ELECTRICAL ACTIVITY OF HUMAN MOTOR UNITS DURING VOLUNTARY CONTRACTION

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Sherrington (17) defined a motor unit as "an individual motor nerve-fibre together with the bunch of muscle-fibres it activates." Eccles and Sherrington (12) and Clark (6) (7) presented evidence which indicates that a single motor neurone may control 100 or more muscle fibers. Adrian and Bronk (3) (4) and Denny-Brown (11) first succeeded in isolating the motor unit as a functional entity.

Adrian and Bronk (4) studied reflex contractions in cats and voluntary contractions (mainly triceps) in man and concluded that the latter like the former are maintained by impulses which range in frequency from 5 to 50 or more per second in each nerve fiber. They further pointed out that gradation of strength of contraction is brought about by changes in the frequency of discharge of each unit and by the number of units active.

Smith (18) studied the motor unit responses in the biceps and triceps muscles of 8 normal subjects during voluntary contraction. Her results agreed essentially with those of Adrian and Bronk. She found no frequency of response above 20 per second but was unable to deal with strong contractions. During sustained contractions she found that a unit might remain continuously active for approximately 15 minutes without evidence of rotational activity.

In the present study an attempt has been made to determine the range of frequency of response of which an individual unit is capable during voluntary contraction, the manner in which gradation of strength of contraction occurs in various muscles and the effect of sustained contractions and fatigue. Records have been obtained from the muscles of 6 normal adult subjects, but for the most part from several representative flexor and extensor muscles of the writer. The muscles studied were the deltoid, biceps, flexor digitorum sublimis, brachio-radialis, rectus femoris, vastus lateralis, sartorius, gastrocnemius and tibialis anticus.

APPARATUS AND METHODS. For most of the work a six stage, transformer-coupled amplifier was used to drive either a loud speaker or a Du Bois oscillograph. A con-

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denser-coupled amplifier and a cathode ray oscillograph (see Garceau and Davis, 14) have also been employed from time to time to check various points.

Four types of electrodes have been used. 1. A fine insulated wire (gauge no. 36) cemented into the lumen of a hypodermic needle (no. 20 or 21) with black baking varnish. The bared tip of the insulated wire led to grid and the outer portion of the needle to ground. 2. Two fine insulated wires inside a hypodermic needle, the bared tips of which were only a fraction of a millimeter apart, led to the primary of an input transformer. The needle was grounded. 3. A fine insulated wire (gauge no. 36) with a minute portion of its insulation scraped off was drawn through a muscle by means of a surgical needle until the bared portion made contact with an active unit. This wire led to grid, and a small metal plate covered with canton flannel soaked in NaCl solution was attached to the skin surface over an inactive region and led to ground. 4. Two fine wires with a knife-edge cut in the insulation were drawn through a muscle together and led to an input transformer.

Electrodes of type 1 served adequately for weak or moderate strengths of contraction but during strong contractions picked up responses from many neighboring units. Electrodes of type 2 were highly selective and served well for strong contractions but required greater amplification and were sensitive to movement. Types 3 and 4, although not easily applied in many muscles, were highly selective and less sensitive to movement than the needle electrodes. When the wires were in a muscle it was possible to move freely without discomfort or fear of displacement.

The needle electrodes were sterilized by autoclaving or soaking in 95 per cent alcohol. They were inserted to various depths in the muscle substance and held in place by a holder capable of tridimensional adjustment. The needles were inserted without anesthesia and except for the initial piercing of the skin did not cause discomfort.

A torsion wire myograph (mechanograph) was used for measuring the strength of contraction in the flexor digitorum sublimis muscle. The shadow of the myograph lever, which was attached to the middle finger, fell upon the film so that an upward deflection of the line indicates increasing tension. For roughly measuring the strength of contraction in the other muscles, hinged levers were arranged to pull against weights hung over a pulley.

RESULTS. When needle electrodes (type 1) were inserted in a muscle which was slightly tense, a rhythmic response was heard in the loud speaker as the electrodes reached the vicinity of an active unit. If the electrodes were inserted deeper or moved about in the muscle the response became louder or fainter depending upon the distance of the recording surfaces from the active unit. In a muscle which was quite tense other units were heard as sounds of slightly different character, indicating that more than one unit was active in the immediate neighborhood of the electrodes.

