Comparison of voluntary and reflex activation of motor units

Functional organization of motor neurones

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The most important mechanism for gradation of muscle contraction is recruitment of new motor units with increasing effort. Whether voluntary and reflex contractions engage the different motor units in a similar order is not known. Since this question is not only of considerable physiological interest but also has clinical implications, we have compared the order in which the motor units are activated in voluntary contraction with that resulting from a polysynaptic and monosynaptic reflex.

The voluntary contraction was increased very slowly or kept constant at a steady level. The polysynaptic reflex was the flexion reflex recorded from the anterior tibial muscle and evoked by painful electrical stimuli applied to the plantar surface of the foot. The monosynaptic reflex was the tendon jerk recorded mainly from the medial and lateral vastus of the quadriceps muscle. The voluntary activation was compared separately either with the flexion reflex or the tendon jerk.

It was necessary to activate the motor units so that they could be identified separately and in order of appearance. This is difficult in the tendon jerk where the units discharge synchronously. No more than the first three potentials recruited within the picking up range of the electrode could be studied in any given needle position. For this reason the investigation was confined to weak contractions.

It was found that in most instances identical motor units were recruited in the same order independently of the source of activation. The differences which did occur were almost always confined to motor units of nearby thresholds. The significance of this finding is discussed.

MATERIAL AND METHOD

Most of the experiments were made on ourselves.

The motor unit potentials were picked up with bipolar needle electrodes, Disa no. 9013K0802, which had been shown to have a selectivity which was neither too high nor too low for experiments of this type. The potentials

were amplified, monitored on an oscilloscope, and displayed on a Tektronix storage oscilloscope no. 564 with a sweep speed of 5 msec./cm. A loudspeaker was used as well.

The technique of eliciting the flexion reflex was that used by Kugelberg, Eklund, and Grimby (1960). Electrical stimuli were applied to the plantar surface of the foot by means of a pair of needles inserted into the skin. The stimulus consisted of a series of shocks delivered over a period of 20 msec. and of a single duration of 1 msec. and a frequency of 500/sec. The sweep of the oscillograph was delayed 60 to 80 msec. in order to display the resulting reflex potentials on the screen at a sweep speed of 5 msec./cm.

The tendon reflex was induced by a reflex hammer attached to a microswitch which triggered the oscillograph after a delay of 10 to 15 msec.

The needle electrode was positioned so that it gave single voluntary potentials of characteristic appearance which could easily be identified. In the quadriceps muscle in addition a position had to be sought where potentials appeared at a comparatively weak contraction, otherwise the needle was displaced by the contraction even if it was isometric. In the smaller anterior tibial muscle this was not necessary since potentials always appeared at a weak contraction irrespective of the placement of the needle.

Great care was taken to ascertain the identity of the motor unit potentials evoked by the different means of activation. The individual motor unit potentials observed on the screen could be identified by their amplitude, duration, shape, and polarity. The appearance of the first three voluntary potentials was first studied. The potentials recruited by reflex activation were then studied by repeatedly trying to grade the reflex response so that one potential was recruited and possibly thereafter just two and then three. The voluntary potentials were then again observed to make certain that the needle electrode had not moved during the procedure. The reflex was generally once more studied followed by control of the voluntary activity unit until we felt convinced that we knew the appearance of the actual potentials.

RESULTS

CONSTANCY OF VOLUNTARY MOTOR UNIT PATTERN A

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prerequisite for comparison of voluntary with reflex activation is some constancy in recruitment of motor units by volition. It is generally acknowledged (Smith, 1934; Lindsley, 1935; Denny-Brown and Pennybacker, 1938; Gilson and Mills, 1941; and others) that a repeated voluntary movement regularly starts with the activity of a particular motor unit and Gilson and Mills (1941) found a constant threshold relationship between the different units for a given movement.

The voluntary contraction in the anterior tibial muscle was a slow dorsiflexion at the ankle joint, and in the quadriceps an extension at the knee joint, during which the subject tried not to contract the other muscles of the leg. When the reflex was induced the subject tried to keep the leg relaxed and to contract neither the agonist nor the antagonist. Repeated recordings of voluntary patterns during the five to 20 minutes the experiment lasted showed that the unit first recruited in voluntary contraction kept constant in 35 out of 39 different needle positions in the anterior tibial muscle and in 35 out of 41 in the quadriceps. The 'rotation' of units was restricted to the first and second but never to the first and the third units recruited. 'Rotation' between the second and the third probably appeared with the same frequency. The pattern of motor unit recruitment in the muscles under study was obviously sufficiently stable to serve as a basis for comparison. This is in agreement with the work cited above.

