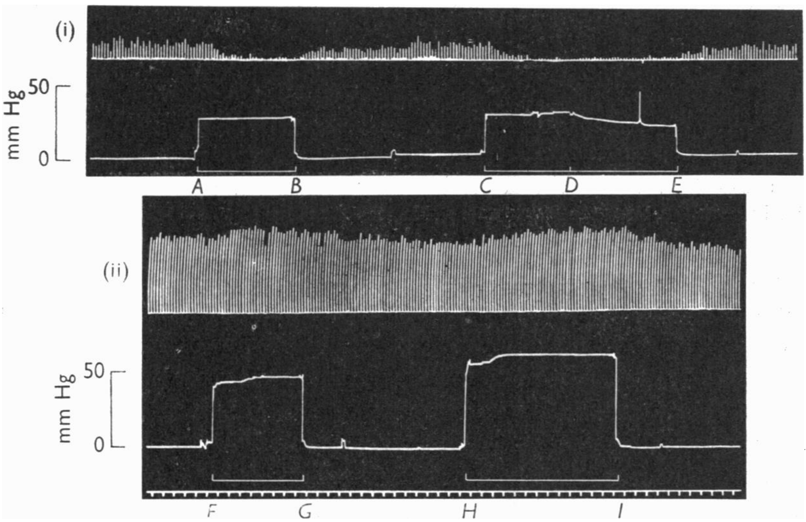

Fig. 6, (i). Decerebrate cat. Upper trace, reflex contractions of semitendinosus muscle following stimulation of the lateral popliteal nerve on the same side; lower trace, pressure in the reservoir system (mm Hg). *A* and *C*, fluid into bladder at constant pressure; at *D* the reservoir tube was clamped and the true intravesical pressure was recorded at constant volume; *B* and *E*, 115 and 125 ml. fluid withdrawn, respectively. (ii). Record obtained later in the same experiment as record (i), 1½ hr after spinal cord transection at T7. *F* and *H*, distension of the bladder at constant pressure; *G* and *I*, 155 and 178 ml. withdrawn, respectively. Time marker, 30 sec.

However, the effect was less frequently seen in the tibialis anterior muscle than in the semitendinosus muscle.

The decrease in the flexor reflexes was particularly pronounced when a spontaneous contraction of the bladder raised the intravesical pressure above 50 mm Hg. At these very high pressures the tone of the flexor muscles was increased. For instance, in the experiment illustrated in Fig. 7 the introduction of 40 ml. of fluid into the bladder led to four bladder contractions which raised the intravesical pressure to 60–80 mm Hg. At the height of each of these contractions the semitendinosus reflex diminished and the muscle tone increased. In the experiment illustrated in Fig. 5, the reflex contractions of the tibialis anterior muscle decreased and the muscle tone increased (middle trace) at the height of each bladder contraction.

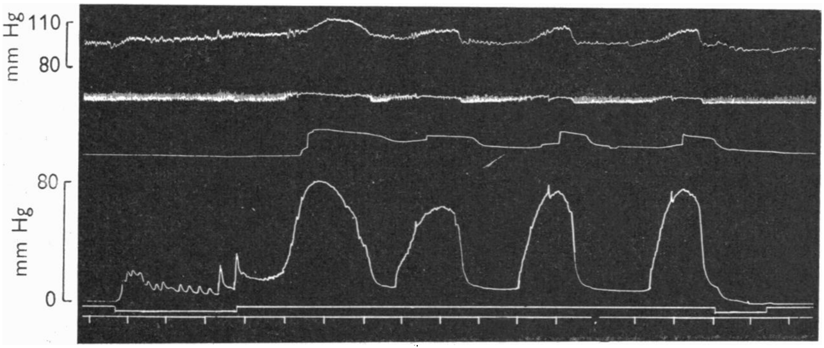

Fig. 7. Cat decerebrated through superior colliculus. Top trace, blood pressure in carotid artery; second trace, reflex contractions of semitendinosus muscle following stimulation of the lateral popliteal nerve on the same side; third trace, tension of contralateral gastrocnemius and soleus muscles; bottom trace, intravesical pressure. At the first signal mark the bladder was distended with 40 ml. of fluid at constant volume; at the second signal mark 40 ml. of fluid was withdrawn from the bladder. Time marker, 1 min.

