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POST-TETANIC EFFECTS IN MOTOR UNITS OF FAST AND SLOW TWITCH MUSCLE OF THE CAT

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SUMMARY

1. Motor unit twitches were examined in cat flexor digitorum longus (fast twitch) and soleus (slow twitch) muscles. The time course of the effects of a standard tetanus on the peak twitch tension was plotted and the maximal potentiation or depression (the post-tetanic ratio) was measured.

2. The post-tetanic ratio decreased continuously as the twitch time to peak of motor units increased; motor units from flexor digitorum longus and soleus could be described as a single population. The closest approximation to a linear relationship was found by plotting post-tetanic ratio against the reciprocal of time to peak.

3. The post-tetanic ratio was also related to the ratio of tetanic to twitch tension. The time of maximum potentiation or depression occurred between 1 and 11 sec, but this variable was unrelated to the time to peak or any other characteristic of the motor unit.

INTRODUCTION

The twitch response of a muscle is modified by a preceding tetanus. In the mammal the nature of the effect depends on the type of muscle: fast-twitch muscle is potentiated following a tetanus but slow-twitch muscle is depressed (e.g. Brown & von Euler, 1938). Motor units show a much greater range of twitch times than do the parent muscles and there is overlap between the slowest motor units of a fast muscle and the fastest motor units of a slow muscle (McPhedran, Weurker & Henneman, 1965; Weurker, McPhedran & Henneman, 1965). We have attempted to discover whether all motor units within one muscle type show the same response to a tetanus or whether the post-tetanic effect is related to the twitch time of the motor unit. Flexor digitorum longus and soleus were used as the fast and slow

muscles. Flexor digitorum longus was referred to as flexor hallucis longus in a preliminary report (Bagust, Lewis & Luck, 1971).

<div style="text-align:center">METHODS</div>

Young adult cats weighing between 1·75 and 3·0 kg were anaesthetized with an initial dose of pentobarbitone sodium (40 mg/kg injected i.p.) and anaesthesia was maintained with subsequent i.v. injections. Either flexor digitorum longus (twelve cats) or soleus muscle (four cats) was prepared for isometric recording. Details of the recording techniques and of the functional isolation of motor units by splitting ventral roots have been described by Bagust, Knott, Lewis, Luck & Westerman (1973) and Bagust (1974). The motor units described generally in these two papers make up the majority of motor units used to obtain the present results. In most experiments the muscle length was adjusted to give the maximum motor unit twitch tension. In one experiment (fifteen motor units) all motor units were examined at the length at which the whole muscle response was maximal. Each motor unit was stimulated regularly once every 10 sec until a consistent twitch response was obtained. A 300 msec tetanus at 100/sec was interposed 1 sec before a twitch and measurements were repeated at 10 sec intervals until the twitch was again stable. In some experiments a second tetanus was interposed 5 sec before a twitch and a further series recorded. The peak active twitch tension was measured in all experiments and in a number of these the electromyogram was full-wave rectified and integrated.

<div style="text-align:center">RESULTS</div>

A total of forty-five motor units were examined in flexor digitorum longus and fifty-four in soleus. Fig. 1 A–D illustrates the responses of two motor units functionally isolated from one flexor digitorum longus muscle. It can be seen that the motor unit with the shorter twitch time to peak (A, B) was markedly potentiated whereas the slower motor unit (C, D) was unchanged by the tetanus. An exact quantitative comparison was made difficult because the time course of the changes after a tetanus differed from one motor unit to another (Fig. 1 E). Arbitrarily, the maximum amount of depression or potentiation (regardless of the time of occurrence) has been used to describe the effect of the tetanus. This twitch tension was expressed as a fraction of the mean pre-tetanic twitch tension and will be called the post-tetanic ratio.

When the post-tetanic ratio was plotted against twitch time to peak (Fig. 2) a continuous relationship was found. In Fig. 2 B a reciprocal scale has been used for the time to peak; this was found to give the closest fit to a linear relationship between the two variables ($r = 0·38$, $P < 0·1$ %). It may be noted that in the region of overlap the fastest motor units of soleus (open circles) were potentiated at least as much as the FDL motor units (filled circles) with the same time to peak. All of the slowest motor units in flexor digitorum longus except one showed little potentiation or depression (cf. Fig. 1 C, D) and in this way they resembled soleus motor units of the

