FORCES AND POWERS OF SLOW AND FAST SKELETAL MUSCLES IN MICE DURING REPEATED CONTRACTIONS

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SUMMARY

1. The normalized force or power developed during each of a series of repeated contractions was averaged over the entire cycle of activity and rest to provide a measure of performance referred to as sustained force or sustained power. We tested the hypotheses that compared with slow soleus muscles, fast extensor digitorum longus (EDL) muscles would attain lower maximum values of sustained force, but higher maximum values of sustained power.

2. During repeated contractions at a stimulation frequency of 150 Hz, forces and powers of soleus and EDL muscles of mice were determined *in situ* at 35 °C. The train rate of repeated contractions was incremented every 5 min to increase duty cycle until a maximum value for sustained force or power was reached.

3. In one set of repeated contractions, each contraction was preceded by a quick stretch and thereafter muscle length was held constant. The stretch minimized active shortening of muscle fibres. Sustained force was calculated from force at constant length. The maximum sustained force developed by soleus muscles of 4.58 ± 0.31 N cm^{-2} (mean $\pm$ S.E.M.) occurred at a duty cycle of 0.48. Compared with soleus muscles, EDL muscles attained a lower ($P < 0.05$) maximum value of 1.38 ± 0.15 N cm^{-2} at a 0.35 duty cycle.

4. During isovelocity shortening contractions, the maximum value for sustained power developed by soleus muscles of 7.4 ± 0.5 W kg^{-1} occurred at a duty cycle of 0.18. Compared with soleus muscles, EDL muscles achieved a significantly greater maximum value of 9.1 ± 0.4 W kg^{-1} at a 0.21 duty cycle.

INTRODUCTION

When compared with soleus muscles, extensor digitorum longus (EDL) muscles have shorter contraction times and half-relaxation times (Close, 1964; Luff, 1981), a greater velocity of shortening for a given load (Brooks & Faulkner, 1988; Close, 1964), a greater maximum power during a single tetanic contraction (Brooks, Faulkner & McCubbrey, 1990), and a more rapid loss of force during repeated isometric contractions (Segal, Faulkner & White, 1986). The greater ability of slow soleus than fast EDL muscles to maintain force over time is consistent with the

difference in fatigability of slow and fast motor units. Fast motor units of all types are more fatigable in terms of maintaining isometric force than slow motor units (Burke, Levine, Zajac, Tsairis & Engel, 1973). Fatigability provides one criterion for the classification of motor units into slow (S), fast-resistant to fatigue (FR), fast intermediate (FI), and fast-fatigable (FF) categories (Burke et al. 1973).

   Based on the observation that peak power is 4-fold higher for bundles of fast than for bundles of slow fibre segments from human skeletal muscles, Faulkner, Claflin & McCully (1986) proposed that fast fatigue-resistant fibres would maintain a greater power during repeated shortening contractions than slow fibres. In contrast, fast-fatigable fibres were expected to lose power rapidly. The experiments reported here tested the hypotheses that compared with slow soleus muscles, fast EDL muscles of mice would attain: (1) lower maximum values for sustained force during repeated contractions at constant length, and (2) higher maximum values for sustained power during repeated isovelocity shortening contractions. Brief reports of these results were presented to the American Biophysical Society (Brooks, Faulkner & McCubbrey, 1988; Faulkner & Brooks, 1990).