Figure 8, which is from the same experiment as Fig. 5, shows that the effect of spontaneous bladder contractions upon the tone of the flexor muscles was greater than the effect produced by a sustained passive distension of a similar intravesical pressure. When the intravesical pressure rose to above 50 mm Hg there was a decrease in the flexor contractions, but the tone of the tibialis anterior muscle increased only slightly (less than 5 g increase of tension). When the flexor reflex had become very small, 20 ml. of fluid was withdrawn from the bladder and the intravesical pressure fell to about 10 mm Hg. This at once increased the reflex to above the original level. A spontaneous bladder contraction then occurred and at its height the reflex was again reduced, but only as long as the bladder contraction maintained a high intravesical pressure. During this bladder contraction the tibialis anterior tone increased by 10–15 g.

The subsequent increased flexor reflex which was produced as the bladder ceased to contract was then again considerably reduced by emptying the bladder.

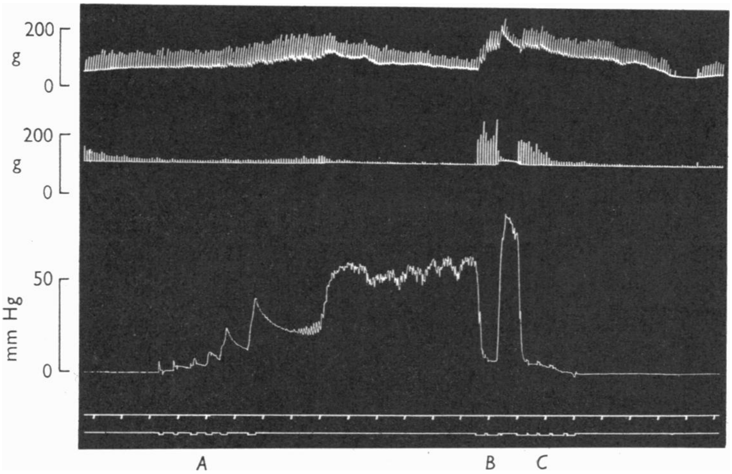

Fig. 8. Pre-collicular decerebrate cat (same experiment as Fig. 5). Top trace, reflex contractions of crossed extensor, recorded from the left gastrocnemius-soleus tendon following stimulation of the right medial popliteal nerve; middle trace, flexor reflex contractions of the right tibialis anterior muscle; lower trace, intravesical pressure. At each of the first 6 signal marks 10 ml. of fluid was introduced into the bladder down one channel of the catheter (*A*); at *B* 20 ml. of fluid was withdrawn, and a spontaneous bladder contraction followed immediately; at *C* the remaining fluid (45 ml.) was withdrawn. Time marker, 1 min.

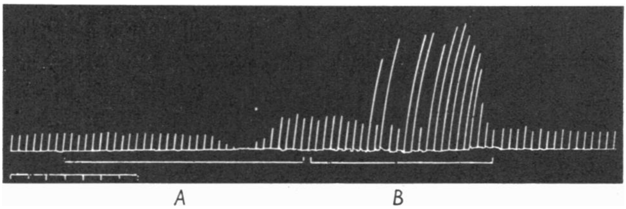

Fig. 9. Reflex contractions of the semitendinosus muscle, following stimulation of the ipsilateral medial popliteal nerve in a decerebrate cat. During the signal *A* the bladder catheter was connected to a constant-pressure reservoir 40 cm above the level of the bladder; during the signal *B* the reservoir was disconnected and the bladder was allowed to empty, 35 ml. being recovered. Time marker, 1 min.

In some experiments the flexor reflexes of the hind limb recovered while the bladder was still distended. This is illustrated in Fig. 9, in which reflex contractions of the semitendinosus muscle evoked by stimulation of the medial popliteal nerve recovered while the bladder was distended at a pressure of about 30 mm Hg (*A*).

A common finding in the decerebrate cat was the increase in amplitude of the flexor reflex above the original level upon emptying the bladder. This is illustrated in the middle trace of Fig. 8 when the intravesical pressure fell abruptly during emptying. In Fig. 9 a similar increase in the reflex response of the semitendinosus muscle occurred while the intravesical pressure was decreasing slowly (*B*), although occasional contractions of the muscles of the whole body were interposed in this section of the record.

Crossed extensor reflexes. During distension of the bladder at low pressure the crossed extensor contractions were often increased in amplitude. This was accompanied by an increase in the tone of the crossed extensor muscles. Bladder distension at high intravesical pressure, however, resulted in a dimi-

