

Motoneurone Properties and Motor Fatigue

An Intracellular Study of Gastrocnemius Motoneurons of the Cat

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Summary. Gastrocnemius motoneurons with different types of muscle unit were compared with respect to their repetitive discharges during 4 min periods of steady intracellular stimulation. The cells were activated by a constant injected current of 5 nA above threshold. Among neurones capable of discharging for 10 s or more, the discharge duration showed no significant correlation to the contraction time or amplitude of the muscle unit twitch. Neither was there any obvious correlation between discharge duration and the sensitivity to contractile fatigue. The slow drop in discharge rate, as measured from the 2nd to the 26th s of firing, was more pronounced for fast-twitch units than for the ones with a slower twitch. Among fast-twitch neurones with about the same initial discharge rate, no difference in the extent of slow frequency drop was found between cells with fatigue-resistant and fatigue-sensitive muscle units. For fast-twitch neurones, measurements and calculations showed that, if the effects of peripheral potentiation and fatigue were disregarded, the drop in firing rate was great enough to cause a decrease in force by more than 60% during the first minute of constant stimulation. Among the fast-twitch units studied, the mean recorded fall in contractile force was initially less than expected (potentiation dominating) and it had become about equal to the expected one at 1 min after the onset of the discharge. It is concluded that, particularly with respect to fast-twitch motoneurons, the late adaptation is likely to be a significant factor for the development of central "fatigue" in voluntary or reflex contractions. Thanks to their small amount of late adaptation, slow-twitch motoneurons are par-

ticularly suitable for producing a steady postural contraction.

Key words: Spinal motoneurone – Repetitive firing – Late adaptation – Muscle unit type – Fatigue

Introduction

Most skeletal muscles contain a mixture of fibres which may differ markedly from each other with respect to their resistance to contractile fatigue. For one of the best-known mammalian muscles, m.gastrocnemius of the cat, it has been estimated that about 40–45% of its motoneurons have fast-twitch muscle fibres that are highly sensitive to fatigue (type FF), about 25–30% have fast-twitch fibres that are relatively fatigue-resistant (type FR) and about 25–30% have slow-twitch fibres that are very resistant to fatigue (type S; Burke et al. 1973). Long-lasting postural contractions are probably predominantly produced by the S units, whereas FF units seem to be used mainly in connexion with brief episodes of very intense motor activity, such as jumping. The FR units are presumably mobilized, together with the S units, in common movements of moderate strength (see Burke 1979, for a review of experimental evidence). To what an extent are the rhythmic properties of the respective motoneurons adapted to their different roles in motor behaviour? Are S motoneurons in any sense more suitable than FF or FR motoneurons for the production of steady contractions? Are FF motoneurons at all capable of sustained firing? These questions have, so far, not been subjected to much experimental investigation. The accommodation to slowly rising currents has been found to be more pronounced among many of the motoneurons with a brief after-hyperpolariza-

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tion (Sasaki and Otani 1961) and a brief twitch (Burke and Nelson 1971) than among those for which the afterpotential and twitch were more long-lasting. It is, however, as yet uncertain what such differences mean in terms of repetitive firing properties. In studies of the rhythmic properties of motoneurons, repetitive impulse discharges are commonly evoked by maintained currents injected through an intracellular microelectrode. In the investigation by Mischevich (1969), hindlimb motoneurons were activated by such steady injected currents. Repetitive impulse discharges could then be maintained for at least 1 s in all slow-twitch cells, but not in all of the neurones whose muscle unit had a twitch contraction time of < 35 ms (fast-twitch units). The interpretation of these findings is, however, complicated by the fact that phasic response properties may arise as a consequence of damage inflicted by the penetrating microelectrode (Kernell 1965a; Schwindt 1973). In a recent study, it has been shown that even FF motoneurons may be capable of continuous impulse firing during several seconds of steady stimulation (Kernell 1979). Thus, phasic discharge properties are at least not consistently present in motoneurons innervating fatiguable muscle fibres.

In a preceding paper we have demonstrated that there is generally an evident fall in firing rate during the first 30–60 s of a motoneuronal discharge that is evoked by constant stimulation ("late adaptation"; Kernell and Monster 1982). In the present paper we will analyze whether motoneurons with different types of muscle unit differ from each other with respect to the extent of their late adaptation.

