Eur J Appl Physiol (1989) 58:369-374

European Journal of Applied Physiology and Occupational Physiology

The fatigability of two agonistic muscles in human isometric voluntary submaximal contraction: an EMG study

II. Motor unit firing rate and recruitment

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Summary. The recruitment and firing rate of biceps brachii (BB) and brachioradialis (BR) motor units (MUs) were studied in the course of fatiguing isometric contractions at 20%–30% of maximal voluntary contraction (MVC). MU recruitment generally occurred throughout the maintained contraction and was similar for BB and BR muscles. Newly recruited MUs started to discharge in the form of bursts, the duration of which increased until a continuous rhythmical firing was achieved. Within each burst, the first interval between two consecutive discharges was usually the shortest. MU threshold was lowered just after the limit time of the maintained contraction. The MU's firing rate either increased or remained stable as a function of the elapsed time. It is concluded that (1) in fatiguing isometric contractions at 20%–30% MVC contractile failure is mainly compensated for by MU recruitment and a lowered MU threshold and (2) differences between in surface changes in the electromyogram of BB and BR muscles cannot easily be explained by related differences in MU firing rate and recruitment.

Key words: Fatigue — Motor units — Agonistic muscles — Isometric submaximal contraction

Introduction

The recruitment and firing rate of motor units (MUs) during prolonged fatiguing voluntary effort have been studied mainly for maximal isometric contractions. Under these conditions, the firing rate and the proportion of MUs firing decrease, as does the maximum force than can be exerted (Bigland-Ritchie and Lippold 1979; Grimby et al. 1981). At the same time, there is a slowing of contractile speed, and it has been suggested (Grimby et al. 1981; Bigland-Ritchie and Woods (1984) that the motoneuron firing rate is controlled in such a way as to optimize force generation.

However, one cannot assume that these changes in MU activity also apply to submaximal fatiguing isometric contractions. The MU activity has been poorly documented during this form of exercise. Progressive recruitment of additional MUs is commonly conjectured or observed (Bigland-Ritchie et al. 1986; Moritani et al. 1986; Scherrer and Bourguignon 1979), whereas changes in motoneuron firing rate remain a matter of debate.

In submaximal isometric contractions of short duration we found (Maton 1981) that the motoneuron firing rate may increase, decrease, or remain stable, depending on the level of the maintained force. These results did not agree with the data of Person and Kudina (1972) which showed a continuous decrease in firing rate throughout the maintained contraction, whatever the force. In contrast to this, Bigland-Ritchie et al. (1986) have described a progressive increase in motoneuron firing rate during 50 min submaximal exercise.

The aim of the present investigation was, therefore, to re-examine MU activity during submaximal isometric contraction held until the limit time, in relation to the surface electromyogram (EMG) changes reported in part I of this study (Gamet and Maton 1989).

Materials and methods

The study of MU activity was carried out during the experiments described in part I of this study (Gamet and Maton

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1989). Except for MU recording and analysis, the procedure and techniques were the same.

The MU activity of biceps brachii (BB) and brachioradialis (BR) muscles was recorded simultaneously by means of wire electrodes similar to those described earlier (Maton 1977). One selective bipolar electrode was inserted into each muscle through a hypodermic needle, which was then removed, following the method proposed by Inman et al. (1952). No attempt was made to keep the depth and location of the electrode constant from one experiment to another. The depth of the electrode was determined by acquisition of a single MU.

Amplifiers of linear bandwith between 10 Hz and 10 kHz and an input resistance of 100 MΩ were used. The MU spikes were selected using an analogue window-trigger and were counted according to two triggering levels for determining the firing rate of a single MU or the density of spikes per second including all the recorded MUs. As in part I of this study (Gamet and Maton 1989), these measurements were made during a series of 9-s consecutive periods of maintained contractions. In order to determine the MU recruitment threshold, the subject was required to perform a torque ramp with a slope of 4 $N \cdot m \cdot s^{-1}$, just before, and immediately after, the maintained contraction. The recruitment threshold was assessed in the usual way (Milner-Brown et al. 1973; Desmedt and Godaux 1977; Freund 1983), by measurement of the external torque level, at the onset of firing.

