Despite the vast literature concerning voluntary contractions of human muscles, there has not yet been presented an adequate description of the discharges from individual nerve cells of the spinal motor horn as they participate in the production of the various movements which occur. In this paper we are presenting material which deals with the responses of those fibers in a muscle which are innervated by one or by a very few motor nerve cells. The spinal motor neurone, which is the final common path (Sherrington, 1) for the activation of skeletal muscle has for its functional element the motor unit. This was defined by Liddell and Sherrington (2) as the "... motoneurone axone and its adjunct muscle fibres..." Adrian and Bronk (3) and Denny-Brown (4) showed that it was possible to record the electrical discharges from single motor units which were responding during reflex activity and Adrian and Bronk recorded discharges from single units of muscles participating in voluntary contractions. Later Smith (5) and Lindsley (6) recorded the responses of single motor units in voluntary activity. Their work established a foundation on which we have attempted to place the beginning of a more complete structure.

In selecting the experimental material which is to be considered below the attempt has been made to use records which would yield an outline description of the activities of single motor units under conditions ranging between threshold and slight to moderate voluntary effort. For the moment we shall avoid detailed quantitative considerations and shall describe the single unit response first as it occurs in quick movements of various intensities, either as isolated single efforts or as a rhythmic series of movements; second, as it participates in sustained movements begun or ended more or less suddenly; and third, as its activities are related to the activities of other near-by motor units whose responses may also be recorded.

METHODS. Action potentials have been recorded on bromide

ACTIVITIES OF SINGLE MOTOR UNITS IN MAN DURING SLIGHT VOLUNTARY EFFORTS

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paper by means of an oscillograph galvanometer of the Duddell type. The galvanometer is activated by a differential amplifier. For lead electrodes we employ three fine steel sewing needles (no. 12). These are lacquered to the extreme tips, sterilized in phenol solution, rinsed in alcohol and inserted into a muscle through a prepared skin area. In most cases the needles are arranged in a triangle about 2 mm. on a side. These electrodes are not satisfactory if intense muscular contractions are produced. They are, however, well suited for use with the slight tension efforts which we have studied. Following each experiment the needles are sharpened and relacquered. They cause but slight discomfort as they are being inserted into the skin and once placed in the muscle should not be noticeable to the subject. Occasionally a needle impinges on a nerve twig and causes pain or muscular twitches with each movement. In these cases the needle is removed and reinserted. A telephone receiver connected with the amplifier furnishes information as to the proximity and activity of muscle units near the needle point and thus acts first as a guide in placing needles and thereafter as an indication to the subject concerning the responses which are being recorded during the tension efforts which he may make. Occasionally we have obtained excellent records of single unit responses with quite uninsulated needles, the ground lead and one grid needle being thrust into the skin and the other grid needle being inserted just deeply enough to record from a unit which lies near the surface of the muscle. This method is not recommended as routinely dependable.

Although single unit responses can sometimes be gotten by other types of electrode, it seems pertinent to point out here that neither the use of the coaxial type of electrode nor the use of “pore” type electrodes such as we have used, guarantees recording from discrete single units. Each record must be interpreted without preconceptions or prejudices as to the specificity of lead relationships for a given type of electrode. In our experiments we have usually placed the needles so that with slight movements only the responses of a single unit are apparent in the records. In almost all cases the responses of additional units appear when somewhat more intense efforts are made. Under favorable circumstances we can obtain records with one, two or three units showing responses which are reproducible and well controlled. Such records have been used in examining the relationship between activities of separate units. With larger numbers of responding units recording we have found it impractical to follow the activities of a given single unit. It is, of course, largely a matter of chance to place the needle points so that a single unit may record without the complicating presence of other near-by units which are
also active. Although, as will be seen below, the different units of a muscle probably keep rather constant threshold relationships for a given movement pattern, the various units of that muscle do not all begin activity at the same effort threshold. Consequently a single unit whose activity is being recorded may be one which comes into activity with a minimum tension of the muscle concerned or it may come into activity only after the muscle has developed considerable tension. Moreover this threshold may be changed by such relatively slight differences in the neuromuscular pattern as may be brought about by changes of limb position or of general muscular tension. In many instances a movement has been found with which the recording unit is brought into activity with a minimum of volitional effort, the subject performing a quick and most delicate tensing of the muscle. In such records, even at high amplifications, the background noise has been so low as to indicate that few if any other near-by units were participating in the effort.

