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SCRATCHING MOVEMENTS AND FACILITATION OF THE SCRATCH REFLEX PRODUCED BY TUBOCURARINE IN CATS

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Recently Feldberg & Fleischhauer (1960) have shown that in cats anaesthetized with pentobarbitone sodium, tubocurarine applied to the dorsal surface of the exposed cervical cord at the level of C1 produces muscular activity in the hind legs. As the pattern of this activity resembled that of the scratch reflex, they concluded that tubocurarine elicits scratching movements by its action on a restricted area of the upper cervical cord. The present experiments are a continuation of this work. They show that tubocurarine is effective also when applied to the level of C2 and that besides eliciting scratching movements, it facilitates the scratch reflex which can be evoked by rubbing the pinna of the ear or the skin behind the ear. When the effects of tubocurarine were compared in cats anaesthetized with pentobarbitone sodium and in decerebrate cats, a difference in the pattern of movements was observed. The movements were usually more rhythmic during pentobarbitone sodium anaesthesia and more sustained in decerebrate cats.

METHODS

Cats weighing 2·1–3·5 kg were used. They were either anaesthetized with pentobarbitone sodium (33 mg/kg) injected intraperitoneally, additional amounts being injected during the course of prolonged experiments, or decerebrated at the anterior collicular level under ethyl chloride–ether anaesthesia.

The experimental procedures were essentially those employed by Feldberg & Fleischhauer (1960). The cat was lying on its belly and the head was fixed to the ear bars of a head holder, similar to the Horsley–Clark stereotaxic instrument. The upper cervical cord was exposed and myographic records were taken from the tibialis anterior muscles.

In order to apply tubocurarine to the exposed dorsal surface of the cervical cord, tubocurarine chloride was dissolved in an artificial cerebrospinal fluid (c.s.f.) of the composition given by Merlis (1940). A pledget of cotton wool was soaked in this solution and placed on the desired region of the cervical cord. The procedure frequently adopted was that of leaving the tubocurarine on the cord for periods of 15 min and washing the cord with pledgets soaked in artificial c.s.f. for periods of 30 min. The pledgets were changed every few minutes.

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The scratch reflex was evoked by rubbing either the pinna of the ear between the fingers or the skin of the neck behind the ear.

In two experiments the effect of chloralose was investigated during pentobarbitone sodium anaesthesia. The chloralose (30 mg/kg) was injected, in a 1% solution, into the superficial vein of the right foreleg.

In several experiments the medulla oblongata was transected below the obex, sometimes after hemisection at the level indicated in Fig. 1 of Feldberg & Fleischhauer (1960).

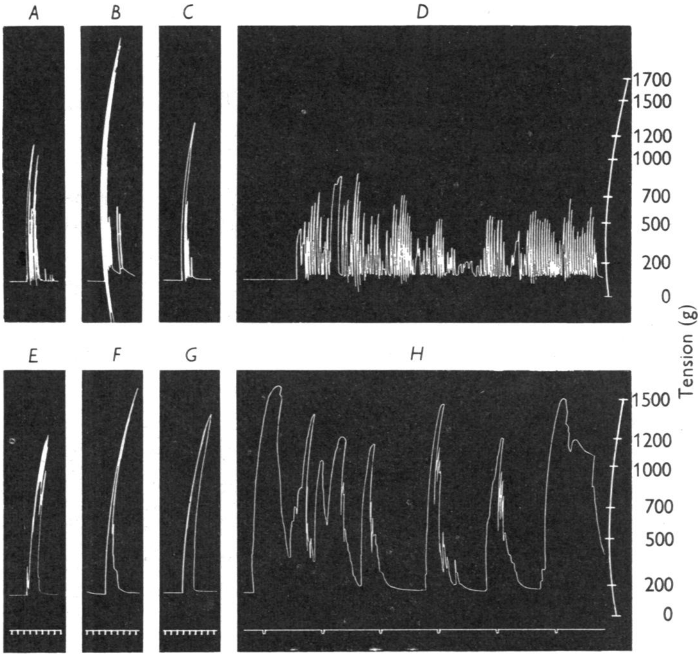

Fig. 1. Records of anterior tibialis muscles of four cats anaesthetized with pentobarbitone sodium (*A* to *D*), and of four decerebrate cats (*E* to *H*). Muscular activity produced by application of tubocurarine 1/1000 to the dorsal surface of the cervical cord at the level of C1, with the exception of cat G where it was applied at the level of C2. Time marker, 10 sec.

RESULTS

Cats anaesthetized with pentobarbitone sodium

Scratching movements of the hind legs were obtained not only on application of tubocurarine dissolved in artificial c.s.f. to the dorsal surface of the cervical cord at the level of C1, but also down the cord to the level of C2, although here higher concentrations of the drug were required.

Spontaneous muscular activity. Figure 1 shows typical bursts of scratching movements at *A–C* and a period of more continuous rhythmic activity at *D* during application of tubocurarine 1/1000 at the level of C1. The effects, which are often associated with extension and adduction of the ipsilateral foreleg, are similar to those described by Feldberg & Fleischhauer (1960). In one experiment the muscular activity in the hind leg consisted of intermittent sustained contractions. The onset of this activity in the left tibialis muscle is illustrated at *H* in Fig. 2.

