Histology and Physiology of the Extraocular Muscles

As described in Chapter 4, the extraocular muscles perform two functions: optostatic and optokinetic. The optostatic function requires that the muscles maintain a state of postural tonicity; the optokinetic function requires that quick, tetanic contractions be performed. These two contradictory functions are served by two different sets of muscles in the skeletal muscle system. Eye muscles, however, are equipped to perform both functions simultaneously. It is important to learn what mechanisms enable them to do so.

In principle the type of response by extraocular muscles would be controlled either by the central nervous system or by peripheral mechanisms residing in the extraocular muscles or by both. We have only sketchy information of the finer details of the central nervous system control of tonic and saccadic extraocular movements, but we have gained a little more insight into the structural differentiation and physiologic and pharmacologic responses of the extraocular muscles. The structure of the extraocular muscles and its possible relation to their function will be discussed first.

In general, two types of striated muscles are distinguished in the skeletal muscle system: (1) “red” or dark muscles composed of fibers of small diameter and rich in sarcoplasm and (2) pale or “white” muscles with fibers of greater diameter and scanty sarcoplasm. Red muscles contract more slowly and are kept in a state of tonic contracture by fewer impulses per second than are white muscles, which contract more quickly. Red muscles relax more slowly than white muscles, and their metabolism increases much less during contraction than that of white muscles. Consequently, red muscles do not tire as easily as white muscles. Red muscles are more continuously active and serve the function of postural activity; white muscles are muscles of locomotion and quick activity.

Structure and Function of the Extraocular Muscles

General Histologic Characteristics

The histologic structure of eye muscles, which perform the functions of both red and white muscles, differs in many respects from that of other striated muscles. Extraocular muscles contain fibers of varying diameters. In general they are the finest fibers found in any striated muscles. They vary in diameter from 9 μm to 17 μm, with fibers as fine as 3 μm having been seen, but these muscles also contain coarse fibers up to 50 μm in width. One can appreciate the fineness of fibers of extraocular muscles if their diameters are compared with those of fibers of the gluteus maximus (90 μm to 100 μm).

It was once believed that each muscle fiber
runs through the entire length of the extraocular muscle. If this were true, one would expect to find the same number of fibers in sections taken from the central or peripheral part of the muscle. This view has not been shown to be valid. Fiber counts from the central portion of the muscle have been consistently higher (44% to 72%) than those taken from the proximal or distal portions.\(^2\)\(^,\)\(^57\) These findings indicate that many fibers must originate and terminate between the origin and the insertion of the muscle, suggesting that an interconnection network of muscle fibers must exist. Indeed, cholinesterase-positive “myomysial” junctions have been described in eye muscles of various species, including humans.\(^55\)

The extraocular muscles can be divided into two distinct portions. One portion is a peripheral orbital layer along the muscle surface and faces the orbit, which contains thin fibers with many mitochondria. This layer encloses a second portion, the central or bulbar layer, close to the globe, which consists of thicker muscle fibers with variable mitochondrial content. Both zones are distinctly separated from each other, sometimes by a thin, dense, fibroelastic tissue. Schiefferdecker\(^66\) therefore believed that the elastic tissue was a factor in the regulation of eye movements. Duke-Elder\(^29\) agreed with this view. However, Eisler\(^33\) believed it to be a secondary, mechanical phenomenon produced by frequent small pulls on the extraocular muscles.

**Nerve Supply**

In Chapter 4, it was mentioned that the nerve supply to extraocular muscles is extraordinarily rich. The motor nerves are very thick, owing to the large number of fibers they contain. The ratio of nerve fibers to muscle fibers is nearly 1:12 in extraocular muscles, whereas in skeletal muscles it may be as high as 1:125.\(^57\) The possibility that this rich nerve supply is partly responsible for fine regulation of eye movements cannot be overlooked.

The abundance of nerve fibers has led to the conclusion that the all-or-nothing law, or law of isobolia, applies to eye muscles.\(^45\) According to this general principle of neuromuscular physiology, individual muscle fibers always respond with a maximum contraction to every supraliminal stimulus. The amount of total contraction of a muscle depends on the number of fibers taking part in a contraction.

