Recruitment order of motor units in man: significance of pre-existing state of facilitation¹

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SUMMARY It has been shown in previous investigations that the recruitment order of motor units is different in tonic and in phasic voluntary activity. The significance of the pre-existing state of facilitation in the motoneurone pool for the recruitment of units is studied, using the phasic flexion reflex in the anterior tibial muscle as test reflex. It is shown that the recruitment order of units in a series of reflexes (1) is unstable if the subject does not expect the stimulus; (2) is stable and identical with that in tonic activity if the subject subliminally facilitates the motoneurone pool before the reflex activation; (3) is stable and almost identical with that in tonic activity if the subject expects the stimulus and therefore involuntarily influences the motoneurone pool; (4) is stable and similar to that in phasic voluntary activity if the subject inhibits the motoneurone pool before the activation and the stimulus strength thus consequentially is increased; and (5) is influenced by blockade of the proprioceptive afferent impulses from the muscle. It is concluded that normal man can select in advance the recruitment order of motor units most appropriate for the work intended.

In electromyographic recordings, single motor units can be identified with complete certainty by the constant and characteristic shape of their potentials.

We have shown in previous papers that the order in which the motor units are recruited can change with a shift from phasic to tonic voluntary activity in normal man (Grimby and Hannerz, 1968) as well as on a shift from phasic to tonic reflex activity in 'spinal man' (Grimby and Hannerz, 1970). The units first recruited in phasic activity have a higher maximal discharge frequency than have the units first recruited in tonic activity. It can be presumed that there is a correlation between maximal discharge frequency and contraction time and thus that faster twitch units are replaced by slow twitch units with a shift from phasic to tonic activity (Hannerz, 1972).

Under certain conditions, however, the recruitment order that is used in tonic activity can be used in phasic activity also. In 'spinal man', subliminal afferent facilitation 'programmes' the motoneurone pool so that the tonic recruit-

ment order is used irrespective of the mode of activation.

The aim of the present investigation is to study the 'programming' effects of different types of cerebral influence on the motoneurone pool.

METHODS

Most of the experiments were performed on the authors themselves but the validity of the results was confirmed in control experiments on other subjects. More than a thousand reflexes were analysed.

In the experiments the anterior tibial muscle was tested. The recording electrodes were inserted proximally close to the tibia to exclude recordings of potentials set up from other muscles, and fairly near the muscle surface to avoid displacement of the recording electrodes. Histochemical analysis of the muscle area under study revealed a mixture of type II or white muscle fibres with a strong reaction for myofibrillar adenosine triphosphatase at pH 9.4 and of type I or red muscle fibres with a weak reaction for this enzyme. Since the motor units are homogeneous as regards muscle fibre type, two types of motor units were thus present within the muscle area.

The motor unit potentials were recorded with bipolar needle electrodes (Disa no. 9013 K0802), which have previously been shown to have a selec-

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FIG. 1. *Difference in recruitment order between (a) phasic and (b) tonic voluntary activity; the unit that is number one in phasic activity is only number four in tonic activity. Time bar: 50 msec.*

tivity that is neither too high nor too low for experiments of this type (Ashworth, Grimby, and Kugelberg, 1967). The potentials were amplified and displayed on two oscilloscopes—namely, a standard oscilloscope with continuous sweep and a Tektronix storage oscilloscope no. 564 which was triggered by the stimulus. All experiments were recorded on magnetic tape and the results obtained were confirmed by repeated playbacks and by film recordings of the principal parts. The pictures were obtained by such film recordings.

To be identified as deriving from a certain unit, the potentials had to be of a characteristic size and shape and remain unchanged during repeated reflex activations as in tonic voluntary activity. A second potential was defined as belonging to a second unit only if it was set up alternately with the first potential. A prerequisite for identifying a third potential as deriving from a third unit was also that its size and shape excluded its being built up from potentials number one and two. And so forth. By the criteria thus established it could be ascertained that the potentials studied represented functionally separate motor units in the muscle. It cannot be ruled out, however, that some of the potentials might be derived from synchronized units, but this would not invalidate the conclusions drawn.

