PHYSIOLOGICAL CHARACTERISTICS OF THE PROPRIOCEPTORS OF THE EXTRAOCULAR MUSCLES OF THE RABBIT

D. P. Matyushkin

UDC 612.846:612.815.2-019

The physiological properties of the stretch receptors of the extraocular muscles (muscle spindles and tendon receptors) have been studied in detail only in goats [18].

According to the histological evidence, spindle-like structures are present in the extraocular muscles of the rabbit, where they take the form of nerve endings enveloping one or two thin muscle fibers, without nuclear sacs or a capsule [10, 17]. There is no definite information regarding the existence of tendon receptors in these muscles [11].

The investigation of the properties of the primitive proprioceptors of the muscles of the rabbit's eye may be useful for many reasons: first, analogous structures are present in the eye muscles of many mammals, including man (in the latter case along with simple spindles); second, these primitive proprioceptors may be a definite stage in the evolution of the spindles; and third, the rabbit is the most convenient object for investigating the activity of the apparatus producing eye movement.

In this paper, the author describes the physiological characteristics of the proprioceptors of the extrinsic eye muscles of the rabbit, the existence of which was hitherto based only on indirect information [3, 4].

EXPERIMENTAL METHOD

Experiments were carried out on 9 thalamic rabbits and 1 rabbit with its brain intact. The animals were anesthetized with ether only during the operation. The active potentials (AP) of the afferent fibers of the branch of nerve III supplying the inferior oblique muscle were investigated. The branch was isolated, divided, and freed from its connective-tissue sheath (after removal of the eyeball). In some experiments the nerve was divided longitudinally into strips. The orbit was irrigated with warm (39°) mineral oil. The action potentials were amplified and recorded from the screen of a cathode-ray oscillograph, during single sweeps of the beam. The frequency of the AP in the branch of the nerve (or its parts) and the number of working units (the number of gradations of amplitude of the AP) were investigated when loads of between 2.7 and 20.5 g were applied to the muscle. The lengthening of the muscle was recorded at the same time. The reactions of the receptors to single contractions of the muscle caused by stimulation of a strip of the nerve branch by short (0.05 msec) pulses of current obtained from an electronic stimulator via a transformer, were studied. The AP was recorded from another part (strip) of the branch of the nerve. In some experiments, parallel with the recording of the afferent AP, the contractions of the muscle were recorded with an isometric optical myograph, and the electromyogram was also obtained.

EXPERIMENTAL RESULTS AND DISCUSSION

When the muscle was stretched by sufficiently heavy loads, as a rule a rhythmic sequence of AP of different amplitudes appeared in its nerve branch, demonstrating the existence of a group of stretch receptors in the muscle. The amplitude of these AP did not exceed 40 μV. The threshold of stimulation of the most readily excited receptors was equivalent to a load of 2-5 g.

As a rule, the reaction to jerking the muscle by the load was much larger than the reaction to a subsequent stationary load, as regards both the aggregated frequency of the impulses and the number of gradations of amplitude of the AP (the number of working receptors). The flow of afferent impulses became weaker during the period from 15-30 sec from the beginning of action of the load, and subsequently its amplitude became constant (Fig. 1), without showing adaptation.

Other conditions being equal, the amplitude of the afferent impulses depended on the magnitude of the load. This relationship was demonstrated accurately only for the reaction to a static load. In these cases the frequency

Department of Normal Physiology, Leningrad Pediatric Medical Institute. (Presented by Active Member of the Medical Sciences of the USSR D. A. Biryukov). Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 63, No. 4, pp. 19-24, April, 1967. Original article submitted April 29, 1965.

