Motoneurone Properties and Motor Fatigue

An Intracellular Study of Gastrocnemius Motoneurones of the Cat

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Summary. Gastrocnemius motoneurones 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 motoneurones, 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 motoneurones are particularly 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 motoneurones 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 motoneurones adapted to their different roles in motor behaviour? Are S motoneurones in any sense more suitable than FF or FR motoneurones for the production of steady contractions? Are FF motoneurones 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 motoneurones with a brief after-hyperpolariza-
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 motoneurones, repetitive impulse discharges are commonly evoked by maintained currents injected through an intracellular microelectrode. In the investigation by Mischelevich (1969), hindlimb motoneurones 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 motoneurones 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 motoneurones 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 motoneurones with different types of muscle unit differ from each other with respect to the extent of their late adaptation.

Methods

The results were of 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 motoneurones 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 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 (T1) and of the peak tension produced 2 min later (T2). A standard "fatigue index" was calculated by dividing T2 by T1. 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 B1 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 motoneurones 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 motoneurones of different muscle unit

![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]