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THE EFFECT OF MOTONEURONE ACTIVITY ON THE SPEED OF CONTRACTION OF STRIATED MUSCLE

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The hypothesis that the motoneurone exerts some 'trophic' influence on the muscle it supplies was based originally on clinical observations of the changes in various organs following disturbances of their innervation. This hypothesis has often been discussed in relation to changes occurring in skeletal muscle, in particular those changes which follow denervation. Those who have opposed this view have usually tried to explain the changes in terms of inactivity, though this has never proved completely successful (Tower, 1937). It is possible, however, that some of the changes observed after denervation occur because the fibres no longer receive impulses from their motoneurones, while some may be due to the fact that the muscle no longer performs mechanical work, and others may still have to be explained by the lack of a 'trophic' influence.

The present paper deals with a phenomenon that appears to fall in the first category, as indeed do most of those which have been studied intensively. For instance, it is now reasonably certain that some of the biochemical changes which follow denervation are attributable mainly to lack of impulse transmission (Gutmann & Vrbová, 1952; Gutmann & Vodička, 1953; Gutmann, Vodička & Vrbová, 1954; Vrbová & Gutmann, 1956). The most detailed study has been made of a biochemical response to contraction first described by Yampolskaja (1950). She found that if a series of single twitches is applied to a normal muscle, its glycogen content, after an initial decrease, increases much above its initial value. The dependence of this increase, or overshoot reaction, on motoneurone activity was subsequently demonstrated in a series of investigations. The reaction was not only shown to be absent in a denervated muscle as early as 48 hr after cutting the nerve, but to disappear also when the motor nerve was left intact, and motoneurone activity was reduced, for instance, by cutting the spinal cord, or by sedation with barbiturates (Gutmann *et al.* 1954; Vrbová & Gutmann, 1956).

The importance of the motoneurone for determining some mechanical responses of striated muscles was recently demonstrated by Buller, Eccles & Eccles (1960*a*, *b*). In their experiments the mechanical response of the slow

soleus, when cross-innervated by a nerve which normally supplied the fast flexor digitorum longus, became that of a fast muscle, and vice versa. They suggested that the speed of contraction and relaxation of striated muscle was determined by a special trophic substance travelling down the motoneurone. The results of the experiments on the overshoot reaction, however, indicated the possible significance of motoneurone activity for such mechanical responses of muscles.

As an initial approach to this problem the patterns of electromyographic activity were studied in slow and fast muscles of conscious rabbits, and a correlation with their twitch speeds was attempted (Vrbová, 1962, 1963). In the slow muscle, soleus, there is continuous e.m.g. activity, whereas the fast muscles are silent except for bursts of activity occurring during 'spontaneous' and reflexly elicited movements. Immediately after tenotomy soleus also becomes silent, except for occasional bursts which seem to be related to postural adjustments. When the twitch speed of soleus was studied it was found to approach that of a fast muscle 2–3 weeks after tenotomy, which led to the conclusion that this change in mechanical properties was brought about by the change in pattern of motoneurone activity previously found (Vrbová, 1962, 1963).

The present paper gives a fuller account of experiments which illustrate the dependence of twitch speed on motoneurone activity.

METHODS

Experiments were performed on rabbits anaesthetized with 25% urethane, and on cats under pentobarbitone anaesthesia (30 mg/kg). Isometric twitches of hind-leg muscles were recorded with a Statham strain gauge, as described by Buller *et al.* (1960*a*). In some experiments a device was used for automatic recording of initial tension, time to peak, time to half-decay and twitch tension (Buller, Lewis & Vrbová, 1962). Both ends of the tibia were drilled and the leg was fixed horizontally to a myograph table. When twitches were recorded from soleus, plantaris or flexor digitorum longus, the muscles were separated and covered with paraffin in a pool constructed from skin flaps. The temperature of the paraffin was kept constant. When twitches from tibialis anterior or extensor digitorum longus were recorded, the tendons of the muscles were separated and freed without exposing the muscles.

Muscles were excited through individual nerves or through the peripheral end of the cut medial or lateral popliteal nerve. In some experiments twitches were elicited by direct stimulation of the muscle through a stainless-steel wire tied round the tendon and the drill in the proximal end of tibia. Twitches were elicited by supramaximal square waves of 0·25 msec duration. The initial tension on the resting muscle was always adjusted to that value at which the maximal twitch tension was developed.

