Some electrical properties of motor units and their effects on the methods of estimating motor unit numbers

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SYNOPSIS Long train (50) electrical pulses were applied to the ulnar, median, and deep peroneal nerves. The probability of firing, or firing index, of the first motor units (MU) recorded by surface and needle electrodes in the first dorsal interosseous, thenar, and extensor digitorum brevis muscles varied from 0-100% as the stimulus was increased from a minimum threshold voltage (V) to $V + \Delta V$ ($\Delta V = 2-4$ volts). The voltage interval, ΔV (firing level range), of even the first few MU recruited greatly overlapped in normal subjects, but may overlap less in some neuromuscular disorders such as amyotrophic lateral sclerosis. The mean size of the single MU isolated by (1) isometric voluntary contraction method, (2) F recurrent discharge method, and (3) stimulation at multiple locations along the nerve, were more than twice as large as the mean size of the incremental steps evoked by graded electrical stimulation. These results suggest that methods of estimating the number of MU in a muscle should incorporate a correction for the fluctuations in excitability and overlap in firing levels of MU, and in addition should include larger MU in the estimation of the mean MU potential.

A method for estimating the number of motor units in the extensor digitorum brevis (EDB) muscle was introduced in 1971 (McComas *et al.*, 1971a) and later extended to other limb muscles (Brown, 1972; Sica *et al.*, 1974). Reports of significantly reduced motor unit estimates in the muscular dystrophies pointed to a possible neurogenic basis for the muscular dystrophies (McComas *et al.*, 1971b, c). A later modification of the original method introduced by Ballantyne and Hansen (1974) did not confirm the evidence of motor unit loss, except in myotonic dystrophy. The motor unit estimates have also been used to quantitate the extent of motor unit loss in peripheral neuropathies and in motor neurone disease (Brown, 1973; Brown and Feasby, 1974; Brown and Jaatoul, 1974).

The method depended on obtaining the mean peak to peak (p-p) voltage of the first 4-10 unit potential steps excited by graded electrical stimulation of the motor nerve. The maximum

compound potential (MCP) evoked in a muscle by a supramaximal motor nerve stimulus could then be divided by the mean motor unit potential (MMUP) voltage to obtain the motor unit estimate (MUE). Of the assumptions considered in detail at the time of the introduction of the method, the two most critical have been (1) that the first five to 10 motor axons excited by graded electrical stimulation have firing levels distinct enough to exclude 'alternation'; (2) that the first one to 10 motor units excited by graded motor nerve stimulation are representative of the range in MU potential p-p and -p voltage in the remainder of the motor unit population.

The two critical assumptions may not be correct, based on evidence that (1) the firing thresholds of human motor axons do frequently overlap to such a degree as to lead to overcounts of the number of motor units used to obtain the MMUP and (2) motor units whose (p-p) and (-p) voltages are much larger than the incremental steps evoked by graded electrical stimulation can be recruited at high isometric contrac-

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tion levels and by the F recurrent discharge method (Brown and Feasby, 1974; Brown *et al.*, 1974; Milner-Brown *et al.*, 1974; Milner-Brown and Stein, 1975).

To provide more information about the possible limitations in the accuracy of the original method and other methods (Ballantyne and Hansen, 1974; Panayiotopoulos *et al.*, 1974), the present investigation was undertaken and designed to provide evidence on: (1) the excitability changes of single motor axons; (2) the extent of overlap of firing levels of two or more motor axons; (3) the comparative ranges in p-p and -p voltages of MU in the EDB and small muscles of the hand by means of the conventional motor unit estimate, isometric contrac-

tion, F discharge, and multiple point motor nerve stimulation methods. The results of this investigation led to the development of two possible modifications of the original method, which will be described in the second paper (Milner-Brown and Brown, 1976).

METHODS

TERMINOLOGY A number of key words will be referred to frequently in the text, and should be clearly defined. When an electrical stimulus is applied to a motor axon, the probability of firing or firing index (FI) of the motor axon, increases from 0–100% as the stimulus voltage is gradually increased from threshold (V) to $V + \Delta V$ (Bergmans, 1970). A plot of the stimulus voltage against the firing index, is the excitability curve (Fig. 1B). The voltage interval ΔV within which the FI varied from 0–100% is defined as the firing level range (FLR) of the particular motor unit. The firing point is the point on the excitability curve at which the MU is first observed to fire using graded motor nerve stimulation and at which the stimulus current was recorded (Methods, p. 251). Except for the first 1–2 MU, observation of distinct potential steps using graded nerve stimulation is uncommon in normal subjects. Trains of higher intensity stimuli frequently lead to multiple potential steps, a phenomenon referred to as alternation. Conventional method refers to the original methods of McComas *et al.* (1971a).