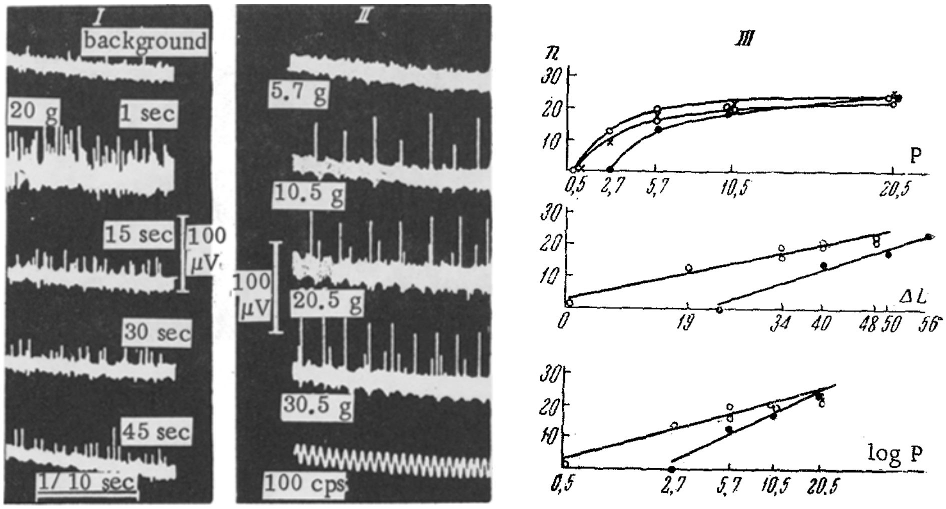

Fig. 1. Flow of impulses in stretch receptors and its relationship to load. I (from top to bottom): background and reaction of the mass of receptors to jerking the muscle with a load of 20 g, and subsequent stationary application of the load; II — afferent impulses with different stationary loads, the large AP belong to a unit; III — relationship between mean frequency of single receptors n (along the axis of ordinates in each case) and the magnitude of the stationary load P (in g), lengthening of the muscle ΔL (in %), and logarithm of the load log P (graphs plotted from results of two experiments).

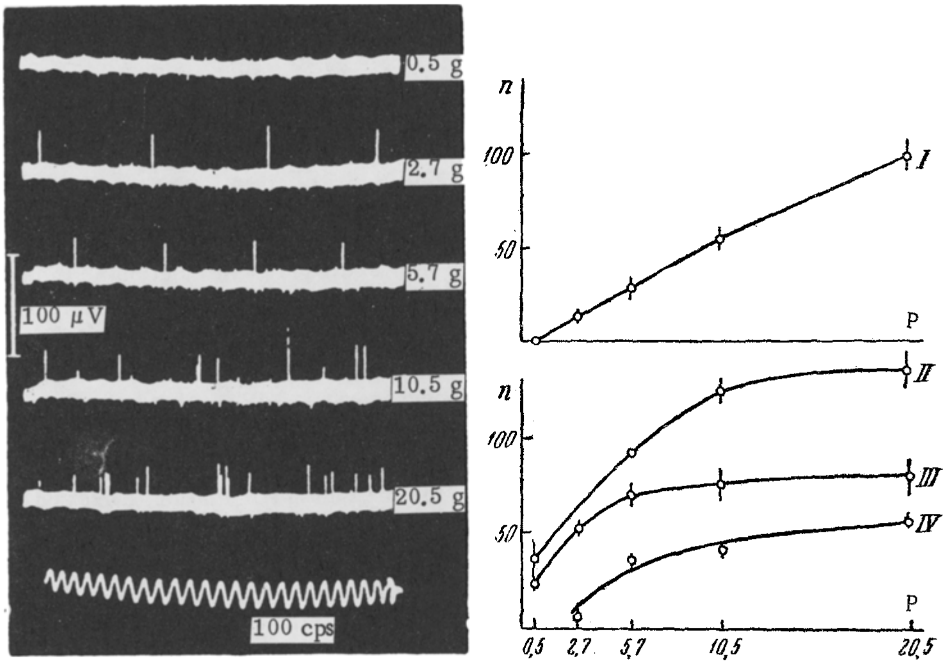

Fig. 2. Discharges of a mass of receptors with different thresholds in response to different stationary loads and relationship between total frequency of discharges n and magnitude of the stationary load in different experiments (I-IV). Vertical lines — standard deviations.

of the AP of the individual afferent units recorded from the thin strips (the bundles of nerve fibers) was proportional to the logarithm of the weight of the load, and also to the degree of lengthening of the muscle* (see Fig. 1).

*This fact was reported by the authors in the Proceedings of the Tenth Congress of Physiologists [9] and in the author's abstract of a dissertation [8]; analogous results were obtained later for the receptors of the frog's muscle [2].

