ACTION POTENTIALS FROM SINGLE MOTOR UNITS IN
VOLUNTARY CONTRACTION

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In 1929 Adrian and Bronk demonstrated a more refined method than
had hitherto been used for obtaining action potentials from muscle, not
only in the laboratory animal, but also in voluntary contraction in man.
These workers devised very small concentric electrodes which detect ac-
tivity of the single motor units in a much restricted area. Such electrodes
have since been used extensively in this laboratory and elsewhere in ani-
mal work, and they have also been used in man by McKinley and Berkowitz
(1933) in determinations of "tonus," and by Hathaway (1932) in a study
of reaction times, but so far as the writer is aware no further systematic
investigation of voluntary contraction by this means has appeared. The
present series of observations has been carried out on eight biceps and
five triceps muscles in eight young normal individuals, four men and four
women.

METHOD. The electrodes are made by inserting a fine insulated copper
wire of 36 \( \mu \) diameter into a 25 gauge steel hypodermic needle. A "bake-
lite" lacquer subsequently hardened by baking, holds the wire firmly
and secures the insulation, and finally both the steel shaft and the copper
point, shaved off to suit the bevel of the needle, are silver plated. The
device may be sterilized by autoclaving. The butt of the needle is made to
fit a small holder in such a way that the central wire leads to the grid of a
three-stage condenser-coupled amplifier,\(^1\) and the shaft is connected to
ground. A Cambridge string galvanometer and an electrocardiograph
camera were used to make permanent records at any desired moment,
while the investigator listened to the discharge through ear phones from
the amplifier.

The subject sat with the wrist hanging in a sling attached to a spring
balance, in such a position that the forearm was at rest approximately at
right angles to the arm. Resting position on the scale varied with the
weight of the forearm and hand of the individual. Contraction in the
biceps was obtained by lifting the forearm from resting position to zero
position on the scale, at which point the forearm was being held, still ap-

\(^1\) Designed and constructed by L. Garceau of this laboratory.
proximately at right angles, completely without support. Contraction of
the triceps was recorded simply as pressure downward. The arrangement
allowed considerable lateral play of the arm as a whole, and also the degree
of rotation at the wrist was not fixed. These two factors are important in
bringing in and dropping out particular motor units, and therefore the
degree of contraction as measured on the scale was by no means the only
determinant of the activity of a given unit. Since there is no means, in any
case, of measuring the tension of the muscle fibers whose action potentials
are being recorded, the scale was used merely as a rough gauge to help
the subject in holding a given pose. Only minimal and submaximal de-
grees of contraction were dealt with, for only when a few units are being
recorded can individual frequencies be distinguished. Tension was
largely regulated in accordance with what was heard in the phones.

Two main questions were studied: the frequency of impulses during in-

Action potentials of single motor units in voluntary contraction with three-stage,
condenser-coupled amplifier and string galvanometer. String aperiodic. All figures
except 3, 4 and 5 are retouched with white ink for reproduction.
Figs. 1 and 2. M. L., male, age 20. April 27, 1933. Time marker in 0.02 second.
Sensitivity, 3 mm. = 10 μv. X 5/7.
1. Onset of contraction. Large waves, 4 in 1.18 seconds, with intervals of 0.29,
0.46 and 0.43 second, and followed by 1 second of silence (not completely shown in
figure). Small waves, 8 to 9/second.

2. Another onset of contraction. Large waves, "random" for 1.24 seconds, fol-
lowed by 4 seconds of silence (not shown in figure). Small waves, 13 to 14/second.
Figs. 3 and 4. M. C., female, age 27. May 13, 1933. Time as in figure 1. Sensi-
tivity figure 3, 3 mm. = 10 μv; figure 4, 1.5 mm. = 10 μv. X 5/7.
3. Steady tension showing one unit alone, rate 12 to 13/second.