Extraocular muscles also are provided with a number of different types of nerve endings. Woollard\(^46\) recognized three types: (1) ordinary single motor end plates associated with coarser muscle fibers; (2) multiple grapelike nerve endings, especially around the tendons, which are believed to be sensory in nature; and (3) very fine, nonmedullated fibers ending in the thinner muscle fibers. Newer studies of these different nerve endings are reported in the following discussion.

**Physiologic and Pharmacologic Properties**

The physiologic and pharmacologic properties of extraocular muscles correspond to the many unusual histologic features of these muscles. Rehms\(^60\) stated that eye muscles require and receive more oxygen than other skeletal muscles. Björk\(^8\) showed by means of electromyography (see p. 109) that responses of extraocular muscles in humans are considerably lower in amplitude (20 to 150 \(\mu\)V), of much shorter duration (1 and 2 ms), and much higher in frequency (up to 150 cps) than those of peripheral skeletal muscles, in which the amplitude is 100 to 3000 \(\mu\)V; the duration, 5 to 10 ms; and the frequency only up to 50 cps. Björk attributed these differences to the low nerve fiber-to-muscle fiber ratio of the motor units in extraocular muscles.

Extraocular muscles contract much more quickly than other voluntary muscles. Contraction times obtained from experiments on cats were: soleus muscle, 100 ms; gastrocnemius muscle, 40 ms; and medial rectus muscle, 8 ms.\(^23\)\(^,\)\(^27\) The great speed of contraction of extraocular muscles is in
keeping with the requirements of saccadic eye movements and with what is known of the structure and innervation of extraocular muscles. It is all the more striking when contrasted with another observation.

Duke-Elder and Duke-Elder\textsuperscript{10} demonstrated that the extrinsic muscles of eyes of cats contract under the influence of acetylcholine. Acetylcholine produces a strong contraction of smooth muscles in invertebrates and of some skeletal muscles in lower vertebrates, but has slight, if any, effect on skeletal muscles of mammals. Only denervated muscles of mammals or embryonic mammalian muscles react strongly to acetylcholine. In the lower vertebrates the differences in reaction to acetylcholine are indicative of the nature of muscles. The more quickly a muscle acts, the less it is apt to respond to acetylcholine; the more its action is one of postural tonicity, the more strongly it will respond to acetylcholine.

Since the discovery that a dual motor system of slow and fast fibers exists in extraocular muscles, experiments have shown that acetylcholine, choline, and nicotine cause slow and tonic contraction of slow fibers, whereas fast fibers respond with a fast twitch. The response of extraocular muscles to neuromuscular blocking agents is of clinical interest, since these drugs are often used during general anesthesia.

**Slow and Fast Twitch Fibers**

Customarily, one thinks of voluntary striated muscles as being characterized by fibers that respond to a single stimulus applied to their nerve with an ungraded fast twitch, followed by speedy relaxation, and accompanied by propagated electrical activity. Repetitive stimuli of relatively high frequency are required to maintain a tetanic contraction, and accompanied by propagated electrical activity. There are also pharmacologic differences between these two systems, which, in general, are present in spatially unrelated muscle groups.

Sommerkamp,\textsuperscript{69} in his pharmacologic studies with acetylcholine, intimated the existence of a slow contractile system in striated muscles of amphibians, which produced a rapid twitch of the sartorius muscle of the frog but a slow maintained contraction of the rectus abdominis muscle. Within iliofibularis muscle of the frog, Sommolkamp was able to separate a group of fibers that responded to acetylcholine by a twitch and a second group of fibers (the “tonus bundle”) in which acetylcholine produced a slow, tonic contraction.