When applied at the level of C1, tubocurarine in a concentration of 1/2000 was effective in all experiments; a concentration of 1/5000 was tested in two experiments but produced muscular movements in only one.

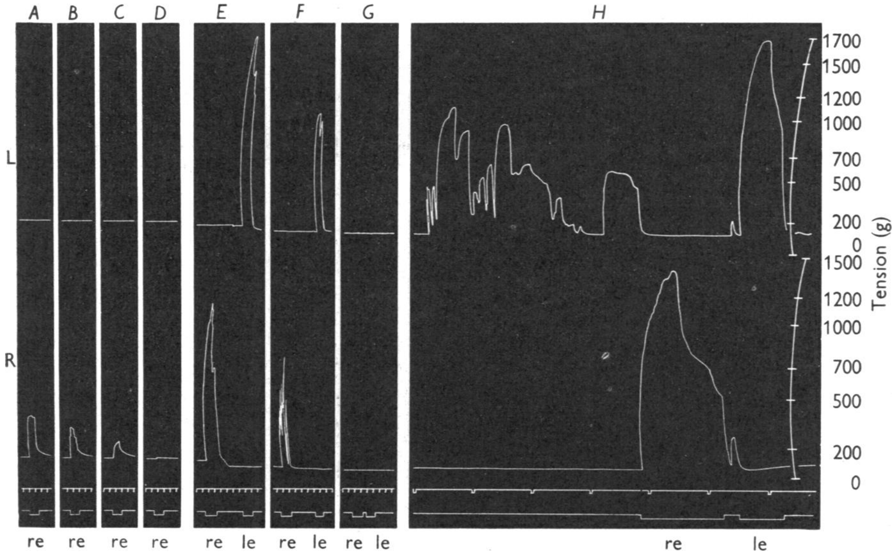

Fig. 2. Records of left (L) and right (R) anterior tibialis muscles of a cat anaesthetized with pentobarbitone sodium. *A*, a few minutes after exposure of the upper cervical cord before application of tubocurarine; *B*, *C* and *D*, 5, 10 and 15 min later. *E*, during application of tubocurarine 1/5000 to the dorsal surface of the cervical cord at the level of C1. *F* and *G*, 10 and 20 min after removal of the tubocurarine. *H*, during application of tubocurarine 1/2000 at the level of C1. On the right, tension in grams. Bottom signals indicate the periods of rubbing the left or right ear (le and re). Time marker, 10 sec.

In this experiment 1/10,000, applied for 15 min, was weakly effective. The response was delayed until 4 min after removal of the tubocurarine and consisted of a few contractions in one leg only. The tension developed in the tibialis muscle was approximately 100 g.

When the tubocurarine was removed and the surface of the cervical cord was washed repeatedly with pledgets soaked in artificial c.s.f., the muscular activity gradually subsided, the contractions becoming progressively weaker and less frequent, and ceasing within 15–40 min, according to the concentration of the tubocurarine used and the duration of its application.

Tubocurarine applied at the level of C2 in a concentration of 1/2000 produced no muscular movements; 1/1000 did so, but not in all experiments, and sometimes in one hind leg only, although the tubocurarine was applied to both sides of the cervical cord. In some experiments the effect consisted of a few weak contractions which occurred after a long delay; in others the contractions were as strong as those obtained with tubocurarine

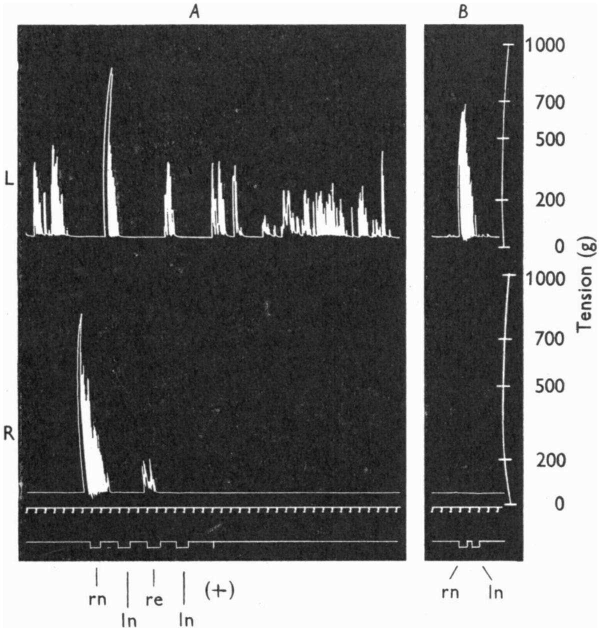

Fig. 3. Records of left (L) and right (R) tibialis anterior muscles of a cat anaesthetized with pentobarbitone sodium. *A*, during the end of a 15 min period of application of tubocurarine 1/1000 to the dorsal spinal surface at the level of C2. Tubocurarine removed at (+). *B*, 25 min after removal of the tubocurarine. Bottom signal indicates the periods of rubbing the left or right ear (le and re) and the skin of the neck behind the left or right ear (ln and rn); for details see text. Time marker, 10 sec.

1/1000 applied at the level of C1. Figure 3 illustrates an experiment in which the application of tubocurarine 1/1000 at the level of C2 caused contractions in the left hind leg only.