4. Steady tension; two units both at rate of 13/second, showing synchronisation
for 6 consecutive beats which is most unusual.
Fig. 5. E. L., female, age 25. April 11, 1933. Time, 1 second between arrows. X
7/0. Steady tension showing a cycle of two waves passing each other, with one syn-
chronous beat. Large waves, 7/second; small, 8.5/second.
Figs. 6, 7, 8. L. M., male, age 22. May 9, 1933. Time marker in 0.02 second
6. Onset, main waves, 8/second; small waves in background.
7. Two seconds later. Main waves, 11/second; background increased in ampli-

8. Height of contraction 5.5 seconds after figure 7. Main waves, 13/second;
background greatly increased in amplitude and complexity.
Figs. 9 and 10. J. R., female, age 28. March 28, 1933. Time marker in 0.01
second. Sensitivity, 1.5 = 10 μv. X 1. Increasing contraction.
9. Small wave (dotted) is the second to come in and has reached a frequency of
16/second. Onset of large wave at 10/second for 2 beats with rapid increase in
frequency to 15/second.
10. Continuation 0.4 second later showing highest frequency distinguishable, 19
to 20/second, in both units at extreme right. One perfectly synchronized beat; four
showing varying degrees of interference.
Figs. 1–10
crease and decrease of tension, and the fatigue of a single unit. Change of tension was carried out in two ways: \( a \), by continuous movement, with continuous exposure on the film, and \( b \), by discontinuous increments and decrements, giving time for exposure at each successive stage. In the trials of endurance of one unit the subject held a given position on the scale for 20 to 30 minutes while the investigator listened throughout the performance, exposures being made at one minute intervals.

**RESULTS. Increase and decrease of tension.** In general the findings corroborated those reported by Adrian and Bronk (1929) while a few supplementary points of interest were noted. With the arm completely at rest, no action potentials were either heard in the phones or registered on the film. In most cases this inactivity was easily obtained, but in one case complete relaxation had to be learned and was accomplished only after several trials. With beginning contraction in both biceps and triceps there is usually heard a faint "distant" discharge in which the ear does not distinguish a single unit, but there appears on the film one repetitive, distinct wave of small amplitude—the record of a single unit at a distance. With increase in tension the first unit increases in frequency until louder second and third ones come in and accelerate in turn (figs. 9 and 10), by which time the first one is too obscured on the film for its frequency to be distinguished. The larger waves may remain clear throughout if the contraction is not too great (fig. 8).

As a rule the frequency at the onset of each new unit is lower than the simultaneous rates of those already present, but this is not always true. Units act with considerable independence and may occasionally change their ratio to each other. But such change is probably due to slight difference in the twist of wrist or shoulder as described above, with resultant difference in the degree of activity of individual muscle fibers. This is probably also the explanation of occasional wide variation of threshold position on different trials, which occurred in two subjects.

Cessation of discharge at the end of relaxation may take place: \( a \), gradually with increasing intervals in the last two or three beats, or \( b \), abruptly after reaching a given slow rate, or \( c \), by the dropping out of impulses in a very irregular way. It is evident that the subject’s control of relaxation is very variable, and in this connection an investigation of highly trained muscle as contrasted with pathological conditions of various kinds would be of special interest.

**Highest frequencies.** The highest frequencies which can be clearly singled out are from 19 to 20 per second in one triceps (figs. 9 and 10), where a step-like onset of different units is also seen. Although the present investigation does not deal with frequencies in maximal contraction, it offers some evidence of the relative importance of accession of new units as compared with acceleration of frequencies. In the records of one bi-
ceps taken on two different days with two different hypodermic needles, one or two single units stand out in sharp contrast to a background which presents the appearance of the classical type of electromyogram, and this affords the unusual opportunity of following one unit amongst the "primary" and "secondary" waves and Nebenzacken so long discussed. Figures 6, 7 and 8 show the single unit increasing in frequency from 8+ per second to 12-13 per second at the height of contraction for that trial, while the background waves increase greatly in amplitude and only very slightly, if at all, in frequency. This is interpreted as an accession of many new units with very moderate acceleration of the single outstanding one. In another trial there is slight progressive deceleration of the single unit for four successive increments of tension while the background increases in amplitude, and subsequent increase or decrease of these two factors irrespective of each other. For one unit to diminish in activity while others increase may or may not be unusual—this was the only clear instance which occurred. It is evident, however, that increase in frequency and accession of new units are two very independent phenomena.

