Journal of Neurology, Neurosurgery, and Psyy, 1980, **43**, 897–906

Regulation of the firing pattern of single motor units

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SUMMARY The normal control of force in the anterior tibial muscle was reflected by a fast regulation of the interval pattern of single motor units. Short and long intervals alternated, the correlation between successive intervals was negative and "double discharges" were present. The discharge rate at 60% of maximal effort was at most 20 Hz.

As the development of selective electrodes has made it possible to record action potentials from single motor units in man at moderate and high levels of voluntary contraction, an increasing number of workers have used "single unit recording" to study recruitment order and to describe the firing pattern during maintained contraction.[1-12]

The aim of this study is to provide a description of the firing pattern of motor units in the anterior tibial muscle during constant isometric contraction. The criteria are the range of firing frequency, the variability of the interspike intervals and the serial correlation coefficient, which describes the relationship between successive intervals.

Methods

Recording

Recordings were obtained from the anterior tibial muscle of four volunteer subjects (table). The subject was lying on a stretcher with the foot firmly strapped to a stiff force transducer. The axis of rotation of the force transducer was aligned with the ankle joint. Thereby only muscles that develop a torque around the ankle contribute to the measured force. The torque at the ankle is mainly due to the anterior tibial muscle. The torque measured by means of a strain gauge was displayed on a large galvanometer suspended in front of the subject. The subject was instructed to keep the reading of the galvanometer constant during a recording.

The electromyogram (EMG) from the anterior tibial muscle was recorded with a bipolar electrode, either a "cut-end" or a "side-hole" wire electrode.[13] The cut-end electrode consisted of three twisted 25 µm enamelled stainless steel wires, insulated except for the end of the wire. The pair of wires was chosen that gave the most selective recording.

The side-hole electrode consisted of two twisted 75 µm stainless steel wires. The wires were threaded medio-laterally across the centre of the belly of the muscle. The recording surfaces were 10-25 µm holes burnt into the Teflon insulation of the wires, with the holes about 75 µm apart.

The EMG was amplified by a DISA amplifier (14A30) with pass-band 20 Hz to 10 kHz. EMG and torque were recorded simultaneously on a FM tape recorder with pass-band 0-7 kHz. During playback the force recording was low-pass filtered with an upper limiting frequency of 100 Hz. The EMG was not filtered further.

About 25 recordings one to four min in duration were made in each subject in two or more sessions. From each recording a representative section of 20 s or longer was selected for measurement of interspike intervals. The sections were selected to avoid large shifts in torque and pauses in motor unit firing longer than one second. The occurrence of irregular fluctuations in torque less than 5% was not a criterion either for selecting or rejecting a section. Twenty seconds corresponded to about 200 interspike intervals, and were the shortest recording that gave a sufficiently accurate estimate of the statistical parameters of the interspike intervals.[14]

Table *Maximal Torque at the ankle joint for ankle dorsiflexion*

Subject	*Sex*	*Age*	*Max torque Nm*	*Max torque Normal average* Nm*
MD	♀	16	40	40
MR	♀	17	60	50
SA	♂	24	60	61
AR	♀	51	60	50

*From Asmussen and Heebøll-Nielsen (1961)[15]

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Accepted 1 April 1980

Measurement of interspike intervals

Interspike intervals between action potentials from the same motor unit were measured in recordings containing action potentials from one, two or occasionally three motor units (fig 1). The torque and EMG was played back from the FM-recorder at 1/10 of the recording speed. A microcomputer sampled the signals with a sampling frequency of 2·2 kHz, corresponding to a sampling frequency of 22 kHz at recording speed. A motor unit potential (MUP) was detected when the amplitude of the EMG exceeded a preset value. From each detected MUP the microcomputer measured three features: (1) peak-to-peak amplitude, (2) maximal positive amplitude and (3) integrated numerical amplitude. Discriminant analysis was used to classify each MUP according to the motor unit which generated it. In a simulation experiment[14 16] where superposition potentials were excluded 99% of the undistorted MUPs were classified correctly from the three features.

In recordings from two motor units three to 10% of the potentials are superimposed. Superposition potentials were classified by calculating the probability of their occurrence from the relatively regular intervals between potentials in a motor unit.[14] The time information was also used to reject artefacts or infrequently occurring motor unit potentials as indicated by a downward pulse in the classification trace (fig 1 top trace).