In one experiment tubocurarine was applied transversely to a restricted region between the levels of insertion of the sensory roots of C1 and C2, by means of a cotton thread used as a wick. Spontaneous scratching movements occurred, as illustrated in Fig. 4.

Tubocurarine 1/1000 applied at the level of C3 failed to produce muscular effects, even in those experiments in which the application at the level of C2 caused strong contractions.

Scratching movements elicited by skin stimulation. Before the tubocurarine was applied, rubbing the pinna of the ear or the skin behind the ear usually produced no muscular effects. In a few experiments, however, there was a short period immediately following the exposure of the upper cervical cord during which such stimulation produced scratching movements in the ipsilateral hind leg. This over-excitability always decreased rapidly and the skin stimulation became ineffective within 15–30 min. In one experiment the response to rubbing an ear during this initial period of

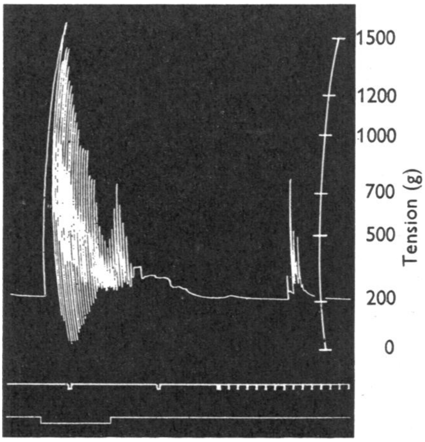

Fig. 4. Record from the left tibialis anterior muscle of a cat anaesthetized with pentobarbitone sodium. A scratch reflex evoked on rubbing the pinna of the left ear and a spontaneous burst of smaller scratching movements during application of tubocurarine 1/1000 between the levels of insertion of the sensory roots of C1 and C2 by means of a cotton thread used as a wick. Bottom signal indicates the period of rubbing the pinna of the left ear. Time marker, 10 sec.

over-excitability did not consist of rhythmic beats but of a weak sustained contraction, as illustrated at *A*, *B* and *C* in Fig. 2. This effect, which occurred on the left side only, was obtained in the experiment in which the spontaneous movements on application of tubocurarine also consisted of sustained contractions.

When tubocurarine was applied to the region of C1 in a concentration evoking spontaneous movements, bursts of scratching movements could always be elicited in a hind leg on rubbing the ipsilateral ear, but not on rubbing the skin behind the ear. When a scratching response was evoked by rubbing the ear, any spontaneous activity present in the opposite hind leg ceased. Rubbing the ear did not evoke movements in the foreleg. A typical evoked scratching response of the left tibialis muscle is illustrated in Fig. 5. The response was obtained on the application of tubocurarine 1/2000 during an interval between spontaneous movements, and was recorded on a fast drum the better to illustrate the individual beats. The left ear was rubbed for about 7 sec; the response began as soon as the ear was touched, but rhythmic beats continued for a few seconds after cessation of stimulation. The evoked scratching movements were often stronger than those occurring spontaneously (see Figs. 3 and 6).

In the one experiment in which the spontaneous movements following application of tubocurarine 1/1000 at the level of C1 consisted of sustained irregular contractions, rubbing the ears also produced sustained contractions without rhythmic beats, as is shown at *H* in Fig. 2.

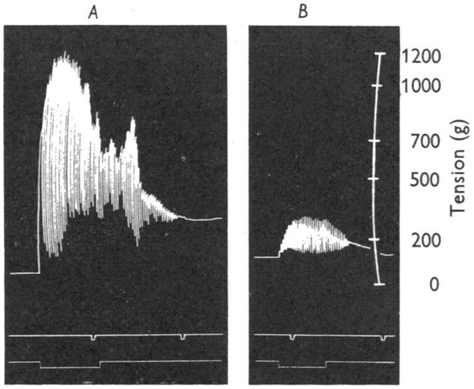

Fig. 5. Records from the left tibialis anterior muscle of a cat anaesthetized with pentobarbitone sodium. Two scratching responses evoked on rubbing the pinna of the left ear during application of tubocurarine 1/2000 (at *A*) and 1/1000 (at *B*) to the dorsal surface of the cervical cord at the level of C1. *B* was taken a few minutes after transection of the medulla just below the obex. Bottom signals indicate the periods of rubbing the pinna. Time marker, 10 sec.

In those experiments in which tubocurarine 1/1000 applied to the region of C2 produced spontaneous movements, scratching movements could be evoked by rubbing the pinna and sometimes also by rubbing the skin behind the ear. In fact, in one experiment this stimulus evoked stronger scratching movements than rubbing the pinna. Usually, however, rubbing the pinna was the stronger, and sometimes the only effective, stimulus. Figure 3 illustrates an experiment in which the scratching movements evoked from the pinnae were stronger than those evoked by rubbing the skin behind the ears; they were also stronger than the movements which occurred spontaneously.

In the one experiment in which the tubocurarine was applied transversely to a restricted region between the levels of insertion of the sensory roots of C1 and C2, rubbing the pinna evoked a strong scratch reflex (see Fig. 4).

