Physiological properties of extraocular muscle fibers are discussed. Several morphological types of fibers are present in these muscles. Studies on fast singly innervated twitch fibers and on slow multi-innervated fibers suggest that the properties of the former are consistent with "phasic" functions, and those of the latter are consistent with "tonic" functions.

Eye movements may be divided grossly into "tonic" and "phasic" movements. Are both of these principal types produced by the same motor nerves and muscle fibers, or are separate systems present that are functionally suited to each of the types of movements? Morphological and physiological studies demonstrate that at least two and possibly three neuromuscular systems are present in eye muscles, and that these have characteristics which would suit them for different types of eye movements.

Hess and Filat\(^1\) have shown that cat extraocular muscles contain singly innervated twitch fibers with "en plaque" type motor endings, and smaller multiply innervated "slow" fibers with endings analogous to "en grappe" motor endings. In human eye muscles, cholinesterase staining techniques have been employed to demonstrate these two fiber types as well as fibers with multiple "en plaque" endings.\(^2\)\(^-\)\(^5\)

Kupfer\(^1\) estimated that two thirds to three quarters of all the extraocular muscle fibers may have multiple motor endings. Recent studies\(^6\) have shown that at least three morphological types of fibers are found in cat eye muscles, including one type characteristic of very fast twitch fibers, one characteristic of slower twitch fibers, and one resembling typical multi-innervated fibers.

In rabbit eye muscles, Matyushkin\(^7\)\(^-\)\(^8\) has recorded from one type of "phasic" and two types of "tonic" fibers. He was able to record action potentials only from the "phasic" fibers. Bach-y-Rita and I\(^9\) have recorded propagated overshoot action potentials from two types of twitch fibers: the large fast singly innervated, and the slow multi-innervated fibers.

The two twitch fiber types are distinguished by their impulse conduction velocities, their range of membrane potentials, the amplitudes and frequencies of their miniature end plate potentials, their responses to the intravenous administration of succinycholine; by the velocities of conduction of the innervating nerve fibers; and by the frequency of stimulation required to produce fused tetanus of each type of fiber. The studies leading to these conclusions have been published in detail elsewhere.\(^9\)

The methods used for recording from cat eye muscles are illustrated in Figs.
Fig. 3. Intracellular records of responses in slow (parts A and B, bottom lines) and fast (parts C and D, bottom lines) muscle fibers of an inferior oblique muscle, in comparison with the extracellular responses displayed on the zero volt reference line (top lines). 

A. Anode break excitation followed by a long latency overshoot spike when the membrane potential was 68 mV. B. A nonovershoot response when the membrane potential (same fiber as in A) had decreased to 45 mV. C. A short latency overshoot spike response to maximal nerve stimulation (cathode excitation) in the fast fiber. D. No response to an anode break excitation in the same fiber as C. Parts A and C have been retouched with dashed lines. (Reprinted by permission of The Rockefeller University Press from The Journal of General Physiology, July, 1966, 49: No. 6, 1177-1198.)

titude distribution suggests that the microelectrode picks up activity from the nearest end plate (largest amplitude), as well as from nearby end plates (smaller amplitudes).

Intracellular stimulation, through an impaling microelectrode, of each type of fiber showed that localized depolarization can produce propagated overshoot action potentials in both types of fibers. Thus, activation of more than one end plate of the multi-innervated twitch fibers may not be necessary to produce propagated impulses. A study of the percentage of fibers activated after cutting two thirds of the nerve to the muscle has suggested that the multi-innervated muscle fibers receive nerve endings from more than one fiber. Thus, they are polyneuronally innervated as well as multi-innervated.

Mechanical studies show that the rise time and total time course of a twitch produced by the multi-innervated twitch fibers was much longer than the twitch of the fast fibers (Fig. 4). The fusion frequency was over 400 per second for the fast, and approximately 25 per second for the slow multi-innervated twitch fibers.

In order to study the differential action of a depolarizing (noncompetitive) blocking agent on the extraocular muscle fibers, intravenous succinylcholine was administered. Fig. 5 illustrates the contracture produced by the multi-innervated muscle fibers, and the inhibition of the tetanic response. The multi-innervated fiber con-
Traction reached maximum earlier and recovered more quickly than the inhibition of the tetanic response, which developed more slowly and greatly outlasted the contracture. These results are in agreement with those reported in this symposium by Katz.10

The physiology of extraocular muscles is, however, more complex than the present studies indicate, since at least three and possibly more types of muscle fibers can be identified histologically.6 Some of these muscle types may not produce overshoot propagated action potentials. In our studies, these responses were not differentiated from the decayed slow multi-innervated twitch responses. Clinical electromyographic (EMG) studies on extraocular muscles are undertaken with extracellular needle electrodes, and undoubtedly do not record activity from muscle fibers which do not produce overshoot propagated action potentials.

Cat extraocular muscles include one that is not found in man or in higher mammals: the retractor bulbi. A study of this muscle revealed that only fast twitch fibers ("phasic" type) are present.11,12 This would be in keeping with the role of this muscle: to retract the globe as part of a protective reflex involving the protrusion of the nictitinating membrane. Thus, in the cat, the recti and obliques, which have both "tonic" and "phasic" functions, contain both types of fibers, whereas the retractor bulbi, which has "phasic" functions, contains only fast "phasic" fibers.

The foregoing studies suggest different roles for each of the two twitch fiber types present in the recti and oblique muscles. The results suggest that the end plate potentials in slow fibers may attain the overshoot spike threshold with the summation of less quanta than in fast fibers. In addition, the fusion frequency of the slow twitch fibers is lower than for the fast

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**Fig. 4.** Isometric twitches in response to nerve stimulation of the inferior oblique muscle. The proximal and central branches of the nerve have been cut, leaving only the distal branch intact. Initial tension 5.5 g. Upper line, a single twitch of fast fibers selectively stimulated by a threshold cathode excitation to the nerve. Lower line, a single twitch of slow fibers, selectively stimulated by anode break excitation. (Modified and reprinted by permission of The Rockefeller University Press from The Journal of General Physiology, July, 1966, 49: No. 6, 1177-1198.)

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**Fig. 5.** Isometric contracture produced by succinylcholine, and the simultaneous decrease in amplitude of the tetanic contraction. Initial tension 2.6 g. A, Before the administration of succinylcholine; maximal nerve stimulation at 350 per second for 150 msec., which produced maximal tetanic tension, was delivered at the rate of 0.13 per second. B, After the administration of succinylcholine; 250 μg in a 2.7 kilogram cat, injected in the femoral vein at the beginning of the trace (arrow). (Reprinted by permission of The Rockefeller University Press from The Journal of General Physiology, July, 1966, 49: No. 6, 1177-1198.)
fibers. It thus appears that neuromuscular transmission in slow twitch fibers is an efficient mechanism for "tonic" muscle activity (which may include pursuit movements, version movements, and possibly the slow phase of vestibular nystagmus), as well as for maintaining contraction of the eye muscles. However, some of these functions may also be mediated by the slow multi-innervated "felderstruktur" type fibers. The tonic discharges recorded on electromyography (EMG) of extraocular muscles, even during rest, could be produced by the slow multi-innervated twitch fibers since the present experiments show they are capable of producing spikes which, with present EMG techniques, are indistinguishable from those produced by the fast innervated fibers.

REFERENCES