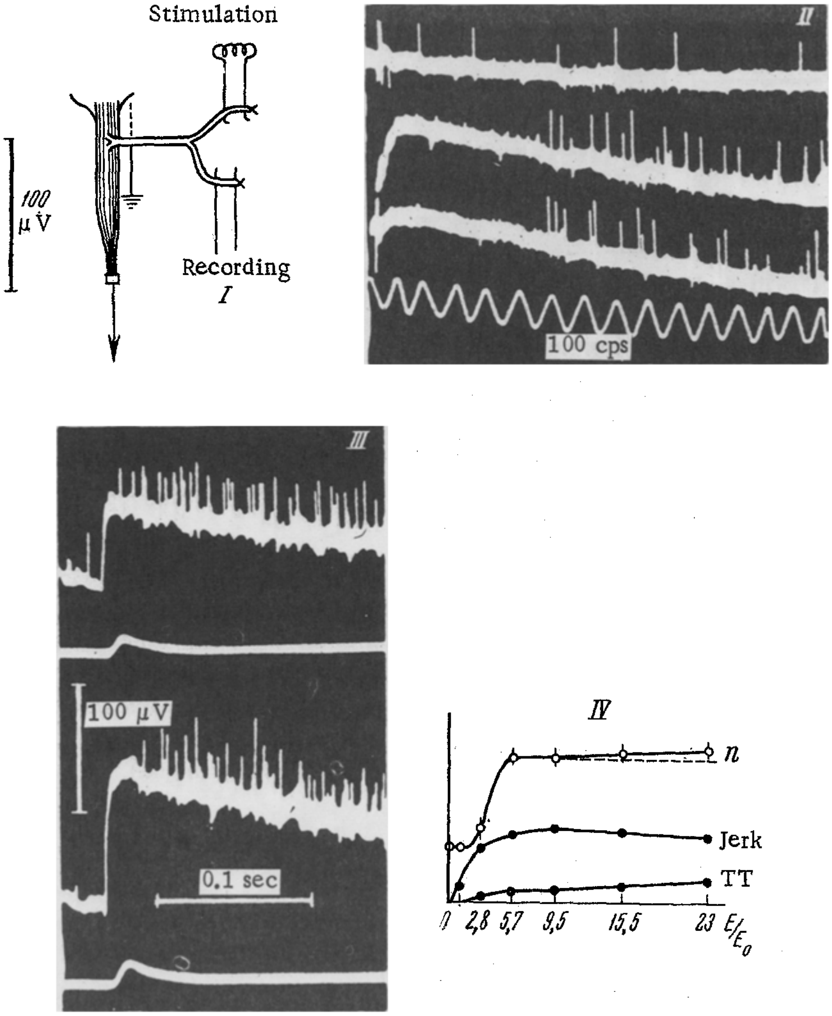

Fig. 3. Reactions of receptors to muscle contractions. I — scheme of experiments; II (from top to bottom) — impulses of receptors in response to constant loads of 20.5 g and two reactions to single isotonic contractions with a strength of stimulation 23 times above the threshold of contraction; the moment of stimulation is at the beginning of the single sweep of the beam on the left; III — two reactions of receptors to single isometric contractions (the curves of the contractions are shown below the electroneurograms) with a strength of stimulation 5.7 and 9.5 times over threshold; IV — relationship between the frequency of the discharges of the mass of receptors n, the magnitude of stretching the muscle with a jerk ("Jerk") after a phased isometric contraction, and the magnitude of the "tonic tail" of the contractile reaction (TT), and the strength of stimulation, expressed in relative units (relative to threshold).

Parallel measurements of the lengthening of the muscle and the weight of the load showed that the degree of lengthening of the muscle was proportional to the logarithm of the load [12]. The logarithmic relationship between the frequency of discharges of the muscle receptors and the weight of the stretching load [1, 13, 15] thus reflected the properties of the muscle carrying them. It may be assumed that the analogous relationship in other types of receptors is also determined by the reactive resistance of their carrier to external influences. The relationship between the total frequency of the AP of the mass of afferent fibers and the load deviated from logarithmic and approached a stright line (Fig. 2). This was due to scatter of the thresholds of the receptors in the range of loads used.