The automatic classification was checked visually against the EMG trace in a paper chart recording (fig 1). To make visual classification reliable the resolution of the paper chart recordings were 1 ms/mm and occasionally 0·4 ms/mm. To show longer sequences of potentials the figures in this paper were recorded at 4 ms/mm. If the automatic classification of a potential differed from the visual classification the automatic classification was changed by typing the corrections on the microcomputer keyboard. The interspike intervals were only used for further statistical analysis, when the operator was convinced that more than 99% of the MUP's were correctly classified. If less than 99% are classified correctly the accuracy of the statistical analysis of variability of intervals and correlation between intervals is compromised.[14 17]

Statistical parameters

The statistical properties of the sequence of intervals from each 20 s recording were described by the mean interval length (MEAN), two measures of the variability of the intervals (FSD and VAR), and a floating serial correlation coefficient (FRHO) which characterises the relation between successive intervals.

A simple measure of variability is the standard deviation of the intervals. This measure is useful when the intervals have a stationary Gaussian distribution. However, a gradual decline in firing frequency is sometimes seen[3 6 18] and the distribution of intervals is often skewed to longer intervals,[3 6 10] and very long intervals "lapses" may occasionally occur.[7] To analyse nonstationary sequences of intervals and to prevent the standard deviation from being dominated by a few very long intervals, two modifications were made in the calculation of the standard deviation.

(1) Intervals exceeding two times the mean interval were omitted from the calculation.

(2) The deviation was calculated relative to a "floating mean interval", calculated from a running square window.

The floating mean interval at interval number i is:

$$\mathrm{FMEAN}_i = \frac{1}{19}\sum_{j=i-9}^{i+9} X_j$$

where X_j is interval number j. The length of the window was 19 intervals, chosen as a compromise

Fig 1 *Action potentials from three different motor units are classified automatically by their (1) peak-to-peak amplitude, (2) maximal positive amplitude, (3) integrated numerical amplitude and (4) expected time of occurrence. The classification is indicated by the height of the pulses in the top trace. Noise and not identifiable potentials are indicated by negative pulses. The third trace is the torque at the ankle and the bottom trace is a time trace.*

A longer window will be less efficient in following trends in the firing frequency, and a shorter window will give the "floating serial correlation coefficient" (FRHO) (see below) a large negative bias. Simulation experiments showed that the bias of FRHO was less than $-0{\cdot}10$ when 19 intervals were used. The "floating standard deviation" was then calculated as

$$\mathrm{FSD}^2 = \frac{1}{N-1}\sum_{i=1}^{N}(X_i\text{-}\mathrm{FMEAN}_i)^2$$

where N is the number of intervals.

Another measure of variability is VAR, as suggested by Prochazka *et al.*[19] VAR measures the variability between successive intervals

$$\mathrm{VAR} = \frac{1}{N-1}\sum_{i=1}^{N-1}\frac{|\,X_i - X_{i+1}\,|}{(X_i + X_{i+1})/2}$$

To compare this measure of variability with FSD, the variation VARI was introduced, defined as the product of VAR and the mean interval

$$\mathrm{VARI} = \mathrm{VAR} \times \mathrm{MEAN}$$

A more detailed characterisation of the relation between successive intervals is provided by the serial correlation coefficient RHO

$$\mathrm{RHO} = \frac{1}{N\text{-}1}\sum_{i=1}^{N-1}(X_i - \mathrm{MEAN})(X_{i+1} - \mathrm{MEAN})/\mathrm{SD}^2$$

A floating serial correlation coefficient FRHO is calculated with the same corrections as made in the calculation of FSD

$$\mathrm{FRHO} = \frac{1}{N-1}\sum_{i=1}^{N-1}\Big[(X_i - \mathrm{FMEAN}_i)\,(X_{i+1} - \mathrm{FMEAN}_{i+1})/\mathrm{FSD}^2\Big]$$

Results

Firing-rates Ninety-seven recordings 20 s or more in duration were obtained from 71 motor units. The variation in torque was less than ± 5%. The mean interval between discharges decreased with increasing torque measured at the ankle (fig 2). The slope of the regression line deviated from zero when all values were pooled ($p < 0{\cdot}001$). In the individual subjects the slope of the regression line was significantly different from zero for MR, AR ($p < 0{\cdot}001$) and MD ($p < 0{\cdot}025$) but not for SA. The shortest mean interval was 49 ms, recorded at 60% of maximal voluntary effort, corresponding to a firing rate of 20 Hz. All mean intervals were shorter than 145 ms with the exception of one mean interval of 163 ms, corresponding to a firing rate of 6 Hz.