The cause of 'rotation' was not clear. It appeared to occur spontaneously but it is evident that subtle changes in contraction pattern of the leg, *e.g.*, co-contraction of the antagonist, might take place during the experiment resulting in 'rotation' of units. Changes in relative thresholds of motor units with change in movement pattern have been described by Seyffarth (1940), Gilson and Mills (1941), and Denny-Brown (1949). However, we have not been able to alter the motor unit pattern in the anterior tibial muscle by a simple change from flexion to flexion with pronation or supination as Seyffarth claimed for the biceps.

On the other hand, the order of recruitment of units could be changed by voluntary control guided by auditory and visual feed back as reported by Harrison and Mortensen (1962) who used plate electrodes. If two units are active and the contraction is slowly decreased it has been possible, by concentrating on the sound, to guide the second unit so that it remains for any desirable length of time although the previous number one unit has dropped out. If the contraction is then stopped but taken up again within a few seconds the second unit can again be recruited alone. After more than 10 seconds' delay the original recruitment order is usually

re-established. The procedure presupposes some mental effort and some of us were much more clever than others in achieving rotation and succeeded in doing so within a few minutes almost constantly. Auditory or visual feed back was certainly essential but changes in direction of movement, if any, were not obvious. We only succeeded in 'rotating' two units nearby in the recruitment order but the possibility that training might give more freedom of choice is not excluded.

COMPARISON BETWEEN VOLUNTARY ACTIVATION AND FLEXION REFLEX Meticulous adjustment of reflex responses is somewhat hampered by the large fluctuations in the threshold due to habituation, sensitization, change in the subject's attention, expectancy, and other cerebral influences (*c.f.* Hagbarth and Kugelberg, 1958; Grimby, 1963). Nevertheless a reflex response of a single potential can repeatedly be reproduced. Moreover, discharges composed of two or perhaps three potentials can in most instances also be evoked. The different potentials in such a weak response follow one another generally in the order of their recruitment at intervals of about 5 msec. (Fig. 1b). Even though the discharge is to some extent asynchronous, interference between potentials is bound to occur. This often makes it difficult to identify with certainty the second and third potentials. We have therefore primarily compared the first unit recruited by the reflex with any of the first three units recruited by volition.

As shown in Table I there is a striking similarity between reflex and voluntary activation. However, its significance depends on how many different discrete motor unit potentials the needle electrode is capable of picking up. By increasing the contraction, seven or eight potentials could generally be followed (for example Fig. 1d). At this point the contraction was not maximal and several more units appeared when a maximal contraction was attempted. We may assume that no less than 10 different potentials appeared. Under these circumstances it

TABLE I

VOLUNTARY CONTRACTION COMPARED WITH FLEXION REFLEX AND TENDON JERK ACTIVATION AT EACH OF 35 DIFFERENT NEEDLE POSITIONS

	First Unit in Flexion Reflex	First Unit in Knee Jerk Reflex
First voluntary unit	29	24
Second voluntary unit	4	4
Third voluntary unit	1	0
Not identified as first, second, or third	1	7
Totals	35	35

FIG. 1. (a) Three motor units during steady voluntary contraction displayed in order of appearance at increasing effort. In this and the following records (except 1c and 1d) sweep speed 5 msec./cm. (grid 1 cm. square).

(b) Flexion reflex discharge composed of the same units in the same order. Latency 113 msec.

(c) Voluntary contraction slightly stronger than in (a), at a slower sweep speed (showing four units).

(d) Strong contraction to show number of units.

could certainly not be the result of pure chance that 29 out of 35 units were identical in reflex and voluntary contraction. Moreover 33 out of 35 of the number one reflex units fell within the first two of 10 available units in voluntary contraction.

The unit activated second in the reflex seemed to follow the same scheme, being in most cases identical with that recruited second in volition. Three different units have sometimes been observed and have appeared in the same order in both voluntary and reflex contraction (Fig. 1a and b).