Methods

The results were from the same experiments as those of our preceding paper (Kernell and Monster 1982), where several of the techniques are described in detail. Cats were anaesthetized with pentobarbitone, and motoneurons of *m.gastrocnemius medialis* (GM) were penetrated with single-barrelled glass microelectrodes filled with potassium citrate. All other hindlimb muscles were denervated. Femur and tibia were rigidly fixed, and the tendon of the GM muscle was attached to a sensitive isometric force transducer. The muscle was kept permanently at the optimal length for a twitch of the whole muscle. Passive muscle tension was then usually close to 100 g (cf. Burke et al. 1973). For each motoneurone, the following recordings were made: (i) muscle unit twitch, (ii) antidromic spike (only cells with spikes > 60 mV accepted), (iii) determination of threshold current for rhythmic firing, (iv) stimulation for 4 min (or until cell stopped firing) with constant injected current of suprathreshold intensity (only cells discharging for ≥ 10 s accepted; only discharges elicited by 5 nA above threshold for rhythmic firing considered in the present paper), (v) fatigue test of muscle unit.

The muscle unit twitch was evoked by activating the motoneurone with a 1 ms pulse of injected current. Amplitude and time course of the twitches were measured from averages of ≥ 10

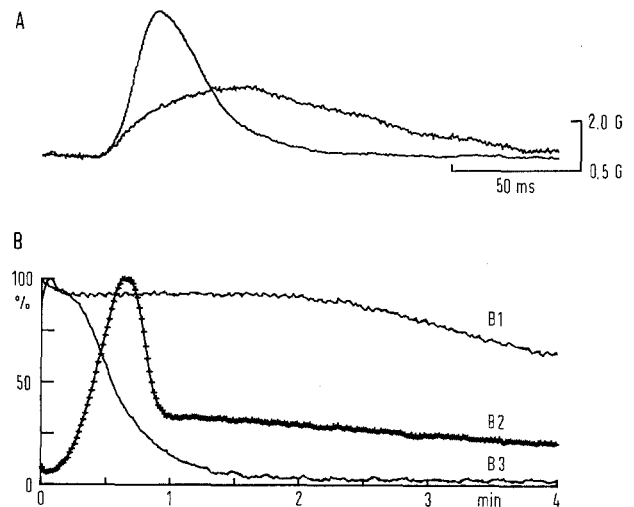


Fig. 1. **A** Twitches of a fast and a slow motor unit drawn superimposed with the same time scale (average of 10 and 23 sweeps respectively). Tension calibration 0.5 g for slow unit and 2 g for fast one. **B** Peak force versus time for series of burst stimuli of three motor units ("fatigue tests"). In each case the muscle unit was activated by a 0.33 s burst at 40 Hz once every second. Neither the fatigue tests, nor the twitches were preceded by any potentiating activity

sweeps (Fig. 1A). These twitches were not preceded by any potentiating activity (cf. Burke et al. 1973; Reinking et al. 1975) and contraction time was measured from the onset of mechanical activity to twitch peak.

Muscle unit fatigue-sensitivity was estimated by methods of Burke et al. (1973), as modified by Kernell et al. (1975). The motoneurone was activated by 1 ms pulses of injected current. Bursts of 40/s stimulation were repeated every second for 4 min. Each burst lasted 0.33 s. Measurements were made of the maximum peak tension produced by any such stimulus burst (T_1) and of the peak tension produced 2 min later (T_2). A standard "fatigue index" was calculated by dividing T_2 by T_1 . As the present fatigue test was not preceded by potentiating activity (cf. Burke et al. 1973), the initial contractions were frequently increasing in size during part of the first minute of the fatigue test (Fig. 1B, curve B2 shows an extreme example; cf. Kernell et al. 1975; Reinking et al. 1975). In a few cases, a small continuous increase in contractile peak force was seen to occur throughout the whole test; the fatigue index was then put equal to 1.0.

