

ACTIVITY OF A HUMAN OCULOROTARY MUSCLE UNIT¹

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In their classical analysis, Adrian and Bronk (1929) provided the definition by which single motor unit action potentials of striated muscles are identified, during weak contraction, by uniform rhythm, amplitude and waveform. Human oculorotary muscles offer a special and difficult problem in unit analysis because of uncontrollable electrode needle movement which alters the recorded amplitude (Buchthal *et al.* 1957). In an analysis of oculorotary single unit activity during progressive contraction, the identification of the unit by rhythm, amplitude and shape is not simple because these characteristics are not fixed. A complete analysis must make use of any of these three characteristics individually or together, simultaneously or in temporal combination, to identify the activity of the response as that from a single unit.

It is ordinarily impossible to study a single unit during moderate or strong contraction because of the mass response of units, many being recorded simultaneously and obscuring one another. Three methods can be used to overcome this plethoric activity: 1. by observing a unit spike of large amplitude standing above the feather edge formed by the tops of the mass of units (Björk and Kugelberg 1953, for ocular muscles); 2. by recording from a severely parietic muscle so that even in maximum contraction only a few units function (Björk and Kugelberg 1953, for ocular muscles); 3. by employing microelectrodes which record single units from strongly contracted muscle by virtue of their small receptive area (Norris and Gastiger 1955). In our investigation of the oculorotary muscles we have used a microelectrode through which, with associated equipment, we were able on occasion to record distinguishable single motor units even during attempted maximum contraction. In this way we have found it possible to describe some characteristics of extraocular unit activity.

METHOD

Basic extraocular electromyographic procedures have been described in a previous publication (Marg *et al.* 1959). In the present experiment the electrode

consisted of a 10 μ or 25 μ insulated platinum-iridium alloy wire which was set in the lumen of a 30 gauge hypodermic needle (outside diameter of 0.3 mm). The Luer fitting was removed to reduce weight and reduce the independent swinging movement of the needle. Leads from the core tip and from the hypodermic shaft were fed into the balanced, high impedance input probe of a Grass P5 preamplifier modified for capacitance coupled input. Half-amplitude cut off occurred at 10 kc. A Tektronix Type 535 dual-trace, cathode-ray oscilloscope provided the display which was recorded with a Grass camera using a constant film velocity of 1-2 m/sec as the sweep. The output of a Tektronix pulse generator displayed on the second trace provided a time reference.

As expected, it was more difficult to find a unit of acceptable amplitude because of the greater selectivity of a micro-conducting surface. The unit was found while the muscle was moderately contracted with the eye straight ahead. After successful insertion, as judged from the staccato sound of the response, the subject was instructed to follow the target with his eyes. The full horizontal version range was stimulated in the oculorotary field for the muscle being recorded.

RESULTS

A graph of 8 sec of activity of a unit is shown in Fig. 1. (Another smaller unit from another subject gave similar results but the records were unfortunately unsuitable for display because the film velocity was not constant.) The graph displays the response of the left lateral rectus during a slow movement from minimum to maximum contraction. The muscle has already been progressively contracting for about 4 or 5 sec before the large unit at 0 sec starts to fire. This is indicated by units of small amplitude and long duration (events before zero time are not shown).

A small amplitude unit of short duration appears for about 2 sec before the start of 0 sec in the graph of Fig. 1, but it cannot be followed much beyond this time because of its small size and lack of a distinctive waveform.

The unit we are analyzing appears as a polyphasic one as seen in inset *A* of Fig. 1. Its characteristic form along with its large amplitude makes the unit particularly easy to follow and analyze even though