Anatomical studies by Krüger\textsuperscript{63} and his school uncovered the structural basis for fast and slow fiber systems in striated muscles. He stated that the system giving twitch responses had a *Fibrillenstruktur*, and the system responsible for the slow contractions had a *Felderstruktur*. In the course of time, the two systems have been demonstrated in skeletal muscles of amphibians, reptiles, and birds, but not of mammals. Although Krüger believed that he had found the two systems also in mammalian muscles, most workers agree with Hess\textsuperscript{37} that these two systems occur in mammals only in extraocular muscles, where they have been found in the rabbit,\textsuperscript{42} guinea pig,\textsuperscript{36} cat,\textsuperscript{18} 38 monkey,\textsuperscript{19, 57} and human.\textsuperscript{10, 28}

The *Fibrillenstruktur* type of the fast fiber system is characterized anatomically by small, well-defined myofibrils, each surrounded by abundant sarcoplasm and having an even, punctate appearance as seen with the light microscope (Fig. 6–1A). Light microscopic and electron microscopic examinations show a well-developed sarcoplasmic reticulum, a regular tubular (T) system in each sarcomere, a straight *Z* line, and a well-marked *M* line or thickening of the filaments in the middle of the *A* band. The nuclei of the fibers are usually located peripherally and are only infrequently centrally located (Figs. 6–2 and 6–3A).

In contrast, slow fibrils of the *Felderstruktur* type are clumped together in a more or less fibrillar-appearing mass of myofilaments with large, partially fused fibrils in scant sarcoplasm (Fig. 6–1B). The sarcoplasmic reticulum is poorly developed; the *T* system is absent or consists of aberrant elements; the *Z* line follows a zigzag course; and the *M* line is absent. Mayr\textsuperscript{55} considers the presence or absence of the *M* band as a distinguishing sign between the two fiber types unreliable. The nuclei are located centrally or slightly eccentrically (Fig. 6–3B). The *Felderstruktur* systems stain more deeply than the *Fibrillenstruktur* systems. Peachey\textsuperscript{59} subdivided fiber types according to their electron microscopic characteristics into five groups, and similar classifications have been suggested by others.\textsuperscript{2, 53} Miller\textsuperscript{84} drew attention to the microstructural changes that extraocular muscles undergo with advancing age.
Fibrillenstruktur fibers are innervated by thick, heavily myelinated nerves joining the muscle fiber with single, typical motor and so-called en plaque end plates (Fig. 6–4), showing junctional folds and numerous synaptic vesicles in the terminal axon. Unlike typical skeletal muscle, Felderstruktur fibers are innervated by multiple grapelike nerve terminals, so-called en grappe endings, derived from efferent nerves of small diameter arranged linearly or in loose collections and scattered throughout the muscle from origin to insertion (see Fig. 6–4). According to Cheng and Breinin, the synaptic membrane of these terminals has only a few rudimentary invaginations and the terminal axon contains granular as well as agranular synaptic vesicles.

With the exception of extraocular muscles, single fibers are innervated by multiple endplates in only two other muscles, the tensor tympani and the stapedius. The presence of multiple endplates indicates that the fiber is innervated by either multiple branches from the same nerve or by input from more than one nerve fiber. Although polyneuronal innervation occurs in several types of vertebrate muscles, Bach-y-Rita and Lennerstrand were not able to demonstrate this function in the extraocular muscles of cats. Lennerstrand distinguished further between multiple innervated fibers that conduct and those that do not conduct action potentials, but his hypothesis has not been universally accepted.

The percentage of multiple innervated muscle
fibers is higher in the orbital region than in the central zone of extraocular muscles and varies with the species. However, the fact that both types of fibers are present in the two zones is of considerable importance when attempting to correlate the structure of the extraocular muscles with their function.

The electron microscopic differences between the fibrillar and field type of fibers emphasize the differences in their functions: the fibrillar type is fast fibers and the field type is slow fibers. The presence of the T system and the abundance of sarcoplasmic reticulum may serve to transmit excitatory impulses with greater rapidity; the large concentration of mitochondria between the fibrils may be related to the considerable oxidative requirements associated with twitch contractions. The virtual absence of the T system and the sparse sarcoplasmic reticulum and mitochondrial concentration may be evidence for the slow, tonic contraction of the field type of fiber structures and their lesser demand for oxidative metabolism. The experimental work of Asmussen and Kiessling has shown that fast twitch fibers respond to denervation with atrophy and slow twitch fibers with hypertrophy.