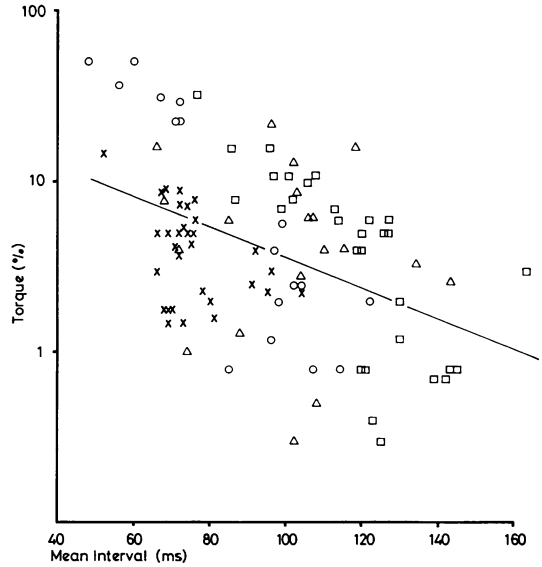

Fig 2 *Relation between torque and mean interspike interval. Ordinate: Torque around the ankle joint as a percentage of the torque exerted at maximal effort (log scale). Abscissa: Mean interval. Ninety-seven recordings from 71 motor units in four subjects: SA△ n=19, MD× n=31, MR□ n=30 and AR○ n=17. n is the number of recordings. Equation of regression line: log (%TORQUE)= —0·0096×MEAN + 1·52 ms.*

Variability The intervals were nearly normally distributed. 93 out of 97 distributions were slightly skewed to longer intervals. This is in agreement with the findings in other muscles: brachial biceps,[20] rectus femoris[3] and first dorsal interosseus muscle.[22] At lower firing rates Kranz and Baumgartner[6] and Derfler and Goldberg[10] found distributions skewed to longer intervals. To obtain a measure of variability also for units with trends in the firing rate or with a few lapses, the variability was described by the floating standard deviation FSD. The values

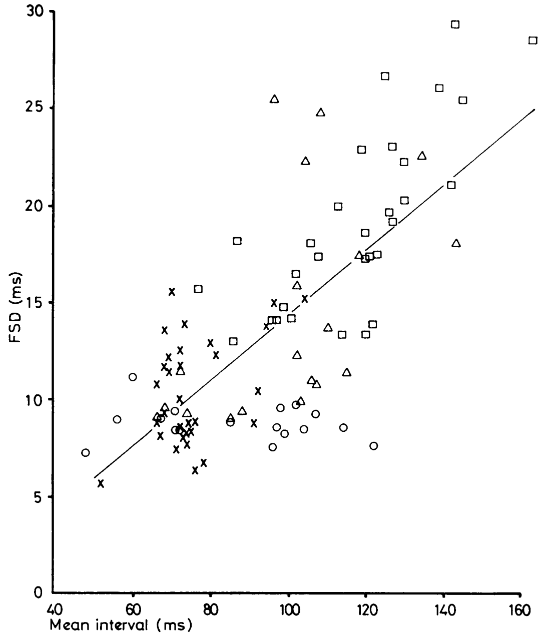

Fig 3 *Floating standard deviation FSD as a function of the mean interspike interval. Ninety-seven recordings from 71 motor units in four subjects: SA△, MD×, MR□, and AR○. Equation of regression line: FSD=0·164× MEAN−1·8 ms.*