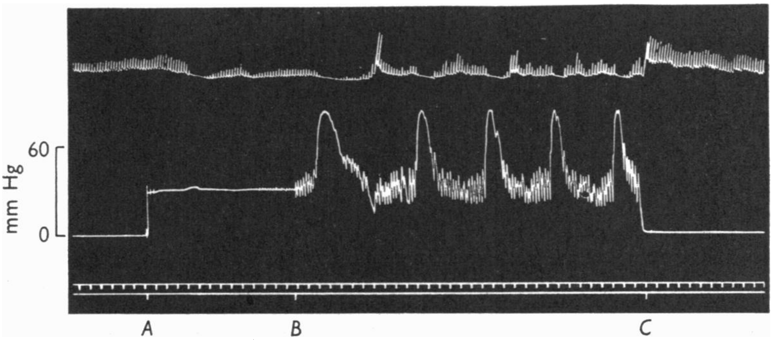

Fig. 10. Top trace, reflex contractions of the quadriceps muscle, following stimulation of the contralateral medial popliteal nerve in a decerebrate cat; lower trace, pressure in reservoir system. *A*, fluid into bladder at constant pressure; at *B* the reservoir tube was clamped and the true intravesical pressure was recorded at constant volume; *C*, bladder emptied of 23 ml. of fluid. Time marker, 30 sec.

nution of the reflex contractions and tended to decrease the crossed extensor muscle tone.

These findings are illustrated in Figs. 5, 8 and 10. The experiment from which Figs. 5 and 8 were obtained has been referred to, but only in connexion with the flexor reflexes. The upper tracings show the contractions recorded from the gastrocnemius-soleus tendon contralateral to the stimulated medial popliteal nerve. In both figures the crossed extensor reflex and gastrocnemius-soleus muscle tone increased when the bladder was distended at pressures up to about 30 mm Hg. Figures 5 and 8 show that at greater intravesical pressures the crossed extensor reflex tended to diminish in amplitude, sometimes becoming smaller than the original amplitude (Fig. 8). The tone of the crossed extensor muscle also commenced to fall at high intravesical pressures, but in the experiment of Figs. 5 and 8 it did not fall below the original level. The same result was obtained in the experiment illustrated in Fig. 10 in which the crossed extensor reflex was recorded from the patellar tendon in a decerebrate cat, after stimulation of the contralateral medial popliteal nerve. In the first portion of the record the catheter was connected to a reservoir about 40 cm above the level of the bladder and the record shows the pressure in the filling system, not the intravesical pressure. The amplitude of the reflex and the tone of the quadriceps muscle increased slightly during the first part of the filling but then declined, and the reflex disappeared during the third minute of bladder distension; muscle tone had by this time fallen to below the original level. Subsequently the crossed extensor reflex recovered partially, although the muscle tone remained decreased. In the latter portion of the record the reservoir tube was clipped and the intravesical pressure was recorded under conditions of constant volume; the spontaneous contractions of the bladder, which produced intravesical pressures up to 82 mm Hg, abolished the crossed extensor reflex and lowered the tone of the quadriceps muscle.

When the bladder was emptied the extensor reflexes and tone often immediately increased above the original level, as is illustrated in Fig. 10. In one preparation (Figs. 5 and 8) this rebound, which occurred upon emptying the bladder, was followed by a 2–3 min period during which the reflex contractions and tone gradually diminished, disappeared for about 1–2 min and then slowly recovered.

In one experiment, illustrated in Fig. 7, in which no crossed extensor reflex was obtained, a high intravesical pressure did not result, as usual, in a decreased extensor muscle tone but in an increased muscle tone. The bladder, which was distended with 40 ml. of Locke's solution, started to contract spontaneously, producing intravesical pressures rising to 60–80 mm Hg, during which the tone increased in the gastrocnemius-soleus muscles.

Acute spinal cats

The hind-limb flexor reflexes returned within a few minutes of transection of the thoracic spinal cord and had greater amplitude than before spinal transection. The crossed extensor reflex returned more slowly, if at all, and had a higher threshold. Bladder distension exerted effects upon these reflexes only after the lapse of 1 hr after spinal transection.

Flexor reflexes. Between 1 and 2 hr after spinal transection a slight increase was seen in the flexor reflexes of the hind limb when the bladder was distended at pressures above about 50 mm Hg (Figs. 6 and 11). Between 5 and 9 hr after spinal transection the increase in the flexor reflex produced by bladder distension was more obvious and in some experiments was accompanied by an increase in flexor tone (Fig. 11). Recovery periods longer than 9 hr have not been investigated. When the bladder was emptied the flexor reflex returned to the original level without passing through any phase of decreased activity.

Crossed extensor reflexes. The crossed extensor reflex was not readily elicited in the acute spinal preparations. In the experiment illustrated by Fig. 11 (i) the spinal cord had been transected at the 6th thoracic level 9 hr previously. Strong stimulation of the whole sciatic nerve 9 hr after transection of the cord produced small contractions of the contralateral gastrocnemius-soleus muscles. These contractions were increased when the bladder was distended with 50 ml. of Locke's solution. The tone of the gastrocnemius-soleus muscles was only slightly increased during the distension. Upon emptying the bladder the reflex contractions diminished slowly, but still remained above the original level 10 min after emptying was complete.