Pharmacologic studies of the behavior of extraocular muscles are of particular interest. Kern showed that the superior rectus muscle of the rabbit consists of two layers, an upper thin layer made up of Felderstruktur fibers, and a lower layer, the bulk of the muscle, composed of Fibrillenstruktur fibers. Kern was able to separate the two muscle strips. When those of the Felderstruktur type were exposed to a low dose of acetylcholine (0.5 μg/mL), a tonic contraction of about 80 mg lasting for more than 6 minutes developed. In contrast, one fifth of the Fibrillen-

**FIGURE 6-2.** Transverse section of human inferior oblique muscle showing Fibrillenstruktur (arrows) and Felderstruktur fibers. (Light micrograph; X400.) Note that the Felderstruktur fibers take a much deeper stain. (From Brandt DE, Leeson CR: Structural differences of fast and slow fibers in human extraocular muscle. Am J Ophthalmol 62:478, 1996.)

**FIGURE 6-3.** Longitudinal sections through superior oblique muscle of cat. Electron micrographs. A, Fast twitch fiber. Separation of fibrils by sarcoplasmic reticulum; straight M and Z lines; regularly occurring T system (arrows) (X16,000). B, Slow twitch fiber. Poor separation of fibrils; sparse sarcoplasmic reticulum; M and Z lines wavy; absent tubular system (X16,000). (From Hess A: The structure of vertebrate slow and fast twitch muscle fibers. Invest Ophthalmol 6:217, 1967.)
Simple en plaque endings common in muscle fibers (F) of Fibrillenstruktur type, 9 to 11. Rare finding of two en plaque endings on one muscle fiber, 12. En grappe nerve endings commonly found on Felderstruktur fibers, 13, 14. (From Dietert SE: The demonstration of different types of muscle fibers in human extraocular muscle by electron microscopy and cholinesterase staining. Invest Ophthalmol 4:51, 1965.)

FIGURE 6–4. Response of rabbit’s superior rectus muscle to acetylcholine (A). a, response of muscle strip comprising only Felderstruktur fibers; b, response of Fibrillenstruktur fibers. Calibration 20 mg/min. (From Kern R: A comparative pharmacologic histologic study of slow- and fast-twitch fibers in the superior rectus muscle of the rabbit. Invest Ophthalmol 4:901, 1965.)

FIGURE 6–5. Struktur strips did not respond at all to acetylcholine, and only a small response rise in tension was noted in the remaining preparations (Fig. 6–5). This minimal response may be explained by some admixture of slow fibers to the preparation. Increased concentrations of acetylcholine (0.1 to 1.0 μg/mL) induced faster and higher rises in both types of preparations. The responses of the Fibrillenstruktur strips were proportionately lower than those of the Felderstruktur strips and returned rapidly to the baseline level, whereas tensions of the latter strips remained elevated for longer than 10 minutes and returned to the baseline level after the drug was washed out.

The presence of two different fiber systems, a slow and a fast system, was confirmed by Katz and Eakins in experiments with succinylcholine and other depolarizing agents. These authors found that the initial effect of succinylcholine on the superior rectus muscle of cats was to increase the baseline tension without an effect on the twitch response. The greater the dose of succinylcholine, the greater the rise of the baseline tension. Eventually the twitch response became depressed, and with a dosage of 128 μg/kg of succinylcholine it was abolished (Fig. 6–6). The anterior tibial muscle did not respond with a rise in baseline tension, but its twitch response was abolished with much lower doses of the drug than in the superior rectus muscle.