The technique of eliciting the phasic reflex was the same as that used by Grimby in 1963. Electric

stimuli were applied to the plantar surface of the foot by means of a pair of needles inserted in the skin. The stimulus consisted of a series of shocks delivered in a period of 10 msec and of a single shock duration of 1 msec with a frequency of 500/sec. The stimulus was experienced as a brief, intense needle prick. The stimulus strength was systematically adjusted to get threshold reflexes.

Only reflexes obtained within 120 msec and having a constant latency from one stimulation to another were studied. It had previously been found that, if a stimulus is applied to a skin area of the foot from which no reflex activity can be evoked and the subject is instructed to bend his foot as soon as he experiences the stimulus, the latencies of the voluntary activity of the anterior tibial muscle thus obtained are highly variable from one stimulation to the other, the subject never being capable of reacting within 150 msec and only exceptionally within 200 msec (Grimby, 1963). There is thus a wide margin between the latencies of the reflex studied and the purely voluntary responses.

RESULTS

The motor units were called according to the order in which they were recruited in voluntary activity, since the aim of the investigation was to study the cerebral influence on the motoneurone

FIG. 2. (a) *Unstable recruitment order in a series of reflexes obtained by unexpected stimuli; five different units appear as number one unit.* (b) *Stable recruitment order in tonic voluntary activity; the five different units are recruited in a certain order.* Time bar: 50 msec.

pool. As was mentioned previously, the recruitment order is different in phasic and in tonic voluntary contraction.

The motor unit with the lowest threshold in a phasic voluntary contraction was called A (Fig. 1a). The unit with the second lowest threshold in a phasic contraction tended to be synchronized with the first unit, and only the unit with the lowest threshold could be studied systematically. In repeated phasic contractions different units had the lowest threshold. The unit most often activated was called A1, the unit next most often activated was called A2, etc.

In the tonic voluntary contraction, it was possible to identify five or six different potentials of units before their interference with one another made further studies impossible. The units were predominantly activated in the same order in repeated tonic contractions. They were called B1, B2, B3, etc., in the order in which they were activated.

Most units appeared both in phasic and in tonic contraction, but some units could be identified only in either tonic or phasic contractions. Figure 1 shows, for example, unit A1 appearing also as unit B4.

REFLEX UPON UNEXPECTED STIMULUS The reflex threshold was lower if the subject experienced the stimulus unexpectedly than it was in any other situation tested. In our experiments a stimulus of 5 V was optimal for studying the recruitment order on unexpected stimulus, as it was strong enough to cause sporadic reflexes and weak enough to make it possible to divert the subject's attention.

Most of the 5 V stimuli did not result in a reflex at all, but, when a reflex was obtained, it usually consisted of several more or less synchronized units, indicating that the threshold differences of the studied units were small.

The reflex achieved by the 5 V stimulus could,

however, consist of a single unit. This unit was not the same in a series of such single unit reflexes. The units most frequently appearing were A1 and B1. Other units appeared more sporadically. The longer the experiment was continued and the more the attention of the subject could be diverted, the greater was the number of units alternating in a series of single unit reflexes. It was not possible to anticipate which unit would appear in the reflex. As many as five different units appeared alternatively in a series of single unit reflexes in an experiment of two hours' duration. Figure 2 shows this experiment. Figure 2a shows the five different single unit reflexes. Figure 2b shows the five units being activated in a stable order in an increasing tonic voluntary contraction.

These results are in accordance with the results achieved in the earlier investigations of 'spinal man'. In these subjects with total interruption of the spinal cord and consequent loss of the cerebral influence on the motoneurone pool, no stable recruitment order of motor units was obtained in a series of phasic reflexes.

REFLEX UPON SUBLIMINAL VOLUNTARY FACILITATION The subject was instructed almost to initiate a contraction of the anterior tibial muscle without actually contracting the muscle. That contraction did not occur could be checked by the subject himself by listening to a loud-speaker connected to the amplifier. To obtain a reflex in this experimental situation a stimulus of 10 V was required—that is, double the strength required for obtaining a reflex when the subject was stimulated unexpectedly.