The scratching movements evoked on skin stimulation occurred not only during periods of spontaneous movements caused by the application of tubocurarine, but also during the latent period before the spontaneous movements began and for some time after their cessation on removing the tubocurarine from the cervical cord. A concentration of tubocurarine too weak to produce spontaneous movements was sufficient to evoke scratching movements on skin stimulation. Some of these results are seen in Figs. 2 and 3.

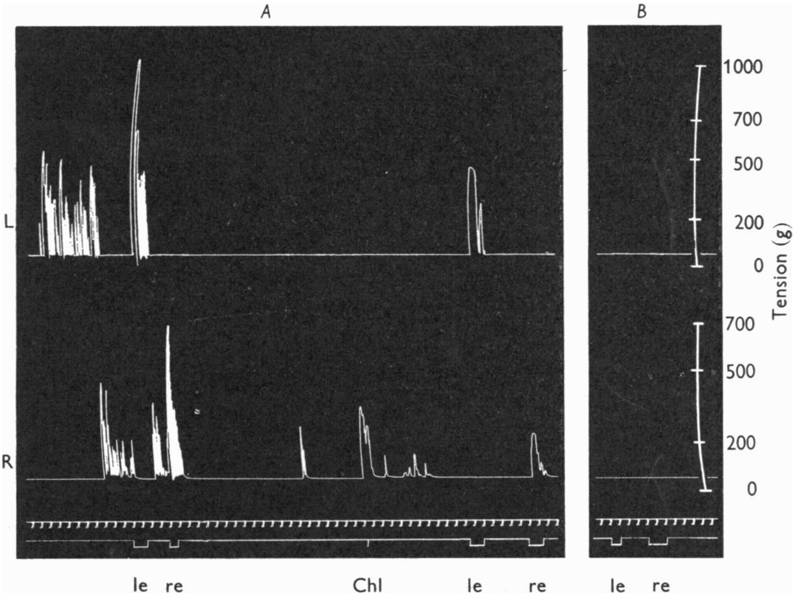

Fig. 6. Records of left (L) and right (R) tibialis anterior muscles of a cat anaesthetized with pentobarbitone sodium. Tubocurarine 1/1000 had been applied for 15 min to the dorsal surface of the cervical cord at the level of C1. *A*, about 15 min after removal of the tubocurarine. *B*, 20 min after *A*, during renewed application of tubocurarine. Bottom signals indicate the periods of rubbing the pinna of the left or right ear (le and re) and the intravenous injection of chloralose 30 mg/kg (Chl). Time marker, 10 sec.

In the experiment of Fig. 2, tubocurarine 1/5000 applied at the level of C1 for 15 min produced no muscular activity, yet during and for some time after its application rubbing a pinna evoked strong responses. These consisted of a sustained contraction without rhythmic beats (at *E* and *F*). In this experiment the spontaneous muscular movements were also sustained contractions.

In the experiment of Fig. 3 (at *A*), the application of tubocurarine 1/1000 to the level of C2 produced spontaneous movements in the left hind leg only, yet rubbing the ear or the skin behind it evoked ipsilateral scratching responses in both hind legs. Thirty minutes after removal of the tubocurarine, when the spontaneous activity in the left tibialis muscle had ceased, rubbing the left ear still produced the characteristic scratching response (Fig. 3 at *B*).

As the evoked scratching responses gradually subsided after removal of the tubocurarine, they not only became weaker but were often delayed as well. The movements no longer began immediately on touching the sensitive skin areas, but only after they had been rubbed for several seconds.

Apart from the two restricted areas, rubbing the skin of any other part of the body, such as the shoulder, the ribs, or the face, did not evoke scratching movements when tubocurarine was applied to the level of C1 or C2. Touching the whiskers was also ineffective.

When tubocurarine 1/1000 was applied to the level of C3, rubbing the skin of any part of the body was ineffective in evoking scratching movements.

Additional pentobarbitone sodium and chloralose. When a dose of pentobarbitone sodium 15 mg/kg, which is a little less than half the dose used initially for the anaesthesia, was injected intraperitoneally, the spontaneous activity produced by the tubocurarine was attenuated for 2–2½ hr. The strength of contractions of the tibialis muscles diminished and the intervals between the bursts of activity lengthened. The degree of attenuation varied in different experiments.

In two cats anaesthetized with pentobarbitone sodium chloralose 30 mg/kg was injected intravenously. This dose, which is a little less than half the full anaesthetic dose, abolished the muscular activity produced by tubocurarine, as is shown in Fig. 6. Both the spontaneous activity and the evoked responses were abolished, without recovery during the following 3 hr.

Hemisection and transection of the medulla. Hemisection of the medulla below the obex did not affect, or only slightly decreased the strength of contractions produced by tubocurarine or of evoked responses in both hind legs. Transection of the medulla, whether or not preceded by hemisection, always resulted in an immediate large reduction in the strength of the spontaneous movements. The evoked responses were also greatly reduced but, as is illustrated in Fig. 5*B*, their rhythm remained unchanged. In those experiments which were continued for 1½–2 hr after the transection the reduced activity persisted.