Many of the results were analyzed on-line by aid of a digital computer. Furthermore, analog data were also recorded on U.V.-sensitive paper and magnetic tape for later analysis. For further technical details, see Kernell and Monster (1982). Because of lack of relevant muscle unit measurements, some of the GM motoneurons of Kernell and Monster (1982) could not be used for the analysis of the present paper.

Results

Classification of Muscle Units

One of the main aims of the present work was to compare motoneurons of different muscle unit

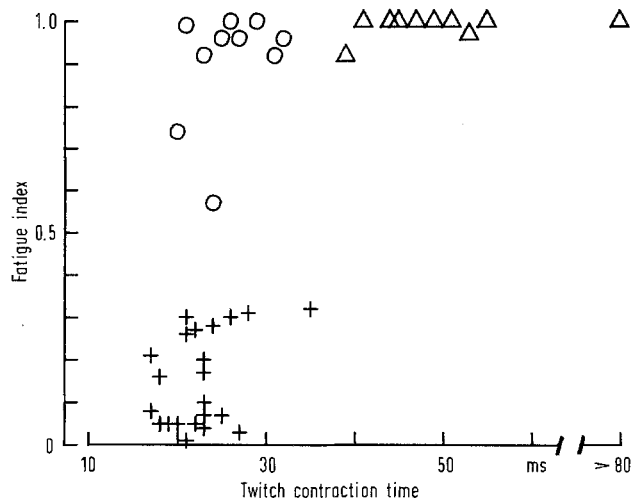


Fig. 2. Fatigue index plotted versus twitch contraction time (ms) for 43 muscle units of *m.gastrocnemius medialis*. Values for fatigue index show the relative amount of peak force remaining at 2 min after the maximum peak force caused by burst stimuli from fatigue tests like those of Fig. 1B. Contraction time measured from onset of mechanical activity to peak force in non-potentiated twitches (cf. Fig. 1A). Separate symbols for “slow-twitch” (S, triangles), “fast-twitch fatigue-resistant” (FR, circles) and “fast-twitch fatigue-sensitive” (FF, crosses) units. Two of the S units had the same coordinates ($x = 44$, $y = 1.0$)

“type” with respect to their late adaptation in repetitive impulse discharges. We determined the type of the muscle units by aid of measurements of (i) the contraction time of a single twitch (Fig. 1A), and (ii) the amount of contractile fatigue during a standardized series of burst stimuli (Fig. 1B). As our experimental procedures were somewhat different from those of several previous investigators, the measurements that we used for muscle unit classification are shown in Fig. 2. For the sake of simplicity, we will refer to all units with a fatigue index greater than 0.5 as “fatigue-resistant” (triangles and circles, Fig. 2). Furthermore, we will refer to units with a twitch contraction time exceeding 35 ms as “slow” (triangles, Fig. 2) and to those with a more rapid twitch as “fast” (crosses and circles, Fig. 2). This dividing value was chosen because all units with a twitch contraction time exceeding 35 ms were also fatigue-resistant (Fig. 2).

Duration of Tonic Firing

All cells of Fig. 3 showed a very well maintained repetitive firing of ≥ 10 s in response to constant stimulation, and this material included motoneurons innervating all the three main types of muscle unit (FF, FR, S; same symbols in Figs. 2 and

