PHYSIOLOGY

ELECTROPHYSIOLOGICAL PROPERTIES OF CERTAIN MUSCLES OF WARM-BLOODED ANIMALS AS RELATED TO THEIR TONICITY

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It has been shown by many Russian and foreign workers [1-11] that considerable differences are to be found in the peripheral motor apparatus of warm-blooded animals: certain muscles are darker in color and show a greater tonicity. These slow, tonically contracting muscles differ in several respects from those which act more rapidly: the time for a single contraction is shorter, their tetanus shows certain distinctive features, the reflex excitability is lower, and they are less readily fatigued.

Practically no studies have been made in which the electrophysiological properties of the "rapid" and "slow" muscles have been compared. On this account, we have used the method of recording action potentials to obtain further information on the mode of action of these two kinds of muscle.

METHOD

The experiments were carried out on 12 cats under amytal anesthesia (80 mg of sodium amytal per kg). Two pairs of muscles were used: m. soleus and m. gastrocnemius, and m. rectus and m. vastus lateralis. The muscles of each of these pairs are synergists (more precisely: heads of the same muscle), but, according to many authors, the m. soleus and m. rectus differ in showing a higher tone than do the corresponding gastrocnemius and lateralis muscles.

Steel needle electrodes were used and the muscle action potentials were led off simultaneously from both muscles of each pair; rhythmic stimulation was applied to the peripheral end of the common nerve trunk (n. femoralis for the m. rectus and m. vastus lateralis, and n. ischiadicus for the m. soleus and m. gastrocnemius). The branches of these nerves to the adjacent muscles were cut. The potentials were recorded on an Ediswan ink writer, whose frequency response was linear from 0.2 up to 90 c/s. The upper frequency limit of the oscillograph is not sufficiently high to avoid distortion in recording the amplitude and shape of the muscle action potentials; however, this does not alter the indication of the functional indices which were used for comparing the different muscles. These indices were as follows: 1) the threshold stimulus strength which caused the appearance of muscle potentials; 2) the kind of alteration in the stimulus rhythm; 3) the amplitude and duration of the so-called "staircase phenomenon"; 4) the constancy of the muscle action potentials following long duration stimulus of the nerve at a frequency corresponding to the development of postural tonic contractions (15-35 per second).

RESULTS

The results of the experiments show that the nerve muscle preparation of the n. ischiadicus – m. soleus usually shows a lower excitability than the n. ischiadicus – m. gastrocnemius preparation (Table 1).

D. Denny-Brown [5], using a myographic method, found a similar distribution of thresholds for these preparations; he observed that, in many cases, with a weak stimulation of the common motor nerve it was possible to elicit a marked contraction of the m. gastrocnemius without any response from the m. soleus.

TABLE 1

Threshold Excitability of Different Nerve Muscle Preparations

Name of muscle pair	Total number of determinations of threshold	Number of determinations in which the threshold was		
m.soleus – m. gastrocnemius	63	the same	higher in m. soleus than in m. gastrocnemius	higher in m. gastrocnemius than in m. soleus
		17	34	12
m.rectus – m. vastus lateralis	21	the same	higher in m. rectus than in m. vastus lateralis	higher in m. vastus lateralis than in m. rectus
		11	4	6

On comparing the thresholds of the n. femoralis – m. rectus with that of the n. femoralis – m. vastus lateralis, it can be seen that in most cases the excitabilities are the same. However, sometimes (see Table 1) there are differences. The indirect excitability of the slow m. rectus is sometimes lower and sometimes higher than that of the m. vastus lateralis.

Observations on change of rhythm occurring in the four nerve muscle preparations described above were made first by steadily increasing the frequency of the stimulus applied to the peripheral end of the nerve of the pair of muscles, and secondly by applying a series of stimuli of known frequency at 10-minute intervals. In spite of the considerable variability of the results, the difference in the transformation of the rhythm by the m. soleus and by the m. gastrocnemium was very marked. For the m. soleus, the first signs of an alteration in the rhythm occurred at a frequency of 80-90 per second. Further increase in the stimulus frequency led to a still more marked alteration (Fig. 1, a), and at values lying within the range 130-150 stimuli per second, the effect of the transformation was to reduce the frequency by two times (see Fig. 1, b). With prolonged stimulation at a frequency of 150 per second, a change-over occurred to a more complex relationship between stimulus frequency and recorded rhythm, and the transformed rhythm became irregular. Typically, the m. soleus was able to maintain this complex transformation of the rhythm for a considerable period lasting several seconds (see Fig. 1, c).