Decerebrate cats

Feldberg & Fleischhauer (1960) showed that decerebration did not abolish the spontaneous movements which occur on topical application of tubocurarine to the upper cervical cord. In their experiments decerebration was carried out during pentobarbitone sodium anaesthesia, so that the effect of this anaesthetic was not excluded. In the present experiments decerebration was performed under a volatile anaesthetic and the tubocurarine effect was investigated later, at a time when it could no longer be influenced by the anaesthetic agent. The characteristics of the response to tubocurarine in these animals were that the strength of the movements in the hind legs was usually stronger, and that the movements tended to be more sustained than in cats anaesthetized with pentobarbitone sodium. These differences applied to the spontaneous activity and to the evoked responses. Movements of the foreleg were also much more pronounced.

Spontaneous muscular activity. When tubocurarine was applied at the level of C1 or C2, spontaneous movements in the hind legs began after a latency which varied between 2 and 15 min. The flexion of the hind leg which initiates a scratching movement was often sustained and not followed by the typical strong beats, so that the response was not easily recognizable as a scratching movement. The tension developed in the tibialis muscles sometimes reached 2 kg or more. Relaxation occurred with or without rhythmic beats. Succeeding similar contractions often followed at random. Sometimes the activity in the tibialis muscle was interrupted by periods of quiescence lasting several minutes. When the tubocurarine was applied by means of a cotton thread to one side of the cord, the response occurred in the ipsilateral leg; when applied to both sides, responses occurred in both hind legs, but alternately. When the application was continued the maximum tension developed during these contractions tended to decrease. On removal of the tubocurarine from the spinal cord the subsidence of spontaneous movements was the same as that described in cats anaesthetized with pentobarbitone sodium. Figure 1 illustrates, in the lower records, typical sustained contractions of the tibialis muscle with no, or only a few, signs of rhythmic beats and, in contrast, in the upper records, the rhythmic pattern of movements obtained under pentobarbitone sodium anaesthesia. The contractions at *E*, *F* and *G* last approximately 20 sec. They are followed by periods of quiescence and correspond to the bursts of rhythmic beats seen during pentobarbitone anaesthesia. At *E* such rhythmic beats are in fact seen to be superimposed on the strong contraction. Even when the record suggests a single sustained contraction, there are often small rhythmic movements of the foot which are too weak to be recorded by the lever system used. At *H* the record is taken on a faster drum and illustrates the random nature of the sustained contractions.

In a few experiments the muscular effect consisted of typical scratching movements or bursts of rhythmic beats characteristic of the experiments in pentobarbitone sodium anaesthesia. In yet other experiments the muscular effect began with a burst of rapid rhythmic activity, followed by more sustained irregular contractions. In all experiments in which the pattern of movements consisted mainly of irregular sustained contractions there were, nevertheless, from time to time, periods in which bursts of rhythmic beats occurred.

The pattern and strength of muscular movements were essentially the same whether the tubocurarine was applied at the level of C1 or C2, but at the level of C1 lower concentrations were effective. At C1 spontaneous movements occurred with a concentration as low as 1/5000, but at C2 only with 1/1000, and at C3 even 1/1000 was ineffective.

Strong activity in a hind leg was associated with extension, elevation and adduction in the ipsilateral foreleg, whilst the claws were often protruded. The movement resembles that made by a cat when wiping something off its face.

Scratching movements elicited by skin stimulation. Before the application of tubocurarine, scratching movements on rubbing the ear, or the skin behind it, were obtained only immediately following the exposure of the dorsal surface of the upper cervical cord. The over-excitability, as in cats under pentobarbitone sodium, decreased rapidly and the skin stimulation became ineffective.

When tubocurarine was applied at the level of C1, rubbing the ear evoked scratching movements in the ipsilateral hind leg, often accompanied by movements of the ipsilateral foreleg. Rubbing the skin behind the ear was ineffective. When tubocurarine was applied at the level of C2, scratching movements of the hind leg were regularly obtained on rubbing the skin behind the ear, but seldom on rubbing the pinna itself. With both sites of application rubbing the skin of any other part of the body was ineffective. When tubocurarine was applied to one side of the cervical cord, the evoked scratching movements were obtainable on the same side only. When tubocurarine was applied at the level of C3, no scratching movement could be evoked on rubbing the ear, the skin behind it, or elsewhere.

The scratching movements evoked by skin stimulation were obtained in the period preceding spontaneous movements, during spontaneous activity, and for some time after it had ceased following removal of the tubocurarine. When spontaneous activity was present the evoked movements were most clearly demonstrated during intervals of quiescence. They could also be elicited with tubocurarine in concentrations too weak to produce spontaneous movements, for instance, with 1/10,000 applied at the level of C1 and with 1/2000 at the level of C2.

The pattern of the evoked scratching movement was usually a sustained contraction with or without a superimposed series of weak beats. Sometimes, however, it consisted of a series of strong rhythmic beats. This appeared to be related to whether the spontaneous activity consisted primarily of bursts of rhythmic beats, or, as was more usual, of sustained contractions; in general, however, the evoked responses tended to be more rhythmic than the spontaneous movements. The evoked responses sometimes outlasted the period of skin stimulation for a few seconds and were often stronger than those occurring spontaneously. Representative results are illustrated in Figs. 7, 8 and 9. In the experiment of Fig. 7 tubocurarine 1/1000 was applied for 15 min to both sides of the cord at the