Katz and Eakins believed that responses of extraocular muscles to succinylcholine and other...
depolarizing agents found in their experiment are explained by the presence of two neuromuscular systems: the increase in baseline tension is attributable to the tonic (slow) system, and the decrease in twitch response is attributable to the twitch (fast) system.40

Although there is abundant ultrastructural and pharmacologic evidence to support the notion of two principal fiber types (slow and fast twitch) in the human extraocular muscle, several authors have proposed classifications that are based on as many as five to six fiber types.2, 3, 53 These classifications take into account a much wider range of structural and contractile features for each fiber type than the older studies cited above.

Some reservations may be in order to distinguish muscle fibers exclusively on the basis of their electron microscopic characteristics, since it has been shown that fibers may change back and forth from Felderstruktur to Fibrillenstruktur along their length.25, 58 Brooke and Kaiser14 introduced a histochemical classification based on the presence of slightly different isoforms of myosin in various types of slow and fast twitch fibers and more recent research has distinguished fiber types on the basis of immunohistochemical studies, using various antimyosin antibodies.62, 65, 75

The main features distinguishing skeletal from extraocular muscle are summarized in Table 6–1 and the various characteristics of slow and fast fiber types are shown in Table 6–2. The reader is referred to several recent reviews for more detailed information.3, 13, 46, 61

**Structural and Functional Correlations**

Inferring a correlation between fast fibers and fast eye movements (saccades) and slow fibers and

| TABLE 6-2. Characteristics of Slow and Fast Twitch Fibers in Extraocular Muscles |
|---------------------------------|---------------------------------|
| **Slow Twitch** | **Fast Twitch** |
| Thin motor nerve fibers | Thick motor nerve fibers |
| Multiply innervated (en grappe) | Singly innervated (en plaque) |
| Large, poorly delineated muscle fibrils (Felderstruktur) | Small, well-delineated muscle fibrils (Fibrillenstruktur) |
| No conduction of action potential | Conduction of action potential |
| Slow, sustained contraction (tonic) | Fast contraction (phasic) |
| Predominantly in orbital layer | Predominantly in central (bulbar) layer |

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**TABLE 6-1. Comparison of Skeletal and Extraocular Muscle**

<table>
<thead>
<tr>
<th></th>
<th>Ocular</th>
<th>Skeletal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fiber diameter</td>
<td>9–17 μm</td>
<td>90–100 μm (gluteus maximus)</td>
</tr>
<tr>
<td>Ratio of nerve to muscle fiber</td>
<td>1:1–17</td>
<td>Up to 1:300</td>
</tr>
<tr>
<td>Contraction time</td>
<td>Fast</td>
<td>Slow</td>
</tr>
<tr>
<td>Acetylcholine sensitivity</td>
<td>High</td>
<td>Low or absent</td>
</tr>
</tbody>
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slow eye movements (vergences) is tempting. If this were so, then two separate neural pathways would exist, one for the saccadic and the other for the tonic function, each with its own separate supranuclear component and subnuclei in the oculomotor complex.

Miller\textsuperscript{56} found the outer part of extraocular muscles of rhesus monkeys to consist of fibers with small cells having the histochemical and electromyographic characteristics of red muscles. The central part of these muscles consisted of fibers with large cells having the characteristics of white muscles. An intermediate area between the outer and central zones was made up of a mixture of large and small cells. Miller attributed slow eye movements to the outer red part of the fibers and faster eye movements to the central white part.\textsuperscript{56}

However, these notions were dispelled by the findings of Keller and Robinson,\textsuperscript{41} which are incompatible with the existence of two muscular systems, one for saccadic and one for tonic function. These authors induced saccadic, pursuit, and vergence movements in alert, unanesthetized monkeys while simultaneously recording the electric responses from cells of the abducens nucleus by means of microelectrodes. All investigated cells responded to all movements; no cells responded selectively. Keller and Robinson concluded that there was a single common pathway for saccadic, pursuit, and vergence movements.\textsuperscript{41} The undeniable differences in muscle fiber types then would have to be correlated with some other functional differences in the oculomotor system. For example, Keller and Robinson found fibers with a discharge frequency of 150 spikes per second with the eye in primary position, that is, during the entire time the animal was awake. As Björk\textsuperscript{8} had already determined from electromyographic studies, this amounts to an intensity and duration far in excess of that required from other muscle systems. On the other hand, units in which the threshold lies lateral to the primary position are recruited into activity for only brief periods of lateral gaze or during lateral saccades. Their role of intermittent activity is not unlike that of other skeletal muscles. Keller and Robinson conclude that it would be remarkable if such large differences in synaptic transmission and muscle metabolism were not reflected in morphologic differences. This observation by Keller and Robinson might well explain the presence of twitch fibers with different physiologic responses,\textsuperscript{41} but one fails to see how it could account for the difference between fast and slow fibers.

