TWITCH FIBERS WITH BINEURONAL INNERVATION IN AN OCULAR MUSCLE OF THE RABBIT

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Among the twitch muscle fibers (T-fibers) of the superior oblique muscle of the rabbit's eye investigated a few fibers (two of 106) with bineuronal innervation were found. The firing patterns of the motoneurons are independent, and the action potentials spreading from the two synaptic regions of such a bineuronal muscle fiber interact (demonstrating both relative and absolute refractory phases). It is postulated that the bineuronal innervation of the twitch fibers increases the speed and strength of their contractions.

The extraocular muscles of mammals differ from the skeletal muscles of these animals, which are more or less uniform in composition, by being composed of fibers which differ in their physiological properties. Chiefly the polar variants of these fibers have been distinguished: a) twitch fibers, with a single innervation and with spreading excitation and b) slow fibers, with multiple innervation and with local excitation [1, 4].

However, the ocular muscles also contain intermediate types of muscle fibers whose identification in the twitch or slow groups is to some extent conventional. These include, for example, the "slow variants" of twitch fibers [2] and also the twitch fibers with bineuronal innervation described in the same paper. Examination of the properties and determination of the number of all the intermediate types are necessary for a general evaluation of the functional spectrum of the neuromotor units of these muscles.

EXPERIMENTAL METHOD

Twitch fibers of the superior oblique muscle of the eye were studied in rabbits anesthetized with urethane (at 32-35°C). Intracellular recording of the potentials was carried out in situ with the aid of glass microelectrodes filled with 2.5 M KCl solution. A type UBP1-02 amplifier and N-102 loop oscillograph (N-135-2 loop, up to 2000 Hz) were used. Full details of the method are given elsewhere [2, 4].*

EXPERIMENTAL RESULTS AND DISCUSSION

Altogether 106 twitch fibers of the rabbit superior oblique muscle were studied. Most of them (85%) had no spontaneous activity and electrical stimuli had to be applied to excite them [2]. It was impossible from their responses to estimate the number of α-motoneurons innervating these fibers. However, constant activity was found in 16 twitch fibers (i.e., in 15%), and in 14 of them it consisted of a more or less regular series of action potentials (APs) characteristic of fibers with a single innervation, while activity of two fibers was more complex: the basic firing pattern was complicated by an additional rhythm of end-plate potentials (EPPs) or APs, evidence of double innervation. The parameters of activity of these fibers will be examined below.

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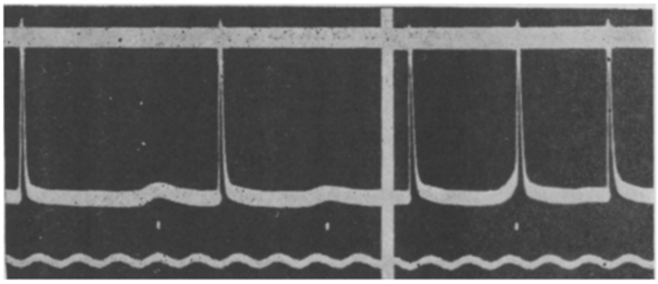

Fig. 1. Electrical activity of twitch fiber No. 1 (two successive cuts of the record). EPPs, shown below as dots, can be seen between the APs. On the right cut the EPP is continuous with the AP. Resting membrane potential (RP) at the beginning of the record is 79 mV. Time marker (100 Hz) shown below.

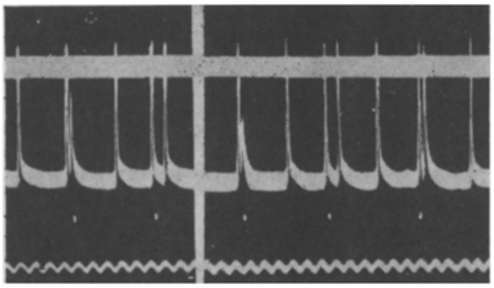

Fig. 2. Activity of twitch fiber No. 21 (successive cuts of the same record). Besides the regular, fast firing pattern there is a slower, additional rhythm (marked by dots below). The closer the approximation of two APs, the greater the decrease in amplitude of the second AP. Membrane RP at the beginning of the record 64 mV. Time marker 100 Hz.

Twitch fiber No. 1 (Fig. 1) had a resting membrane potential of 79 mV. Its firing rate was 19/sec, and the mean parameters were as follows: amplitude 80 ± 0.4 mV, rise time 0.71 ± 0.03 msec, half-decay time 0.32 ± 0.01 msec. The APs had no prepotentials, indicating that they were generated in the region of the synapse distant from the microelectrode. Meanwhile, slower and lower fluctuations of potential, with a frequency of 26 /sec, independent of the firing rate specified above, were found in the same fiber. The parameters of these waves were: amplitude 2.1 ± 0.18 mV, rise time (t_r) 5 ± 0.12 msec, half decay time (t_{hd}) 5.2 ± 0.17 msec. The shape and parameters of these waves indicate that they are EPPs of reduced amplitude. Presumably these EPPs were generated by the synapse of the second motoneuron lying near to the recording electrode and, for some reason or another, lacking in quantum composition. It is worth noting that the amplitude of these EPPs varied and sometimes reached sufficient magnitudes to enable an AP to arise on the basis of the EPP (Fig. 1).