Trained subjects were able with this procedure constantly to obtain the B1 unit as the motor unit with the lowest threshold in the reflex. If more units than the B1 unit were activated, there was an interval between the different units of about 5 msec which made the identification of the different units possible. Such 'multi-unit reflexes' always started with B1 followed by B2, B3, etc., in the usual tonic recruitment order as in Fig. 2b.

The same result—that is, a stable recruitment order identical with that in tonic activity—was obtained after tonic afferent facilitation of the motoneurone pool in 'spinal man'. It can be concluded that tonic afferent or cerebral

facilitation programmes the motoneurone pool so that the units are recruited in the tonic order independently of the mode of activation.

REFLEX UPON HABITUATION When the stimulus was repeated at short intervals, the reflex threshold successively increased but after about 10 stimuli the reflex threshold was stabilized at about 30 V. If the 30 V stimulus was then repeated at intervals of one to two minutes, the rather stable reflex threshold was maintained for hours without any active cooperation from the

FIG. 3. Influence of pre-existing state of facilitation and stimulus strength on the recruitment order in the reflex: (a) on subliminal voluntary facilitation a 10 V stimulus is enough for a reflex to appear and then a certain unit regularly has the lowest threshold; (b) on habituation the reflex threshold is 30 V and then another unit is regularly first recruited; (c) on voluntary inhibition a 150 V stimulus is required and then a third unit has the lowest threshold; (d) in a very strong reflex the three potentials appear together which proves that they belong to three different units. Time bar: 50 msec.

subject. The 30 V stimulus was painful and when it was used the subject's attention could not easily be diverted from the experiment situation, as was possible when the 5 V stimulus was used in the experiment described above. If, nevertheless, the subject's attention was diverted, the reflex threshold markedly decreased.

No electromyographic activity could be registered between the reflexes during these experiments of one to two hours' duration. It is thus not likely that any of the alpha motoneurons in the anterior tibial muscle discharged continuously during these habituation experiments.

The recruitment order was mainly stable in a series of habituated reflexes. In most of the experiments, the B1 motor unit had the lowest threshold. In some experiments the unit first recruited was, however, the B2 unit. Habituation thus has almost the same programming effect as voluntary facilitation of the motoneurone pool.

REFLEX UPON STRONG STIMULUS One of the authors was able to suppress the reflex voluntarily so that the threshold increased to 150–400 V, provided he knew exactly when the stimulus was going to be elicited. The recruitment order was mainly stable in a series of single motor unit reflexes elicited by such strong stimuli. In some reflexes the first unit to be recruited was A1, in others A2.

Figure 3 shows the significance of reflex threshold and stimulus strength for the recruitment order. In Fig. 3a the motoneurone pool was voluntarily facilitated and a 10 V stimulus was enough to result in a reflex; the unit B1 had the lowest threshold. In Fig. 3b the subject was habituated and a 30 V stimulus was needed to obtain a reflex; the unit B2 was the first to be recruited. In Fig. 3c the subject voluntarily inhibited the reflex and a 150 V stimulus was needed to get a reflex; the unit A1 had then the lowest threshold. In Fig. 3d the three potentials A1, B2, and B1 are seen together, proving that they belong to different units.

The voluntary inhibition of the motoneurone pool and consequent increase of the stimulus strength thus results in a 'phasic' instead of a 'tonic' recruitment order. It is apparent that the long-lasting state of facilitation in the motoneurone pool programmes the pool for one

recruitment order, while the strong stimulus tends to activate the units in another order.