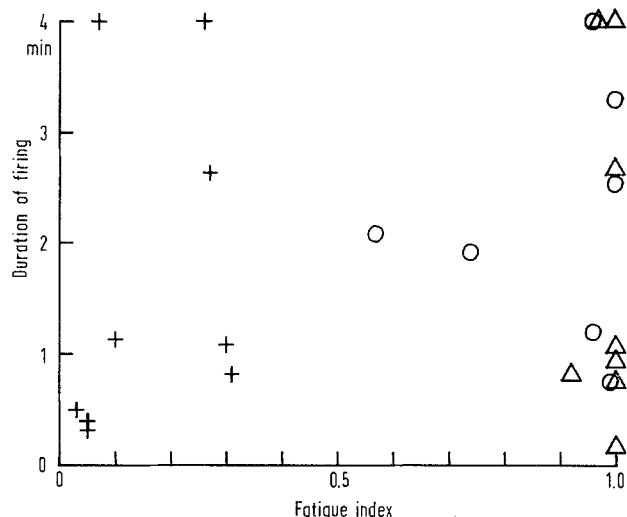


Fig. 3. Maximum duration of firing (min) to constant stimulation plotted versus fatigue index. All neurones stimulated by 5 nA above threshold for rhythmic firing. Fatigue index and symbols for S, FR, and FF units as in Fig. 2. There was not statistically significant correlation between the two plotted parameters ($r = 0.28$, $n = 27$, $P > 0.1$). The same coordinates were obtained for 2 of the FF units ($x = 0.05$, $y = 0.4$), 2 of the FR units ($x = 0.96$, $y = 4.0$) and 2 of the S units ($x = 1.0$, $y = 4.0$)

3). As is evident from Fig. 3, there was no significant correlation between the standard fatigue index and maximum discharge duration in response to steady stimulation (5 nA above threshold in all cases). Even some motoneurons with a very low fatigue index could sustain firing during the whole test period of 4 min. Furthermore, it is evident from Fig. 3 that the discharge durations of slow-twitch (triangles) and fast-twitch (crosses, circles) units were distributed over about the same range. There was no significant correlation between the discharge durations of Fig. 3 and the contraction time ($r = 0.06$, $n = 27$, $P > 0.1$) or amplitude ($r = -0.14$, $n = 27$, $P > 0.1$) of twitches of the respective muscle units.

The standard fatigue index of Figs. 2 and 3 gave a measure of the drop in force during 2 min following the maximum peak tension of a fatigue test (Fig. 1B). This method of calculation was chosen in order to make our data as compatible as possible with those obtained in experiments where a fatigue test was started after the muscle unit had been brought into a state of maximum potentiation (Burke et al. 1973; cf. Kernell et al. 1975). If, however, we would have classified all our units on the basis of an “initial” fatigue index, given by the ratio between the peak forces of the 120th and the first contractions of the fatigue test, then four out of the ten FF units of Fig. 3 would have been characterized as fatigue-resistant (cf. Fig. 1B, curve B2). This change of classification would have included the three FF units for which the

discharge duration exceeded 2 min (Fig. 3). The correlation between "initial" fatigue index and discharge duration was statistically significant ($r = 0.54$, $n = 27$, $P < 0.01$). The interpretation of this result is, however, somewhat complex, because the fatigue resistance of the muscle units was investigated after tests for late adaptation. Maybe some of the most "tonic" FF units of Fig. 3 showed a small initial contraction followed by a huge potentiation (Fig. 1B, curve B2) because they had been fired repetitively during unusually prolonged periods just prior to the fatigue test. A large "initial" fatigue index might then have been caused by the prolonged discharge duration during the test for late adaptation, and the presence of a significant correlation between "initial" fatigue index and discharge duration would then represent a methodological artefact. Further experiments are needed for a resolution of these problems. We also used, however, a third method for calculating a fatigue index: we computed the accumulated tension during 4 min of the fatigue-test stimulation, and we calculated a "cumulative" fatigue index by dividing the summed tensions of min 3–4 by the summed tensions of min 1–2 (cf. Reinking et al. 1975). This could be done for 25 of the 27 units of Fig. 3, including the three FF units with rhythmic discharges of > 2 min. The correlation between discharge duration and "cumulative" fatigue index was not statistically significant ($r = 0.22$, $n = 25$, $P > 0.1$).

Extent of Late Adaptation

As we have shown in our preceding paper (Kernell and Monster 1982), most of the drop in discharge rate that is associated with late adaptation takes place during the first 20–30 s of firing. Furthermore, the extent of the frequency-drop is strongly correlated to the impulse rate at the beginning of the respective discharges (Kernell and Monster 1982). The diagram of Fig. 4 shows this relationship for motoneurons with different types of muscle unit. There was no difference in late adaptation between fast-twitch units with fatigue-sensitive (crosses) and fatigue-resistant (circles) muscle fibres. Very evident differences were found, however, between motoneurons innervating muscle fibres of different contractile speed: slow-twitch units (triangles) typically showed lower initial rates and less adaptation than those of fast-twitch units (crosses and circles, Fig. 4). There was a highly significant correlation between the plotted values for adaptational frequency-drop (cf. Fig. 4) and twitch contraction time ($r = -0.76$, $n = 23$, $P < 0.001$).