Most normal subjects can relax a muscle so completely that, although full amplification is used and the electrodes are inserted in different parts of the muscle, no active units are found. Relaxation sometimes requires conscious effort and in some cases special training, although in none of the 6 normal subjects used in this study was the complete relaxation of a muscle difficult.

The recorded responses of a single motor unit (fig. 1) during a voluntary
contraction are characterized by a distinctive pattern, which serves to distinguish them from the responses of other units, uniform amplitude and a fairly regular rhythm. The rhythm in this case varies by approximately 10 per cent of the average interval between successive responses, which is the usual amount of variation. In some cases, however, the rhythm may vary by as much as 30 per cent (see fig. 4 A). In general the rhythm is less regular during weak than during moderate or strong contractions.

The frequency range of motor unit responses during voluntary contraction did not vary significantly in different parts of the same muscle or in the several muscles studied, with the exception of the biceps in which the upper frequency limit was on the average a little higher than in the other muscles. Motor units usually began to respond regularly at frequencies of 5 to 10 per second during the weakest voluntary contractions which could be made, although occasionally a unit began to discharge at a rate of 12 to 15 per second if a number of other units were already active. It was sometimes possible to obtain regular responses at a frequency as low as 3 per second if an attempt was made to slow down a unit which was already discharging. Usually, however, when such attempts were made the responses became irregular and ceased entirely.

When the strength of contraction was gradually increased, the frequency of response of the motor units increased and at the same time more and more units throughout the muscle became active. This is illustrated in the records in figure 2, which were taken during a series of contractions of increasing strength in the biceps muscle. Record A was obtained during the weakest voluntary contraction which could be initiated and shows a unit responding fairly regularly at a frequency of 5 to 6 per second. Record B shows the frequency increased to 9 per second and C to 11 per second with the accession of a new unit. With still stronger contractions the frequency of each unit increased further and responses of other units appeared.

It is difficult to evaluate the part played by the two mechanisms (change of frequency in each unit and variation in the number of units active) for grading the strength of a contraction, since both operate throughout the

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2 A transformer-coupled amplifier of the type used for obtaining most of the records distorts the wave-form of the action potential, but does not interfere with the identification of individual units by their general pattern which is determined largely by the relation of the recording surfaces of the electrodes to the active units.
entire range. In one experiment during a very weak contraction of the flexor digitorum sublimis (a small muscle) slow rhythmic responses (5 per second) of a motor unit were correlated with slight undulations of the myograph curve of tension recorded from the middle finger. This indicates that there was probably only one unit active in the entire muscle and that there was not complete summation of contractile effect. In weak contractions, when the frequency of response in each unit is low, smoothness of the contraction depends upon the asynchronous response of several units. Since the frequency of response in individual units increases quite evenly with gradually increased effort, whereas the accession of each new unit represents a discrete step, it appears that the change in frequency is the more delicate method of grading the strength of contraction. The accession of units is probably a quicker and more potent factor in increasing the strength of a contraction.

During the ordinary range of voluntary muscular activity, including weak to moderately strong contractions, the frequency of motor unit responses does not exceed 30 per second. Only during very strong contractions involving maximal or near maximal effort does the frequency of
response become higher. As Adrian and Bronk (4) have pointed out, it is difficult to study the upper frequency limit of response of single motor units during very strong contractions because of the swamping of the rhythm by other units. With electrodes of types 2 and 4 we have found it possible to isolate and record the response of single motor units in several muscles during maximum effort. The highest frequencies of response we have found in the muscles of normal subjects were in the neighborhood of 40 per second. Figure 3 C shows responses of a single motor unit in the biceps muscle during the strongest voluntary contraction the subject could make. The frequency of the responses is on the average about 40 per second, although the highest frequency attained by any two successive responses is approximately 45 per second.