Scott and Collins\textsuperscript{67} and Collins\textsuperscript{21} recorded from slow and fast fibers in the orbital and central layers of human extraocular muscles to analyze their contribution to various types of eye movements. During fixation in different eye positions, the fast fibers are inactive outside the field of action of the muscle. As the muscle approaches its maximal field of action, their activity begins to increase. Conversely, slow fibers are active even in extreme positions of gaze outside the field of action of the muscle. Their activity increases nonlinearly as the eye begins to fixate more and more in the field of action of the muscle. This innervational pattern is similar during slow following movements; however, during fast saccades, both slow and fast fibers are activated maximally during the first phase of the saccades, then begin to decay logarithmically to their new equilibrium with a time constant of about half the duration of the saccade. The work of these investigators leaves little doubt that both slow and fast fibers contribute to tonic and phasic activity but not necessarily simultaneously in the case of tonic activity. Scott and Collins suggested that various muscle fiber types are functionally differentiated by the amount of work they do rather than by the type of eye movement to which they contribute.\textsuperscript{67}

One may hope that future work will permit application of laboratory findings in extraocular muscles to the clinical study of strabismus. Extraocular muscles contain different types of muscle fibrils with intricate ultramicroscopic structures and fibers with highly differentiated nerve endings. They are surely there to subserve specific functional needs. This seems more probable when one considers that even such anatomically and embryologically closely related muscles as the levator of the upper lid in humans\textsuperscript{28} and the retractor bulbi in the rabbit\textsuperscript{42} do not share the peculiarities of extraocular muscles.

There is justification in comparing the action of extraocular muscles with the action of flexor muscles of amphibians. Flexor muscles of frogs contain tonic bundles required for the amplexus. Kuffler and Vaughan Williams\textsuperscript{44} established that slow and fast fibers in these muscles are synergistic, that the state of tension of slow fibers is directly related to stimulus frequency, and that any amount of slow fiber tension could collapse instantly by superimposition of a single twitch.
contraction. A comparable phenomenon may take place in extraocular muscles.

Regardless of what future studies may uncover, the uniqueness of the structure and function of extraocular muscles remains unquestionable. These muscles have many structural and therefore functional features that are present in some skeletal muscle systems and absent in others which enable them to carry out their complex and highly specialized tasks.

The effect of the autonomous nervous system on extraocular muscles is uncertain because morphologic, pharmacologic, and electrophysiologic studies have produced contradictory results. There is no convincing evidence for sympathetic innervation of extraocular muscles.

Muscle Spindles and Palisade Endings in the Extraocular Muscles

Groups of fine cross-striated fibers with centrally located nuclei surrounded by a thin, torpedo-shaped capsule are found in all skeletal muscles. These so-called muscle spindles are proprioceptive sensory organs. Since publication of the studies by Daniel, Cooper and Daniel, and others, there is no doubt that human extraocular muscles also contain muscle spindles. The density of these spindles is about the same as in skeletal muscle and their presence is not, as had originally been assumed, age-related. Whether extraocular muscle spindles are capable of providing proprioceptive information is a subject of debate. In view of distinct histologic differences from spindles found in skeletal muscles, Ruskell doubts this capacity. On the other hand, passive stretching of an extraocular muscle causes changes in ocular alignment and lack of pointing accuracy and visual illusions can be elicited by muscle vibration. Lennerstrand and coworkers reported that vibration-induced eye movements differed in normal and exotropic subjects. Most current research seems to indicate that there may indeed be sensory feedback from muscle spindles even though the role of this inflow under casual conditions of seeing is by no means clear (see also p. 30).