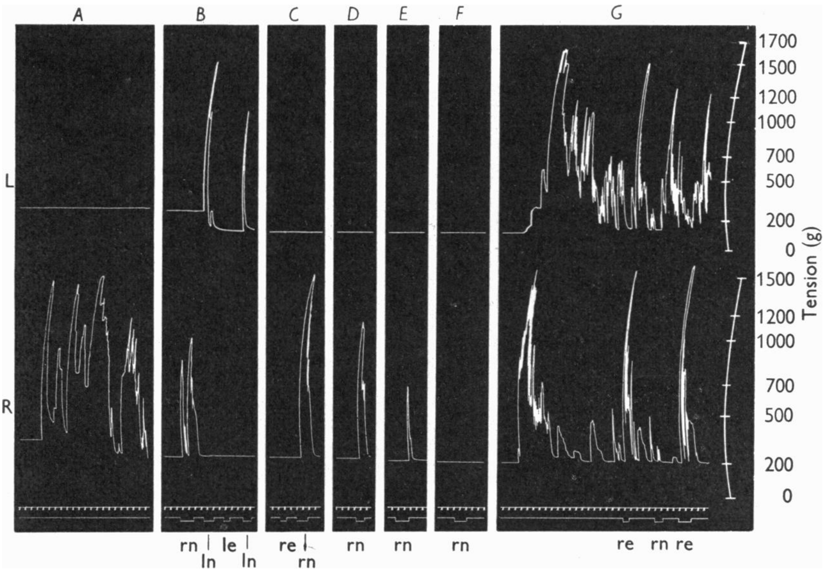

Fig. 7. Records of left (L) and right (R) anterior tibialis muscles of a decerebrate cat. *A*, during application of tubocurarine 1/1000 dorsally at the level of C2. *B*, 8 min after removal of the tubocurarine and subsidence of the spontaneous movements. *C*, *D*, *E* and *F*, 15, 30, 35 and 40 min, respectively, after removal of the tubocurarine. *G*, during application of tubocurarine 1/1000 at the level of C1. Bottom signal indicates the periods of rubbing the pinna of the left or right ear (le and re) and the skin of the neck behind the left or right ear (ln and rn); for details see text. Time marker, 10 sec.

level of C2. Spontaneous muscular activity occurred on the right side only (at *A*); yet (at *B*) the right hind leg as well as the left responded to stimulation of the skin behind the ear, but rubbing the pinna itself was ineffective. Following removal of the tubocurarine this evoked response disappeared on the left side within 15 min whilst it was still obtainable on the right side (at *C*). It decreased gradually on this side too, and 35 min after removal of the tubocurarine the response was reduced and occurred only after the skin had been rubbed for 20 sec (at *E*). Forty minutes after removal of the tubocurarine the response was absent (at *F*). On the other hand, when tubocurarine was applied at the level of C1, rubbing the ears produced strong evoked responses in both legs. This is illustrated for the right tibialis muscle at *G*. The moment the ear was touched a strong contraction occurred followed by weaker rhythmic beats. Rubbing the skin behind the ear was ineffective.

Figures 8 and 9 illustrate two patterns of responses evoked by rubbing the ear, recorded on a faster drum. The effects were obtained after the

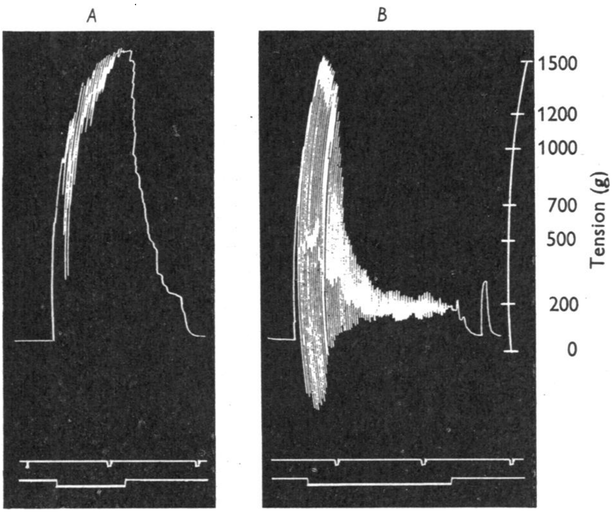

Fig. 8. Records of the left anterior tibialis muscle of a decerebrate cat. Evoked responses on rubbing the pinna of the left ear before (at *A*) and 2 hr after (at *B*) an intraperitoneal injection of pentobarbitone sodium 30 mg/kg. The responses were obtained a few minutes after removal of tubocurarine 1/5000 (at *A*) and 1/1000 (at *B*), after spontaneous activity had ceased. The tubocurarine had been applied dorsally at the level of C1 each time for 15 min. Bottom signals indicate the periods of rubbing the pinna of the left ear; for details see text. Time marker, 10 sec.

disappearance of spontaneous movements following removal of tubocurarine from the region of C1. In the experiment of Fig. 8 the pattern of spontaneous activity produced by tubocurarine had been that of sustained irregular contractions, whereas Fig. 9 is from one of the few experiments in which the spontaneous activity was characterized by bursts of rhythmic beats. These two patterns are reflected in the evoked responses as well. Figure 9 also illustrates that the evoked response occurs in the ipsilateral leg only.