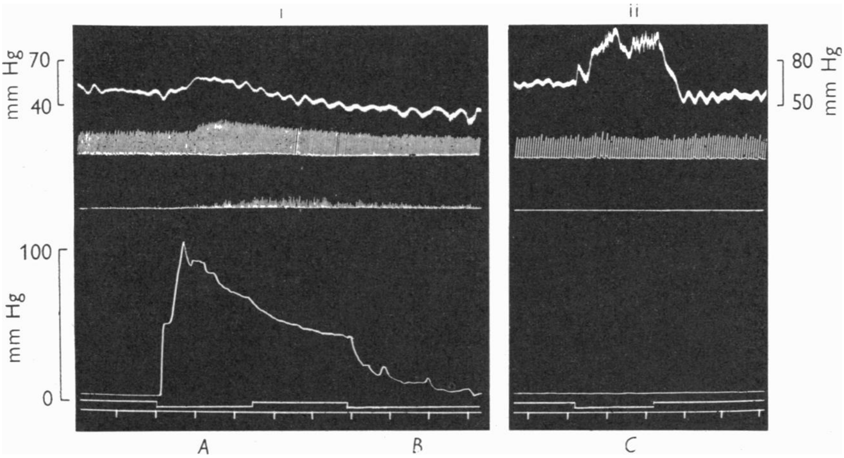

Fig. 11. Decerebrate cat with spinal cord transected 9 hr previously at the 6th thoracic level. (i). During the signal *A* 50 ml. of fluid was introduced into the bladder down one channel of the catheter, and withdrawn at signal *B*. (ii). During the signal *C* adrenaline hydrochloride 7 μg was infused intravenously. Top trace, blood pressure in carotid artery, second trace, flexor reflex contractions of the right semitendinosus muscle following stimulation of the ipsilateral sciatic nerve in record (i) and the medial popliteal nerve in record (ii); third trace, in record (i) crossed extensor contractions recorded in left gastrocnemius-soleus tendon (in (ii) no extensor reflex contractions were obtained); bottom trace, intravesical pressure. Time marker, 1 min.

Cats anaesthetized with chloralose

Flexor reflexes. At low intravesical pressures the flexor reflexes in chloralosed cats were unchanged. At high intravesical pressures the reflexes were either unchanged or were decreased in amplitude. When the bladder was emptied the reflexes returned to the original level without showing any enhancement. Figure 12 illustrates the diminution of the reflex contractions of the semitendinosus muscle during slow distension of the bladder from a constant-pressure reservoir. Approximately 3 min after the start of the distension the reflex contractions of the semitendinosus muscle became smaller and remained diminished while the bladder was distended. The reflex returned to the original amplitude immediately the bladder was allowed to empty.

Crossed extensor reflexes. The crossed extensor reflexes in chloralosed cats were never increased during bladder distension. The only effect of distending the bladder was to decrease the amplitude of the crossed extensor reflex, and this occurred at low and high pressures. Figure 13 illustrates the diminution in the reflex during distension of the bladder at a constant pressure of 7·5 mm Hg. At this low pressure the reflex partially recovered during the period of distension.

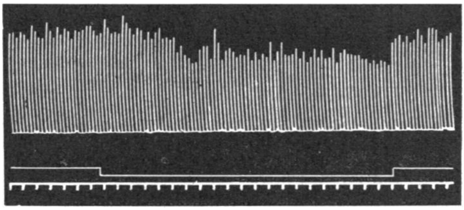

Fig. 12. Reflex contractions of semitendinosus muscle following stimulation of the ipsilateral medial popliteal nerve in a cat anaesthetized with chloralose. During the signal mark the bladder catheter was connected to a constant-pressure reservoir of Locke's solution 60 cm above the level of the bladder, which was allowed to fill slowly; 45 ml. of fluid was recovered at the end of distension. Time marker, 30 sec.