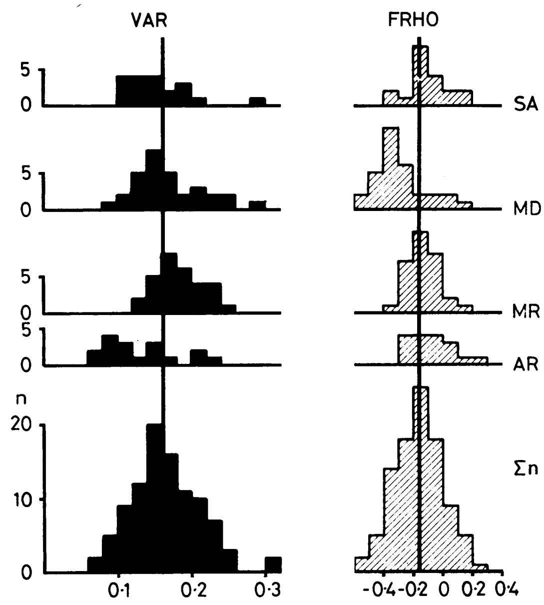

Fig 4 *Histograms for VAR and FRHO for 97 recordings (Σn) from 71 motor units in four subjects. Mean and standard deviation (S) of VAR and FRHO for the n recordings in each normal subject. P is the significance of deviation of the mean from the values for the normal subjects pooled. (NS=not significant).*

Normal		*VAR*			*FRHO*		
subjects	*n*	*mean*	*S*	*P*	*mean*	*S*	*P*
SA	19	0·158	0·046	NS	−0·09	0·13	0·10
MD	31	0·169	0·046	NS	−0·28	0·16	0·001
MR	30	0·184	0·032	0·05	−0·12	0·11	0·25
AR	17	0·130	0·048	0·02	−0·07	0·14	0·10
Σn	97	0·162	0·047		−0·16	0·16	

of FSD increased with the mean interval (fig 3). The variability emphasising short term variations was obtained from VAR (fig 4, left) and VARI (fig 5). Although the distributions of FSD and VARI were quite similar for normal subjects, VAR and VARI were useful when findings in patients were compared with those in normal subjects.[21]

Serial correlation A serial dependence between successive intervals was present in most recordings. Long intervals tended to be followed by short, and short intervals by long (fig 6). This dependence was measured by the serial correlation coefficient. Assuming a Gaussian distribution of the intervals, the axis a and b in a contour ellipse of the joint interval histogram were related to the serial correlation coefficient by[14]:

$$\mathrm{RHO}=\frac{a^2-b^2}{a^2+b^2}$$

The tendency for alternating long and short intervals therefore corresponded to a negative value of RHO. To avoid errors in RHO due to trends in the interval sequences the floating serial correlation coefficient FRHO was used (fig 6). The regression line for FRHO as a function of mean interval showed a moderate increase in FRHO with mean interval (fig. 7). Significantly negative values of FRHO were found even at low firing rates. FRHO ranged from −0·56 to 0·22 and more than half of the values were below −0·14. 0·14 is the 5% significance limit for deviations from FRHO=0 for recordings with 200 intervals.[14] Histograms of FRHO were plotted for each subject in fig 4. The standard deviation of FRHO in the individual subject was smaller than that for all subjects pooled. Hence, although the mean values FRHO for individual subjects differed significantly, all motor units in the muscle of a given subject behaved similarly. The data suggest that the mean value of FRHO increased with age, although the number of subjects was too small to confirm it statistically.

Double discharges In many of the recordings double discharges were observed, the criterion for a

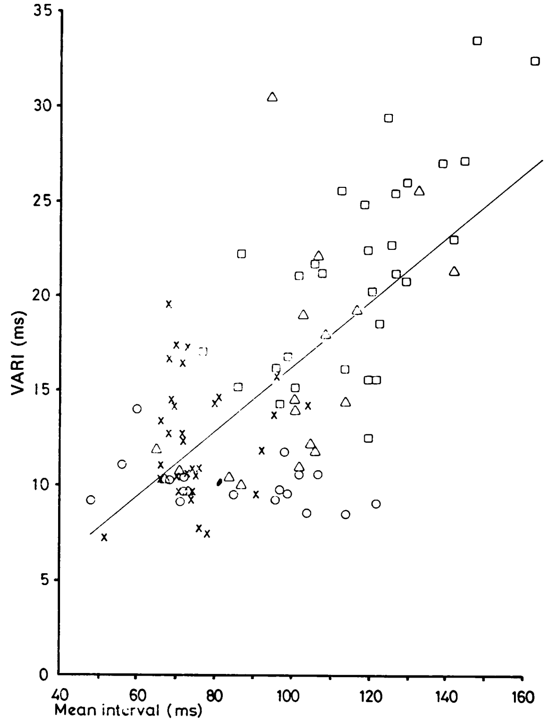

Fig 5 *The variation VARI, defined as VAR×MEAN, as a function of mean interval. Ninety-seven recordings from 71 motor units in four subjects: SA△, MD×, MR□ and AR○ Equation of regression line:* $VARI = 0{\cdot}168 \times MEAN - 0{\cdot}5$ *ms.*