COMPARISON BETWEEN VOLUNTARY ACTIVATION AND TENDON JERK Since the potentials in the tendon jerk are well synchronized we have only been able to identify the unit of lowest threshold.

By a tendon tap it is possible with some training and persistence to evoke only one motor unit potential. The criteria for a single unit versus a

synchronized potential have been a potential of constant appearance and one which responds in an all or nothing manner. It is, however, clear that the experimental error is greater here than in voluntary and flexion reflex activation. Some units, which we have not been able to identify among the voluntary population, may in reality have been synchronized units of nearby thresholds which were difficult to separate. Nevertheless, enough units have been identified. Some not clearly identified were of smaller amplitude than the voluntary units and had characteristic form so it was very unlikely that they represented synchronized activity of any of the low threshold voluntary units observed.

This is exemplified in Fig. 2 where the potential first recruited by a tendon tap and by volition is compared in five consecutive needle positions. In the first four the potentials are obviously identical but the fifth is different.

FIG. 2. Five experiments showing first unit evoked by knee jerk (upper record) and by volition (lower record). Reflex latency about 25 msec.

A striking similarity was again found between reflex and the voluntary activation which could not be the result of pure chance (Table I). The maximal number of recruited units within the picking-up range of the electrode is somewhat less in the quadriceps muscle than in the anterior tibial muscle but this does not invalidate the conclusion. A similar study was performed on the ankle jerk in the soleus with essentially the same result.

As mentioned before, in some instances rotation occurred between the first two units in voluntary contraction. The same was observed in both the

flexion and the tendon jerk in a few needle positions. It has been considered most correct not to include them in the table since they could be counted either as number one or two or both. However, whatever is done they do not change the principal results.

INTERACTION OF VOLUNTARY AND REFLEX ACTIVITY

It is well known that slight or moderate volition decreases the threshold and increases the strength of both human spinal polysynaptic reflexes (c.f. Kugelberg *et al.*, 1958) and tendon jerks (Hoffmann, 1922). As shown above, the first unit recruited in

FIG. 3. (a) I and II, first and second units recruited by voluntary effort.

(b) First reflex unit evoked in flexion reflex (I) and by knee jerk (II) being second voluntary unit. Latency 93 and 35 msec. respectively.

(c) First reflex unit recruited under slight voluntary effort being first voluntary unit. Latency 94 and 30 msec. respectively.

FIG. 4. (a) *First voluntary unit.*
 (b) *First flexion reflex unit, same as in (a). Latency 73 msec.*
 (c) *Willed rotation of voluntary unit.*
 (d) *First flexion reflex unit, same as in (c). Latency 80 msec.*

reflex and voluntary activation was not always the same. It was possible, however, with great regularity to change the reflex unit if it was elicited under slight voluntary effort. The unit then obtained was identical with the voluntary unit. This was equally valid for both the flexion and the stretch reflex.

In Fig. 3 the unit number one in flexion reflex (Ib) and in knee jerk (IIb) was number two in voluntary contraction (Ia, IIa). If the subject was told to attempt a slight voluntary effort which in itself neither evoked any visible muscle contraction nor any potential the reflex unit switched over to the number one voluntary unit (Ic, IIc).

The same was accomplished by willed rotation. Number one unit in voluntary contraction (Fig. 4a)

is identical with number one in the flexion reflex (Fig. 4b). The subject could by willed rotation get his second voluntary unit running as number one (Fig. 4c). If this unit was stopped and the flexion reflex was induced within a few seconds the same unit was still evoked (Fig. 4d). Some seconds later the original pattern was again obtained on voluntary as well as reflex activation.

Another change which took place was most easily observed in the tendon jerk. Generally it is difficult to grade the stimulus to recruit only one potential. There is a strong tendency to synchronized discharge of several units. Under attempted voluntary contraction, however, with the greatest ease just one unit could be evoked, that is, the voluntary unit of lowest threshold.

Evidently reflex excitation of the common motor neurone pool discharged the unit which had been brought near to threshold by subliminal volition. The ease with which a voluntary unit is singled out depends probably on the graded character of the voluntary discharge which is impressed upon the reflex.

The order of units in the reflex may also influence the voluntary sequence. Voluntary activation immediately after the flexion reflex showed persistence of the reflex unit which had been evoked instead of the voluntary one. Moreover, synchronization of voluntary units by the tendon jerk or vibratory stretch stimuli is a well known and easily reproducible phenomenon (e.g. Sommer, 1941).