In different groups of animals operations were performed aseptically under ether or pentobarbitone anaesthesia some time before the final experiment. These were: section of all tendons round one ankle joint, or section of the tendons of gastrocnemius and soleus only: in some of these animals the tendons were subsequently reattached to their original insertions by a catgut suture at different intervals after tenotomy. Sometimes the section of all tendons round one ankle joint was combined with section of either the spinal cord or the sciatic nerve. In one group of rabbits gastrocnemius, soleus and plantaris muscles were excised on one side.

RESULTS

Changes in contraction and relaxation times following tenotomy in fast and slow muscles

Rabbits. Isometric twitches of soleus and plantaris were recorded at different intervals after cutting all the tendons round one ankle joint. No appreciable change in twitch speed occurred in the tenotomized plantaris. This is illustrated by Fig. 1, which shows isometric twitches of the control, and of the tenotomized plantaris muscles 50 days after the operation, the time to peak being 23 msec in the control and 24 msec in the tenotomized muscle. By contrast, the twitch speed of soleus changed considerably 2–3

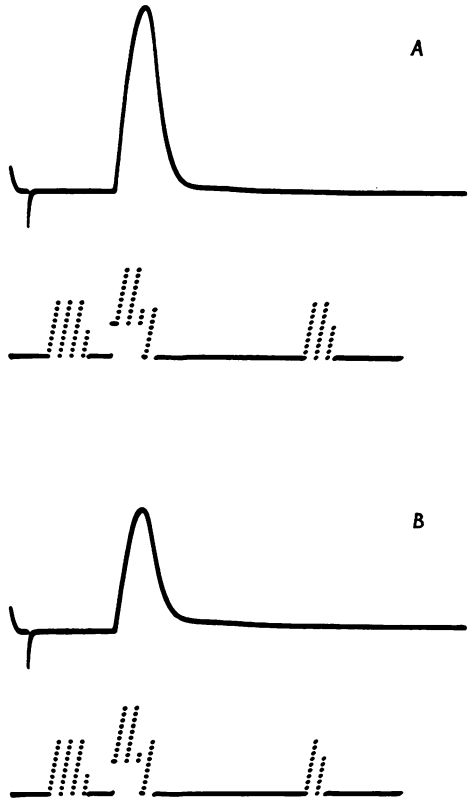

Fig. 1. Isometric twitches of rabbit plantaris. *A*, Control plantaris; *B*, plantaris 50 days after tenotomy. The dots under each twitch indicate: first group, initial tension, each dot representing 5 g; second group, separated from the first by a horizontal gap, contraction time, each dot representing 1 msec; third group, separated from the second by a change of base line, half-relaxation time, each dot representing 1 msec; fourth group, separated from the third by a horizontal gap, twitch tension, each dot representing 50 g.

weeks after tenotomy. The time to peak and half-relaxation time shortened, the values becoming comparable with those of plantaris. In the experiment of Fig. 2 the time to peak of the 50 days tenotomized soleus was 17 msec and that of the control muscle was 69 msec. It would naturally be expected that fusion frequency would be greater in the tenotomized soleus muscle, and this is also illustrated in Fig. 2. If the operated animals were followed for longer periods, the tenotomized soleus remained fast. The time