Effect of pentobarbitone sodium. In the decerebrate cat the intraperitoneal injection of pentobarbitone sodium 20–30 mg/kg not only diminished the strength of the spontaneous contractions to a varying extent but also changed their character, i.e. they became more rhythmic. The evoked responses showed the same change but did not necessarily decrease in strength. These results are illustrated in Figs. 8 and 10. Figure 8 shows the change in pattern of the evoked response on rubbing the left ear and Fig. 10, from the same experiment, the changes in spontaneous activity

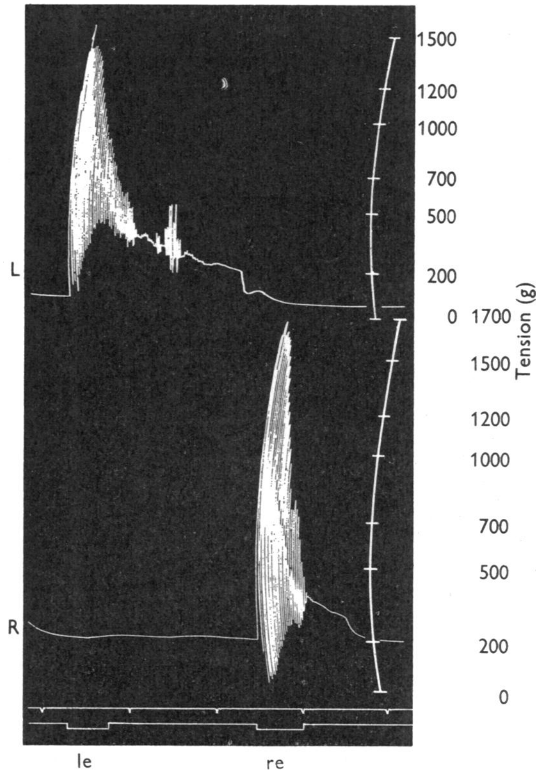

Fig. 9. Records of the left (L) and right (R) anterior tibialis muscles of a decerebrated cat. Evoked responses on rubbing the left (le) and right (re) ear a few minutes after removal of tubocurarine 1/1000 and after cessation of spontaneous activity. The tubocurarine had been applied dorsally at the level of C1 for 15 min. Bottom signals indicate the periods of rubbing the pinnae of the ears. Time marker, 10 sec.

following intraperitoneal injection of pentobarbitone sodium 30 mg/kg. The spontaneous activity produced by the application of tubocurarine 1/5000 decreased in the left hind leg and became more rhythmic in character. In the right hind leg it was abolished, but rubbing the ear was still effective (at *B*). When the concentration of tubocurarine was increased to 1/1000 spontaneous activity reappeared in both legs (at *C*).

Transection of the medulla. Transection of the medulla below the obex greatly reduced spontaneous activity produced by tubocurarine as well as the evoked responses, which in addition became more rhythmic in character. Unlike the results obtained in the cats under pentobarbitone sodium anaesthesia, in decerebrate cats the activity ceased within 10 min of transection.

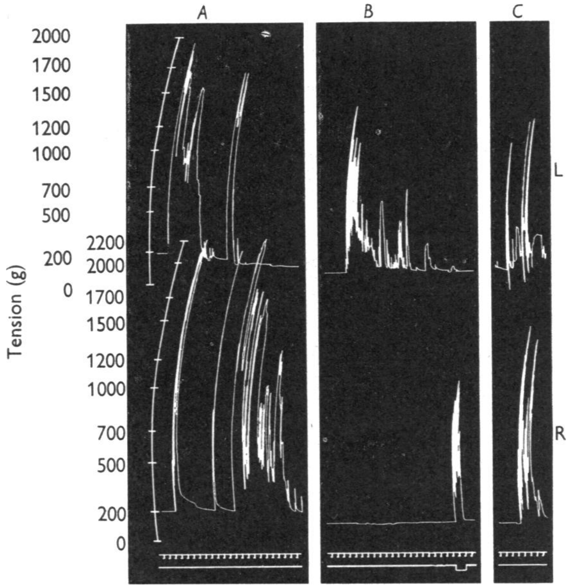

Fig. 10. Records of left (L) and right (R) anterior tibialis muscles of a decerebrate cat before (at *A*) and after (at *B* and *C*) intraperitoneal injection of pentobarbitone sodium 30 mg/kg, during the dorsal application of tubocurarine 1/5000 (at *A* and *B*) and 1/1000 (at *C*) at the level of C1. Bottom signal in *B* indicates a period of rubbing the pinna of the right ear. Time marker, 10 sec.

DISCUSSION

Feldberg & Fleischhauer's (1960) conclusion that the movements seen during tubocurarine application to a restricted area of the cervical cord at the level of C1 were scratching movements was based on the observed similarity between these movements and those a cat makes when scratching itself. The movements of the hind legs were considered to be those of a scratch reflex. These conclusions are no longer based solely on this similarity but also on the finding that tubocurarine facilitates the scratch reflex evoked on rubbing the pinna of the ear or the skin behind it.