METHODS

   Measurements were made *in situ* on twelve soleus and fifteen EDL muscles from young (1- to 2-month-old) male albino mice. All operations and experiments were conducted in compliance with the Guide for the Care and Use of Laboratory Animals (United States Public Health Service, Publication number 85–23). Mice were anaesthetized with an initial intraperitoneal injection of sodium pentobarbitone (40 mg kg^{-1}). Supplemental injections were given as necessary to maintain an adequate depth of anaesthesia. The distal tendon of the soleus or EDL muscle, including the distal portion of the muscle, were exposed and freed from attached connective tissue and surrounding muscles. A 5-0 silk suture was tied around the distal tendon and the tendon was severed distal to the suture. To prevent pulling on the soleus muscle by other portions of the triceps surae muscle group during contractions, the tendons to the gastrocnemius and plantaris muscles were severed and the muscles reflected. Throughout all experiments the exposed portions of the muscle and tendon were bathed regularly with saline warmed to 35 °C.
   The mouse was placed on a plexiglass platform which was maintained at 35 °C by a temperature-controlled circulating water bath. In order to stabilize the hindlimb to be used in the experiments, the knee was pinned and the foot was secured to the platform. The tendon of the soleus or EDL muscle was tied directly to the lever arm of a servomotor (Cambridge Technology Inc., Model 300H). The motor moved the lever at a constant velocity through a given displacement. Data on the displacement and on the development of force were displayed on a storage oscilloscope and photographed.
   The soleus or EDL muscle was stimulated by electrodes inserted beneath the skin adjacent to the tibial or peroneal nerve respectively. The voltage was increased to elicit a maximal isometric twitch response. The muscle length was then adjusted to the length at which the isometric twitch force was maximum. This muscle length, defined as L_0, is also the optimum length for the development of maximum isometric tetanic force (Brooks & Faulkner, 1988). The optimum fibre length (L_f) was determined by multiplying the L_0 for each muscle by a previously determined fibre length to muscle length ratio of 0·70 for soleus muscles (Brooks & Faulkner, 1988) and 0·44 for EDL muscles (McCully & Faulkner, 1985). The frequency–force relation for each muscle was determined at L_0 from records of the force exerted during periods of stimulation at increasing frequencies. F_0 was defined as the maximum isometric tetanic force on the frequency–force curve.

Stimulation protocol for repeated contractions
   During single isometric contractions, a stimulation frequency of 150 Hz produced 100 % of F_0 for soleus muscles and 80 % of F_0 for EDL muscles. In contrast, during single isovelocity shortening contractions, a rapid decrease in the ability to develop power was observed for both soleus and

EDL muscles as stimulation frequency was decreased from 150 Hz (Brooks *et al.* 1990). For stimulation frequencies higher than 150 Hz, values for sustained power decreased significantly with repeated contractions. Therefore, a stimulation frequency of 150 Hz was used for all experiments on each muscle. Throughout the protocols of shortening contractions, the velocity of shortening and displacement of each contraction were held constant, resulting in fixed train durations of 57.5 ± 3.9 ms for soleus muscles and 29.3 ± 0.8 ms for EDL muscles. These train durations were also used during the protocol of repeated constant length contractions.

During each protocol of repeated contractions, the number of contractions per unit time (train rate) was gradually increased. The duty cycle is the product of train rate (in Hz) and train duration (in seconds). Increments in duty cycle were continued, by increasing train rate while maintaining a constant train duration, until the value for sustained force or sustained power plateaued at a maximum level or reached a peak and declined. If the duty cycle required for a maximum value of sustained power was approached in this way, any level of force or power that could be maintained for 5 min could be maintained for at least 30 min. Preliminary experiments showed that high values for sustained power were achieved only when duty cycle was increased gradually.

Force measurements

During a fixed end contraction, the fibres within a muscle shorten by as much as 25 % (Griffiths, 1987). The energetic cost for shortening is greater than that of maintaining isometric force (Loiselle & Walmsley, 1982). Therefore, to minimize the active shortening of muscle fibres and keep the energetic cost of isometric contractions as low as possible, a quick stretch preceded the isometric portion of each contraction. The quick stretch acted to bring the force rapidly to a steady-state level. The stretches, through 10 % of L_f at velocities of $5 L_f \ \mathrm{s^{-1}}$ and $10 L_f \ \mathrm{s^{-1}}$ for soleus and EDL muscles respectively, were completed in less than 20 ms for soleus muscles and less than 10 ms for EDL muscles. Stimulation of the nerve occurred as late during the quick stretch as possible to achieve a level of force greater than 80 % of F_o (Fig. 1).

The average force (F_c) from the time the stretch ended to the end of stimulation was calculated for individual contractions from the integrated area under the force curve. Sustained force (F_s) was defined as:

$$F_s = F_c \times C_d,$$

where C_d was the duty cycle. The product of C_d and F_c distributed the force developed during individual contractions over the entire period of activity and rest. In preliminary experiments, all of the contractions were measured. We found that at any given duty cycle, F_c reached a steady state within the first few contractions, and remained virtually constant for the 5 min period at that duty cycle (Fig. 1). Consequently, the F_c determined from only the last contraction of the 5 min period was used to calculate F_s.