In no muscle have we found a predictable distribution of muscle units of lower or of higher response thresholds. We have frequently obtained excellent records with an active needle near the surface of a muscle or near its tendinous end but we have also obtained excellent records from the muscle belly. However, the main requirement for a readable record is that a unit close to a recording needle shall become active at a tension level considerably below that at which closely adjacent units become active. With a fairly random distribution of thresholds for different units throughout the muscle such a requirement as the foregoing might be met most readily at the muscle surface. It seems probable therefore that the apparently optimal situation for recording sometimes found at a muscle surface is a matter of statistical rather than of functional anatomy. Likewise we believe it to be largely a matter of sampling that we usually find, as did Smith, that the first units to be heard responding as the needle is thrust into the muscle are relatively remote from the lead needle and consequently give but a faint click in the telephone or a low amplitude of galvanometer excursion. It is entirely possible that there may be a functional organization of units within a muscle. However, the nature of such organization has not yet been demonstrated.

As regards the constancy of spike heights recorded from single unit responses, the accompanying records are typical of those which we have obtained. Frequently records have shown but a few per cent difference of spike heights with wide ranges of the tension effort and of the resulting unit discharge frequency. The record of figure 1-K shows a considerable fluctuation of recorded spike heights. Because we have found, as have others previously, that slight changes in needle position may result in
marked changes of recorded amplitude, we have attributed such changes of amplitude as are seen in figure 1-K to mechanical disturbance of the spatial relationships between the active unit and the lead needles. We have found no reason to believe that there is an increase of the amplitude of the single unit spike with increased tension or frequency of unit discharge. An increase of "spike" amplitude with increased tension is, of course, seen where multiple units are recorded so that with increased tension and increased number of recording units there is increased summation of unit discharges.

Records of tension exerted have been obtained by use of spring torsion levers. Because the recorded movement of a part has usually involved the participation of more than one muscle, the records so far obtained have been of service merely as guides to time and tension relationships. Records for finger muscle contractions have been the most satisfactory in this respect, but even these cannot be regarded as precision records of the tension changes of a single muscle.

**RESULTS.** 1. *Responses with brief efforts.* It has been a generally held belief that even the shortest of volitional efforts involves a brief but rhythmic discharge of those motor neurones concerned in the activation of muscle fibers. In recent years it has seemed clear that in sustained voluntary contractions the individual motor neurones discharge more or less asynchronously but at relatively slow rates. For a sustained movement, the discharge frequency for a given motor neurone may for the moment be considered to range upward from Lindsley's minimum figure of 3 per second. Stetson and Bouman (7) used skin electrodes to record action potentials from the muscles in the forearm while tapping movements were being made with the hand. They reported a tendency for action potentials to be grouped into unit bursts which had a duration of about 50 msec. Since sustained discharge of single motor units at rates less than 20 per second (that is, with discharge intervals greater than 50 msec.) are easily obtained, there seemed to be ample possibility of making a volitional movement so brief and so slight that a single recording motor unit might respond once and only once for each volitional effort.

This has been attempted and found possible. Eight normal individuals have so far acted as subjects. Each of these individuals has yielded records from one or more of fourteen different muscles. In all cases it has been possible to record single motor unit discharges with discrete volitional efforts. Figure 1-A illustrates the case in point. While this record was being made the finger could exert a steady tension of about twenty grams on the lever without discharge of the recording unit. For the first and last two responses of figure 1-A the finger made a quick flexion movement representing a further tension on the lever of about ten grams. The movement at the finger was about $\frac{1}{2}$ mm. Comparison of the elec-
Fig. 1
trical and mechanical records shows that each tension effort produced a single spike discharge which is interpreted as representing the discharge from a single motor unit. Such an interpretation is based on the fact that if the tension is not quickly released but is sustained, there occurs the simple rhythmic discharge of recorded spikes of essentially constant height and form. This criterion of single unit activity has been considered acceptable by previous workers. It does include certain assumptions which are made in this as in previous studies by other workers. Single spike (i.e., single unit) discharges may also be obtained when the subject makes a slow tensing effort until the telephone indicates a discharge, the effort then being immediately discontinued (fig. 1-A, second response). Because the subject's reaction time is involved in such a procedure he must be in a good state of motor control if his attempt is to be successful. On the other hand, under favorable conditions, this is perhaps the most dependable method of eliciting such single spike responses. In a subject under general tension the method usually produces only multiple spike discharges.