In the present experiments scratching movements as well as facilitation of the scratch reflex were obtained when the tubocurarine was applied not only at the level of C1 but also at the level of C2. At the level of C2, however, a stronger concentration of tubocurarine was required to produce these effects; even a concentration of 1/1000 was not always effective. This explains why Feldberg & Fleischhauer did not obtain an effect when they applied the tubocurarine at this level. The present results are in accord with the assumption that the tubocurarine acts at the synapses of the afferent filaments of those nerve roots which are activated in the scratch reflex. It is known from the early experiments of Sherrington (1908–9, 1910, 1917) on the scratch reflex in cats that these roots are those of C1 and C2 and of the 5th cranial nerve, all of which have synapses at the spinal levels where the tubocurarine was applied. Sherrington had found that stimulation of these roots elicits the scratch reflex, as did stimulation of cross-sections of the bulb or cord at points in the little crescentic field formed by the descending root of the trigeminal nerve which extends to the level of C2 (Gerard, 1923) and is undoubtedly reached by the tubocurarine when applied at this level. The evidence for this is the finding of Feldberg & Fleischhauer (1960) that the dye bromophenol blue which, like tubocurarine, produces scratching movements, stains this field intensely when applied to the dorsal surface of the cervical cord at the level of C1.

Sherrington (1910) found that in cats the scratch reflex is also elicited from skin regions, the afferent fibres of which reach the cord at a lower level than C2, i.e. 'from the skin covering the shoulder, the back and outer edge of the upper arm even down to the elbow'; yet when applied at the level of C3 the tubocurarine was ineffective. This could be due to the fact that in this region the synapses of the afferent filaments are located more remotely from the surface or that they are less abundant. The latter possibility is compatible with Sherrington's (1910) finding that 'the skin about the root of the pinna and just behind it...appears to constitute the region whence the scratch reflex...is most easily excited'.

Sherrington (1908–9) regularly obtained the scratch reflex on rubbing the pinna or the neck behind it in normal, decapitate and decerebrate cats. In the present experiments these stimuli were ineffective in eliciting the scratch reflex before the tubocurarine application. Only occasionally did they elicit a scratch reflex and then only during a short period following the exposure of the upper cervical cord. This disparity can be accounted for by differences in the experimental set-up. In our experiments the head of the cat was immobilized with the aid of ear bars which produced a constant stimulus. It is possible that this stimulus suppressed the scratch reflex evoked on rubbing the ear or the skin behind it, either because this stimulus is capable of causing the scratch reflex and adaptation has occurred, or because the stimulus is of a kind which inhibits the normal scratch reflex. Therefore the conditions in our experiments required the facilitation by tubocurarine in order to elicit the scratch reflex.

As synapses of the filaments of the trigeminal nerve extend down to the level of C2, it is not possible to say whether the site of action of tubocurarine is mainly on these synapses or on those formed by the sensory filaments of C1 and C2. It is interesting, however, that stimulation by tubocurarine of the restricted area between the sensory filaments of C1 and C2 is sufficient to cause both spontaneous scratching movements and facilitation of the scratch reflex.

The present experiments confirm the observation of Feldberg & Fleischhauer (1960) that chloralose abolishes the effect of tubocurarine. This effect was obtained with less than half the dose normally used for full anaesthesia. Pentobarbitone sodium also affected the tubocurarine responses but usually did not abolish them. The responses were diminished in strength. When the effect of pentobarbitone sodium was investigated in decerebrate cats the responses became not only attenuated but often also more rhythmic in character. The attenuating effect of pentobarbitone sodium is compatible with the observation that it reduces the convulsive activity which is elicited in unanaesthetized cats by an injection of tubocurarine into the cerebral ventricles (Feldberg & Sherwood, 1954). No explanation is apparent for the observation that when tubocurarine was applied to the level of C2 in decerebrate cats a scratch reflex was usually elicited more easily by rubbing the skin behind the ear than by rubbing the pinna itself, whereas in cats anaesthetized with pentobarbitone sodium rubbing the pinna was the more effective stimulus.

The finding that transection of the medulla greatly reduces, but does not abolish, the effects of tubocurarine suggests that the higher nervous centres enhance the tubocurarine effects, but that the pattern of the scratch reflex and of the scratching movements is intrinsic to the spinal cord. Le Gros Clark (1958) has suggested 'that the lower sensory centres of the central nervous system function as sorting stations' and 'that the regrouping of somatic sensory fibres (and of the impulses conveyed by them) as they enter the nervous system must be determined by some sort of positive selectivity exerted by the different groups of receiving cells in the lower sensory centres—that is to say, the analysis of the sensory inflow must depend primarily on their activity'. The fact that tubocurarine applied to the upper cervical cord produces a pattern of spontaneous movements which is that of the scratch reflex is compatible with this concept, in that the lower sensory centres, when exposed to drug stimulation, exhibit this property of 'selective sorting'.

SUMMARY

1. Application of tubocurarine to the dorsal surface of the cervical cord of cats produced both spontaneous scratching movements and facilitation of the scratch reflex elicited by rubbing the pinna and the skin behind the ears. The area of application from which these effects were obtained

extended from the level of C1 down the cord to the level of C2. At this lower level a stronger concentration of tubocurarine was required.

2. The pattern of movements produced by tubocurarine in decerebrate animals was usually more sustained than that seen in cats anaesthetized with pentobarbitone sodium. In both conditions these movements were decreased in strength by the addition of pentobarbitone sodium. The addition of chloralose abolished them.

3. Transection of the medulla below the obex greatly diminished the strength of the movements.

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