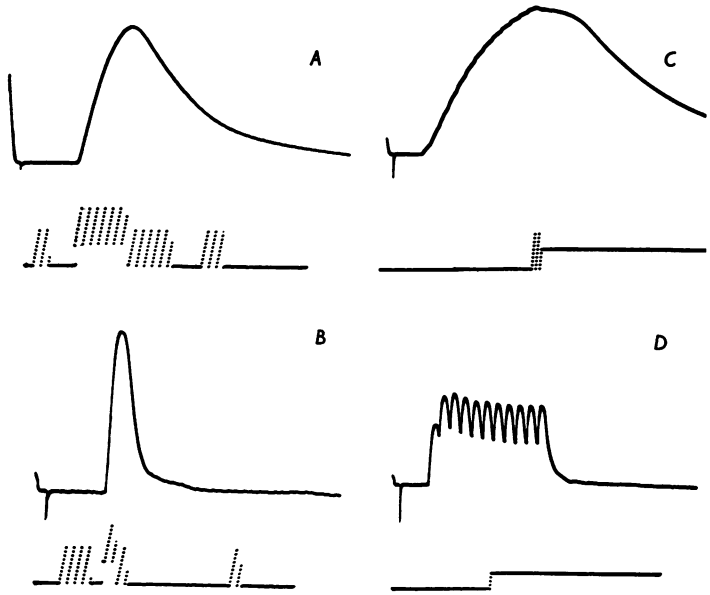

Fig. 2. Isometric contractions of rabbit soleus. *A*, Control soleus; *B*, isometric twitch of soleus 50 days after tenotomy; *C*, response of the same muscle as *A* to a repetitive stimulus at 30/sec; *D*, response of the same muscle as *B* to a repetitive stimulus at 30/sec. The dots under the twitches in *A* and *B* indicate: first group, initial tension; in *A* each dot represents 5 g, in *B* each dot represents 1 g; second group, contraction time, each dot representing 1 msec; third group, half-relaxation time, each dot representing 1 msec; fourth group, twitch tension; in *A* each dot representing 10 g, in *B* each dot representing 1 g; in *C* and *D* the dots indicate tension developed, each dot in *C* representing 50 g, and in *D* 4 g.

course of the change in soleus from a slow to a fast muscle is illustrated in Fig. 3. No such change in twitch speed of plantaris occurs after tenotomy, as shown in Fig. 4.

These changes in speed of contraction and relaxation of soleus were partially reversed when the tendons were re-attached to their original insertions. This operation was performed at different intervals after tenotomy, at which soleus would be expected to have become fast; and when tested at the intervals shown in Table 1, it was found to have

become slower again. The similarity of the twitch of such a re-attached muscle to that of a normal soleus is illustrated in Fig. 5.

In a normal soleus continuous e.m.g. activity is recorded, no matter whether the animal is standing, sitting, or moving in its cage. When all the tendons round one ankle joint were cut this continuous activity was no longer observed. Short bursts of activity could be recorded, but only when the position of the animal was suddenly changed (Vrbová, 1962, 1963).

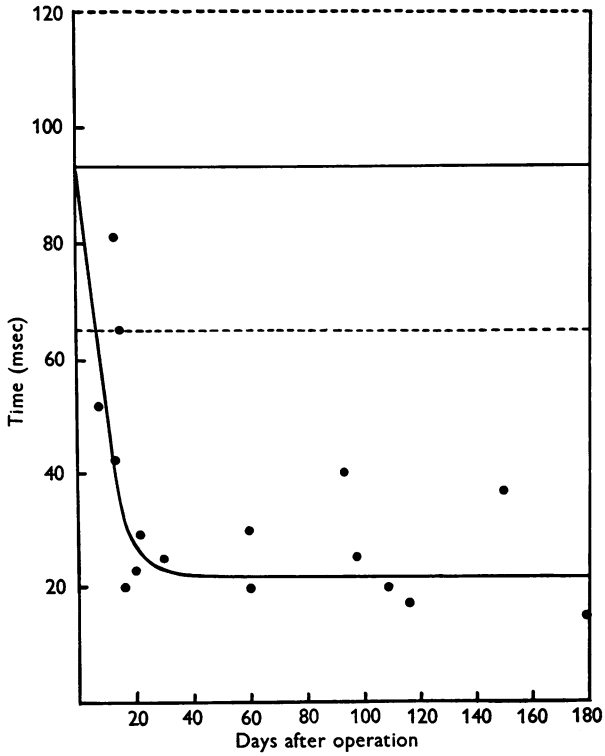

Fig. 3. The time course of the changes in contraction time of rabbit soleus, following tenotomy. Each circle represents the contraction time of one tenotomized soleus muscle. The thick horizontal line represents the mean value of the contraction time of soleus muscles on the unoperated side; the interrupted lines, the extreme values for these muscles.