On further raising the stimulus frequency, it could be seen that the frequency range over which the alteration in the rhythm could be observed (from the frequency at which the alteration first appeared to that at which there was a definite counting down effect) was quite small. In our opinion, this indicates a fairly high degree of uniformity of the action time of the motor units of the n. ischiadicus – m. soleus preparation.

The reaction of the m. gastrocnemius to an increase in stimulus frequency is very much more complex. At a comparatively low stimulus frequency (about 50 per second), fluctuations in the amplitude of the potentials are to be observed (Fig. 2, b). With increase in frequency, these fluctuations become more marked, and the trace presents the appearance of a number of spindles placed end to end. Superimposed on these fluctuations, there may also be an alternating rhythm (see Fig. 2, c). However, it is not easy to determine the frequency of stimulation which corresponds to the appearance of this alternating rhythm, since in most cases it is irregular and not well marked. The maximal frequency of the electrical response which we were able to record was 130-150 per second, the limitation being due to the frequency response of the apparatus. In many cases, the m. gastrocnemius reproduced the stimulus frequency unaltered. In other cases, stimulation of the nerve with a frequency of 150 per second led to a frequency division of two. However, in both cases, the amplitude of the muscle spikes fell to zero within a fraction of a second (see Fig. 1, b' and c').

From what has been said, it can be seen that it is scarcely possible to draw any conclusion as to the absolute values of the lability of these preparations, because the experiments were carried out on anesthetized animals. The facts reported indicate only that the m. gastrocnemius can reproduce, unaltered, a higher frequency stimulus

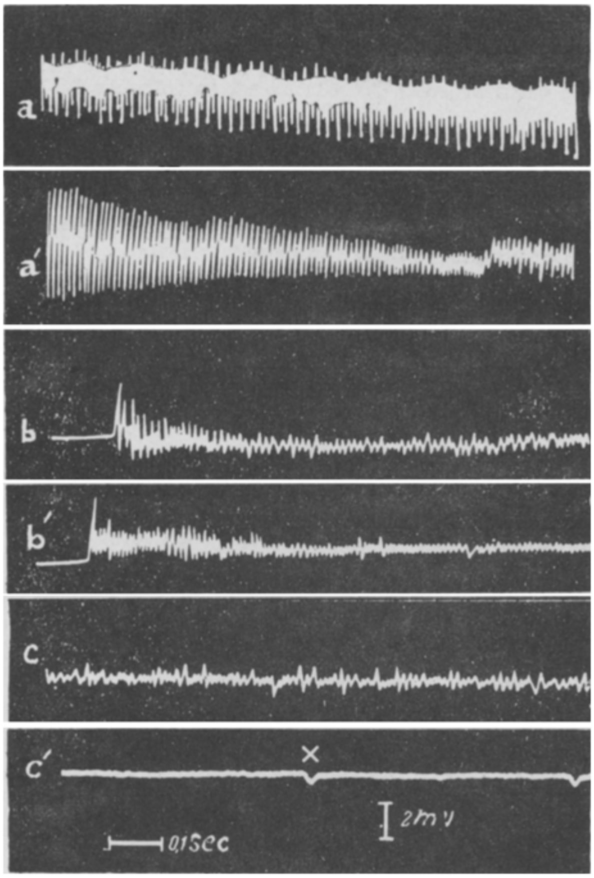

Fig. 1. Electrical response of the m. soleus and m. gastrocnemius to stimulation of the sciatic nerve. a) Action potential of the m. soleus at a stimulus frequency of 105 per second; a') potentials led off simultaneously from the gastrocnemius; b) potentials of the m. soleus at a stimulus frequency of 160 per second (the frequency of electrical response of the muscle is 80 per second); b') potentials of the m. gastrocnemius for the same frequency of stimulation (there is no transformation of the rhythm at the onset of stimulation); c) continuation of trace b after 7 seconds; c') continuation of trace b' (the cross shows a peak of the electrocardiogram).

than can the m. soleus. However, the response to such a high frequency stimulus lasts only for a very short time, and is followed by complete cessation of activity, whereas the m. soleus continues to respond to the stimulus for a considerable time, and does so by producing action potentials at an altered rhythm. There is no need to describe separately the transformations in rhythm of the m. rectus and m. vastus lateralis, since their reactions to an increase in stimulus frequency closely resembled those of the m. soleus and m. gastrocnemius, respectively.