same twitch time. The correlation between the two variables was still found if the motor units from either muscle type were tested alone. A more critical test was made in soleus by excluding the two very fast motor units with twitch times to peak of less than 30 msec. The correlation coefficient for soleus was then less high (0·49) but it was significant ($P < 0·1\%$, $n = 52$). The same was true in flexor digitorum longus after excluding the slowest motor units with a time to peak of 30 msec or more ($r = 0·44$, $n = 33$, $P = 1\%$).
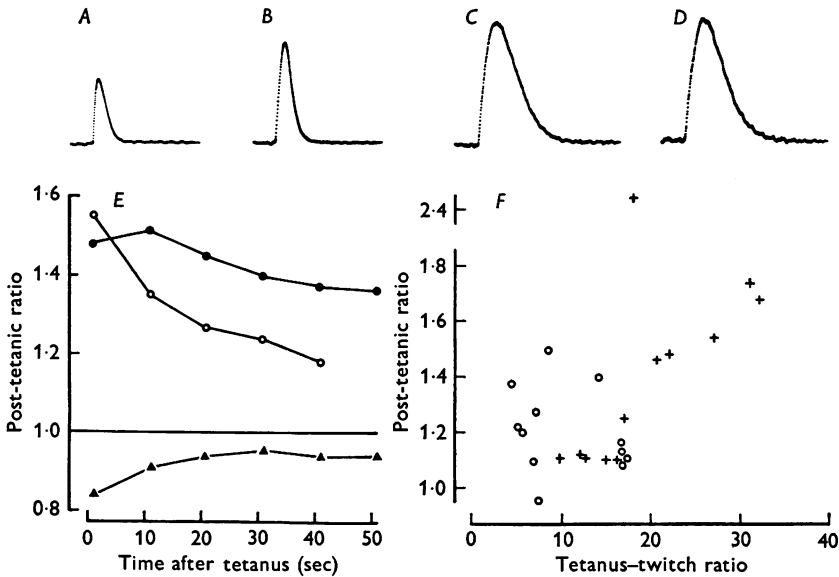

Fig. 1. *A–D*, twitches of two motor units from a single flexor digitorum longus muscle. *A* and *C* are pre-tetanic twitches (peak tension and time to peak were 7·5 mN and 18 msec in *A* and 5·7 mN and 32 msec in *C*). *B* and *D* are twitches of the same two motor units recorded 1 sec after a 300 msec tetanus at 100/sec. *E* shows the time course of the post-tetanic effects in three motor units from flexor digitorum longus (circles) and soleus (triangles): times to peak 16 msec (●), 18 msec (○) and 76 msec (▲). The ordinate shows the peak twitch tension expressed as a ratio of the mean pretetanic twitch tension. *F* shows the maximum post-tetanic potentiation plotted against the ratio of maximum tetanic tension to peak twitch tension for motor units with twitch times to peak within the range of 16–23 msec. +, results of a single experiment; ○, from seven other experiments.

In no case tested was there any change in the electromyogram of a motor unit following a tetanus. Changes in neuromuscular transmission were not therefore thought to be important. In no motor units tested was the twitch time to peak prolonged by more than a few milliseconds. This indicated the absence of repetitive firing: a short tetanus duration had been chosen to achieve this (cf. Olson & Swett, 1970).

In the fastest motor units post-tetanic potentiation did not result in any large or consistent change in the time to peak or the time to half relaxation of the twitch. There was an increase in the maximal rate of rise of twitch tension which was slightly larger (expressed as a ratio) than the change in peak tension, but followed the same time course. The time to the maximum rate of rise of tension shortened by 10–20 % (e.g. from 7 to 6 msec). In the slower motor units of soleus the post-tetanic depression was accompanied by a reduction in the time to peak. In these respects the
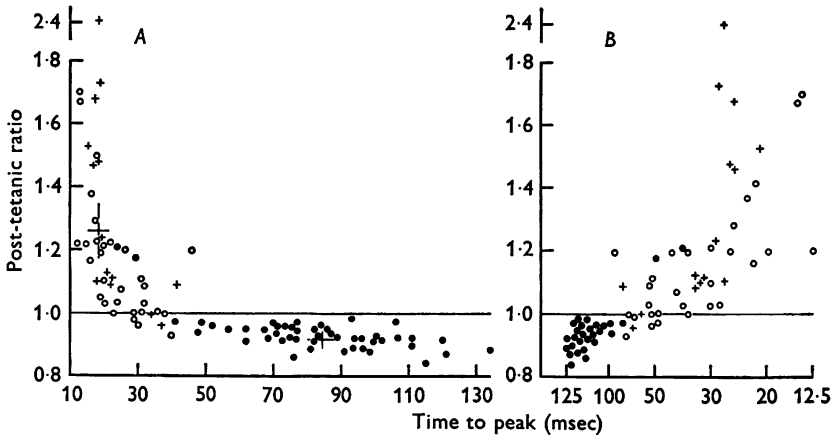

Fig. 2. Post-tetanic ratio plotted against twitch time to peak. ●, Soleus motor units; ○, +, flexor digitorum longus motor units (as Fig. 1 *F*). The large crosses indicate the means (± S.D.) of the time to peak and of the post-tetanic ratio of the whole muscle contractions. The abscissa in *B* uses a reciprocal scale. Some of the motor units (especially of soleus) have been omitted to avoid overlap: these may not be the same ones in *A* and *B*. Where this has been necessary only those points in the middle of a cluster have been excluded.

motor units resembled their parent muscles. The motor units from both muscles which had a post-tetanic ratio close to unity showed no changes in other characteristics of their twitches.