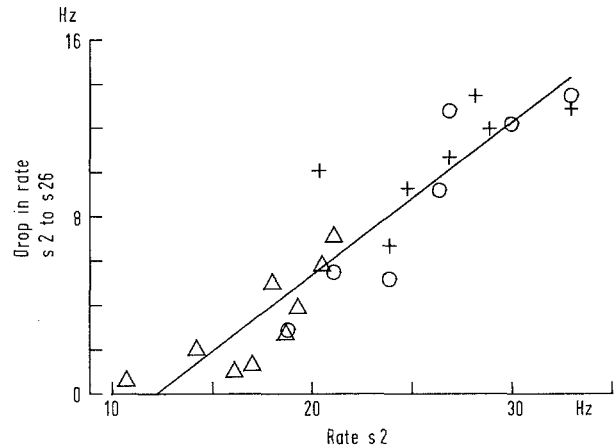


Fig. 4. Drop in discharge rate from 2nd to 26th s of regular firing (Hz) plotted versus rate of 2nd s (Hz) for cells stimulated with 5 nA above threshold for rhythmic firing. Regression line calculated by method of least squares ($r = 0.92$, $n = 23$, $P < 0.001$). Symbols for S, FR, and FF units as in Fig. 2

Contractile Consequences of Late Adaptation

The findings represented in Fig. 4 suggest that, at least at the excitation level studied (5 nA above threshold for repetitive firing), the late adaptation would have a more marked effect on muscle force in fast-twitch than in slow-twitch units. This was confirmed by actual force-recordings, and results from two individual cells are illustrated in Fig. 5. Both these cells were capable of discharging throughout the test period of 4 min. The S unit showed little late adaptation (Fig. 5A) and little force loss (Fig. 5B). The FF unit showed a pronounced drop in rate (Fig. 5A) as well as in mean force (Fig. 5B). With respect to FF units, however, such a drop in force would be expected to result from the combined effects of motoneuronal adaptation and peripheral fatigue. Furthermore, it is obvious from Fig. 5 that, for the FF unit, the time course of the force change is also influenced by peripheral potentiation processes (cf. Kernell et al. 1975): at 5–10 s after onset of stimulation the force even increases while firing rate is decreasing. These complexities in the responses of fast-twitch units have been further analyzed, as illustrated in Fig. 6.

The curve of Fig. 6A shows the mean frequency-time relation for five fast-twitch motoneurons. The "computed" curve of Fig. 6B was calculated from the one of Fig. 6A, using the experimentally determined relation between contractile force and stimulus rate among correspondingly fast gastrocnemius units. The respective force-frequency relations were, in these latter cases, measured from series of relatively brief trains of stimuli; mean force was measured during the