**Lowest frequencies.** Low frequencies as seen in the records of 6 biceps and 2 triceps, either in steady tension, or at threshold in increase-decrease trials, range for the most part between 5 and 7 per second. In evaluating such frequencies the arbitrary criterion has been taken of a discharge of 4 or more impulses occurring without either definite change to a different rhythm, or change to such total irregularity as to make the term "rhythm" meaningless. Such extreme irregularities may be designated as "random" discharges.

The lowest frequencies under this evaluation are in one case 4½ per second for 1.24 seconds followed by an interval equal to double the average interval in the foregoing rate; in another subject (fig. 1), four discharges at intervals of 0.29, 0.46 and 0.43 occur in 1.18 seconds followed by silence for the remaining 1 second on the film. This frequency of 2½ per second is so very exceptional that it is a question whether it may best be termed a low frequency or a "random" discharge.

"Random" discharges occur often in a way that cannot be accounted for merely on the hypothesis of dropped beats; e.g., a single beat at onset of contraction with succeeding silence for 1 second before establishment of a rhythm. Another beginning contraction shows 6 totally irregular discharges in 1.24 seconds (fig. 2), silence for 4 seconds, and then two beats before onset at a rate of 7 per second. Such irregularity is often found also at the end of relaxation. In general it may be said that at threshold a unit may discharge in a quite random way without establishing any rhythm at all.

* Dr. D. B. Lindsley now working in this laboratory finds indications that this may often be true.
Fatigue. Four satisfactory experiments on fatigue of a single unit were obtained in the biceps of one man and three women. The subject, sitting in as comfortable a position as possible, flexed the arm to a point at which loud single discharges were prominent, and the attempt was made to maintain the discharge, as heard in the phones by the investigator, over a period of 20 to 30 minutes, whether or not this entailed fluctuations on the scale of the spring balance.

In L. M. a loud clear unit was heard continuously and is recorded on the film at a rate of 9± per second up to 3 minutes during a gradual change of position from 600 to 200 on the scale (cf. p. 629). It dropped out of the discharge as heard in the phones for a moment just before 3 minutes and reappeared immediately on shifting to position 150, frequency 7-8. At five minutes it stopped again momentarily and came in at position 100, rate 6 ±; it then persisted with fluctuations in frequency, up to 18 minutes. In the record taken at 11 minutes, a second, slightly smaller unit (nearer the electrodes), appears on the film and the frequencies of both are accelerated; the original at this point is 12-14 per second. At 15 minutes a third appears, of about the same amplitude as the second, and all three are present to the end; the original varies in frequency from 10 to 12 per second in the last eight exposures. The acquisition of new units is, then, not a substitution of units, but an indication of increased activity in the vicinity of the electrodes. The “patient’s” subjective feelings were noted during the latter part of the time as “general tiredness through the arm, pectoral muscles and whole shoulder, with a crick in the neck.” The important finding is that the original unit has discharged at varying rates for 18 minutes with two momentary stops in the early stages and without stop for 13 minutes. After 15 minutes’ rest it came in alone at position 900 on the scale showing the same form and amplitude as before. The change in the threshold position is not significant, as such changes were frequent in this subject.

In the next two subjects, C. B. and M. C., an individual unit was kept going for 21 and 30 minutes respectively with two momentary stops in the former case and four in the latter. In C. B. other units are present throughout the record and take a prominent part in some exposures, while in M. C. the main unit is present alone in the exposures at 7, 11 and 12 minutes and in the rest of the film the number varies from 2 to 4 irrespective of scale position. In this experiment a “momentary” pause was caught by the camera and shows a duration of 1.1 second.

In the fourth experiment, E. L. maintained approximately the same scale position for 22 minutes with a slight tendency to fluctuate toward the end. The film shows frequencies of the main unit for the most part within a range of 7 to 10 per second, but occasionally dropping to 5 or 6 and twice, to “random.” Small (distant) units are present in the back-
ground and at times a second large (near) unit takes part. The longest consecutive discharge of the original was 14 minutes without stop either in the phones or on the film.