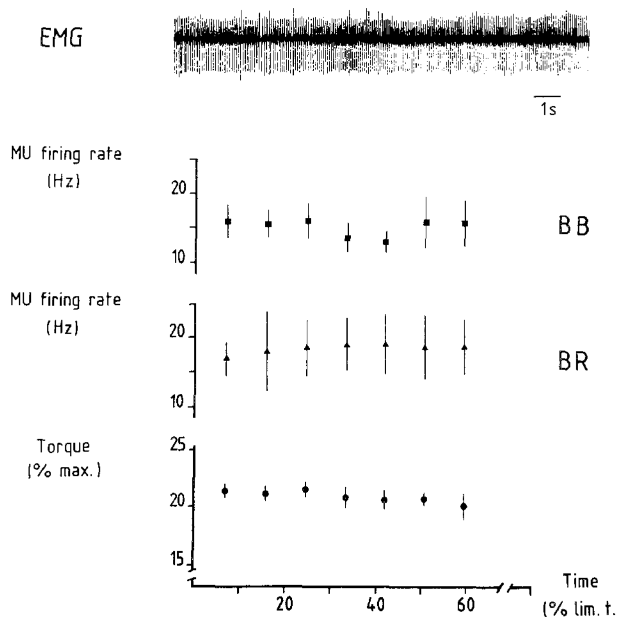

Fig. 1. Firing rates of biceps brachii *(BB)* and brachioradialis *(BR)* continuously firing motor units (MUs) and external torque, in relation to the duration of maintained contractions. An example of MU recording (EMG) is inserted at the top of the figure. Each *point* represents the mean value of the instantaneous firing rate, or of the torque, over a period of 9 s. The *vertical lines* above and below each point indicate the corresponding standard deviations

Results

Firing rate of motoneurons during fatigue

Two types of MU activity were observed in both BB and BR intramuscular recordings during the maintained contraction: either continuous discharge of the motoneuron, or an intermittent series of discharges, referred to here as bursting activity.

The mean discharge frequency of continuously firing MUs of both BB and BR muscles was between 12 Hz and 19 Hz. Regardless of the muscle, the discharge frequency of these MUs, already firing from the very beginning of the maintained contraction, either slightly increased or remained stable at least to 60%-70% of the limit time, as illustrated in Fig. 1.

Beyond the limit time, we were never able to follow unambiguously the activity of a single MU because of the recruitment of other neighbouring MUs with action potentials of similar shape. Bursting motoneurons started to discharge at different times after the beginning of the maintained contractions. For a single MU the occurrence and duration of the burst increased progressively, leading finally to continuous firing (Fig. 2).

Within each burst of an MU, the first interval of discharge was the shortest, as shown in Fig. 3. Double discharges at the onset of motoneuron activity are also known to occur during isometric anisotonic contraction as well as during anisometric anisotonic contraction (Gurfinkel et al. 1972; Maton and Bouisset 1975; Zajac 1981) or in H reflex activation (Eccles and Hoff 1932; Hoff and Grant 1944), in the absence of fatigue. Thus, it can be suggested that the double discharges observed under the present conditions corresponded to force and perhaps length oscillations.

Motor unit recruitment during fatigue

In an attempt to assess MU recruitment, the spike frequency in each intramuscular EMG was measured. Spike frequency of BB and BR recordings changed in a similar way as a function of time. As shown by a Student's *t*-test, the spike frequency was greater at the end of the maintained contraction in 8 out of 15 experiments ($p \leq 0.01$). A typical set of data is shown in Fig. 4. However, the spike frequency remained stable in five maintained contractions and significantly decreased ($p \leq 0.05$) in the two remaining contractions. In the case of increasing spike frequency, the mean increase was 61.8% of the initial mean spike frequency, whereas in the two cases of decreasing spike frequency, the mean decrease was 23.4%.