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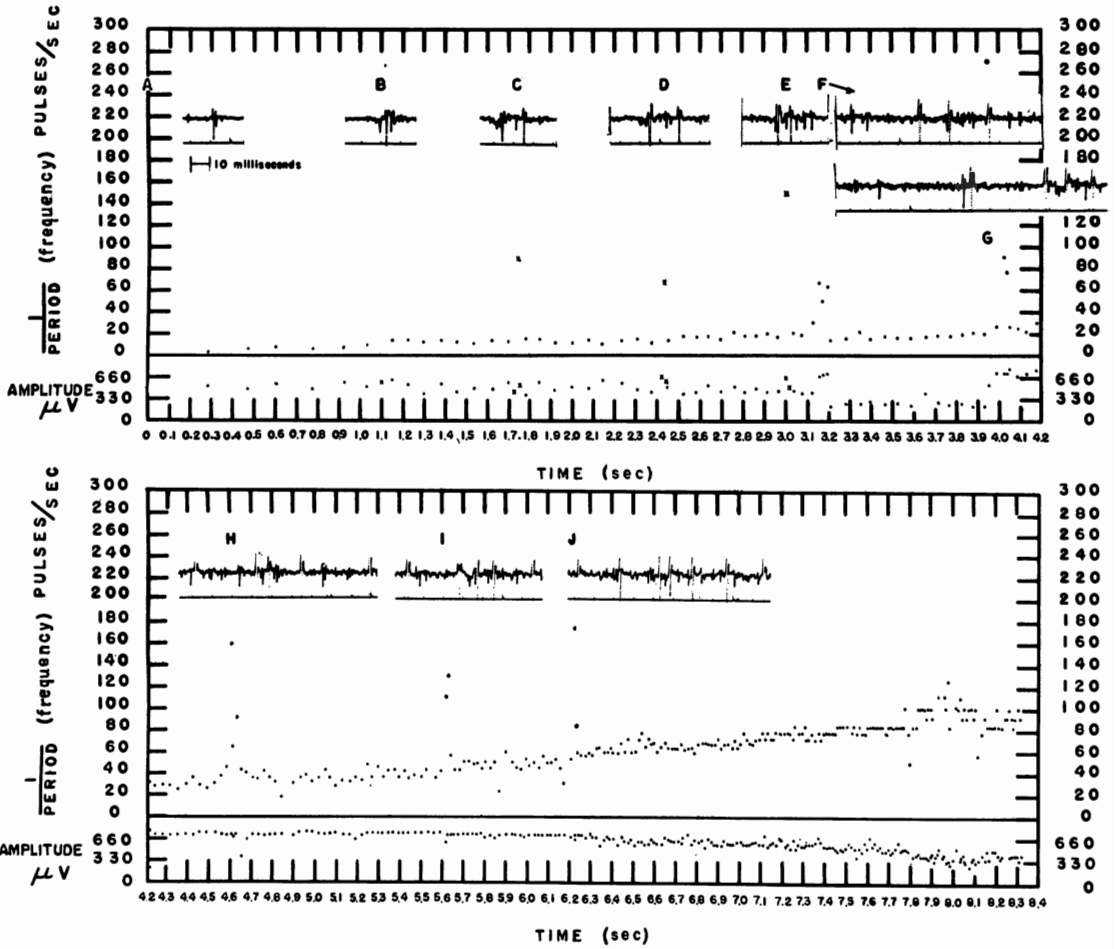


Fig. 1

A unit from the lateral rectus during a following movement of the eye from extreme adduction (relaxation) to extreme abduction (contraction). The two graphs are continuous. The movement started 4 or 5 sec before the observed unit first appeared at time 0.0 sec on the abscissa. The unit was followed for 8.3 sec. Insets A to J with expanded time scale show the action potentials at specific points of interest, the position of the letter on the abscissa indicating the time of occurrence of the inset. The amplitude is measured from the trough of the negative wave to the crest of the following positive wave. The crosses signify some doubt that the datum point is based on the same single unit. Note that the maximum frequency (or minimum period) displayed is 270/sec at time 3.94 sec. The amplitude indicates the relative position or movement of the electrode tip. For further explanation see text.

its form gradually changes. The unit starts out at a very low tonic frequency of 4-7 spikes/sec and gradually increases while the amplitude is fairly constant. The total amplitude was measured from the trough of the downward negative wave to the following positive crest. Variations in size of both negative and positive deflections of the spike appear to occur together and their sum is graphed because it is more constant and easier to measure precisely. Bursts of activity are seen superimposed on the slowly increasing rate of firing (tonic activity).

DISCUSSION

Is tonic activity separate and distinct from bursts of activity? It appears that tonic activity provides the steady state innervation for maintaining a given eye position. Tonic activity is limited in frequency to about 100-140 spikes/sec. Slow eye movements can take place during such type of activity without the high frequency bursts. However, it is possible that fast or saccadic movements, large or small, may be elicited by bursts of activity. Generally, the maximum

frequency of a burst, up to 350/sec, is higher than the maximum tonic frequency, but it is not necessarily always so. For example, the burst of activity near time 3.2 sec in Fig. 1 does not exceed 70 spikes/sec. This frequency might be considered tonic but the briefness of the change leads to the burst classification. Thus, there may be an overlapping of tonic and burst frequency responses but they are clearly separate and distinct at low steady state frequencies and at high transient frequencies.

The maximum burst frequency in Fig. 1 was 270/sec. Generally, the burst frequency did not exceed 180/sec. If one is not careful to identify the spikes as being from the same unit it is easy to find erroneous frequencies of 300/sec or more. However, as already mentioned, we have been able to follow in excellent isolation another easily identified unit of low amplitude for 14 sec through minimum to maximum contraction during three complete cycles. A similar picture of that of Fig. 1 was observed except that the burst frequency often climbed to the order of 300/sec often for three of four spikes and with a maximum of 350/sec. The tonic frequency started at 40/sec, and during relaxation again stopped after descending to 6–12/sec. The maximum mean tonic frequency was about 140/sec.