The speed of contraction of soleus can therefore be related to the impulse traffic proceeding down the motoneurone, and the increase in twitch speed of soleus appears to be associated with the great decrease of impulse activity reaching it. In four rabbits the spinal cord was cut at the same time as the tendons, for it had previously been found that the bursts of e.m.g. activity could then be recorded no longer in the tenotomized soleus (Vrbová, 1962, 1963), and when isometric twitches of soleus were recorded

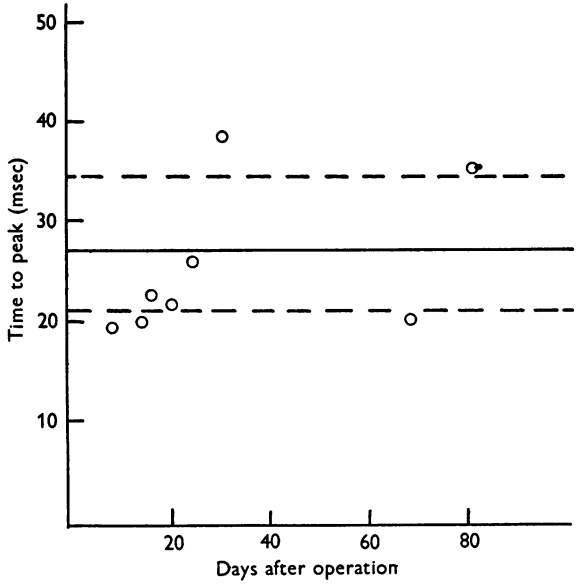

Fig. 4. Effect of tenotomy on the contraction time of rabbit plantaris. Each circle represents the contraction time of one tenotomized plantaris muscle. The thick line represents the mean value of the contraction time; the interrupted lines, the extreme values of the control plantaris muscles.

2–3 weeks after the operation the contraction and relaxation times of soleus were similar to those found with tenotomy alone (Fig. 6 and Table 2).

Supporting evidence for the role of impulse activity in determining the twitch speed of soleus was provided in the next experiments, in which the tendon of plantaris was left intact and only gastrocnemius and soleus tendons were cut. These experiments were initiated by some observations of Eccles, Eccles & Lundberg (1957) that soleus motoneurones can be monosynaptically activated by afferent impulses from synergistic muscles; from which it could be assumed that, if some synergists of soleus are left intact, the tenotomized soleus motoneurones will receive more impulses than if all the synergists are tenotomized. As is shown in Table 3, when

TABLE 1. Twitch characteristics of rabbit's soleus following tenotomy and subsequent re-attachment of tendons

Days after tenotomy	Days after re-attachment	Tension (g)		Time to peak (msec)		Half-relaxation time (msec)	
		Unoperated side	Operated side	Unoperated side	Operated side	Unoperated side	Operated side
16	8	290	180	98	98	117	130
21	14	110	25	60	40	60	40
37	68	290	36	64	42	67	30
35	35	230	100	65	62	42	36

plantaris was left intact, soleus did not become so fast as if the tendons of all the synergists had been cut (compare Table 3 with Fig. 3).

The presence of the intact motoneurone seems to be essential for production of the change in twitch speed. In five rabbits the sciatic nerve was cut at the same time as the tendons, and twitches were subsequently recorded. The denervated and tenotomized soleus muscles did not become 'fast' (Table 4 and Fig. 7).