Since subthreshold voluntary facilitation had such strong influence on the order of recruitment of reflex units it may be asked if the identity of voluntary and reflex pattern observed at most needle positions is not the result of such cerebral effects.

To minimize its effect the subject was asked to contract the antagonist voluntarily. Under this procedure the reflex was inhibited and the threshold raised, showing that the instructions had been followed. In the majority of cases the units first recruited were still the same.

The validity of the observations above depends upon the possibility of distinguishing reflex from voluntary discharges. This could be done on the constant latency relationship between the reflex discharge and the stimulus which evoked it. Moreover the latency of the stretch reflex was about 25 msec. and the flexion reflex about 80 msec., which is too short for a voluntary response to the stimulus.

COMPARISON OF DIFFERENT TYPES OF REFLEX ACTIVATION The order of recruitment of motor units in voluntary contraction has been shown to be similar to that obtained in the flexion reflex and also the

FIG. 5. (I) Normal subject. Soleus muscle.
(a) Polysynaptic extension reflex. Latency 110 msec.
(b) Ankle jerk. Latency 30 msec.

FIG. 5. (II) Pathological case (spastic paraplegia). Anterior tibial muscle.

(a) Flexion reflex. Latency not measured.
(b) Tendon jerk. Latency 30 msec.

tendon jerk. It is therefore to be expected that the sequence of units recruited, in the same muscle, in response to flexion reflex and tendon jerk stimulation, would be similar but this is not easy to demonstrate. In most normal subjects it is difficult to elicit a tendon jerk in the anterior tibial muscle without a strong blow on the tendon which displaces the needle electrode. However, by strong painful stimulation of the heel it is possible (in normal people) to evoke a polysynaptic spinal extension reflex as a component of the general defence reflex for the leg (Kugelberg *et al.*, 1960; Habgarth, 1960). The unit first recruited in this reflex was also number one in the ankle jerk (Fig. 5Ia, b).

To decide whether the similar recruitment order in these two reflexes was due to cerebral influences two patients with spastic paraplegia were investigated. Both had complete loss of voluntary power in the lower limbs. In these patients the first unit recruited in the flexion reflex and the tendon jerk recorded, from the anterior tibial muscle, was the same (Fig. 5IIa, b).

DISCUSSION

Each muscle was examined at more than 10 needle positions and 10 to 20 units could be recorded from each position. Approximately 445 motor units are found in the human anterior tibial muscle according to Feinstein, Lindegård, Nyman, and Wohlfart (1955). Thus, a fairly large proportion of the units

was available within the picking-up range of the electrodes. It must be emphasized that only low threshold units were actually studied. Moreover, the observations were restricted to a few muscles which were specially suitable.

The motor units were activated through three different routes: supraspinal, spinal polysynaptic, and spinal monosynaptic. The voluntary discharge was tonic in the sense that it could be maintained, if required, for hours at a constant slow pace. The reflex discharges were phasic. It was found that in most instances identical units responded and in the same order independently of the mode of excitation. When there was a difference in recruitment order it was confined to units of nearby threshold. The motor neurone pool is apparently homogeneously excited by different inputs.

Since the motor neurone is the only cell common to all three routes of activation it is likely that its inherent properties are the main factor determining the order of recruitment. An alternative explanation is that the different inputs superimpose their activity on a powerful background stimulation which determined the excitability level and excitability order of the individual motor neurone. Thus any discordance between voluntary and reflex activation order of units could be eliminated by increasing the cerebral influence on the motor neurone pool. However, this cerebral background excitation is obviously not essential. Voluntary contraction of the antagonist muscles gave a large increase in reflex threshold but hardly any change in recruitment order. The same basic order of recruitment in the different types of reflex stimulation still occurs in patients in whom all supraspinal influence is blocked. Moreover Henneman, Somjen, and Carpenter (1965a) found in the cat that interruption of the gamma loop did not alter the sequence of recruitment. It is not likely that background excitation, in general, plays a major part in recruitment order.