Units have been kept discharging, then, for 18 to 30 minutes with momentary stops which could hardly be regarded as recovery periods. There is no evidence in these records of substitution, or rotation of units. There may be accession of new units brought in by the effort to hold a position, but since this accession is entirely irregular and may come and go without loss of the original, it is interpreted as due to the fact noted throughout this work—that marked change in what is picked up by the electrodes may result from very delicate change in twist of wrist or shoulder. The indications are that the single unit could continue long after “fatigue” of the individual as an entity brings the test to an end.

Discussion. The present method of recording has greatly simplified the voluntary electromyogram. Adrian and Bronk (1929) have discussed in particular the findings and interpretations of Wachholder (1923) and Richter (1927) and point out that the detailed structure of the electromyogram has become clearer as the electrodes have become more selective. The complicated curves made up of “primary” and “secondary” waves and Nebenzacken have thereby been reduced to one type of simple discharge occurring in independent rhythms in different neuromuscular units. It is interesting that where “selection” takes place by elimination of many motor units in certain diseases of the anterior horn cells, a comparatively simple electromyogram is obtained even with plate electrodes and skin puncture (Richter and Ford, 1928), showing frequencies much in accord with present findings. Evidence appears to be all against the arguments in favor of a motor fiber discharge too high to be followed by the muscle (Forbes and Rappleye, 1917; Forbes and Olmsted, 1925) and also against a “proper” rhythm intrinsic in the motor neurone broken up by the play of centripetal impulses (v. Weiszäcker, 1921, and Dusser de Barenne and Brevée, 1926). Again, although the muscle itself may be a limiting factor in certain circumstances there appears to be no “proper” rhythm here either. Indeed the work of Adrian and Bronk (1928, 1929) finally re-establishes one contention in Piper’s (1912) original thesis, viz., that the rhythm in the muscle is directly determined by the rhythm of the impulses from the central nervous system.

The question of duality of neuromuscular function has recently been brought up again by Rijlant (1933f, g) who reports two types of action potentials in striated muscle, “fast waves of high potential corresponding to contraction; much slower and smaller waves corresponding to tonic activity.” He states also that such action potentials can be obtained from human triceps and quadriceps. In his original article on tonus in the rabbit (1933d), however, he says, “L’exploration électrique des muscles des
mammifères ne permet pas de mettre clairement en évidence cette dualité réactionnelle si manifeste chez l'Oiseau et chez la Grenouille. Toutes les ondes observées sont rapides sans qu'il soit possible de les différencier en ondes rapides et lentes, quoique de légères différences existent entre elles.”

His very clear figures in this paper show that this is indeed true. But, apparently basing his hypothesis on the finding that the action potentials of greatest amplitude disappear with depression of muscular activity in light hypnosis, he maintains that the smaller action potentials which remain represent “tonic activity” as a specific neuromuscular function. The small waves disappear in deep hypnosis when the animal becomes atonic. In articles on the human electromyogram he shows figures designated as “tonus normal” (1932a, b) presenting waves of great and small amplitude of varying degrees during this state alone; and in a following paper (1932c) the statement appears that in voluntary contraction in a muscle not showing tonic activity, waves are produced which are “comparable en intensité et en durée aux ondes toniques.” Comparison of the figures again shows this to be true. There seem to be, then, some inconsistencies in Rijlant’s interpretations. He further appears to disregard one fact in particular. The recorded amplitude is a function not only of the potential changes in the muscle fibers, but of the distance of the fibers from the electrodes. It should be noted incidentally that ordinary needle electrodes can and do pick up potentials from considerable distance (Forbes and Barbeau, 1927) and not merely from fibers in the immediate vicinity. Even coaxial electrodes, which are far more selective, record action potentials from varying distances. If, during a clear discharge, the needle is pushed slightly deeper into the muscle the discharge becomes louder (or fainter) and the simultaneous deflections of the string shadow change in amplitude, and these two phenomena are seen to be directly correlated.