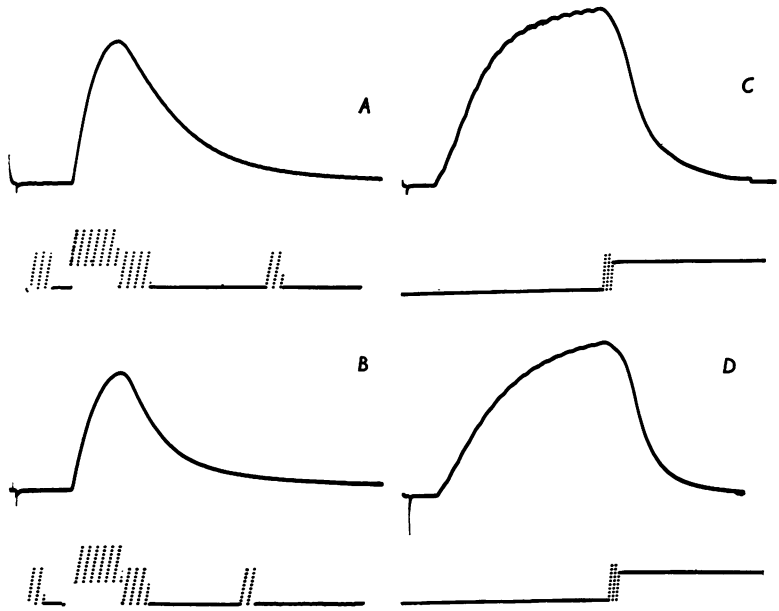

Fig. 5. Contractions of rabbit soleus. *A*, Isometric twitch of control soleus; *B*, isometric twitch of soleus which, 38 days after tenotomy, had been re-attached for 35 days; *C*, the response of the same muscle as *A* to a repetitive stimulus at 20/sec; *D*, the response of the same muscle as *B* to a repetitive stimulus at 20/sec. The dots under twitches *A* and *B* indicate: first group, initial tension, each dot representing in *A* 5 g, in *B* 1 g; second group, contraction time, each dot representing 1 msec; third group, half-relaxation time, each dot representing 1 msec; fourth group, twitch tension, each dot representing in *A* 10 g, in *B* 1 g. The dots under *C* and *D* indicate tension developed; in *C* each dot represents 50 g, in *D* 4 g.

When compared with the 'control' muscle the denervated and tenotomized soleus appears to be slightly faster than the 'control' soleus. The contraction time of the denervated tenotomized soleus is in the range of that observed in soleus muscles of unoperated animals (61·4 msec, $\pm$ 2·1 S.E. of mean), whereas that of the tenotomized soleus is much shorter (see Fig. 3). It is possible that the apparent difference between the denervated tenotomized soleus and 'control' soleus is due to a 'slowing' in the 'control' soleus, which is discussed later.

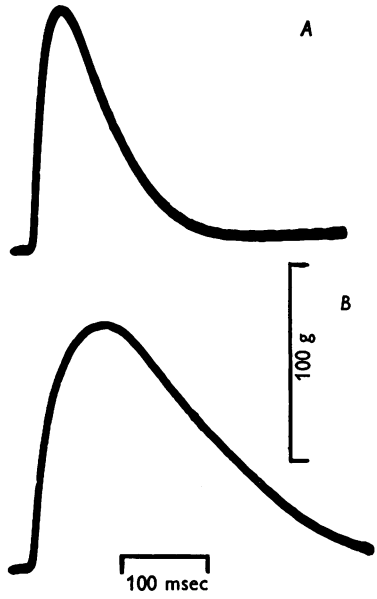

Fig. 6. Isometric twitches of rabbit soleus. *A*, 22 days after section of the spinal cord and all tendons; *B*, control muscle, 22 days after transecting the spinal cord.

TABLE 2. Twitch characteristics of rabbit's soleus after spinal cord section and tenotomy

Days after operation	Tension (g)		Time to peak (msec)		Half-relaxation time (msec)	
	Unoperated side	Operated side	Unoperated side	Operated side	Unoperated side	Operated side
17	150	60	66	27	99	38
18	230	60	65	50	67	50
17	80	96	80	52	80	50
22	128	128	80	40	128	64

TABLE 3. Twitch characteristics of rabbit's soleus at different intervals after cutting the tendons of gastrocnemius and soleus and leaving plantaris intact

Days after operation	Tension (g)		Time to peak (msec)		Half-relaxation time (msec)	
	Unoperated side	Operated side	Unoperated side	Operated side	Unoperated side	Operated side
59	110	16	66	48	70	50
58	240	32	60	32	—	—
78	85	44	120	64	150	88
75	270	46	64	64	135	96
100	190	80	110	80	120	90
160	200	90	76	58	30	36

Cats. Since the results described above could explain the findings of Buller *et al.* (1960*b*) on changes in twitch speed of cross-innervated muscles in cats, the effect of tenotomy on the speed of contraction of soleus was tested in cats. In six cats all the tendons round one ankle joint were cut

and isometric twitches recorded at different intervals after the operation. Figure 8 and Table 5 show that soleus on the tenotomized side was faster, though it did not become so fast as in rabbits. J. C. Eccles (personal communication) has obtained similar results with cats.