The major question concerns the nature of the bursts of unit activity. Two hypotheses present themselves. First the bursts of activity are elicited by the irritation of the tonic unit by the electrode needle tip. It is not possible to prevent movement of the needle tip relative to the source of potentials as is indicated by the several jumps in the amplitude of the potential shown in Fig. 1. These jumps show some correlation with the bursts, although it is not possible to state a cause and effect relationship. It has been demonstrated in larger muscles that insertion and bending of the needle electrode can cause bursts of unit activity up to 200/sec (Kugelberg and Petersen 1949). We tried to avoid bending our inserted electrodes but some bending occurred during eye rotation since only the pointed end is fixed by the insertion through the conjunctiva. Björk and Kugelberg (1953) evoked insertion activity in the extraocular muscles but did not note other injury discharges.

The second hypothesis is that the bursts of activity are purposeful, innervated activity of a unit concerned with phasic ocular motility. This phasic activity hypothesis is tenable because bending of the electrode did not elicit bursts.

It does not seem possible at this time to perform a crucial experiment which would distinguish between the irritation and phasic hypotheses. Smaller, lighter electrode needles and/or isometric contraction of the muscle should help make the distinction.

In regard to the maximum burst frequency recorded of 350/sec, it is interesting to note that this is the same rate required to produce a completely fused tetanus in the internal rectus muscle of the cat (Cooper and Eccles 1930).

The sequence of multiple pulses giving the high maximum frequencies found here shows little resemblance to classical "double discharge". This phenomenon is seen in larger skeletal muscles where the period between a single pair of spikes may correspond to a frequency as high as 350–500/sec (Hoff and Grant 1944; Norris and Gastiger 1955). Regular double or triple rhythms at higher than normal frequencies are not seen in the extraocular muscles.

Within our very limited sampling, there does not appear to be in the oculorotary muscles the kind of relation of response frequency and degree of contraction as reported by Norris and Gastiger for postural muscles of the leg.

Kuboki (1957) found the increase of tonic response with contraction in a single extraocular unit, although his maximum tonic frequency was never shown over 65–70/sec. This can be explained if his data did not represent maximum contraction because of the interference pattern.

In a subsequent publication, Kuboki (1959), using a large tip electrode, noted that the EMG had two rhythms, a slow and a fast. Fourier analysis demonstrated peaks in the power spectra at two loci, 60–120 per sec and 120–250/sec. The maximum value of the slow rhythm peak increased with contraction of the muscle. These slow rhythms were not observed in contractions of less than about 30° abduction (greater abduction meant relaxation of the muscle). The fast rhythm appeared at about 30° or more adduction. Kuboki presumes that the slow rhythm represents the activity of the tonic muscle units and the fast rhythm represents the activity of the "kinetic" muscle units.

The frequency and other response characteristics of our single unit allow us to offer an explanation of the analysis of the data presented by Kuboki. It may be that our tonic rhythm is his slow rhythm and our bursts his fast or kinetic rhythm.

Although the rate of movement of our target stimulus was not strictly controlled, an attempt was made to make it constant. The relatively constant slope of about 16/sec per sec in the lower graph of Fig. 1 raises several points. If the frequency of a unit is strictly associated with the eye position, does a given change of position merely require a given incremental change in the tonic frequency of innervation? Co-contraction may change the level of frequency but may not alter the rate of change. Fast movements may be accomplished by a superposed phasic frequency to speed the eye to its new tonic position. Kuboki's analysis indicates that most units respond in the same two octaves of frequency from 60–120 and 120–250.

Another question is raised in the relation of tonic frequency to eye tremor which is generally considered to have a dominant frequency of 50–100/sec. A plausible hypothesis has been offered that the tremor is a result of the synchrony of some of the units firing at their tonic rate (Hebbard and Marg 1960). On the basis of the data obtained here, this hypothesis may

be tested by a Fourier analysis of tremor with the eye not only in the primary position but in extreme adduction and abduction. One would expect two peaks in the power spectra at a higher and a lower value than the single peak found in the primary position, although the higher value may be largely damped by the mass of the globe.

SUMMARY

Single unit responses were recorded, even during strong contraction, by means of a concentric electrode with a 10–25 μ diameter core. During progressively increasing contraction which lasted 8 sec, a single unit was followed and its amplitude and frequency (or period) plotted. Two patterns of activity are distinguished. A tonic activity is seen, starting at fewer than 10/sec, increasing in frequency as the muscle contracts to more than 100/sec. Superimposed on this tonic response the same unit exhibits brief bursts of one to four spikes, as high as 270/sec, which may occur as often as at half second intervals. In another subject, a unit reached the frequency of 350/sec. These bursts of activity can be interpreted as either a response to irritation by the electrode or as genuine phasic activity. The theoretical significance of the pattern interpretation is discussed.

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