Another possible source of proprioceptive input is the palisade endings, which have been described in the tendinous insertion of human extraocular muscle. Lewis and Zee believe that the tendon organs rather than the muscle spindles are providing feedback as to the position of the eye, a view that is also shared by Steinbach and Smith and by Richmond and coworkers.

The peripheral and central pathways of extraocular muscle proprioception have been defined by Manni and Bortolami, who showed, on the basis of histologic and electrophysiologic studies, that the perikarya of first-order neurons are located in the semilunar ganglion. Whereas the peripheral nerve process innervates the muscle spindle, the central nerve processes terminate in the ipsilateral portion of the spinal trigeminal nucleus and in the main sensory trigeminal nucleus. Second-order neurons have been identified in these nuclei and project on the cerebellum and the mesodiencephalic areas. These data refer to animal studies and there is no information yet on the route of centripetal information from the extraocular muscles in humans.

The functional significance of the muscle spindles, palisade endings, and other proprioceptive sensors is discussed in Chapter 2. For additional reviews of current theories, see Bach-y-Rita, Lennerstrand, and Steinbach.

Electromyography

Electrical responses have been recorded from extraocular muscles of animal eyes for many years. Following Björk’s study of electromyography of human eyes in 1952 and subsequent elaboration by a number of researchers, important contributions have been made toward understanding of the function of extraocular muscles in normal and pathologic states. Basically, electromyography consists of oscilloscopic recording of suitably amplified electrical activities of a muscle. Monopolar or bipolar electrodes are inserted into the muscle to record the current. The electrodes are placed extracellularly. This basic technique may be highly refined by use of various electronic components for integration, analysis, and storage of responses.

Extraocular muscles are especially interesting to those engaged in electromyographic studies because of their low nerve fiber-to-muscle fiber ratio. The anatomical motor unit consists of the neuron cell body, its axon, and the muscle fibers innervated by that axon. All these fibers discharge synchronously when the axon is stimulated. The integrated voltage of this discharge constitutes the
electric motor unit. Since only a few fibers of an extraocular muscle are innervated by one axon, electromyography comes close to recording the electrical activity of a single anatomical motor neuron in such a muscle.

Electromyography has proved to be of value in assessing paretic and pseudoparetic conditions of extraocular muscles, in myopathies, and in elucidating the pathophysiology of the retraction syndrome (see Chapter 21). No specific abnormalities are revealed in patients with comitant strabismus. Great difficulties are encountered in quantifying electromyograms. The smallest movement distinguishable by means of ocular electromyography is about 5°. All this puts limitations on the use of electromyography in studying the physiology of the motor functions of the eyes. It should be be noted that the applicability of electromyography is, for technical reasons, limited. The introduction of electrodes into the muscles is easy only for rectus muscles, although some discomfort is always part of this procedure. The insertion of electrodes into the oblique muscle is far more difficult. Generally, no more than two muscles in each eye can be studied simultaneously. Multichannel recordings have recently been obtained after insertion of electrodes into the muscles during surgical procedures. The recordings were performed days after surgery and without discomfort to the patient, after which the electrodes simply pulled out of the muscle. This approach may hopefully provide better information on electrical activity of the extraocular muscles.

Despite these limitations electromyography has resulted in important contributions to the kinesiology of extraocular muscles. In essence, electromyographic studies have given incontrovertible proof for certain basic facts that were known, or assumed to be known, from physiologic or clinical experience. The contributions of electromyography to the anomalies of ocular movements are discussed in the appropriate place in various chapters dealing with these anomalies.

Electromyographically, there is no “rest” of the extraocular muscles (and no “position of rest” of the eyes). In primary position and with the eyes grossly fixed, extraocular muscles are never electrically silent but manifest a tonic activity. Complete inactivity of electrical discharge in extraocular muscles is encountered only in deep sleep or deep anesthesia.