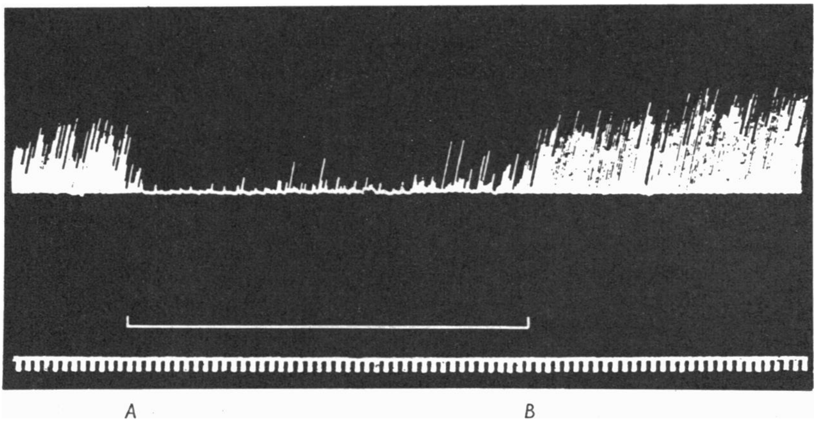

Fig. 13. Reflex extension of the whole leg recorded at the ankle, following stimulation of the contralateral medial popliteal nerve in a chloralosed cat. At *A* the bladder was filled with fluid from a reservoir 10 cm above the bladder; at *B* 22 ml. of fluid was withdrawn. Time marker, 10 sec.

Changes in blood pressure and respiration

The arterial blood pressure was increased by distension of the bladder at high intravesical pressures, but these blood-pressure changes were not responsible for the changes in hind-limb reflexes and muscle tone observed during bladder distension. For example, in the experiment illustrated in

Fig. 7 the spontaneous contractions of the bladder which changed the hind-limb reflexes of the decerebrated cat were accompanied by rises in blood pressure of about 10 mm Hg, shown on the top trace. In the same experiment the intravenous infusion of adrenaline HCl 15 μg during a period of 4 min 15 sec resulted in a rise of blood pressure of about 20 mm Hg, but apart from a slight transient increase in muscle tone the flexor contractions of the semitendinosus muscle remained unchanged.

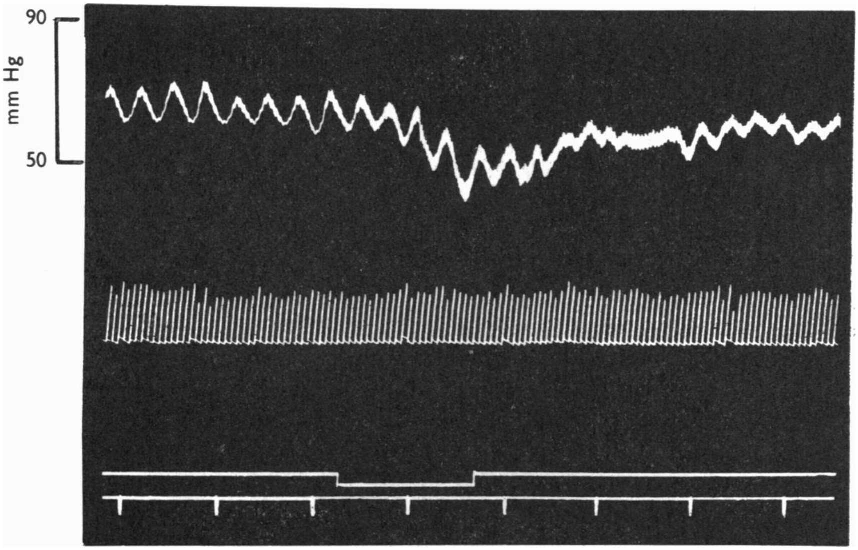

Fig. 14. Upper trace, blood pressure in the carotid artery of a decerebrate cat with spinal cord transected at T6 about 9 hr previously; middle trace, reflex contractions of the semitendinosus muscle following stimulation of the ipsilateral medial popliteal nerve. During the signal mark 20 ml. polyvinyl pyrrolidone was injected intravenously. Time marker, 1 min.

Figure 11 illustrates an experiment on a spinal cat in which bladder distension was accompanied by an increase in the flexor and crossed extensor reflexes and by a transient rise in blood pressure. When the bladder was empty, adrenaline HCl 7 μg was slowly infused intravenously and this raised the arterial blood pressure by about 30 mm Hg, but the flexor reflex and the tone in the semitendinosus and gastrocnemius-soleus muscles was unchanged.

In Fig. 14, from the same experiment as Fig. 11, the flexor reflex of the semitendinosus muscle is shown in the middle trace. During the signal mark, 3·8% 'polyvidone' was given by rapid intravenous injection (20 ml. in 1½ min). The subsequent 20 mm Hg fall in blood pressure had no effect upon either the tone or the reflex contractions of the semitendinosus muscle.

Bladder distension at high pressure was sometimes accompanied by an increase in the rate and depth of respiration and by sighing and gasping. These respiratory changes were not responsible for the effects upon the tone and reflexes in the hind limbs, for these changes in the reflexes and muscle tone often occurred when no changes in respiration were detectable. In the experiment illustrated by Fig. 15 the lower trace shows the flexor reflex contractions of the semitendinosus muscle, evoked by stimulation of the ipsilateral medial popliteal nerve. During the signal mark 4½ min of manual overventilation, which was followed by a short period of apnoea, had no effect on the tone or on reflex contractions of the semitendinosus muscle.