double discharge being that the interspike interval is less than half the mean interval. Double discharges often occurred when a unit was recruited. In fig 8 two units with almost identical recruitment threshold were recruited by slowly increasing the torque. Although the initial instantaneous frequency for both units was 143 Hz, the frequency calculated from the first two intervals was only 11·7 Hz and 12·3 Hz respectively. This is within the range of 5–15 Hz of initial frequencies given by Desmedt and Godaux[11] for single motor units in the anterior tibial muscle recruited during slow increases in torque. Double discharges also occurred during maintained contraction in about 30% of the 20 s recordings. Double discharges often preceded small increases in torque or followed immediately after a small decrease in torque (fig 9).

Double discharges in different units usually did not occur at the same points of time, as exemplified by fig 10, which shows two simultaneously recorded units. Double discharges did not seem to have any preferred interval, and intervals shorter than 10 ms were quite rare.

Discussion

Firing rates of most human muscles during constant isometric contraction lie within 6–25 Hz (brachial biceps 7–25 Hz,[1,23]; anterior tibialis 7–25 Hz[1]; first dorsal interosseus, flexor digitorum profundus and extensor digitorum indicis 5–20 Hz[6]) except for the hand muscles where firing rates up to 35 Hz have been reported.[5] The mechanism responsible for the limitation of firing rate is still unknown. Recurrent inhibition has been suggested to regulate firing rate.[24] However, the firing rate is limited in the masseter muscle although no recurrent collaterals have been identified.[10] After-hyperpolarisation (AHP) of the motor neuron has also been suggested to regulate the firing rate. The time course of the AHP is related to the minimal firing frequency of a motor neuron,[25] but not to the maximal firing frequency. Experiments with intracellular current injection into motor neurons showed a linear relation between firing rate and injected current.[26,27] The firing rate increased proportional to the injected current from the minimal firing frequency to a frequency well above the frequencies found during voluntary contraction (the primary firing range). The limitation of firing rate can therefore not readily be explained by the membrane properties of the motor neuron. Disturbance of the peripheral feedback from the muscle can eliminate the limitation of the firing rate.[28] Marsden *et al* blocked the ulnar nerve by applying xylocaine. This left the adductor pollicis muscle without both efferent and afferent innervation except for a few aberrant motor axons that followed the median nerve and crossed to the ulnar nerve in the forearm distal to the nerve block. These few motor units fired at rates up to 150 Hz and could for several seconds maintain discharge rates of 50 Hz. A discharge rate of 50 Hz is higher than discharge rates found during sustained voluntary contractions under normal conditions.

The temporal summation of AHP can account for other characteristics of the firing pattern, for example, the negative serial correlation, the variability of interspike intervals and the occurrence of double discharges. Due to the summation of AHP, the motor neuron has a high dynamic sensitivity, that is, a higher sensitivity to rapid fluctuations in synaptic input than to static changes in the level of synaptic input. When, for example, the synaptic excitatory drive is increased a motor neuron responds with an "overshoot" in firing rate. As the AHP builds up during the next few discharges the discharge rate drops to the static level. This dynamic sensitivity amplifies the synaptic noise and thereby contributes to the variability in the interspike