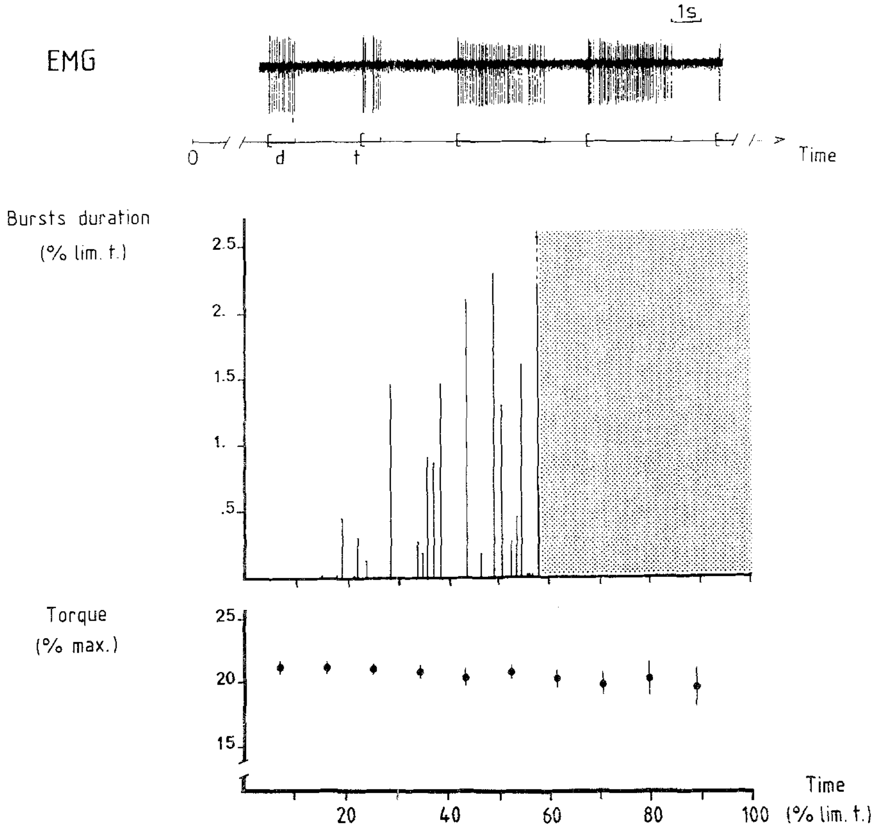

Fig. 2. Activity from a bursting type of MU from the beginning to the end of a fatiguing maintained contraction. An example of MU bursting activity (EMG) is inserted at the top of the figure. *Horizontal bars* under the bursts indicate how the duration (*d*) and time of onset of the burst (*t*) were measured. The limit of a burst was arbitrarily determined as the time at which an inter-spike interval was five times greater than the preceding interval. The *stippled bar* indicates that bursting activity had changed to continuous firing activity. Burst duration was expressed in per cent of the limit time

However, in the interpretation of these data it should be borne in mind that the mean torque value was usually slightly lower just before the limit time, due to the difficulty of sustaining the initial torque, because of tremor and fatigue, at the end of the maintained contraction. Since there was no clear change in MU firing rate, these results provide some evidence for recruitment of additional MUs in most maintained contractions.

The significance of spike frequency in terms

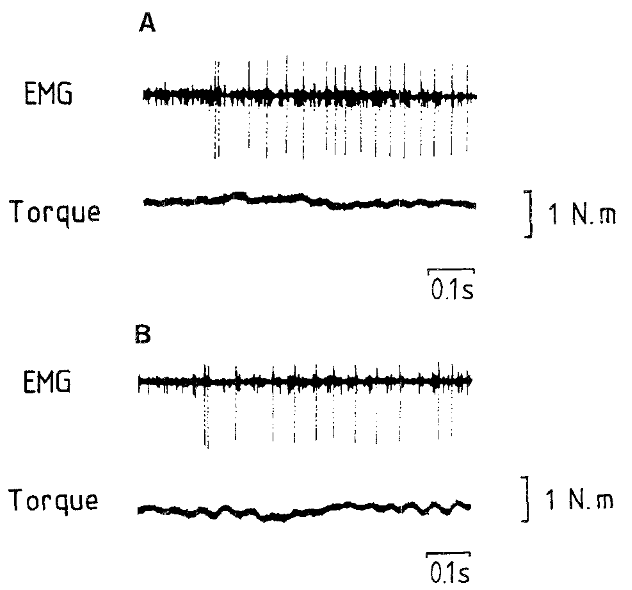

Fig. 3. Details of the MU activity within two bursts (**A** and **B**), showing the initial doublet of discharges

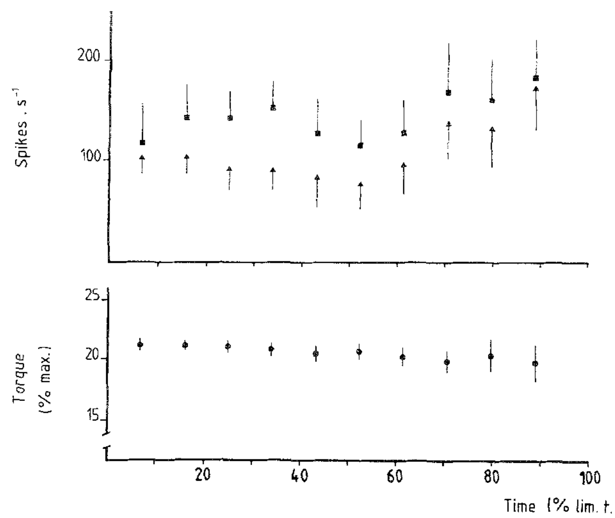

Fig. 4. Spike frequency from BB (■) and BR (▲) intramuscular recordings as a function of time. Each *point* indicates the mean spike frequency or torque value, over a period of 9 s. *Vertical lines* correspond to standard deviations. The same subject, and the same experiment as for the preceding figures