Very frequently in the text reference will be made to peak-peak (p-p) and/or negative peak (-p) voltages. This is because some of the data were accumulated independently by the authors; W.F.B. generally used -p voltages as a measure of the amplitude of the evoked potentials, while H.S.M.B. measured (p-p) voltage. The parameter measured will always be specified in the legend to the figure.

SUBJECTS The investigations were carried out on members of the hospital and laboratory staff and on patients with a variety of peripheral neuropathies. The type of neuropathy has been specified in the examples used in the text.

FIG. 1 Illustration of the key words used in the text. A. Four 'distinct' potential steps evoked by graded electrical stimulation: each step corresponds to one point on the excitability curves (firing points). The possibility of observing distinct potential steps depends on the extent of overlap in firing levels (see Appendix A). B. Shows excitability curves of four motor units, which represent the change in the firing index from 0–100% as the stimulus voltage is increased by ΔV (firing level range).

ELECTROPHYSIOLOGICAL INVESTIGATIONS The muscles investigated included the hypothenar (HT), thenar (T), first dorsal interosseous (IDI), and extensor digitorum brevis (EDB) groups, using methods previously reported (Brown and Feasby, 1974; Milner-Brown *et al.*, 1973, 1974).

The investigations could be subdivided into:

Excitability curves and firing levels of single motor units That the probability of firing or firing index

FIG. 2 Excitability curves of three MU recorded from two normal subjects (MU₁, MU₂, and MU₃) and one MU from a patient with diabetic neuropathy (MU₄). Fifty electrical pulses were applied to the median, ulnar, and deep peroneal nerves, and MU responses recorded by surface electrodes on thenar (MU₁, MU₂), and needle electrodes in IDI (MU₃) and EDB (MU₄). The number of MU responses at a fixed stimulus voltage divided by 50 is the firing index (FI). The voltage was increased in 0.2–0.5 V steps until the FI was 100%. The excitability curve of MU₂ was not completed because of a change in the subject's posture.

(FI) of motor axons increases from 0 to 100% as the stimulus intensity is increased from threshold, was reported by Bergmans (1970). In the present context, it was important to determine the firing level ranges and plot the excitability curves of single EDB and hand muscle motor units. To do this, the stimulus voltage delivered to the motor nerve (pulse duration 0.05–0.1 ms) was increased in 0.2–0.5 V steps and, at each voltage, the frequency of occurrence of the all or nothing discharges of the MU produced by trains (50) of constant voltage pulses was determined. It was possible to plot FIs of the first 1–2 MU activated only because, when the stimulus voltage was high enough to excite more than two MU, the constant voltage trains produced multiple distinct potential steps.

Movement of the limb or stimulating electrode (Disa 13K62) altered the excitability of single axons and, as a result, special efforts were made to prevent movement of the limb under study. For each of the motor nerves, the stimulating electrode position was distal—that is, at the ankle or wrist.

Intramuscular concentric needle electrodes were used in preference to surface electrodes at times (Fig. 2, MU₃) because the more restricted pick-up territory of the needle electrode made it more possible to exclude MU potentials of axons with nearly identical firing levels.

Examination of degree to which firing points of first one to 10 motor axons overlap In this part of the investigation, the firing points of one or more motor axons were recorded by a modification of the conventional method. By means of a sample and hold amplifier, the stimulus current was recorded at the point that the MU first fired and could be superimposed two or more times; no other MU potential

being observed. If other potential steps were observed, the stimulus voltage was maintained constant and a train of 50 pulses delivered in order to count the number of distinct potential steps produced by the train. No attempt was made to count the numbers of potential steps if that number was too high to preclude errors in the identification of the distinct potentials.

Other methods for determining mean motor unit potential The methods for isolating single MU using the isometric contraction and F-discharge methods have been reported before (Milner-Brown *et al.*, 1973; Brown and Feasby, 1974). The new modification introduced in this report was to stimulate the respective motor nerves at 10–20 points along the length of the nerve from the level of the upper arm to the wrist in the case of the median and ulnar nerves and from the popliteal fossa to the level of the ankle in the case of the peroneal nerve. At each point, only the first, all or nothing MU potential excited was included. The p-p or negative p voltage of single MU and of MMUPs from all four methods were then compared.

RESULTS

EXCITABILITY CURVES AND FIRING POINTS OF MOTOR UNITS Excitability curves of single motor units from control and abnormal subjects had a sigmoid (Fig. 2, MU₃, MU₄), not a Gaussian distribution in agreement with Bergmans (1970). This excitability curve is actually a property of the axon; however, in the text, reference will often be made to the excitability and firing threshold levels of the motor unit as a whole.