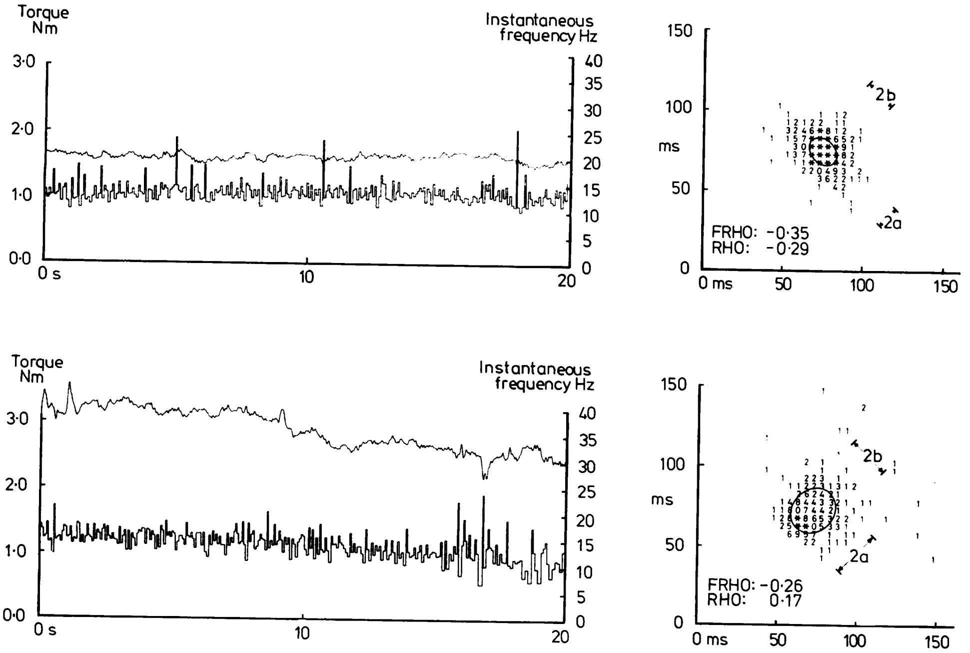

Fig 6 *Left: Torque and instantaneous frequency as a function of time. Above: The torque was kept within±5%. Below: The torque and instantaneous frequency decreased. Right: Joint interval histograms for the recordings shown to the left. Above: The axis* $a=2SD\sqrt{1+RHO}$ *of the contour ellipse is smaller than the axis* $b=2SD\sqrt{1-RHO}$ *corresponding to a negative serial correlation coefficient RHO* ($a=7$ *ms;* $b=10$ *ms). Below: a axis is longer than b due to the decrease in instantaneous frequency and RHO is positive* ($a=16$ *ms;* $b=13$ *ms). The floating serial correlation coefficient FRHO calculated relative to a floating mean interval is negative for both recordings and reflects the interval pattern when long and short intervals alternate. Normal subject MD.*

intervals. In this context the double discharges and the lapses can be considered to be responses to maybe only moderate fluctuations in synaptic input. The behaviour of neuron models with temporal summation of AHP can be made to resemble the behaviour of cat motor neurons when tested with steps of injected current.[29–30] Such neuron models can be made to produce double discharges in response to a current step.

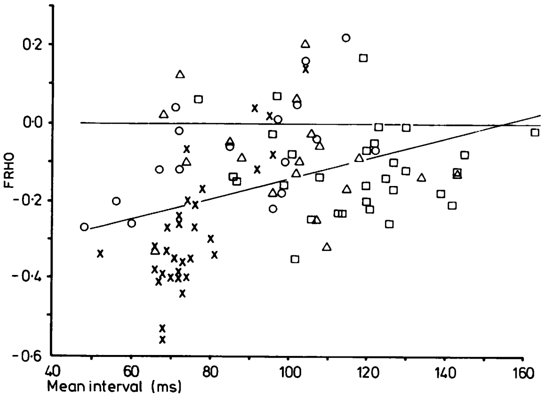

Fig 7 *Floating serial correlation coefficient FRHO as a function of mean interval. Ninety-seven recordings from 71 motor units in four subjects: SA△, MD×, MR□ and AR○ Equation of regression line:* $FRHO=0{\cdot}0026\times MEAN-0{\cdot}4$ *ms.*

The temporal summation of AHP is apt to cause short and long intervals to alternate, i.e., to produce a negative serial correlation between interspike intervals. The large AHP following a short interspike interval delays the next discharge until most of the AHP has decayed thereby producing a long interval.[3 6 10] Elble and Randall[31] give a different interpretation for the negative correlation associated with 8–12 Hz tremor: they suggest the negative correlation to be due to recurrent Renshaw inhibition. Recurrent inhibition and AHP produce effects with approximately the same time course and any effect that the AHP may have on the variability of interspike intervals, double discharges and serial correlation can equally well be ascribed to recurrent inhibition. The finding of negative serial correlation in the masseter muscle, where no recurrent collaterals have been identified[10] makes