When the frequency of stimulation of the motor nerve is sufficiently low (from 10 to 50 stimuli per second), the action potentials in all four muscles investigated do not attain their maximum size immediately. For a quite considerable time after the onset of stimulation, the phenomenon known as the "staircase effect" can be observed. Table 2 shows the average results for a staricase effect (relation of maximum amplitude of spike to the initial value), and the time during which the spike amplitude increases.

It can be seen from Table 2 that during the first few seconds of excitation, the amplitude of the action potentials of all four muscles increases almost twofold. The m. soleus and m. rectus show a somewhat greater increase in amplitude than do the m. gastrocnemius and m. vastus lateralis. However, there is no apprecialbe difference between the quick and the slow muscles in this respect. However, the difference between them emerges very clearly when a comparison is made of the time during which the increase in spike amplitude occurs. In whatever way the staircase phenomenon is explained, whether it is due to a long-continued increase in excitability or whether to a gradual increase in the neuromuscular units involved, the figures show that the attainment of the maximum level of activity in the muscles with the higher tone takes considerably longer than in the more quickly acting muscles. These results of ours agree completely with the myographic observations of other authors [6, 12, and others].

The right hand part of Table 2 shows the average time of continuous tetanic stimulation in the different muscles which is required to cause the amplitude of the spike to fall to 50% of the maximum value. It can be seen that the rate of reduction of the electrical response in the m. soleus and m. rectus is several times less than in the m. gastrocnemius and m. vastus lateralis. This shows the far greater stability of the excitatory process of the slow muscles in relation to continuous stimulation.

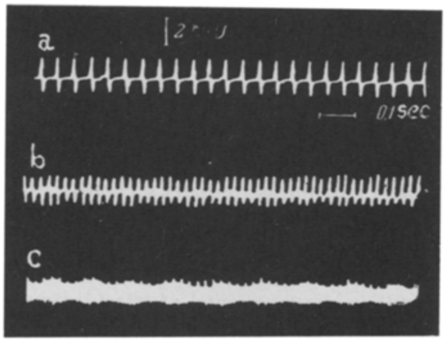

Fig. 2. Action potentials of the m. gastrocnemius on stimulating the sciatic nerve. a) Stimulus frequency of 23 per second; b) stimulus frequency of 48 per second (noticeable sinusoidal fluctuation in amplitude of potentials); c) stimulus frequency of 100 per second.

To sum up these experimental results, we may note:

1. The slow muscles of the cat attain maximum activity far more slowly than do the quick muscles, and similarly, when measuring the response from the onset of rhythmical stimulation, they are also much more stable in maintaining a response to maintained stimulation at various frequencies from 10 to 150 per second.

2. The nerve fibers of the common nerve trunk innervating slow muscles are,in most cases,less excitable than those supplying quick muscles, although the reverse relationship may sometimes be found.

3. In the case of indirect stimulation of the slow muscles, transformation of the rhythm occurs at a lower stimulus frequency than for the quick muscles. The former are able to maintain a transformed rhythm for a long time. The quick muscles are capable of responding to a higher rate of stimulation without any change of frequency, but they lose the ability to respond within a fraction of a second.

All these considerations must be taken into account in working with a nerve muscle preparation which includes several muscle heads. It is only in this way that it is possible to give a correct description of the relationship between the type of contraction and the frequency, strength, and duration of the stimulus.

TABLE 2

Time to reach the maximum spike amplitude (in seconds)		Ratio of maximum to initial amplitude (in %)		Time for amplitude of spike to fall to one half (in minutes)	
m. soleus	m. gastrocnemius	m. soleus	m.gastrocnemius	m. soleus	m.gastrocnemius
55	17	176	156	9.2	1.5
m. rectus	m. vastus lateralis	m. rectus	m. vastus lateralis	m. rectus	m. vastus lateralis
45	10	199	128	6.3	0.8

SUMMARY

Action potentials in response to rhythmic stimulation of the motor nerve were registered from the quickly and slowly contracting cat's muscles. Slow muscles take a much longer time to reach the maximal amplitude of the spikes, counting from the commencement of the stimulation,and are characterized by a much greater stability of the amplitude in prolonged stimulation. The nerve fibers innervating the slow muscles are,in the majority of cases,the less exitable ones. In indirect stimulation,slow muscles begin to transform the rhythm at a lower frequency of stimulation than the quick ones. These muscles are capable of maintaining the transformed rhythm for a long time. Quick muscles, producing a higher rhythm without its transformation,lose their ability to respond to frequent stimulations very rapidly (in fractions of a seond).

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