Twitch fiber No. 21 (Fig. 2) had a resting membrane potential of 64 mV. Only APs were found in the fiber, but their pattern was very irregular. Sometimes the APs came so close together that the second potential was sharply reduced compared with the first (refractoriness). Analysis of this activity showed that it includes two independent and relatively regular firing patterns: a faster rhythm of 30/sec and a slower of about 9/sec. APs forming these two rhythms were indistinguishable in their parameters. Their

TABLE 1. Comparison of Parameters of Twitch Fibers with Bineuronal Innervation and General Parameters of Twitch and Slow Fibers

Object	Mean parameters of AP			Mean param. of EPP (PSP)			Source
	amplit. (in mV)	t_r (in msec)	t_{hd} (in msec)	amplit. (in mV)	t_r (in msec)	t_{hd} (in msec)	
Twitch fibers with bineuronal innervation:							
No. 1	80	0,71	0,32	2,1	5,0	5,2	This investigation
No. 21	72	0,8	0,8				
All twitch fibers studied in the given muscle	48—132	0,32—0,8	0,25—0,8				[2]
All slow fibers studied in the given muscle	None			24,0	2,1—3,5	1,8—7,7	[4]

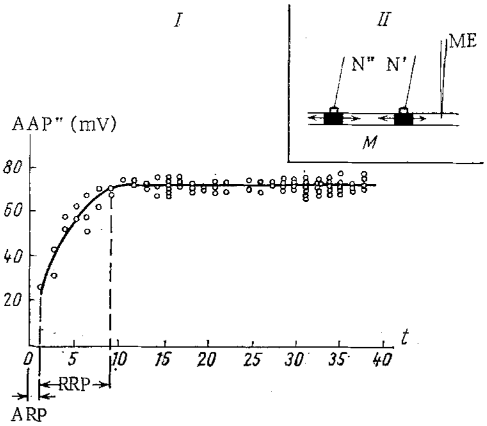

Fig. 3. Amplitude of second AP (AAP) as a function of interval (t) between that and the previous AP: I) graph of function. Abscissa, intervals (in msec); ordinate, AAP (in mV); II) diagram showing appearance of "double rhythm" in twitch muscle fiber (M). N^{I} and N^{II} – axons of two motoneurons. Regions of generation of independent series of APs spreading along the fiber shown in black. ME) microelectrode, RRP) relative refractory period, ARP) absolute refractory period.

mean amplitude was 72.4 ± 0.7 mV. Because of this interaction between the APs, special measurements were made of the total duration of the spike and the duration of its negative after-potential. The duration of the spike (approximately equal to $t_r + 2\ t_{hd}$ was 1.6 ± 0.11 msec. The mean duration of the negative after-potential was 9.1 ± 0.23 msec. There is every reason to suppose that these two firing patterns were produced by two motoneurons innervating this particular twitch fiber. Under these conditions interaction between APs evoked by different motoneurons demonstrates the refractoriness of the muscle fiber uncomplicated by the refractoriness of the motoneurons. The duration of the absolute (ARP) and relative (RRP) refractory periods of the twitch fiber can be estimated from the graph in Fig. 3, which shows the ratio between the amplitude of each AP (AAP) and the interval between it and the preceding AP. It follows from this graph that ARP of the muscle fiber was less than 2.5 msec while RRP was about 9 msec. It will be noted that ARP corresponded to the spike duration and RRP to the duration of the negative after-potential of the twitch fiber.

The characteristics of the two twitch fibers examined above (their membrane resting potential, the values of t for AP, ARP, and RRP) were typical for the fibers of this group [2] and differed sharply from those of the slow group [3] (Table 1). The somewhat lower AAP than that described previously from twitch fibers [2] is explained in this case by the conditions of recording (the piling up of the high frequencies on the N-102 loop).

It is thus the bineuronal innervation which clearly distinguishes these two twitch fibers from the mass of the other twitch fibers. Incidentally, bineuronal innervation in certain variants of fibers of this type in the ocular muscles could be predicted on morphological grounds [5, 6]. The meaning of this double innervation in the twitch fibers which are designed for rapid jerks is probably to reduce the time loss in the conduction of excitation along the muscle fiber and to synchronize the beginning of activity in its various parts.* With a conduction velocity of 3 m/sec [4] and a fiber length of 30 mm doubling the innervation could be equivalent to shortening the time taken to produce excitation of the fiber from 5 to 2.5 msec. As a result, the speed and strength of the contraction are both increased [4].

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