TABLE 4. Twitch characteristics of rabbit's soleus after tenotomy and denervation

	Tension (g)		Time to peak (msec)	
Days after operation	Unoperated side	Operated side	Unoperated side	Operated side
28	240	20	54	44
28	87	26	100	85
29	140	52	108	77
21	350	70	80	60
37	180	40	76	64

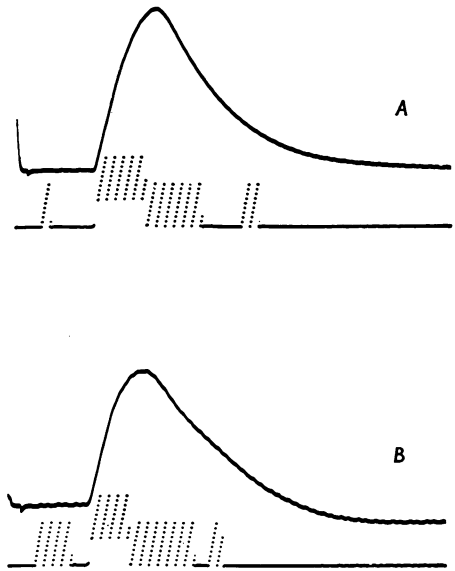

Fig. 7. Isometric twitches of rabbit soleus. *A*, control soleus; *B*, soleus 28 days after section of the tendons and sciatic nerve. The dots under the twitches indicate: first group, initial tension, each dot representing in *A* 5 g, in *B* 1 g; second group, contraction time, each dot representing 1 msec; third group, half-relaxation time, each dot representing 1 msec; fourth group, twitch tension, each group representing 10 g in *A* and 1 g in *B*.

Changes of twitch speed after excessive use

Soleus. It was noticed by Jewell & Zaimis (1954) that in the soleus of cats, in which the tendons of gastrocnemius and plantaris had been cut, fusion frequency of the soleus decreased and the twitch became slower. In rabbits in which all tendons round one ankle joint are cut the soleus on the opposite side is excessively used. The contraction time of these

eighteen soleus muscles 20–180 days after operation was found to be 93 msec (S.E. of mean 1·6) as compared with that of ten normal soleus muscles, which was 61·4 msec (S.E. of mean 2·1). The difference between these two groups is highly significant ($P < 0{\cdot}01$). These results suggest that increased activity can prolong the contraction time of soleus.

TABLE 5. Twitch characteristics of cat soleus following tenotomy

	Tension (g)		Time to peak (msec)	
Days after operation	Unoperated side	Operated side	Unoperated side	Operated side
14	500	143	96	81
27	580	52	120	108
30	472	252	75	60
42	570	140	100	65
88	380	90	117	65
90	483	46	86	56

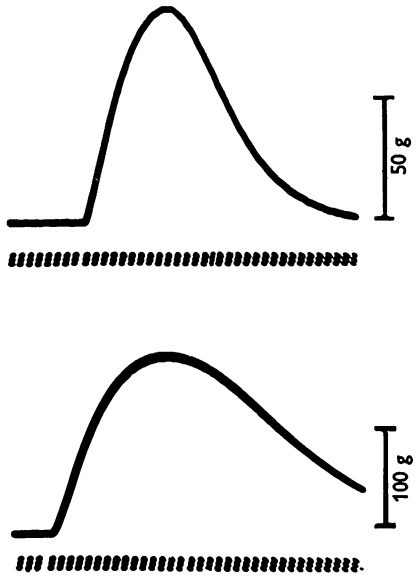

Fig. 8. Isometric twitches of cat soleus. *A*, 90 days after tenotomy; *B*, control muscle. The distance between successive dots represents 10 msec.

Fast muscles. Increased motoneurone activity has a similar effect on fast muscles. In a group of rabbits soleus and plantaris muscles were excised, or the tendons of soleus and gastrocnemius were cut. After such operations the animals walked on their heels with the toes flexed. Thus, flexor digitorum longus was being almost continuously used, together with the physiological flexors of the ankle joint, tibialis anterior and extensor digitorum longus. It is, of course, difficult to know just how much more than normal these muscles were being used, but, as Table 6 shows, when

tests were made 46–75 days after the initial operation these muscles were always slower than their controls on the unoperated side. The mean value of the time to peak was 32 msec (S.E. of mean 2·1), and that of the unoperated side 23 msec (S.E. of mean 0·8) ($P < 0·01$). The size of the change