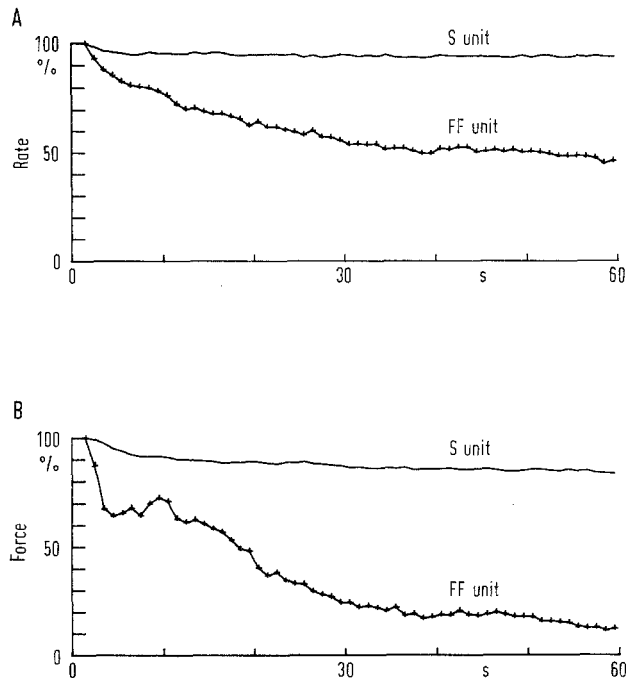


Fig. 5. **A** Plot of firing rate (%) versus time (s) for 1st min of discharges produced by current of 5 nA above threshold for rhythmic firing. For consecutive seconds of discharge, mean firing rates have been connected by straight lines. Firing rates given as percentage of rate during 2nd s of discharge (= first value plotted = 16.1 Hz for the S unit and 28.9 Hz for the FF unit). Twitch contraction time was 53 ms for the S unit and 25 ms for the FF unit. The standard fatigue index was 0.97 for the S unit and 0.07 for the FF unit. **B** Contractile force produced by the discharges in **A**. Force given as percentage of value for 2nd s of discharge. In non-fused contractions, mean force was calculated over time periods of 1 s

last half of constant-frequency trains lasting 1 s (cf. Kernell 1979). Hence, the “computed” curve of Fig. 6B gives an impression of the drop in force that one would expect to result from the decrease in firing rate (Fig. 6A) if no strongly potentiating or fatiguing processes were operating in the muscle units. The mean force actually produced by the units of Fig. 6 was at first greater than expected (potentiation dominating), but became about equal to expectations at the end of the first minute (apparent balance between potentiating and fatiguing processes; cf. “recorded” and “computed” curves of Fig. 6B). Thus, the results of Fig. 6 indicate that, among fast-twitch units, the late adaptation may cause mean muscle tension to drop by more than 60% within the 1st min of constant stimulation. The activation level employed in the experiments of Fig. 6 was relatively low; in the 2nd s of discharge the mean firing rate was 24.5 Hz which, for these fast units, corresponded to a “computed” mean force of only about 12% of the maximum tetanic tension. At somewhat stronger

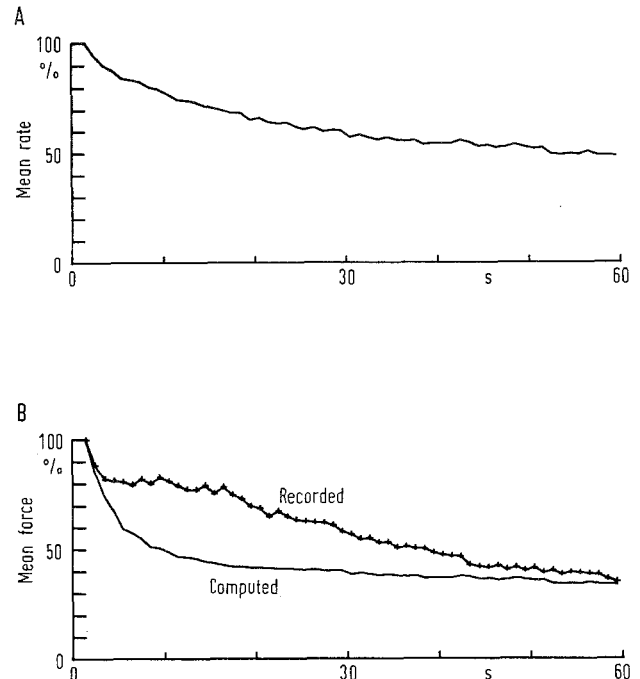


Fig. 6. **A** Plot of mean firing rate (%) versus time (s) for five fast-twitch motoneurons whose contractile responses were recorded during late adaptation. The discharges were produced by constant stimulation at 5 nA above threshold for rhythmic firing, and a regular discharge was in all these cases kept up for at least 60 s. Firing rate expressed as percentage of rate during 2nd s of discharge (= first value plotted = 24.5 Hz). The units had a twitch contraction time of 22–26 ms. **B** “Recorded” curve shows the mean force produced by the discharges of **A**. Before calculating the plotted average values, the force measurements were for each unit expressed as a percentage of the force for the 2nd s of the same discharge. The force values of the “computed” curve were calculated from the firing rates of **A** by aid of the experimentally determined relationship between mean muscle tension and stimulus rate in fast-twitch gastrocnemius units. The force-frequency-curve used for these calculations was an average of measurements from five units from the material of Kernell (1979) and the twitch contraction time of these latter units was 23–26 ms. In non-fused contractions, the mean force has in all individual cases been calculated over time periods of 0.5–1 s

stimulus intensities and higher discharge rates, the force-frequency curve would be steeper and the late adaptation would be more prominent (Kernell and Monster 1982). Thus, still stronger effects than those of Fig. 6 would be expected to occur at higher levels of activation.