Injury to fibres occurs following repeated lengthening contractions with the greatest injury observed 3 days afterward (McCully & Faulkner, 1985). The quick stretches did not injure fibres in the EDL muscles, since force development was not different from control 3 days following the protocol for sustained force. Soleus muscles are injured much less by lengthening contractions than EDL muscles (Lian & Faulkner, 1987). Consequently, a protocol that did not injure EDL muscles would not be likely to injure soleus muscles.

Power measurements

Power measurements were made using isovelocity shortening contractions through 10 % of L_f at optimum velocity (Fig. 1). Optimum velocity, defined as the velocity of shortening that resulted in the maximum value for the development of power (Brooks *et al.* 1990), was 10.9 ± 0.7 mm $\mathrm{s^{-1}}$ for soleus muscles and 18.8 ± 0.4 mm $\mathrm{s^{-1}}$ for EDL muscles. This velocity was maintained for each shortening ramp throughout the protocols of repeated isovelocity contractions. A displacement through 10 % of L_f was selected because soleus muscles could not maintain force through displacements greater than 10 % of L_f. To allow the muscles to shorten around L_o, each muscle was stretched to 105 % of L_f prior to shortening and shortened to 95 % of L_f. Stimulation of the nerve and initiation of the isovelocity shortening ramp occurred simultaneously. Stimulation was terminated at the end of the shortening ramp. An increase in force occurred as the muscle was stretched back to resting length. The immediate return to resting length was necessary to permit adequate increases in train rate.

Average force (F_c) during the shortening period of each contraction was calculated from the integrated area under the force curve. The value of sustained power (P_s) was defined as:

$$P_s = F_c \times V_{opt} \times C_d,$$

where V_{opt} was the optimum shortening velocity and C_d was the duty cycle. After the first few contractions at a given duty cycle, F_c did not vary from contraction to contraction and only the final shortening contraction of the 5 min period at any duty cycle was used for the calculation of P_s (Fig. 1).
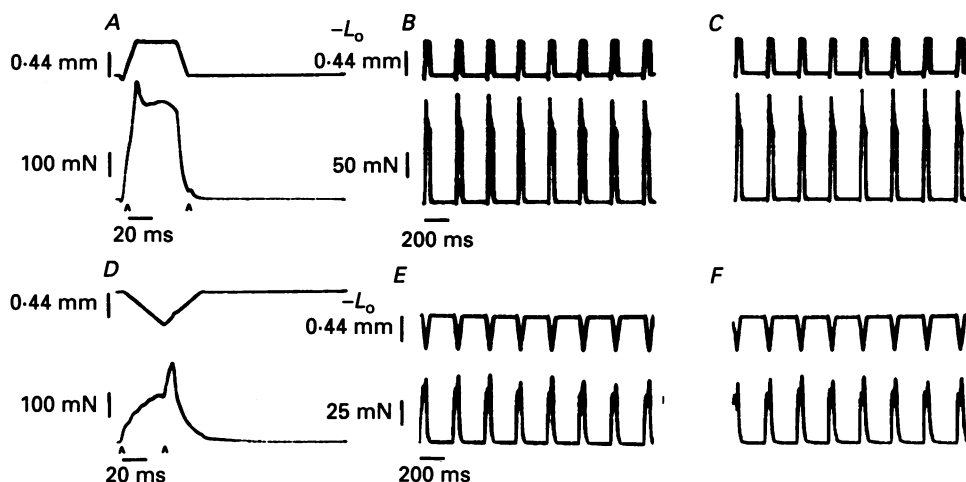

Fig. 1. Experimental records for an EDL muscle of a single isometric contraction (A) and an isovelocity shortening contraction (D) and examples of repeated isometric (B, C) and shortening (E, F) contractions at a train rate of 4 Hz. In each panel, the upper trace indicates displacement of the distal end of the muscle and the lower trace shows the force developed by the muscle. Length changes are 10% of fibre length (L_f) and an upward deflection indicates lengthening of the muscle. Isometric contractions (A) were preceded by a quick stretch from 90% of L_f to L_f and isovelocity shortening contractions (D) occurred from 105% to 95% of L_f. Stimulation was turned on and off at the times indicated by the arrows in panels A and D. Panels B and E show the first 2 s of repeated contractions. Panels C and F show another set 4 min later. Scales are identical in panels C and F to those in B and E respectively.