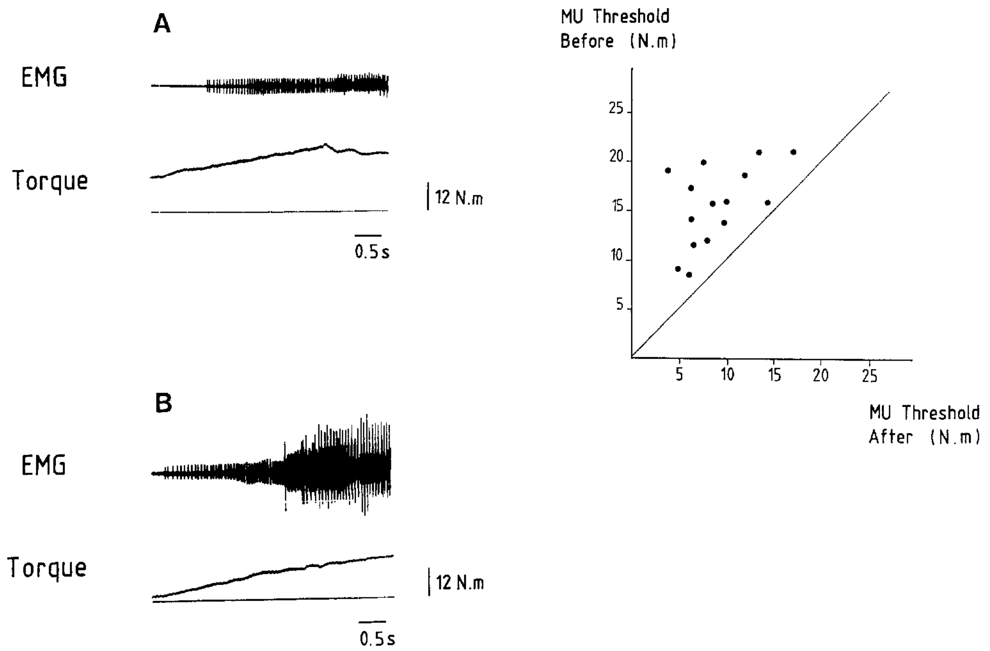

Fig. 5. MU threshold before and after fatigue. *A and B* MU during a torque ramp recording before and after the fatiguing maintained contraction respectively. The correlation diagram of MU threshold before and after fatigue is represented on the right of the figure. Note that all experimental points are distributed above the line of unit slope

of MU recruitment may depend on the location and selectivity of the electrodes. It follows that this measurement is in no way an absolute quantification of the number of the additional MUs recruited.

Motor unit threshold change due to fatigue

The recruitment threshold torque for BB and BR MUs was measured during identical ramps of force performed just before and just after the fatiguing maintained contractions. A significant decrease of threshold after fatigue was noted in all cases, as can be seen from the two records, and from the diagram of the correlation between pre- and post-fatigue threshold values (Fig. 5).

Discussion

Motoneuron firing frequency and recruitment

The discharge properties of motoneurons during fatiguing submaximal voluntary contraction are poorly documented because of technical difficulties. Indeed, monitoring by any recording technique of the activity of a single MU throughout a maintained contraction is problematical, due to the difficulty of unambiguous selection of the action potential of this MU up to the limit time. In the present study, wire eletrodes allowed analysis of the firing rate of single motoneurons up to at least 60%–70% of the limit time.

The firing rates of continuously firing motoneurons remained stable, or did not substantially increase, whereas the number of active motoneurons significantly increased from the beginning to the end of the maintained contraction. Thus, in fatiguing contractions, BB and BR muscle at 20%–30% maximal voluntary contractions (MVC), contractile failure was only compensated for by recruitment of additional motoneurons, and not by rate coding of the motoneurons already active at the beginning of the maintained contraction. This agrees with, and extends, our previous findings (Maton 1981) obtained for shorter periods of maintained contraction.

Once recruited during the maintained contraction single motoneurons discharged intermittently for increasing periods of time until they reached a steady state, or fired continuously; i.e. motoneurons began to discharge phasically before discharging tonically. This pattern of recruitment mirrored the inactivation of motoneurons during the sustained maximal contraction described by Grimby et al. (1981). An attractive hypothesis would be that this process of activation/inactivation of motoneurons during fatigue is a general rule, although more data are required to confirm this hypothesis.