The five cells of Fig. 6 comprised four FF units and one FR unit. The force response of the FR unit did not deviate by more than about 5–10% from the average “recorded” curve of Fig. 6B and, in this particular sample, the smallest force loss was actually seen in a unit classified as type FF. It should be noted, however, that the FF/FR classification was based on reactions to test stimuli occurring at sub-

stantially higher rates (40 Hz; Fig. 1B) than the discharges of Fig. 6A (initial mean rate of the curve: 24.5 Hz).

Discussion

The present findings clearly indicate that, thanks to their small amount of late adaptation, slow-twitch motoneurons are more suitable than the fast-twitch cells for producing a steady postural contraction (Figs. 4–6). This is consistent with the well-known fact that slow-twitch muscle units have a high degree of resistance to contractile fatigue (Fig. 2; Burke et al. 1973; Reinking et al. 1975; Kernell et al. 1975). Furthermore, our findings fit well to the classical view (Denny-Brown 1929) that the slow-twitch units of a muscle or muscle group are those preferentially used for long-lasting postural contractions (for a discussion of experimental evidence, see Burke 1979). In voluntary contractions, prolonged steady discharges are easily maintained in slow-twitch units but not in the more rapidly firing fast-twitch ones (Grimby et al. 1979). Our findings show that, in repetitive firing caused by steady stimulation, the amount of late adaptation is strongly dependent on the initial rate of the discharge (Fig. 4; Kernell and Monster 1982). Such a dependence on firing rate is fully in accordance with the view that late adaptation is caused by cumulative after-effects of the discharging spikes (Kernell and Monster 1982). When stimulated by the same amount of suprathreshold current, initial firing rates are lower for slow-twitch gastrocnemius motoneurons than for the fast-twitch cells (Fig. 4). This difference is mainly due to the fact that the minimum firing rate (i.e. the rate obtained just above the threshold for rhythmic firing) is lower in slow-twitch gastrocnemius motoneurons than in fast-twitch cells (Kernell 1979; cf. also Grimby et al. 1979). The minimum firing rate is strongly dependent on the duration of the after-hyperpolarization that follows a soma-dendritic spike (Kernell 1965b). Thus, the comparatively small amount of late adaptation among slow-twitch motoneurons seems mainly to be a consequence of the fact that these cells are equipped with a comparatively long-lasting after-hyperpolarization (Eccles et al. 1958; Burke 1967).

The findings of Figs. 4–6 suggest that late adaptation may be of importance in connexion with phenomena related to "motor fatigue". Even at comparatively low levels of constant activation, late adaptation will lead to a conspicuous drop in the contractile tension of fast-twitch units (Figs. 5 and 6). At higher intensities of stimulation, late adaptation would be still more prominent than the one of Fig. 6

(cf. Kernell and Monster 1982). Thus, even in the absence of peripheral fatigue processes, a steady contractile output of fast-twitch units would only be produced by aid of a progressively increasing excitatory drive of the motoneurone pool. In voluntary contractions, the production of such an increase of motor drive might be associated with an increased sense of effort (McCloskey 1978). In the experiments of Person and Kudina (1972), the impulse activity was recorded simultaneously for several units while a human subject maintained a steady submaximal contraction for ≥ 2 min. During such contractions, there was a slow progressive fall in the discharge rate of all continuously active units (see Figs. 3 and 4 of Person and Kudina 1972). This drop in firing rate might have been partly caused by late adaptation of the motoneurons. The resulting loss of motor unit force was, in these cases, apparently compensated for by the recruitment of more motoneurons (Person and Kudina 1972). Other investigators have shown that, in maximal voluntary contractions, there is a marked decline of discharge rate of the motoneurons during the initial 0.5–1 min (Marsden et al. 1971; Grimby et al. 1981; cf. also Bigland-Ritchie and Lippold 1979). In this case, however, the decline in discharge rate appears to help to optimize force production: due to peripheral fatigue-processes, less total force is produced by a steady high-frequency discharge than by a discharge of decreasing rate (Jones et al. 1979; Grimby et al. 1981). Thus, in very strong maintained contractions, late adaptation of the motoneurons might actually help to counteract undesirable effects of peripheral fatigue. It should be emphasized, however, that the fall in motoneuronal firing rate that occurs during voluntary contractions may well be due to combined effects of late adaptation and changes in the net amount of excitation received by the motoneurons.