In the case of the frog (1933a, b) Rijlant himself interprets the wide, slow waves as a complex made up of grouped fibrillary activities slightly asynchronous (1933f, discussion). Figures for the hen (1933c) under normal and hypnotic conditions present much the same sort of composite picture in the slow waves. The findings in the curarised cat (1933e) corroborate the known action of this drug, viz., the loss of the sustained contraction of posture before complete loss of power of active movement, but this does not offer any new proof that sustained contraction is a different function brought about by a different mechanism.

There does not appear to be in Rijlant’s work any type of discharge which is not found in different degrees of sustained voluntary contraction. I believe his records demonstrate action potentials of one type varying in recorded amplitude with the distance of muscle fibers from the electrode. They demonstrate also the stretch reflex and the changes in different de-
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Degrees of muscle tension, but they do not present any evidence of a duality of neuromuscular function.

Differently interpreted, the dropping out of large (near) units with beginning relaxation in hypnosis is a point of interest in Rijlant's work. In the present investigation it was a common finding that relatively distant units were active in small degrees of tension while the nearer ones were associated with greater contraction. This brings up the question suggested by Adrian and Bronk (1929) as to whether active fibers are more numerous in the deeper parts than in the periphery of the muscle, and is suggestive of such a possibility. There is, however, a statistical probability involved which should be considered. Since the number of units at a given distance increases with the square of the distance from the active electrode, it may be merely on these grounds that distant activity is usually the first to appear and the last to disappear. The point is one needing further investigation.

The question of rotation of activity among units suggested by Forbes (1922) to explain "tonus," or sustained contraction, in skeletal muscle without fatigue has been much discussed, but more recent work has not upheld the theory. The emphasis has all been on the surprisingly slow rates of discharge, which are in themselves sufficient to explain absence of fatigue in moderate degrees of tension. Adrian and Bronk (1929) and Denny-Brown (1929) find no indication of rotation in the single unit rhythm. The findings in the present work militate further against it. Units have been kept going without stop for 13 and 14 minutes which are periods beyond all consideration in Forbes's original idea. The momentary pauses described are hardly an indication of fatigue even at these points and neither can the appearance of other units during a 20 to 30 minute experiment be considered a rotation, since these accessions occur without loss of the original. The fact that units at very low frequencies maintain a sustained contraction by virtue of their independence is in a way, however, a modification of the idea of rotation in the original sense. If each unit plays its part independently the result is still an alternation of activity in succeeding fractions of time though the individual unit maintains its rhythm for long periods without cessation. It is, then, a combination of the two factors which brings about smooth moderate sustained activity in the muscle as a whole without fatigue.

SUMMARY

An investigation of action potentials in single motor units in the biceps and triceps muscles of eight young normal individuals has been made with concentric needle electrodes. The electromyogram so recorded is of simple form in moderate degrees of contraction and allows analysis of constituent rhythms.
Increase of contraction involves both increase of frequency of impulses in the individual unit and accession of new units. There is great independence of rhythm in different units.

The highest frequencies distinguishable were 19 to 20 per second. Low frequencies most often found were 5 to 7 per second, but much slower, highly irregular discharge may occur at threshold. Discharge tends to be more irregular at the end of relaxation than at onset of contraction.

In fatigue tests, individual units have maintained a continuous discharge without stop for 13 and 14 minutes, and have continued for 20 to 30 minutes with momentary pauses too short to be considered recovery periods. There is no evidence of rotation of activity, or substitution of units.

The question of duality of neuromuscular function is discussed. Since the type of discharge in moderate sustained voluntary contraction is essentially the same as that found by other investigators in "tonic" activity there is no evidence of separate "tonic" and "voluntary" mechanisms.

It is with great appreciation that I express my thanks to Dr. Alexander Forbes and Dr. Hallowell Davis for the privilege of working in this laboratory, and my indebtedness to Doctor Davis in particular, for the interest and suggestions which have formed the basis of this work.

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