![Fig. 3. Action potentials from single motor units during the strongest voluntary effort possible. A and B from biceps muscles of patient with progressive muscular atrophy, frequencies, 30 to 40 and 45 to 50 per second, respectively. C from biceps of normal subject, frequency, 40 per second. Time units equal 0.023 second.](http://ajplegacy.physiology.org/)

Patients with progressive muscular atrophy have provided a rather unique situation for investigating further the upper frequency limit of the motor unit response during voluntary contraction. In several such patients the biceps and triceps muscles were atrophied to such an extent that only a small strand of muscle tissue remained. On examination it was found that the few remaining units in these muscles appeared to function normally. It was possible therefore to study maximal voluntary effort in these units without interference from other units. Figure 3 A and B are records from different units in the severely atrophied muscles of one of these patients during an attempt to flex the arm at the elbow. In A a motor unit responds at a frequency of 30 to 40 per second and in B at 45 to 50 per second. The biceps of this patient was only about as large in diameter as his little finger and he was not able to flex the arm against gravity.
On several occasions a single motor unit has been kept continuously active for periods ranging from 15 to 30 minutes during a sustained contraction which did not cause fatigue. Records were taken at regular intervals during the course of the contraction and the unit's response followed by ear with the loud speaker between records. Figure 4 A was taken at the start of a sustained contraction of the tibialis anticus muscle and B 30 minutes later. Throughout the duration of the contraction the unit was continuously active and there was no evidence of the substitution of one unit for another. The records show that the frequency and amplitude of the motor unit responses remained the same.

Records of single motor unit responses have also been obtained during strong sustained contractions which produced fatigue within a few minutes. These records show progressive decrease in amplitude of the motor unit responses as fatigue develops. Figure 5 shows a series of records from the tibialis anticus muscle of a normal subject during a strong contraction maintained as long as possible. Record A was taken at the start of the contraction. The single motor unit responses are of uniform amplitude and at a frequency of 9 per second. Record B, obtained 4 minutes later when fatigue was first felt, shows the unit at the same frequency but with a slight diminution of the amplitude of the responses. Record C, obtained 1 minute later and just prior to complete fatigue, shows the unit responding at approximately the same frequency but with greatly diminished amplitude.

Further confirmation of the decrease in amplitude of the motor unit responses with fatigue has been demonstrated in the muscles of the patients with progressive muscular atrophy. Figure 6 shows records obtained from the flexor digitorum sublimis muscle of the forearm, which was greatly atrophied. The middle finger was attached to a myograph lever and a constant voluntary contraction maintained until fatigue ensued. In record A, taken at the start, a motor unit responds at a frequency of 13 per second. Record B taken 5 minutes later, when fatigue was very marked, shows reduced amplitude of the motor unit responses, although the frequency remains approximately the same. One also notes irregularities of the myograph curve resulting from fatigue.

Some information about the relative size of the groups of muscle fibers
Fig. 5. Action potentials from tibialis anticus muscle during a strong contraction, showing progressive diminution of amplitude with fatigue. A, at start; B, 4 minutes later; C, 1 minute later and just prior to complete fatigue. Time units equal 0.023 second.

Fig. 6. Motor unit responses from flexor digitorum sublimis muscle of a patient with progressive muscular atrophy during a contraction which caused fatigue. A, at start; B, 5 minutes later, showing reduced amplitude of response. White line indicates tension against myograph. Time units equal 0.023 second.
which compose a unit and the distribution of the fibers has been obtained with the highly localizing electrodes (types 2 and 4). The movement of the electrodes a millimeter one way or the other often completely eliminated the response of a unit, thus indicating that the diameter of such a group of fibers is somewhere in the neighborhood of one millimeter. Adrian (1) has shown that a nerve fiber may divide and send branches to both halves of the tenuissimus muscle of the cat, but for the most part the muscle fibers which compose a unit are probably not widely separated. Our experience indicates that muscle fibers of a unit are grouped, possibly in longitudinal chains, as Cooper (8) showed, rather than widely distributed throughout a muscle. If such is the case, it would make the response of a single active unit effective, as we have observed, and would result in greater effectiveness of all units during sub-maximal contractions.

Discussion. Of particular interest is the fact that the frequency of motor unit responses during voluntary contraction did not exceed 40 to 50 per second and for the most part fell within the range of 5 to 30 per second. Although it may be possible that the frequency of response could be increased still further during so-called "super-human" feats of strength, the strongest voluntary effort that could be produced in an experimental situation would not drive motor units at frequencies above 50 per second.