To determine whether these stretch receptors belonged to the spindle-like or the tendon category, their reactions to single contractions of the muscle were investigated during application of a stationary load (from 5 to 20 g). These showed that a phased [5, 8] contraction of the muscle, if of adequate strength, slowed or stopped the discharge of the proprioceptors during contraction (a pause of 20-60 msec), and this was followed by an increase in the

Changes in Total Frequency of Afferent Impulses (ENG) and Amplitude of Fast Action Potential (EMG) during an Increase in the Strength of Stimulation

Experimental conditions	Strength of stimulation (relative to threshold of fast AP)	Mean amplitude of fast AP (in mV)	Mean frequency of afferent discharges after pause
Isotonic contraction	0	0	$n_0 = 277 \pm 16$
Load of 5.7 g	2.8	3.86 ± 0.19	$n_1 = 330 \pm 29$
	5.7 (maximum for fast AP)	4.74 ± 0.03	$n_2 = 320 \pm 26$
The same	9.5	4.67 ± 0.35	$n_3 = 358 \pm 19$
" "	15.0	4.67 ± 0.26	$n_4 = 398 \pm 16$

Note. The difference between n_2 and n_4 is statistically significant ($P < 0.05$).

frequency of the discharge, with the involvement of new units, lasting for 1-2 sec. This effect was hardly visible for contractions of near-threshold level, but was clearly detected in response to maximal contractions, evoked by powerful (5 or more times over threshold) stimulation of the nerve trunk (Fig. 3). With such powerful stimulation, the stimulus could also spread to the afferent fibers from which recordings were made, generating antidromic impulses in them.

However, single antidromic impulses have practically no effect on the rhythm of the proprioceptors [13, 15], and the observed effects could not be attributed to them. The pause in the discharge of the receptors during fast contraction of the muscle shows that the receptors are brought into action parallel to the fast muscle fibers and are discharged during their contraction. The increase in the intensity of the discharge of the proprioceptors after the pause (observed in all 6 experiments of this series) may partly be attributed to the jerky stretching of the muscle by the load after completion of its contraction. However, with an increase in the intensity of stimulation, this afferent reaction may also become intensified when the fast contractions and jerks of the muscle by the load can no longer increase (because they have reached the maximum). This was clearly seen in the two experiments whose results are given in Fig. 3, IV and in the table. These very demonstrable results show that the proprioceptors of the ocular muscles are activated by tonic muscle fibers receiving their motor innervation from high-threshold γ-motor neurons [6].

Probably the receptors of the investigated muscle are located on some of its tonic fibers and are stretched (stimulated) when a contraction arises in the zone of efferent innervation of these nonconducting fibers [7, 8]. The investigated primitive proprioceptors of the extraocular muscles of the rabbit are thus functionally similar to spindles. No receptors of the tendon type (reacting by excitation to a fast contraction) could be found in this object.

LITERATURE CITED

1. R. Granit, The Electrophysiological Investigation of Reception [Russian translation], Moscow (1957).
2. G. V. Zarapov, Z. A. Metreveli, and Ts. A. Lezhava, Biofizika, 11, No. 3 (1966), p. 544.
3. D. G. Kvasov, G. N. Bylyginskii, and I. G. Antonova, Byull. éksp. biol., No. 7 (1951), p. 16.
4. M. V. Korovina, Data Relating to the Physiology of the Extraocular Muscles and Their Central Nervous Regulation, Candidate Dissertation, Leningrad (1956).
5. D. P. Matyushkin, Fiziol. Zh. SSSR, No. 2 (1962), p. 188.
6. D. P. Matyushkin, Fiziol. Zh. SSSR, No. 5 (1962), p. 534.
7. D. P. Matyushkin, Fiziol. Zh. SSSR, No. 5 (1963), p. 603.
8. D. P. Matyushkin, The Fast (Phased) and Slow (Tonic) Systems of the Eye Muscles, Doctorate Dissertation, Leningrad (1964).
9. D. P. Matyushkin, in the book: Abstracts of Scientific Proceedings of the Tenth Congress of the All-Union Physiological Society [in Russian], 2, No. 2 (1964), p. 69.
10. V. M. Starshinova, Trudy Smolensk. Med. Inst., 12 (1961), p. 186.
11. E. Davson, The Eye, 3, New York (1962).
12. J. Ernst, Biophysics of the Striated Muscle, Budapest (1963), p. 247.
13. B. H. Matthews, J. Physiol. (London), 71 (1931), p. 64.
14. B. H. Matthews. J. Physiol. (London), 78 (1933), p. 1.

15. P. B. Matthews, Physiol. Rev., 44 (1964), p. 219.
16. I. Tasaki, Conduction of the Nerve Impulse [Russian translation], Moscow (1957).
17. F. M. Tozer and C. S. Sherrington, Proc. Roy. Soc., B., 82 (1910), p. 450.
18. D. B. Whitteridge, in the book: Handbook of Physiology, 2, Sec. 1, New York (1959), p. 1089.