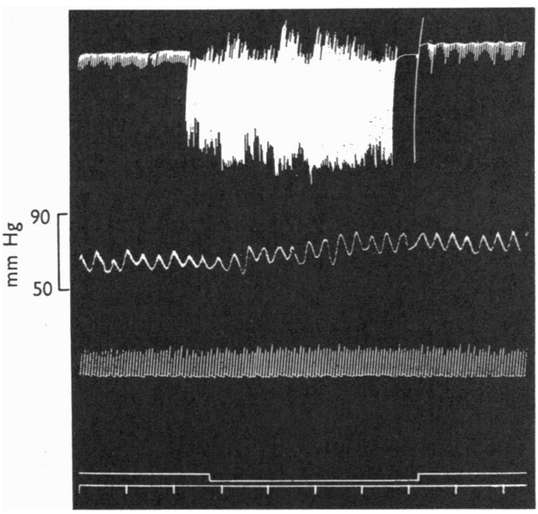

Fig. 15. Same experiment as Figs. 11 and 14. Top trace, respiration record from pneumograph, inspiration downwards; middle trace, blood pressure in the carotid artery; bottom trace, reflex contractions of the semitendinosus muscle following stimulation of the ipsilateral medial popliteal nerve. During the signal mark the animal was artificially over-ventilated. Time marker, 1 min.

DISCUSSION

In our previous experiments (Evans & McPherson, 1958) the effects of bladder distension on somatic reflexes were studied with electrophysiological methods. The finding that bladder distension decreased the mono- and polysynaptic reflexes was confirmed in the present series of experiments. The present experiments were mainly concerned, however, with the myographic examination of the effects of bladder distension on the hind-limb reflexes. Dusser de Barenne & Ward (1937) found that the knee jerk was depressed by distension of the bladder of the decerebrate cat and this is in agreement with our finding that the monosynaptic reflexes in the hind limb are depressed by bladder distension. Chernigovsky (1947) found that the flexor reflex in the hind limb of decerebrate cats was depressed by bladder distension and this was also confirmed in our experiments.

From the finding that bladder distension decreases the size of the monosynaptic response in both flexor and extensor reflex arcs, it may be inferred that afferent nerve fibres from the bladder have an inhibitory influence upon flexor and extensor motoneurones during rapid bladder distension. Since this inhibition is most marked in decerebrate cats, less marked in chloralosed and least marked in spinal cats, it appears that the visceral afferent pathways are depressed by anaesthesia and during spinal shock. Visceral reflexes are known to be depressed during spinal shock for a longer period than somatic reflexes (Creed, Denny-Brown, Eccles, Liddell & Sherrington, 1932).

In the previous series of experiments (Evans & McPherson, 1958) it was found that polysynaptic reflexes could be depressed by bladder distension in the absence of any decrease in the size of the monosynaptic response. From this it was inferred that afferent pathways from the bladder also exert an inhibitory effect on somatic interneurones. By using standard myographic techniques it has been possible to examine the polysynaptic reflexes of the hind limb in more detail, and to show that bladder distension exerts both inhibitory and excitatory influences on spinal somatic reflex arcs.

From the work of Talaat (1937) and Iggo (1955) it would seem likely that the excitatory influence of bladder distension at low intravesical pressures, upon flexor and crossed extensor reflexes in the decerebrate animal, is exerted by means of afferent nerve fibres from the bladder tension receptors. These authors showed that bladder tension receptors are activated at intravesical pressures of only a few millimetres of mercury, and adapt rapidly after firing at relatively high rates during the phase of rising intravesical pressure. If the excitatory effects of bladder distension, seen in our experiments at low pressures, were due to direct facilitation at either the motoneurones or somatic interneurones, one would expect to see evidence of facilitation of monosynaptic reflexes during the rising phase of bladder distension. This was never seen. Therefore, an alternative explanation of the excitatory effects must be sought.

The enhancement of hind-limb reflexes and tone at low intravesical pressures might be explained by an excitation of the gamma efferent (small motor nerve) system by afferents from tension receptors in the bladder. Such excitation would not facilitate the monosynaptic reflexes in our experiments because the peripheral nerves or spinal roots were divided. The gamma efferent system is known to be more active in cats decerebrated by supra- or intercollicular section than in anaesthetized preparations (Granit & Kaada, 1953). This would conform with our findings that the enhancement of the hind-limb reflexes and tone at low intravesical pressures has been seen in decerebrate but not in anaesthetized cats. Furthermore, the enhancement has always been more pronounced in the extensor muscles than in the flexor, and it is known that in decerebrate cats the activity of the gamma efferent system is greater in the nerves to the extensor muscles than in those to the flexor muscles.