TABLE 6. Twitch characteristics of rabbit's fast muscles following excessive use

Days after initial experiment	Muscle	Type of experiment	Tension (g)		Time to peak (msec)		Half-relaxation time (msec)	
			Unoperated side	Operated side	Unoperated side	Operated side	Unoperated side	Operated side
46	Tibialis ant.	Gastroc., soleus and plantaris excised	326	632	20	41	23	52
46	Ext. dig. l.		380	760	23	42	25	55
60	Tibialis ant.		360	250	19	26	29	54
60	Ext. dig. l.		480	500	26	32	36	40
51	Flexor dig. l.		300	500	22	30	33	35
65	Flexor dig. l.		530	480	20	24	33	35
58	Flexor dig. l.	All tendons cut except plantaris	890	950	24	27	18	20
57			720	1200	22	38	23	36
75			1200	850	25	27	20	24

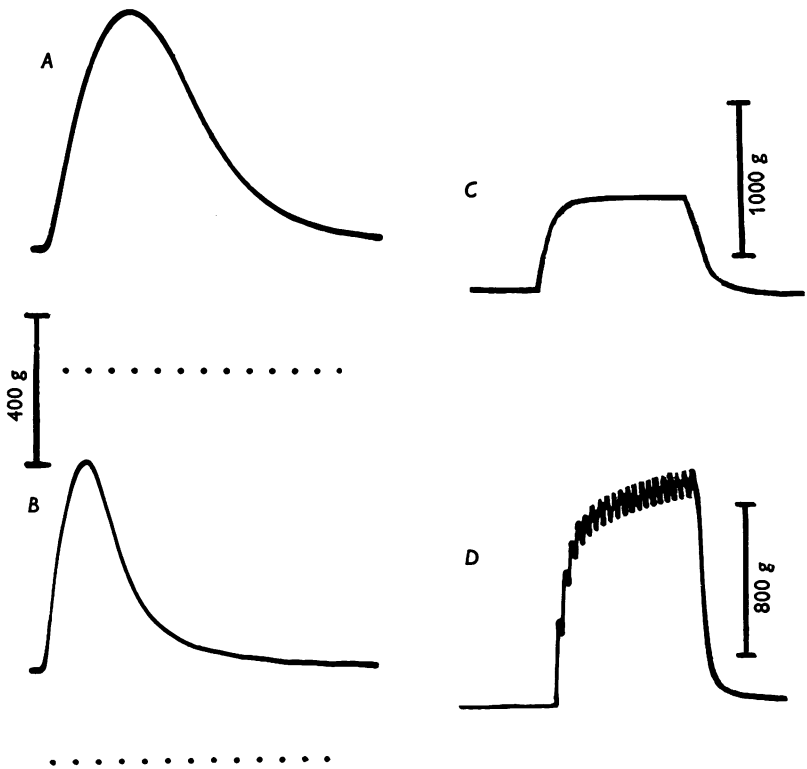

Fig. 9. Isometric contractions of rabbit extensor digitorum longus. *A*, 46 days after gastrocnemius, soleus and plantaris had been excised; *B*, control extensor digitorum longus; *C*, the response of the same muscle as that of *A* to repetitive stimulation at 64/sec; *D*, the response of the same muscle as that of *B* to repetitive stimulation at 64/sec.

that can be produced is illustrated by the experiment of Fig. 9, which shows single twitches and responses to repetitive stimulation of each extensor digitorum longus muscle in an animal in which, 46 days previously, gastrocnemius, soleus and plantaris muscles had been excised on one side. The values for the control muscles of operated animals do not differ from those of normal, unoperated animals. In six normal rabbits the twitches of plantaris, flexor digitorum longus, tibialis anterior and extensor digitorum longus of both legs were recorded; the mean value for muscles of the right leg was 23 msec (S.E. of mean 0·5) and for those of the left 23 msec (S.E. of mean 0·7). It is concluded that increased impulse activity affects fast muscles in the same sense as slow muscles, i.e. the speed of contraction and relaxation becomes slower. It shows that by continuous impulse activation fast muscles can become slow.