There was considerable scatter in the results. It was of course more difficult to estimate the post-tetanic ratio in the small contractions of the motor units than in those of the whole muscle, but other factors may have played a part. First, the number of observations made after a tetanus was limited so we are unable to define the maximum or minimum effect accurately. It was clear, however, that it could occur at any time up to 11 sec and therefore was not consistent, even with motor units with similar times to peak (Fig. 1*E*, circles). If the time course had been followed in more detail, the post-tetanic ratio would have been measured more accurately

and this might have reduced the scatter, but probably not to a large extent.

A second factor which may have increased the variance was the dependence of the post-tetanic ratio upon the ratio of tetanic to twitch tension. This has been described for whole muscle contractions (Smith, 1970) and was found to apply to motor units. Fig. 1F illustrates this by plotting the two variables for all motor units with twitch times to peak within a limited range: the correlation was significant at the 1 % level ($r = 0.53, n = 24$). It is possible that the association between the two factors is due to a common cause (but see Discussion); if not it would result in increased scatter if all measurements were not made under comparable conditions. In one experiment the motor units were measured at the muscle optimum rather than their own optimum length and this procedure resulted in a wider range of tetanus-twitch ratios (Lewis, Luck & Knott, 1972): these motor units are indicated as crosses in Figs. 1F and 2. If they were excluded, the correlation between post-tetanic ratio and tetanus-twitch ratio would not be seen, but there would be a marked reduction in the scatter from a linear relationship in Fig. 2B. The correlation coefficient would increase from 0.38 to 0.84 ($n = 99$ and 84 respectively) with a change in the level of significance from $< 10^{-3}$ to $\ll 10^{-10}$ ($t = 4.0$ and 14.4 respectively).

<center>DISCUSSION</center>

The most marked feature of the results is that there was apparently a continuous range of variation of post-tetanic ratio with twitch time to peak as seen in Fig. 2. There was considerable scatter but none of this could be related to the type of the muscle of origin of a motor unit. Moreover, the correlations within one muscle did not depend on the few exceptional motor units which were faster (in soleus) or slower (in flexor digitorum longus) than average. These observations must be fitted into any hypothesis about post-tetanic effects. For example, an attempt to explain post-tetanic effects in terms of the nature of the contractile proteins would require that each motor unit should contain different proportions of myosins, whether mixed within or between individual muscle fibres. This would allow the continuous gradation of post-tetanic effect to occur despite the limited number of types of myosin (Weeds & Pope, 1971).

The correlation between the post-tetanic effect and tetanus-twitch ratio together with a correlation between time to peak and tetanus-twitch ratio which has been described for these motor units (Bagust *et al.* 1973; Bagust, 1974) might be thought to be sufficient to explain the relationship between post-tetanic ratio and time to peak. However, this does not work quantitatively. The most marked discrepancy is that the regression linking time

to peak to tetanus-twitch ratio in flexor digitorum longus motor units is different from that for soleus; the quantitative deduction from this is that there would be a discontinuity between the plots for flexor digitorum longus and soleus in Fig. 2. Further the influence of tetanus-twitch ratio on post-tetanic ratio was too small; the correlation was only marked in one experiment in which an artificially wide range of tetanus-twitch ratios was obtained.

It is clear that no simple explanation has been offered for the fact that the results from a fast and a slow twitch muscle can be described by a single relationship. It may be that the scatter has prevented a more complex relationship being revealed, but the explanation may lie in a mechanism by which the factors that control the time to peak are also the ones which can be influenced by a preceding tetanus.

The interpretation of these results would be complicated by the interpretation of post-tetanic effects in frog muscle as being the resultant of two processes: one of potentiation and one of depression, each with its own time constant of decay (Connelly, Gough & Winegrad, 1971). An indication of these two independent processes in cat muscle has also been seen in a comparison of the post-tetanic responses of flexor digitorum longus and soleus whole muscle contractions (Smith, 1970). If the initial potentiation and depression and the two rates of decay varied independently between motor units, this would explain the variation found in the time at which a maximal effect (potentiation or depression) was observed after a tetanus.

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