FIG. 3 Shows negative potential steps evoked by graded electrical stimulus to peripheral nerves of two patients and three controls. A. The remaining three EDB motor units in a patient with amyotrophic lateral sclerosis produced distinct potential steps. C. All four MU in the thenar muscles from a patient with diabetic mononeuritis multiplex produced four distinct potential steps (firing points). B, D. In controls, however, 'alternation' is observed in thenar muscles after the second unit. The occurrence of distinct firing points depends on the extent of overlap in firing levels as explained in Appendix.

The range of stimulus voltage over which the four illustrated and representative motor unit FIs changed from 0–100% was 2.0–4.2 V (firing level range) and notably less than the voltage changes between most of the 'distinct' potential steps observed by means of graded motor nerve stimulation. Even though minor variations in shape of the excitability curves of single motor axons were noted, no obvious differences were observed between motor axons belonging to the median, ulnar, and deep peroneal nerves.

In Fig. 3, only one point on the excitability curve (firing points) of each MU has been plotted. It is important to note that the points do not mean that the firing level ranges of MU 1–4 in Fig. 3C and MU 1–2 in Fig. 3D do not overlap, but that the degree of overlap is such that the probability of noting other possible MU and MU combinations was too low using the method described above (p. 251). (A theoretical explanation is given in Appendix B.) Even so, in healthy motor nerves, using the same method,

only the first one to a maximum of five MU had firing points distinctive enough for 'alternation' not to be expected to make a significant contribution to the observed number of potential steps.

In a limited number of controls, and even of patients with peripheral neuropathies, trains of stimulus pulses at motor threshold produced multiple potential steps pointing to an overlap in the firing levels of even the first motor axons excited. The numbers of distinct potential steps produced by the constant voltage trains at motor threshold or at stimulus voltages higher than that producing distinct single motor unit increments are plotted in the histogram (Fig. 4). An important feature is the presence of peaks

FIG. 4 Shows multiple potential steps evoked by applying long trains of above threshold stimulus pulses to motor nerves of normal subjects and patients with peripheral neuropathies. Peaks are centred around 3, 7, 15, which correspond to the maximum number of possible combinations of n motor units with overlapping firing levels, given by $2^n - 1$. Only the experimental observations that permitted an accurate count of the number of potential steps are included.

centred around numbers of distinct potential steps, which corresponded to the maximum number of possible combinations of n motor units with overlapping firing levels, given by $2^n - 1$. Only the experimental observations that permitted an accurate count of the number of potential steps are included and, as a consequence, no proper conclusion can be made about the relative frequencies of occurrence of potential steps close to three, seven, 15, 31....

FIG. 5 Comparison of single MU isolated during isometric voluntary contractions, and F recurrent discharges, with incremental steps evoked by graded electrical stimulation of ulnar and median nerves. The parameter measured was the negative peak voltage recorded from the IDI muscle of one patient with polymyositis.

FIG. 6 A. EMG amplitudes of single motor units recorded from IDI muscles of 10 normal subjects during isometric voluntary contractions (—). Amplitudes of incremental responses evoked by electrical stimulation to ulnar nerve at the wrist and recorded from IDI muscle of 10 normal subjects (---). Mean $\pm$ SD: $235 \pm 285 \mu V$ (voluntary contraction); $100 \pm 65 \mu V$ (nerve stimulation). B. Single motor units from thenar muscles isolated by stimulating at different locations along the median nerves of three normal subjects. Similar results were obtained from hypothenar muscles. The mean $\pm$ SD was $332 \pm 625 \mu V$. The parameter measured in these figures was (p-p) voltage.

Quite frequently the number of potential steps was much higher than 31, pointing to a probable overlap of at least five or more motor axon firing levels at that stimulus intensity.

Even though the actual numbers of potential steps observed were close to the expected 2^n-1 , in other motor nerves the number of potential steps was obviously less. Clearly, the number of potential steps observed could have been less than the expected number, particularly if the firing index of certain MU combinations was too low, the train duration too short, or if two or more of the MU or MU combinations had identical amplitudes and excitability curves. The observed number could have been larger than the expected number if the firing indexes of the motor axons changed as could have happened if ischaemia occurred or, much more commonly, if the position of the stimulating electrodes changed in relation to the motor nerve.