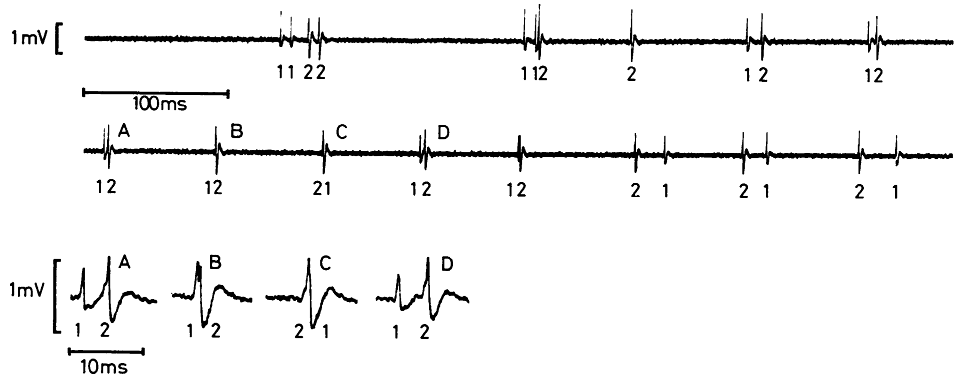

Fig 8 *Two motor units with initial double discharges recruited during slowly increasing torque. The first four intervals of motor unit 1 are: 7 ms, 164 ms, 8 ms and 148 ms and for motor unit 2: 7 ms, 155 ms, 65 ms and 91 ms. Both motor units stabilise with intervals around 80 ms after 5 discharges. All potentials were identified by their shape from recordings at 5 times faster time scale as exemplified in the lower trace (ABCD)*

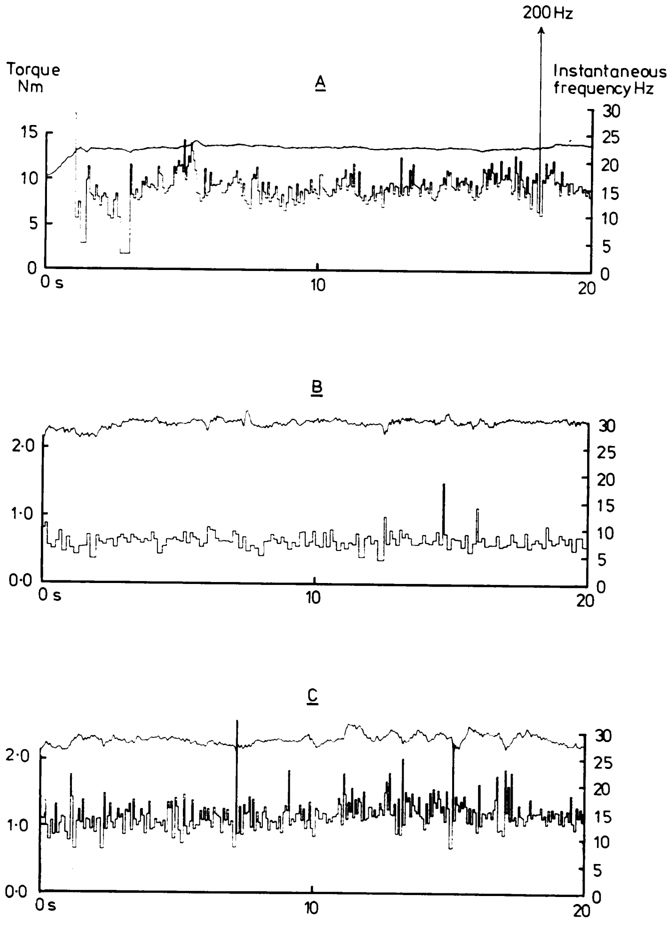

Fig 9 *(A) Recording with an initial double discharge, a lapse at 3 s and a 5 ms double discharge at 18 s. 5 ms is the shortest interspike interval observed in the material. Subject: AR. (B) Double discharge at 15 s immediately preceding a small increase in torque. Subject: MR. (C) Double discharge at 7·8 s immediately following a small decrease in torque. The short interval at 15·5 s also follows a drop in torque. Subject: MD.*