In view of the findings of Adrian and Bronk (3) (4) that the frequency of impulses in individual fibers of the phrenic nerve of the cat ranged from 15 to 90 per second, it might have been expected that motor units generally would be capable of such a range. However, in single nerve fibers to other muscles of the cat they found the highest frequencies per second during reflex excitation were as follows: peroneus longus, 30; tibialis anticus, 44; quadriceps, 90; vastus lateralis, 25; vastus medialis, 65. They also demonstrated that stimulation of the whole nerve to the gastrocnemius and tibialis anticus produced curves of tension which showed but little increase in response to stimulating frequencies above 50 to 60 per second. Liddell and Sherrington (15) and Cooper and Eccles (9), on the other hand, have shown that stimuli at the rate of 90 per second or more are required in some cases to produce a completely smooth contraction. It would appear therefore that some muscles require impulses in the neighborhood of 70 to 90 per second to produce a completely fused tetanus, whereas other muscles require frequencies of only 30 to 50 or 60 per second. However, during normal reflex or voluntary excitation muscles probably seldom produce a completely fused contraction.

It is interesting that action potentials of single motor units recorded from muscles during reflex contractions (4) (11) (10) have not apparently exceeded 20 to 30 per second in most cases. Similarly the responses of single motor units recorded from the intercostal muscles of the cat during normal inspiration by Adrian (2) and during hyperpnea by Anderson
and Lindsley (5) have not exceeded rates of 15 to 30 per second. These examples as well as the highest frequencies of response found during voluntary contraction of human muscles in this study fail to correspond with the highest frequencies of response reported in the individual nerve fibers of the phrenic and elsewhere by Adrian and Bronk (3) (4).

A point which calls for further explanation is the fact that a motor unit during fatigue (fig. 5) shows a progressive diminution of amplitude whereas a motor unit during sustained contraction (fig. 4), which does not cause fatigue, shows no variation in amplitude or frequency of response, although it discharges at the same rate and for a longer period of time. The difference might be accounted for in terms of the available oxygen supply, which is proportionally less per unit in the former case, in which the contraction is much stronger and a greater number of units are active. Therefore there is probably a greater accumulation of lactic acid and metabolites in the fatigued muscle. It is also probable that the blood flow is less during a strong contraction than a weak one.

Fatigue in normal subjects does not appear to be of the same type as the weakness and fatigability of the muscles of patients with myasthenia gravis, for in the latter Lindsley (16) demonstrated not a uniform and progressive decrease in amplitude of motor unit responses but irregular amplitude from the start.

Both Denny-Brown (11) and Adrian and Bronk (4) have failed to find evidence of rotational activity of motor units during sustained reflex contractions. The present evidence, as well as that presented by Smith (18), on voluntary contractions in man has likewise failed to substantiate Forbes' (13) original suggestion of the rotational activity of units as an explanation of the lack of fatigue in long-sustained contractions.

**SUMMARY**

Action potentials have been recorded from single motor units in several flexor and extensor muscles of 6 normal human subjects during various strengths of contraction, sustained effort and fatigue.

No electrical activity has been demonstrated in any part of a relaxed muscle. During a voluntary contraction the response of a motor unit is characterized by a distinctive pattern of uniform amplitude and fairly regular rhythm. The rhythm may vary by as much as 10 to 30 per cent during a constantly maintained voluntary effort.

The two means by which the strength of contraction may be graded, namely, change in frequency of discharge in each unit and in number of units active, operate together throughout the range of contraction intensities. Change in frequency is probably the most delicate grading mechanism and change in number of units the most effective.

The lowest regular frequency of response found during voluntary con-
traction was 3 per second, the highest frequency 50 per second. During the weakest voluntary contraction which could be initiated, motor units usually began to respond at frequencies between 5 to 10 per second. With the exception of the upper frequency limit, which was slightly higher in the biceps than in the other muscles, motor unit responses did not differ significantly from one muscle to another or in different parts of the same muscle.

Motor units kept continuously active for 15 to 30 minutes during a weak sustained contraction showed no sign of rotational activity or variation in frequency and amplitude.

During fatigue produced by strong, constantly maintained contractions, single motor unit responses progressively diminish in amplitude but maintain the same frequency.

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