RANGE OF MOTOR UNIT SIZES In isometric contraction at high force levels large p-p voltage motor units, up to 10–20 times the p-p voltage of MU recruited at low force levels, are recruited. Such large motor unit potentials correspond approximately to the p-p voltage of large units isolated by the F recurrent discharge method and are clearly greater in p-p amplitude if compared with the first few motor units activated by motor nerve stimulation as illustrated for a few subjects in Fig. 5. Since the F recurrent discharge method was used on only a few subjects, Fig. 6A shows a separate comparison between the amplitudes of over 200 MU recorded from 10 normal subjects during isometric voluntary contraction (Milner-Brown *et al.*, 1973) and the (p-p) amplitudes of the incremental steps evoked by electrical stimulation to the ulnar nerve and recorded from IDI. The presence of large MU recruited during isometric voluntary contraction is clearly evident; the mean $\pm$ SD were 235 ± 285 μ V for voluntary contraction and 100 ± 65 μ V for nerve stimulation.

In an attempt to isolate single MU by an independent method, the motor nerve was stimulated at different locations along the nerve. At each location at the wrist, forearm, elbow, and above elbow a number of motor units were isolated. Figure 6B shows preliminary data obtained from normal subjects. The fact that

this method is not subject to alternation and that there is a fairly wide range of MU sizes does suggest that the method could be considered as a way of obtaining a more representative mean motor unit size. However, because of the obvious differences in the latencies of the single motor units isolated, a method has to be devised for obtaining a satisfactory MMUP from the MU isolated at the different locations along the nerve.

DISCUSSION

It is obviously important to determine the probable accuracy of methods for estimating motor unit numbers if meaningful interpretations of changes in motor unit numbers based on the method are to be justified. McComas *et al.* (1971a) identified most of the possible errors in their conventional method and for each in turn and collectively concluded that the errors could not account for the magnitude of MU loss in the muscular dystrophies. The findings in the present report do not bear directly on this last finding but have questioned the major assumptions that were made in their conventional motor unit estimates. It became obvious, particularly when long trains of constant amplitude stimuli were used, that the firing levels of two or more motor axons frequently overlap in the first one to 10 motor axons excited. This evidence was based on the finding that the firing level ranges of single motor axons extend over 2–4 V, and that the separation of single increment steps in the evoked compound potential with graded stimulation was often of that order. The occurrence of alternation—that is, the fluctuation in the number of potential steps at constant stimulus intensity—frequently at motor threshold, would lead to errors in the calculation of the mean motor unit potential.

Much larger p-p and negative p voltage motor units have been isolated using the isometric contraction method in IDI and the F response method in the thenar and EDB muscle groups and both findings pointed to the existence of motor units much larger than motor units included within the first group excited above motor threshold. Unfortunately, the F discharge and isometric contraction methods give no indication of how quantitatively important

such larger units are to the motor unit estimate—that is, the proportion of the total motor unit population that are large units. Moreover, even if a representative population of single motor units could be obtained (representative not only in terms of p-p voltage but in numbers of motor units in each amplitude group), there has been no good method to date to correct for the variations in latency to potential peak that would be necessary in the calculations of the MMUP before the MMUP could be used as the denominator in the calculation of the MUE.

In conclusion, this investigation strongly suggests, firstly, that motor unit estimation methods should incorporate the phenomena of fluctuations in excitability and overlap in firing levels of motor axons. Secondly, the sample of motor units used in estimating the mean motor unit potential should include larger motor units. From these important findings have evolved two new modifications to the original method of estimating the number of motor units in a muscle, which is described by Milner-Brown and Brown (1976).

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APPENDIX A

To examine the effect a change in the degree of overlap of the firing level of two motor axons would have on the FI of MU and MU combinations, Fig. 7A has been constructed from the excitability curves. The excitability curves used to represent the changes in FI of the motor axons were close to those of MU₃ and MU₄ in Fig. 4 and that reported by Bergmans (1970).

The probability of observing the sum of MU potentials (MU₁ + MU₂ . . . + MU_N) is equal to FI MU₁ × MU₂ × . . . FI MU_N. Fig. 7B shows plots of the probabilities of observing MU₁, MU₄, MU₁ + MU₄ when the firing levels of MU₁ and MU₄ overlap 50%, and Fig. 7C shows the same plots of MU₁, MU₂, MU₁ + MU₂ with 98% overlap. In the case of an overlap of 50% in the firing levels of two MU, the probability (P) of observing MU₄ at any point between E and K was less than 5% compared with the P of MU₁ of over 70% at H (Fig. 7B). Based on the comparative Ps of MU₁ and MU₄, it is most unlikely that MU₄ would have been observed in the conventional method of obtaining the motor unit estimate but a train of constant voltage stimuli (50–100) may have identified the extra potential step