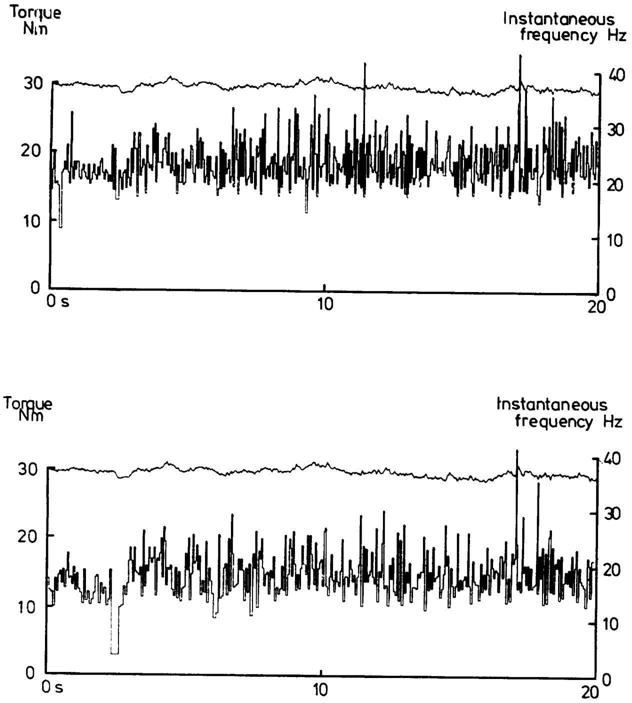

Fig 10 *Simultaneous recording from two motor units. Double discharges occur simultaneously in both units at 17 s just preceding a small increase in torque. The lapse at 0·5 s and the double discharge at 11·4 s in the upper unit occur independently of the lapse at 2·5 s and the double discharge at 17·8 s in the lower unit.*

it unlikely that negative correlation is mainly due to recurrent inhibition. The point raised by Elble and Randall's suggestion[31] is that any reflex effect on the motor neuron pool with an appropriate time course affects the firing pattern. Taking the serial correlation as an example, feedback from Ia and Ib afferents produces negative correlation. A short interspike interval increases the muscle contraction and, allowing time for neural conduction delay and excitation-contraction coupling, Ia disfacilitation and Ib inhibition reaches the motor neuron pool 50–100 ms later. This timing is appropriate to increase the next interspike interval.

A number of phenomena, AHP, recurrent inhibition, Ia and Ib feedback, of unknown relative importance may affect the pattern of discharge of the motoneuron in about the same way. The functional value of these effects lies in the increased dynamic sensitivity of the motor neuron pool. The motor neuron pool thereby enhances the higher frequencies in the synaptic input which partially compensates for the pronounced low-pass characteristics of muscle. The cat soleus muscle for example has a frequency response corresponding approximately to a second order low-pass filter with a characteristic frequency ranging from 2–8 Hz.[32] In recordings from cat hindlimb flexors and extensors during walking double discharges are found in most motor units.[33 34] Double discharges increase the tension[35] as well as the rate of rise in force[36] beyond what can be expected from a linear model of muscle behaviour.

AHP, recurrent inhibition and peripheral feedback thus play an important role in producing a discharge pattern of motor neurons that is tuned to optimise muscle performance. Both in normal subjects[31 37] and in for example Parkinsonian patients the presence of tremor causes substantial changes in the discharge pattern of single motor units. The sensitivity of tremor to changes in peripheral feedback[38 39] suggests that peripheral feedback may have a relatively important effect on the discharge pattern. The findings in spastic patients[?1] with partial paralysis due to cerebral or cerebellar haemorrhage supports this idea. In these patients the firing rate is reduced, double discharges are rarely found, variability of interspike intervals is reduced and the serial correlation coefficients are close to zero or positive.

This study was supported by the Danish Medical Research Council and the Danish Council for Scientific and Industrial Research. We thank Professor F. Buchthal for helpful criticism during

the work and in the preparation of the manuscript. The work was initiated at the Institute of Neurophysiology, University of Copenhagen and at the Electronics Institute, Technical University of Denmark.

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