When a muscle rotates an eye into its field of action, there is an increment of electrical activity accompanied by graded inhibition of the activity of the direct antagonist (Sherrington’s law of reciprocal innervation). Similarly, in extreme gaze to the right, the left medial rectus fires maximally while the left lateral rectus is electrically silent. The opposite is true in extreme gaze to the left (Fig. 6–7). Figure 6–7 also shows that in a waking person a muscle may be electrically silent only when in extreme positions out of its field of action. Whenever an eye diverges, an increment in the electrical activity occurs in the lateral rectus muscle. For the electromyographic behavior of extra-

**FIGURE 6–7.** Simultaneous electromyograms of the four rectus muscles. Note the graded increase in electrical activity in the right medial (RMR) and left lateral rectus (LLR) muscles with corresponding decrease in activity all the way to zero in the right lateral (RLR) and left medial rectus (LMR) muscles as the eyes perform a levoversion movement. With return to the primary position the RLR and LMR resume their activity and increase it in the ensuing dextroversion while the activity in the RMR and LLR decreases. (Courtesy of Prof. Alfred Huber, Zurich.)
ocular muscles in vergences and a discussion surrounding it, see Chapter 4.

Saccadic movements differ from vergence movements in their innervational pattern. Miller\textsuperscript{55} found that they are initiated by a sudden burst of motor unit activity of the agonist with corresponding inhibition in the antagonist (Fig. 6–8). The duration of the initial burst is proportional to the extent of the movement (30 ms for a 2.5° movement to 150 ms for a 40° movement).

This initial burst is followed immediately by an orderly series of uniformly firing motor units. The firing rate of the motor unit depends on the angular displacement from primary position. Large movements (15° to 20°) cause a second or third saccadic burst representing efforts to overcome a lag in fixation. These findings are in accord with those made by optical and electro-oculographic recordings of eye movements.

**Sources of Tonus of the Extraocular Muscles**

The presence of fast and slow fibers in extraocular muscles and their electrophysiologic characteristics and pharmacologic properties provide evidence for some of the peripheral mechanisms that contribute to the tonus of these muscles. This exciting new knowledge must not obscure the fact that the tonus of extraocular muscles is basically regulated by neural influences.

Neurophysiologists have established that there are differences in the frequency of firing of motor neurons innervating slow and fast muscles in the hind limbs of cats and other experimental animals. Buller and coworkers\textsuperscript{16} stated that the shorter afterpolarization of motor neurons supplying fast muscles\textsuperscript{32} permits fast frequency of firing and is appropriately related to the contraction time of muscles. As a consequence, motor neurons with larger afterhyperpolarization have frequencies of discharge appropriate to the slow muscles they innervate. Buller and coworkers also made the observation in cross-union experiments that when a nerve from a fast motor neuron is made to innervate a slow muscle, the muscle is transformed into a fast muscle; slow or tonic motor neurons, similarly transferred, convert fast muscles into slow.\textsuperscript{16} No corresponding observations exist for extraocular muscles or other muscles innervated by cranial nerves.

Irrespective of peripheral mechanisms, the most important source of tonus of extraocular muscles is reflex in origin. A certain tonus within the central nervous system is kept up by stimuli from sensory sources. Light itself is a powerful source of tonus. In adult humans, reflex tonus from neck muscles appears to be of minor importance. All the more important are reflexes resulting from vestibular stimulations. These stimulations to a large degree control the position of the eyes in space. They are active when the head is erect, and they also regulate the position of the eyes with every movement of the head.

In humans, with their highly developed binocular vision, however, the most powerful tonic impulses flow from the process of vision. Psycho-optical reflexes have superseded in importance such unconditioned reflexes as those that arise from proprioception and the vestibular system. In uniconal and binocular vision, these impulses produce the fixation reflex. In binocular vision, disparate stimulation elicits fusional movements.
and maintains the proper relative position of the eyes.

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