When we focused on the intermittent or bursting activity of motoneurons recruited during the maintained contraction, it was apparent that the first interval between the discharges was the shortest of the burst. This pattern of discharge generates a faster and larger development of tension than a regular firing rate (Zajac 1981). In this way, newly recruited MUs could develop a significant amount of force, despite intermittent activity. The possibility of a connection between these double discharges and the tremor cannot be excluded. Unfortunately, we cannot infer from the present data whether or not these doublets reinforced, or resulted from, tremor oscillations.

Immediately after the limit time, MUs can be voluntarily recruited with a torque threshold lower than before the maintained contraction. It can be speculated that the loss of tension, due to contractile failure of fatigued MUs may release the motoneurons from part of the Ib inhibitory disynaptic influence from Golgi tendon organs. An alternative or complementary explanation could be that the gain is lowered under supraspinal influences. Some evidence for this mechanism has been recently provided by Kirsch and Rymer (1987). However, these authors stressed that changes in spindle, and even free nerve ending, activity are also likely to play an important role in compensation for fatigue.

Motor unit activity and surface EMG

In our study of surface EMG changes in fatiguing submaximal isometric contraction [part I of this study (Gamet and Maton 1989)], we found that the integrated electromyogram (IEMG) increased while EMG-MPF (mean power frequency) decreased. These changes are usually attributed to both the recruitment of additional MUs and to the increase in firing rate of already active MUs (Edwards and Lippold 1956; Lind and Petrofsky 1979; Scherrer and Bourguignon 1979).

Slowing of muscle fibre conduction velocity is also of importance (Lindström et al. 1970). Indeed, because of muscle tissue low-pass filtering effects, MU action potentials are more readily transmitted to the skin. The present MU study demonstrates that during 20%–30% MVC sustained elbow flexor contraction, IEMG increases did not result from increases in MU firing rate, at least until 60%–70% of the limit time, while the EMG-MPF study [part I of the study (Gamet and Maton 1989)] suggests that the IEMG increase due to MU recruitment is enhanced by slowing of muscle fibre conduction velocity. This is partly in accordance with the findings of Bigland-Ritchie et al. (1986), who showed that during 50% MVC isometric contraction of the quadriceps muscle, with brief MVCs performed at a rate of about 1/min, there was a fourfold increase in IEMG, and only a 30%–80% increase in MU firing rate. Nevertheless, in contrast to our data, these authors described a significant increase in MU firing rate. It therefore seems likely that the mechanisms responsible for surface EMG changes in fatigue of submaximal isometric contraction may vary with the type of exercise or/and the type of muscle.

In part I of this study (Gamet and Maton 1989), we also emphasized that surface EMG changes, due to fatigue, are dependent on the existence and magnitude of tremor. Elble and Randall (1976) established that the 8–12 Hz component of finger tremor is caused by synchronous MUs firing at 8–12 Hz, as suggested by Lippold et al. (1957), and also by the activity of MUs firing at a higher frequency of discharge. In the present experiments, we did not examine this aspect of MU activity, but it should be noted that the firing frequency range of all the BB and BR recorded MUs was within the range of the tremor frequency. Moreover, experiments on arm and leg muscles (Hogan and Mann 1980; Lago and Jones 1981; Verroust et al. 1981) and on facial muscles (Van Boxtel and Shomaker 1984), as well as mathematical models of surface EMG-PSDF (power spectrum density function) (Blinowska et al. 1980; De Luca 1985), have shown that a distinct maximum, at the dominant firing rate of the MUs, can be observed in the EMG power spectrum. The amplitude of the peak of this firing rate depends, among other factors, on the homogeneity of firing rate of different MUs and is amplified by the existence of double discharges. It was found here that BB and BR MUs were firing at a similar mean frequency and that double discharges also occurred. We conclude that under the present conditions of maintained contraction, the so called "tremor peak" in the surface EMG spectrum was also the peak for the dominant firing rate of the MU.

However, the differences between BB and BR surface EMG changes reported in part I of this study (Gamet and Maton 1989) can not be explained on the basis of MU firing rate and recruitment. The more important changes of BR EMG may be due largely to a greater slowing of muscle fibre conduction velocity, or to a higher degree of synchronization between MUs. Alternatively, they may have resulted from differences in muscle tissue conductivity or representation of the surface EMG with regard to the recruitment of additional MUs.

Acknowledgements. This study was supported by grants from the DGRST and from UER Pitié-Salpêtrière, Paris.

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Accepted September 15, 1988