DISCUSSION

The most striking result of the present investigation is that the mechanical response of soleus becomes that of a fast muscle when the tendons of all muscles round one ankle joint are cut. The contraction time of the rabbit's tenotomized soleus becomes even faster than that of plantaris or flexor digitorum longus. There are several possible ways in which such a change of twitch speed could be brought about. Extensive degenerative changes occur in soleus after tenotomy (McMinn & Vrbová, 1962). It might be thought that all the slow muscle fibres have degenerated and only the fast ones remain, had it not been claimed that the rabbit's soleus consists only of slow fibres (Krüger, 1952). In any case, it was found in the present investigation that soleus became fast when the spinal cord was divided at the time of the tenotomy, although under such experimental conditions no degeneration of muscle fibres can be detected (McMinn & Vrbová, 1962). The change of twitch speed in these experiments can thus only be due to a transformation of the slow muscle fibres into fast ones. Such a transformation may to some extent be the effect of extreme shortening ('contracture') of the muscle, which is known to occur after tenotomy. There is at present, however, no evidence to connect shortening and change in twitch speed. When a tenotomized soleus was denervated it still shortened, but it remained slow. Fast muscles, such as plantaris or flexor digitorum longus, also shorten, yet their twitch speed does not change. Similarly Buller *et al.* (1960*b*) found that when the spinal cord and dorsal roots in cats were cut soleus became fast, although no shortening was observed.

It is therefore most likely that it is not the shortening, but the decrease of impulse activity, observed after tenotomy, which is responsible for this change. In previous experiments on e.m.g. activity it was found that normally the slow soleus is continuously activated, whereas the tibialis

anterior is activated only during reflex activity (Vrobvá, 1962, 1963). Whenever continuous activity in soleus with an intact motor innervation ceases, as after tenotomy, tenotomy combined with section of the spinal cord, or section of the spinal cord and dorsal roots, the slow soleus becomes fast (Buller *et al.* 1960; Vrbová, 1962, 1963). It is concluded that the change in twitch speed of soleus is brought about by cessation of continuous impulse activity. There is evidence that the pharmacological properties of skeletal muscle depend in a similar way on motoneurone activity. The cat's soleus responds to neuromuscular blocking agents in a different way from the tibialis anterior or pure fast muscles (Paton & Zaimis, 1951), but if soleus is tenotomized the reactivity of its neuromuscular junctions becomes similar to that of fast muscles (Jewell & Zaimis, 1954). These results reinforce the view that it is no longer necessary to invoke a special trophic influence of the motoneurone in order to explain changes of mechanical responses.

The results of the present investigation also show that if impulse activity in slow or fast muscles is increased, their contractions become slower. This finding also supports the hypothesis that continuous activity has a slowing effect on the twitch.

More recently, Eccles, Eccles & Kozák (1962), when reconsidering the interpretation of these experiments on nerve crossing, discussed the possibility that frequency of motoneurone discharge may determine the twitch speed of skeletal muscle. According to the idea discussed, a fast muscle, if activated at a rate of about 10/sec, would be submitted to a vibratory stress to which it would respond by becoming slow. Eccles *et al.* (1962) did not think that the results obtained by nerve crossing could be satisfactorily explained by such a hypothesis, since they found that if muscles of spinal cats were stimulated for periods of up to 10 min a day at a rate of 10/sec for 8 weeks their twitch speeds were only slightly altered. This is not surprising in view of the present results, which show that when *continuous* activity of soleus ceases its contraction becomes fast. It is not yet possible to say whether the frequency, as distinct from the duration, of motoneurone discharge plays a role in determining the mechanical responses of skeletal muscle.

SUMMARY

1. The contraction and relaxation time of the rabbit's soleus shortens within 3 weeks after tenotomy, whereas no such change was observed in the fast plantaris.

2. This change in speed of contraction and relaxation of soleus also occurred when the spinal cord was cut as well as the tendons. It is concluded that continuous impulse activity, which is normally present in the postural soleus, is responsible for the slow contraction and relaxation time

of this muscle, and when this continuous activity ceases soleus becomes a fast muscle.

3. The contraction and relaxation time of soleus became slower following excessive use.

4. The contraction and relaxation time of tibialis anterior, extensor digitorum longus and flexor digitorum longus was also prolonged when these muscles were continuously used.

5. It is suggested that impulse activity plays a decisive role in determining the speed of contraction and relaxation of mammalian skeletal muscles.

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