FIG. 7 A. Diagram of three excitability curves in which MU₁ and MU₂ overlap 98%, and MU₁ and MU₄ overlap 50%. B. Probability of observing MU₁ or MU₄ alone and MU₁ + MU₄. C. Probability of observing MU₁ or MU₂ alone and MU₁ + MU₂. In B and C the probability of observing a MU at any particular voltage (A to P) was read directly from A. The probability of observing a sum MU₁ + MU₄ is equal to FI MU₁ × FI MU₄.

corresponding to MU₄ alone. When the firing levels overlap by 98%, however, the maximum Ps of MU₁ and MU₂ became almost identical and each less than 30% (Fig. 7C). In this case, the conventional method was quite likely to record MU₂ as an isolated potential if an effort were made not only to identify MU₁ but to superimpose that potential trace two or

FIG. 8 A. Diagram of three excitability curves: MU₁ and MU₂ overlap 98% and MU₁ and MU₃ overlap 96%. B. Probabilities of observing the seven possible combinations of MU₁, MU₂ and MU₃ read directly from A. The probability of observing MU₁ + MU₂ + MU₃ is equal to FI MU₁ × FI MU₂ × FI MU₃ at any voltage.

more times as is the usual practice in the conventional method.

Figure 8A is an illustration of three motor units whose firing levels overlap; each MU overlaps the preceding MU by 98%. The probabilities of observing each single MU or combination of MU are plotted in Fig. 8B. In this example, the probability of observing any individual MU or MU combination potential was between 10–20% and trains of stimuli at voltage levels E, F, and G were likely to produce the maximum number of possible distinct potential steps of seven. Of course, the probability of observing 'alternation' is dependent not only on the

FIG. 9 Single responses of the first two motor units (MU_1 and MU_2) evoked by stimulating the exposed deep peroneal nerve of a macaque, and recorded from EDB muscle. At stimulus voltages 10.1 V and 10.2 V, the two motor units produced three incremental steps due to MU_1 , MU_2 , and $MU_1 + MU_2$; at a higher stimulus voltage of 10.4 V, however, separate potentials due to MU_1 and MU_2 were not observed.

degree of overlap of the motor axon firing levels but on the firing level ranges and the slope of the excitability curve—that is, the rate of change of the FI with increasing stimulus.

The above illustrations make it clear that, if alternation can be observed frequently among the first one to 10 motor axons excited and the number of potential steps observed are close to the maximum number possible for n number of axons with overlapping firing levels, it is likely that the degree of overlap of the axon firing levels is high (more than 90%) and that, even when MU potentials appear to have clearly distinct firing points, the overlap may still be substantial.

APPENDIX B

After the theoretical calculations were made in Appendix A, we had the opportunity of experimentally substantiating the theoretical predictions. The exposed deep peroneal nerve of a macaque was directly stimulated with bipolar, 0.1 ms duration electrical pulses and the response pattern of the first two motor units recruited from the extensor digitorum brevis (EDB) muscle was studied. Figure 9 shows single evoked responses recorded from EDB muscle at different stimulus voltages. The figure illustrates two instances (at 10.1 V and 10.2 V) in which the first two motor units (MU_1 and MU_2) with overlapping firing levels produced three incremental steps due to MU_1 , MU_2 , and $MU_1 + MU_2$. At

FIG. 10 Number of observations of MU_1 , MU_2 , and $MU_1 + MU_2$ from EDB muscle when 50 pulses were applied to the exposed deep peroneal nerve of a macaque. At a stimulus voltage of 10.1 V there is approximately an equal probability of observing the three combinations MU_1 , MU_2 and $MU_1 + MU_2$; at higher voltages above 10.2 V, however, the number of observations of $MU_1 + MU_2$ predominates.

a higher stimulus voltage of 10.4 V, however, it was possible not to observe the separate responses of MU_1 and MU_2 . How frequently the motor unit responses followed this pattern was investigated in detail by applying 50 pulses to the nerve at the different stimulus voltages. Figure 10 is a plot of the number of observations of single motor units MU_1 and MU_2 and their sum $MU_1 + MU_2$. This figure shows that at a stimulus voltage of 10.1 V, the probabilities of observing the three combinations MU_1 , MU_2 , and $MU_1 + MU_2$ are approximately equal, while at voltages above 10.2 V, the number of observations of $MU_1 + MU_2$ predominates. This result is the same as the theoretical prediction (Fig. 7C) and forms the basis of a modified method of estimating the mean motor unit potential described by Milner-Brown and Brown (1976).