To complete the record it may be said that single spike responses have been produced in two other ways. The first of these has consisted in the

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Fig. 1. All records except H, I and J were taken from the flexor digitorum sublimis over a period of about two hours. II, I and J were recorded from an adjacent region of the same muscle at another time. Time lines, inked for reproduction, mark intervals of ½ second. Mechanical record from spring lever attached to finger by a thread. Mechanical movement amplified about 20X. Spring lever tension for records H, I and J indicated on record H. Tension calibration for other records indicated on record F.

A. Discrete volitional movements resulted in single unit discharges for each movement.

B and C. With greater effort the single unit shows a double discharge.

D. With still greater effort additional units near the lead-off point become active.

E. Response of single unit with repetitive movement. Toward the latter part of the strip a second unit is responding.

F and G. Slow increase and decrease of unit discharge frequency with slow increase and decrease of tension, respectively. In G, the last discharge of the unit is included in the figure. There followed a period of several seconds during which the recording unit showed no discharges.

H. Double discharge followed by a pause at the beginning of a movement. Interruption of discharge with quick partial release of tension and sudden cessation of discharge with quick final tension release.

I. Double discharge with duration of second interval nearly equal to that of the third when initial tension increase is smoothly continued.

J. Double discharge without long pause with but brief interruption of tension increase.

K. Record of flexion of third digit.

L. Record of flexion of fourth digit immediately after recording of K. Position of needles unchanged from that for K.
development of a brief instant of muscular resistance when a quick "passive movement" is applied by the subject himself. A highly coordinated resistance effort is thus permitted. A second method has occasionally been used when there has existed a tonic "resting" activity of the unit recording. This "resting" discharge has been due to the effort of maintaining immobility of a limb which has not been properly supported. Under these conditions the "resting" discharge of the recording unit can sometimes be stopped by an appropriate antagonistic effort. During a momentary release of such an antagonistic effort a single discharge of the recording unit may occur.

If the subject makes a quick effort of somewhat greater intensity than that considered above, double discharges may appear. Figures 1-B and 1-C illustrate such responses. The records are typical of many which have been obtained. Although the spike heights are frequently not the same it seems probable that they represent discharges from the same unit. The reasons for this interpretation follow. First, an equal or greater dissimilarity of spike height may be seen during repetitive discharges of the same unit during sustained effort. Second, in many cases the unit of next higher threshold to appear in records of greater tension efforts shows grossly different spike height or form. Third, because the double responses seen in our records are similar in occurrence to the double responses recorded by other workers, as for example, by Denny-Brown for crossed extension reflexes and interpreted by him on a basis of still further evidence as responses of the same unit.

With quick efforts of somewhat greater intensity (fig. 1-D) the two spikes of the double response fall more closely together and the responses of other units also begin to appear. The units of lower threshold appear to show increasingly shorter latencies so that the record may show a marked summation of spike potentials. Occasionally the spikes of the double response have been separated by as little as 10 msec., a value in accord with that found by Denny-Brown in certain of the reflex responses in his experiments. If a rhythmic series of discrete efforts are made, a single unit response may be recorded for each movement (fig. 1-E). With an effort to achieve too high a rate of alternation, the movement becomes less well controlled and additional units are introduced into activity, with or without the appearance of the double spike responses. It is to be seen from the above that a sudden movement may be expected to have a high degree of muscular effectiveness because of the approach to simultaneity of discharge of the more promptly responding muscle fibers and because the double discharge of some of the responding units will fall within time limits which will yield considerable mechanical summation. On a basis of our experiences, it would seem probable that the quicker of the tapping movements employed by Stetson and Bouman might well have produced
a single discharge of the units of higher threshold and a double discharge of units of lower threshold.