Our findings and conclusions agree, in this respect, with those of Henneman *et al.* (1965a, b) and Somjen, Carpenter, and Henneman (1965). They compared the order of recruitment of different spike sizes in ventral root filaments of the cat during various reflexes and supraspinal electrical stimulation. The spike size was taken as an index of axon diameter and relative motor neurone size. A small spike was thought to arise from an axon of small diameter connected to a cell of smaller size than a spike with relatively larger amplitude. In general, the smaller of any two spikes discharged at a lower intensity of stimulation than the larger one. Some 10 to 15% of units had reversed recruitment order in relation to spike size which was attributed to fibre damage in the separation of the thin filaments rather than to

neuronal factors. Henneman *et al.* and Somjen *et al.* concluded that the excitability of motor neurones is an inverse function of the cell size which, in turn, determines the order of recruitment. The relationship between the electrical threshold and size of the motor fibres to the order of recruitment of motor neurones has earlier been discussed by Kugelberg and Skoglund (1946) and Hyde, Kugelberg, and Skoglund (1953).

Our results differ in some respects from those of Henneman *et al.* and Somjen *et al.* The inherent properties of the motor neurone, though important, cannot be the only determining factor in the order of recruitment. When voluntary and reflex activation were compared about 20% of motor neurones were discordant. Moreover, in such cases the recruitment order could be changed in both voluntary and reflex activation by superimposing the one on subliminal excitation of the other. This shows that specificity of input determines to some extent the excitability of motor neurones.

The discrepancy may be explained by the fact that reflex excitation in the decerebrate cat is a much more stereotyped event than spinal reflex activity under cerebral control, or voluntary activity, in the human subject. Technical factors may have also influenced the results. In our experiments identification of units was based not only on amplitude but also on shape, which was often characteristic. In our 10-20 unit samples the difference in threshold between adjacent units is likely to be less than in a sample of only a few fibres.

As mentioned above, some variability in recruitment order from test to test was found as well as some discordance between voluntary and reflex recruitment. However, using auditory feedback, if the subject tried to change the recruitment order of two nearby units he could do so in up to 100% of attempts provided that he was adept. The greater tendency for input specificity to show up under auditory feedback might be expected. In the basic experiments the voluntary and reflex movements were simple flexion and extension. The voluntary movement under auditory feedback could take advantage of any combination of contraction in synergists and antagonists and any posture until a combination was found which produced a change in recruitment order of two units. It is clear that input specificity cannot be ignored even within the restricted boundary of the motor neurone pool. But only units of nearby threshold have been altered in recruitment order. It would seem that the properties of the motor neurones themselves are the main factor in recruitment.

In so far as the functions investigated are representative it is clear that a population of motor units

have a low threshold for any stimulus and will be used for all the day. Training and disuse therefore seems to be concerned mainly with high threshold units. This is probably the theoretical background to the popular use of heavy weights in the athlete's training. Furthermore the low threshold units in a tonic and a phasic discharge were identical.

From the clinical point of view it is interesting to note the close interaction between voluntary and reflex activity even at the motor unit level. It forms a rational basis for different types of physical therapy in which reflex activity is used to reinforce voluntary effort.

SUMMARY

Voluntary, polysynaptic, and monosynaptic spinal reflex activation of motor units have been compared in normal human subjects. The motor unit potentials were recorded with a bipolar needle electrode and identified by their shape, size, amplitude, and polarity.

The order in which low threshold units are recruited in initiating voluntary contraction was found to be sufficiently stable to serve as a basis for comparison.

The first unit recruited out of at least 10 available units was the same in voluntary and flexion reflex activation in 29 out of 35 registrations. The comparable figures for the tendon jerk were 24 out of 35. The first reflex unit corresponded with the second voluntary unit on four occasions in each series.

Voluntary and reflex activation interact. During subliminal voluntary effort, the reflex was enhanced, the order of recruitment was made identical with that of volition, and recruitment of units was made more gradual. Voluntary contraction just after a flexion reflex discharge brought up the reflex order of recruitment.

By using auditory feedback in voluntary contraction a trained subject could bring out reversal of recruitment order of nearby units almost constantly. This could also be impressed on the reflex discharge.

In two patients with spastic paraplegia and no voluntary power the same unit appeared first in both monosynaptic and polysynaptic reflex stimulation.

It was concluded that the inherent properties of the motor neurone are the most important factor in determining the order of recruitment of motor units but that there is some specificity of input concerning units of nearby threshold.

The significance of these findings in relation to training and disuse is briefly discussed.

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