The contrasting effects of high intravesical pressure require further explanation. Talaat (1937) demonstrated afferent fibres from the bladder which were not active at low pressures but which discharged at high rates when the intravesical pressure was above a certain threshold, which varied between 8 and 25 cm H_2O (6–18 mm Hg). These afferents accommodated slowly, continuing to discharge for 15–20 min when the intravesical pressure was greater than 45 cm H_2O (33 mm Hg). These afferents are probably nociceptive, as Denny-Brown & Robertson (1933) reported that discomfort is felt when intravesical pressure in man is about 18 cm H_2O (13 mm Hg).

At high intravesical pressures the somatic reflexes diminish in the decerebrate cat, and this diminution could be due to activity in the nociceptive bladder afferents. The facilitatory effects seen at lower pressures would be overcome by the high pressure effects, because nociceptive afferents are known to be prepotent in their actions (Sherrington, 1906). The diminution of the flexor and crossed extensor reflexes produced by high intravesical pressure in decerebrate or chloralosed cats might be due either to inhibition or occlusion. As both reflexes and tone fall together and there is a considerable rebound of the reflexes after distension ceases, it would seem more likely that a process of inhibition rather than occlusion is involved, except in the case of the flexor reflex at intravesical pressures greater than 50 mm Hg when the reflex is diminished but flexor muscle tone increases.

It has been shown by monosynaptic testing that there is some direct inhibition of motoneurones by bladder distension, but the degree of this inhibition is never sufficient to explain the total suppression of the flexor and crossed extensor polysynaptic reflex arcs which is so frequently observed. It must be assumed therefore that there is additional inhibition of the interneurones of these somatic polysynaptic reflex arcs. The mechanism that mediates this inhibition of the somatic arc interneurones is unknown at present.

The finding that, in decerebrate cats, the polysynaptic reflexes are depressed more than the monosynaptic reflex can perhaps be explained on the assumption that the somatic interneurones are inhibited by visceral afferents, entirely at the spinal level. However, in spinal animals the flexor and crossed extensor reflexes are increased by bladder distension at high pressures, and it is difficult to see how a segmental inhibition in a decerebrate animal could be changed to a facilitation by transection of the thoracic spinal cord. In order to explain the different effects of high-pressure bladder distension upon hind-limb reflexes, in decerebrate and acute spinal cats, it is necessary to consider supraspinal mechanisms. Certain regions of the medullary reticular formation are known to exert inhibitory influences upon hind-limb reflexes (Magoun & Rhines, 1946). Downman & Hussain (1958) have demonstrated a pathway which descends from the medial medullary reticular formation along the dorsolateral quadrant of the spinal cord. Cutting this descending inhibitory pathway results in augmentation of visceral and somatic polysynaptic reflexes in the spinal cat and also alters the pattern of interaction between visceral and somatic polysynaptic reflexes.

It seems probable that bladder afferents activated at high intravesical pressures would project to supraspinal centres along pathways in the ventrolateral quadrants of the spinal cord, similar to the splanchnic afferent pathways mapped by Downman & Evans (1957). This rostral projection of bladder nociceptors might provoke an increased inhibitory activity descending from the medial medullary reticular formation, and thus bring about a diminution in somatic reflex activity, when the intravesical pressure exceeded 15–30 mm Hg. Spinal transection would interrupt the pathways for such an inhibitory system and account for the fact that inhibition of somatic polysynaptic reflexes never occurred in the acute spinal cats of the present experiments. This supraspinal inhibition would not exclude the further possibility of occlusion of the flexor reflex in decerebrate cats, in the special circumstances in which the reflex decreases but muscle tone increases when the bladder is distended at pressures greater than 50 mm Hg.

The augmentation of the flexor and crossed extensor reflexes seen in acute spinal cats when the bladder is distended at high pressures is probably due to the unmasking of excitatory mechanisms which, in the decerebrate cat, are largely over-ridden by supraspinal inhibitory processes. Even in the decerebrate cat there is evidence that some excitatory mechanisms are operating when the intravesical pressure is above 50 mm Hg, e.g. the tone of the flexor muscles is increased and generalized movements of the trunk and limbs occur. Such generalized movements have also been described by Mellanby & Pratt (1940) at the height of a bladder contraction.