2. Responses with sustained efforts. Several features typical of the single unit response during the beginning, maintenance and ending of a sustained tension are indicated by figure 1-F to 1-J, inclusive. If the tension is developed smoothly there is a gradual increase of discharge frequency to the maximal rate attained and then a gradual decrease in frequency as the tension is slowly released. Under such conditions there may be rather close agreement between the tension levels at which the unit discharge begins and that at which it ends. Such a case is seen in figures 1-F and 1-G. These figures were recorded at the beginning and ending of a sustained movement, the intermediate part of the record covering several seconds of the effort being omitted. A frequent type of start is that indicated by figure 1-H in which there is seen an initial double discharge, a long pause and then continued discharge. The long pause, in our material, has been associated with a brief interruption of the tensing effort. This does not seem to apply, for example, to certain of the published reflex responses recorded by Eccles and Hoff (8). If, in our experiments, the tension interruption does not occur the long pause may be absent.

Cessation of discharge may be gradual as in figure 1-G or abrupt as in figures 1-H, 1-J and 1-K. If there is a quick release of tension from a higher to a lower tension level (figs. 1-H and 1-K) there is a brief cessation of discharge followed by a new discharge rhythm at a lower frequency. It is apparent that with sudden onset and cessation of activity there is no necessary quantitative relationship between the lever tensions at which the unit discharge begins or ends.

For a tension achieved quickly and then maintained constant, the early responses are followed by a continuous discharge which, at slight tensions, may continue almost indefinitely. If the responses of several units are being recorded it is seen each unit will discharge at its own rate so that the responses of the various units quickly become completely asynchronous. In such a sustained tension a given motor unit will continue its discharge without interruption or alternation as long as the tension is sustained and provided that the motor pattern is unchanged. It is difficult to continue a smooth tension effort without change of the movement pattern and such maintained efforts have not been made for periods longer than three minutes. On several occasions tension efforts sustained for one to two minutes have been made repeatedly over a period of thirty to forty minutes. The records were comparable in all cases. In one case such sampling was repeated over a two hour period.

3. Relationships between activities of different units. Threshold and discharge relationships between different units in the same muscle have
been discussed by various authors. The possibility of rotational activity of motor units suggested by Forbes (9) dealt with a situation involving a frequency of motor fiber discharge much greater than that which has been indicated by the later work on single motor units. The work of Denny-Brown, of Smith and of Lindsley has shown that a single motor unit set into activity, whether by reflex activity or by voluntary motor effort, will continue to show a rather constant rate of discharge without interruption as long as the smooth maintenance of tension continues. Within the limits of interpretation permitted by the sampling methods which these authors have used, their work may well be considered to indicate that alternation of motor units, rotational activity, or haphazard and irregular changes in unit activity do not occur in a sustained or smoothly changing effort. Recently Hoefer and Putnam (10) have presented the conclusion that (p. 218) "... individual motor units are independent in their frequencies of each other..." so that "... the individual units may alternate in their activity..." The records from which their discharge frequencies and "unit" relationships were determined appear to have been in considerable part typical records of responses of multiple units (as, for example, their fig. 3, lower record of each strip). Consequently the high unit frequencies and the apparent independence of the activities of the different units which they report may well be held subject to question.

We have undertaken to obtain data dealing with this point. Our first method of procedure yielded results in complete confirmation of Lindsley's observation that a single unit may be kept active for long periods of time with no sign of its dropping out, as would be expected if there occurred any rotational or alternating activity. Moreover with repeated trials, starting, maintaining, stopping and again starting the tension effort, the same unit repeatedly became active before other units and continued in action throughout the period of tension even though other units might have been brought into activity when the tension was increased to levels above that which was threshold only for the first unit. An example of this latter situation is seen in figure 1-L where a unit which may be designated as A appeared with a lever tension lower than that at which a second unit, B, became active. However, unit A continues discharging regularly even after unit B becomes active. A further complication was first noticed in a record being made from the biceps muscle of the arm where it was first thought that at times one and at times another motor unit responded at lower tension efforts. More careful attention to the movement showed that both units were responding at very close to threshold for forearm flexion. However, the one unit showed a slightly lower response threshold when the movement was flexion with pronation and the other unit showed the lower response threshold when the movement was
flexion with supernation. Similar results were obtained on another occasion with the lateral division of the triceps muscle of the arm.