REFLEX UPON DECREASE OF MUSCLE SPINDLE DISCHARGE The muscle spindle discharge can be reduced by injection of local anaesthetics into a muscle nerve without eliminating the activity of the alpha motoneurons (Matthews and Rushworth, 1957). Most authors are of opinion that this is due to blocking of the gamma motoneurons, but others consider that blocking of the large afferent nerve fibres is also involved (Gassel and Diamantopoulos, 1964). It has fur-

FIG. 4. Influence of partial lidocaine blockade of the muscle nerve on the recruitment order in the reflex: (a) before the blockade a certain unit has the lowest threshold; (b) on the blockade another unit has the lowest threshold; (c) after the blockade the original unit again has the lowest threshold; (d) despite the blockade the two potentials can appear together which proves that the change in recruitment order is not due to blockade of the alpha motoneurone fibres. Time bar: 50 msec.

ther been shown that such a blocking makes the alpha motoneurone discharge at more irregular intervals than normally occurs (Tokizane and Shimazu, 1964).

In two experiments in which the motor unit B1 had been the first recruited unit in 30 reflexes at two minute intervals, the peroneal nerve was injected with lidocaine during voluntary contraction. The injection was continued until the B1 unit began to discharge at irregular intervals—that is, until it could be assumed that the lidocaine had acted on the muscle spindle discharge but not on the alpha motoneurone of the B1 unit. The voluntary activity was then discontinued and a reflex elicited. A new unit thereupon appeared in the reflex. As long as the B unit discharged at irregular intervals in voluntary contraction, the new unit remained first in the reflex. As soon as the effect of the lidocaine on the voluntary discharge pattern disappeared, the B1 unit returned as the number one unit in the reflex (Fig. 4).

Local cooling of the muscle decreases, among other things, the sensitivity of the muscle spindles (Eldred, Lindsley, and Buchwald, 1960). By applying a cold pack to the muscle for 20 minutes, the same change in the recruitment order in the reflex could occur as upon injection of the muscle nerve with lidocaine.

It can be assumed that the proprioceptive afferent activity contributes to the programming of the motoneurone pool in normal man (*cf* Discussion).

DISCUSSION

It was shown in a previous study of 'spinal man' that recruitment order of motor units for tonic activity is used also in phasic activity after subliminal sustained afferent facilitation of the motoneurone pool. It was assumed that this 'programming' was due to changes in the pre-existing subliminal state of facilitation of the motoneurone pool. However, the possibility could not be excluded that feedback effects from alpha motoneurone activity might be necessary for 'programming' to occur.

It is shown in this paper that cerebral influences can 'programme' the motoneurone pool in normal man for use of tonic recruitment order irrespectively of the mode of activation, in the

same way as sustained afferent facilitation 'programmes' the pool in 'spinal man'. This cerebral 'programming' can be accomplished without previous alpha motoneurone activity and feedback effects—for example, via Renshaw collateral fibres. Moreover, the thresholds of some units can increase so much upon 'programming' that it is likely that not only facilitating but also inhibitory mechanisms are involved.

It is generally thought that phasic voluntary activity is mediated via direct activation of the motoneurone pool but that tonic voluntary activity is dependent on indirect facilitation via the gamma loop. It is thus pertinent to ask to what extent the muscle spindle discharge is responsible for the tonic recruitment order.

It is shown in this paper that the subject has difficulties in maintaining the 'programming' when the muscle spindle discharge is blocked. Further experiments are, however, needed before it is possible to decide whether this is due to decreased afferent facilitation of the motoneurone pool or to changed cerebral influence on the motoneurone pool because of changed feedback to cerebral centres.

As different units have different properties, it is functionally essential that they are recruited in the order that is most appropriate for the work intended.

For maximal precision of the contraction, the recruitment order should be stable so that it can be anticipated which unit will discharge. Maximal stability of the recruitment order is achieved by 'programming' which thus can be seen as an adaptation to precise movements.

For maximal rapidity of the contraction, especially in alternating movements, however, high-frequency units with a presumably short contraction time should be used. The normal subject can indeed voluntarily interrupt the 'programming' so that the importance of high-frequency units increases.

The conclusion is drawn that cerebral centres are capable of selecting in advance the recruitment order that is most appropriate for the work intended.

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