The finding that in the decerebrate cat distension of the bladder at pressures greater than 50 mm Hg increases flexor muscle tone and decreases the hind-limb reflexes is probably relevant to the rigidity of the abdominal muscles and the attitude of flexion seen during intra-abdominal disease. It is extremely likely that at intravesical pressures above 50 mm Hg pain afferents from the bladder are stimulated. A mechanism that gives protection to the abdominal contents by increasing muscle tone, and obviates the painful consequences of movement by inhibiting reflex activity, would be of considerable biological advantage to the organism.

SUMMARY

1. Somatic hind-limb reflexes have been studied during distension of the urinary bladder in decerebrate and acute spinal cats and in cats anaesthetized with chloralose.

2. Monosynaptic reflexes recorded electrically, with the dorsal and ventral spinal roots cut, were depressed during rapid distension of the bladder. This depression suggests a direct visceral influence upon motoneurones and was most marked in decerebrate cats.

3. Myographic techniques have shown that the flexor reflex in tibialis anterior and semitendinosus muscles, and the crossed extensor reflex in the quadriceps and gastrocnemius-soleus muscles, were depressed by bladder distension in chloralosed cats. This depression was often accompanied by a slight loss of muscle tone.

4. The flexor and crossed extensor reflexes were slightly enhanced by bladder distension at high pressures in acute spinal cats, but not during the first one or two hours after spinal transection. The enhancement was often accompanied by a slight rise in muscle tone.

5. The flexor and crossed extensor reflexes and tone were enhanced by bladder distension in decerebrate cats when the intravesical pressure was less than 15–30 mm Hg, but were depressed when the intravesical pressure was greater than this. At pressures above 50 mm Hg the reflexes remained depressed, but flexor muscle tone increased and generalized contractions of trunk and limb muscles were often seen.

6. It is suggested that in the decerebrate animal the enhancement of the somatic reflexes at low intravesical pressures may be mediated by bladder tension receptors acting upon the small-motor-nerve (gamma-efferent) system. The high pressure depression of somatic reflexes may be partly due to increased supraspinal inhibition, provoked by nociceptive bladder afferents. The excitatory effects of high intravesical pressures are probably due to spinal mechanisms.

We should like to acknowledge the advice and encouragement of Sir Lindor Brown, Dr W. Feldberg and Dr J. L. Malcolm.

REFERENCES

Chernigovsky, B. N. (1947). Enteroceptors and skeletal muscles. *Physiological Journal, U.S.S.R.* **33**, 657–672.

Creed, R. S., Denny-Brown, D., Eccles, J. C., Liddell, E. G. T. & Sherrington, C. S. (1932). *Reflex Activity of the Spinal Cord.* Oxford University Press.

Denny-Brown, D. & Robertson, E. G. (1933). On the physiology of micturition. *Brain*, **56**, 149–190.

Downman, C. B. B. & Evans, M. H. (1957). The distribution of splanchnic afferents in the spinal cord of cat. *J. Physiol.* **137**, 66–79.

Downman, C. B. B. & Hussain, A. (1958). Spinal tracts and supraspinal centres influencing visceromotor and allied reflexes in cats. *J. Physiol.* **141**, 489–499.

Dusser de Barenne, J. G. & Ward, A. A. (1937). Reflex inhibition of the knee-jerk from intestinal organs. *Amer. J. Physiol.* **120**, 340–344.

Evans, M. H. (1958). A simple intensity modulator for electrophysiology. *J. Physiol.* **142**, 8–9*P*.

Evans, M. H. & McPherson, A. (1958). The effects of stimulation of visceral afferent nerve fibres on somatic reflexes. *J. Physiol.* **140**, 201–212.

Fulton, J. F. (1955). *A Textbook of Physiology*, 17th ed. pp. 205–206. Philadelphia: Saunders.

GRANIT, R. & KAADA, B. R. (1953). Influence of stimulation of central nervous structures on muscle spindles in cat. *Acta physiol. scand.* **27**, 130–160.

IGGO, A. (1955). Tension receptors in the stomach and the urinary bladder. *J. Physiol.* **128**, 593–607.

MAGOUN, H. W. & RHINES, R. (1946). An inhibitory mechanism in the bulbar reticular formation. *J. Neurophysiol.* **9**, 165–172.

MELLANBY, J. & PRATT, C. L. G. (1940). The reactions of the urinary bladder of the cat under conditions of constant volume. *Proc. Roy. Soc.* B, **128**, 186–201.

RIDDOCH, G. (1917). The reflex functions of the completely divided spinal cord in man, compared with those associated with less severe lesions. *Brain*, **40**, 264–402.

SHERRINGTON, C. S. S. (1906). *The Integrative Action of the Nervous System.* Yale University Press.

TALAAT, M. (1937). Afferent impulses in the nerves supplying the urinary bladder. *J. Physiol.* **89**, 1–13.