Figures 1-K and 1-L illustrate another instance of the same sort. Needles were inserted in the superficial flexor muscle to the fingers. The needle points were separated by about 4 mm., one being somewhat deeper than the others. Movement of the index or little fingers gave no recorded activity, even with rather intense flexion effort. Flexion of the third finger produced threshold recorded activity as indicated in figure 1-K and flexion of the fourth finger gave threshold recorded activity as recorded in figure 1-L. To obtain the mechanical records which are reproduced, a thread loop attached to the recording lever was carefully changed from one finger to the other by an assistant. However, the procedure of recording cannot be held responsible for the shift of the unit recording because of shift of the needle positions as the transfer was accomplished with little or no disturbance and was repeated several times. Moreover, it was observed that a similar change of threshold unit response occurred when the fingers were alternately flexed either free or against an unyielding surface and with no attachment to the spring lever. For figures 1-K and 1-L it is obvious that the recording units were significantly closer in the one case to one of the needles and closer to the other needle in the other case. In two of our records it seems probable that a similar functionally different pair of units lay mainly within the very limited range of lead of a single needle point but such an interpretation must for the moment be held as merely tentative. For the case of figure 1-K and 1-L it is recognized that the superficial finger flexor muscle is not a simple muscle and that movement of the third or of the fourth fingers may be more or less independently. For this case, therefore, we could merely conclude that for the position of the needles which happened to apply, the recorded response of "flexing the fingers" might well have indicated an apparent independence of threshold of the units involved. On the other hand, carefully repeated movements of a single digital joint showed consistent and reproducible responses.

For the present it may be said without qualification that in none of our records, obtained when both subject and operator have been satisfied that the movement pattern has remained unchanged, has a unit, A, appearing at a tension threshold lower than that of a second unit, B, shown any failure to continue in activity under maintained tension effort. Usually A will at all times have a frequency of discharge higher than that for B. This is not invariable in our records, however, though the frequency of B has never been more than slightly higher than that of A and in these cases the effort has always been sufficiently great so that there has always been the possibility of an unconscious slight change in the movement pattern. Lindsley's summary (p. 98) of the means by which the strength of a muscle
contraction may be graded may therefore be used with but slight modification to describe the means by which a muscle may slowly and smoothly develop a contraction of considerable tension. The movement begins with a slow response of a very few units perhaps even of a single unit. As the contraction increases these units increase in the frequency of their discharge and other units are brought into action. When the tension increase is halted and the effort is continued as a smoothly sustained tension, all the responding units continue in their asynchronous, rhythmic discharge probably until voluntary effort of a postural or other change disturbs the total movement pattern.

SUMMARY

1. Electrical records have been obtained from one or a few units of normal human muscle under various conditions of slight voluntary effort.
2. Discrete, slight and brief voluntary efforts may each be accompanied by a single discharge of the motor unit whose activity is being recorded.
3. For quick movements of slightly greater force there may be double discharges of a single recording unit.
4. Rhythmic movements, repeated several times per second, may each show a single response of a single recording unit.
5. With more intense, quick movements additional motor units are brought into activity. The more intense the movement the more are summated potential spikes to be observed in the initial phase of the response.
6. Sustained movements may be begun slowly with a gradual increase of discharge frequency of the units of lowest threshold and with a gradual accession of additional units. If the movement is begun suddenly there is usually a double discharge of the units of lowest threshold and an approach toward a simultaneity of discharge of the various units. Following this first burst the discharge of the various units quickly becomes quite asynchronous.
7. Cessation of movement may be due either to gradual or to sudden cessation of unit activity.
8. No records have shown rotation or alternation of unit activity in sustained tension efforts provided that the movement pattern has remained unchanged.
9. No evidence has been observed which would seem to support the statement that there is increased amplitude of the single unit spike with increased muscular tension.

REFERENCES

SINGLE MOTOR UNIT ACTIVITY