It is interesting to note that, for some time, post-activity potentiation of the muscle units will tend to compensate for effects of motoneuronal late adaptation on muscle unit force (Figs. 5 and 6). It has previously been demonstrated that, in non-fused contractions, peripheral potentiation will also temporarily compensate for effects of peripheral fatigue (Kernell et al. 1975). Peripheral post-activity potentiation is typically less noticeable in slow-twitch units than in fast-twitch ones (Bagust et al. 1974; Stephens and Stuart 1975; Kernell et al. 1975; cf., however, Burke et al. 1973). In slow-twitch units this compensatory mechanism would, however, be of little use because these motoneurons have comparatively little late adaptation (Fig. 4) and little peripheral fatigue-sensitivity (Fig. 2; Burke et al. 1973; Reinking et al. 1975; Kernell et al. 1975).

Among cells that were capable of prolonged repetitive firing, no evident relationship was found between maximum discharge duration and muscle unit type (Fig. 3). Maximum discharge duration did not, however, seem to be a very constant property of a motoneurone; depending on the state of an individual cell, its maximum discharge duration may change over a wide range (Kernell 1965a; Kernell and Monster 1982). At least with respect to the briefest maximum discharge durations ("phasic" discharges) there is considerable evidence that such response patterns may arise because of some noxious effect of microelectrode penetration (Kernell 1965a; Schwindt 1973). According to our experience, no type of motoneurone, not even the slow-twitch ones, is immune against this kind of reaction to damage. We used microelectrodes filled with K-citrate. Phasic response patterns have, however, also been commonly encountered in studies employing mainly KCl-filled microelectrodes (Mischelevich 1969; cf. also Schwindt 1973). Furthermore, the presence of a large antidromic spike is no safe guarantee that the capability for maintained repetitive firing has not been deteriorating (see Discussion by Kernell and Sjöholm 1973). Thus, it would be very difficult to prove or disprove the existence of genuinely phasic motoneurons by intracellular techniques. In spite of these difficulties of interpretation, which were also discussed by Mischelevich (1969), it remains very interesting that he found phasic response patterns to occur more often among fast-twitch motoneurons than among the slow-twitch cells. One possible interpretation would be that, in comparison to other motoneurons, fast-twitch cells might tend to be particularly susceptible to damage by microelectrode penetration. Mischelevich (1969) did not measure the fatigue sensitivity of the muscle units; at the time of his investigation, this kind of measurement did not yet belong to the standard procedures for muscle unit classification (cf. Burke et al. 1973). It is, however, of interest to note that the material of Mischelevich (1969) fails to support the hypothesis that fast-twitch motoneurons with fatigue-sensitive muscle fibres (FF) would tend to show phasic responses more often than the fast-twitch cells with fatigue-resistant fibres (FR): on average, FF units are stronger than FR units (Burke et al. 1973) whereas the phasic fast-twitch units of Mischelevich (1969) were no stronger than his tonic ones. Our present observations demonstrate directly that many cells with fatigue-sensitive muscle fibres are capable of discharging continuously for tens of seconds or, in some cases, several minutes in response to constant stimulation (Figs. 3–6). Such a capability for very prolonged firing might, at first sight, seem to be rather inappropriate for a moto-

neurone that is equipped with fatigue-sensitive muscle fibres. However, it should be noted that, at low levels of activity, even FF units may keep up a significant amount of tension during a comparatively long time (Figs. 5 and 6). Furthermore, it is important to bear in mind that the fatigue sensitivity of a muscle or muscle unit is markedly dependent on its long-term use (e.g. Holloszy and Booth 1976). A general capability for tonic firing among motoneurons might be of great importance in connexion with the endurance training of muscle.

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