In some measurements of power made previously (Sargeant, Hoinville & Young, 1981; Joseph, 1985; de Haan, van Ingen Schenau, Ettema, Huijing & Lodder, 1989), the investigators chose to subtract the work done on the muscle to return it to its original position. For studies of muscle efficiency of an organism this 'negative work' performed by antagonistic muscles is an important element. In contrast, the present and other studies (Sargeant *et al.* 1981), focus on the capability of individual muscles or groups of muscles to develop or maintain a level of power. Under these circumstances, to subtract the 'negative work' component is inappropriate.

Following the measurements of sustained force or power, the muscle was removed from the animal. The animals were then killed by a lethal dose of sodium pentobarbitone. The tendons were trimmed off the muscle, and the muscle was blotted and weighed immediately. The mean cross-sectional area of each muscle was estimated by dividing the muscle wet mass by the product of L_f and 1·06 mg mm^{-3}, the density of mammalian skeletal muscle (Mendez & Keys, 1960). Based on this cross-sectional area, specific F_o (N cm^{-2}) was estimated. Values for sustained force were also normalized. Values for specific F_o of soleus and EDL muscles normally range from 20–28 N cm^{-2} (Brooks & Faulkner, 1988). This range was used as a criterion for a viable muscle preparation. On

this basis, data on fewer than 10 % of the muscles tested were rejected. Because power is a function of both force development and shortening velocity, values for sustained power were normalized by muscle wet mass to reflect the contribution of both muscle cross-sectional area and fibre length.

For each variable, data are presented as the means ± 1 s.e.m. Differences between groups were determined by Student's t tests. Significance was accepted *a priori* at $P < 0.05$.

TABLE 1. Data for soleus and EDL muscles

	Soleus muscles ($n = 12$)	EDL muscles ($n = 16$)
Body mass (g)	29.8 ± 1.3	26.8 ± 1.3
Muscle mass (mg)	8.1 ± 0.4	8.9 ± 0.5
L_o (mm)	9.1 ± 0.3	12.6 ± 0.2
Total fibre area (mm²)	1.17 ± 0.07	1.50 ± 0.07
TPT (ms)	14.1 ± 0.6	9.6 ± 0.3
F_o (mN)	273 ± 0.8	363 ± 17
Specific F_o (N cm⁻²)	23.7 ± 0.9	24.5 ± 0.7
	($n = 6$)	($n = 10$)
V_{opt} (L_f s⁻¹)	1.80 ± 0.14	3.48 ± 0.10
P_s (W kg⁻¹)	7.4 ± 0.5	9.1 ± 0.4
	($n = 6$)	($n = 6$)
F_s (N cm⁻²)	4.58 ± 0.31	1.38 ± 0.15

Data are given (means ± 1 s.e.m.) for body mass; muscle wet mass; optimum length (L_o); total cross-sectional area of muscle fibres (total fibre area), estimated by dividing muscle mass by the product of fibre length and 1·06 mg mm⁻³, the density of mammalian skeletal muscle; time to peak twitch force (TPT); maximum isometric tetanic force (F_o); and maximum specific tetanic force (specific F_o); optimum velocity for power (V_{opt}); the maximum power sustained during repeated isovelocity shortening contractions (P_s); and the maximum force sustained during repeated isometric contractions preceded by a quick stretch (F_s).

RESULTS

The mean values for specific F_o were 23.7 ± 0.9 N cm⁻² for soleus muscles and 24.5 ± 0.7 N cm⁻² for EDL muscles (Table 1). The mean displacements for shortening contractions were 0.65 ± 0.02 mm and 0.55 ± 0.01 mm for soleus and EDL muscles respectively. These values corresponded to 10 % of L_f for each of the two muscles.

Force measurements

As the duty cycle was increased, the average force generated during each constant length contraction decreased more rapidly for EDL muscles than for soleus muscles. Soleus muscles continued to generate ~ 50 % of F_o during each contraction at a duty cycle of 0·48 (Fig. 2 *A*), whereas EDL muscles generated less than 25 % of F_o at a duty cycle of 0·35 (Fig. 2 *A*). When sustained force was calculated from these data, the maximum value for soleus muscles, of 4.58 ± 0.31 N cm⁻², occurred at a duty cycle of 0·48 (Fig. 2 *B*). The value of 1.38 ± 0.15 N cm⁻² for EDL muscles, achieved at a duty cycle of 0·35, was significantly lower than the value for soleus muscles (Fig. 2 *B*).

Power measurements

During the initial single shortening contraction with a stimulation frequency of 150 Hz, the maximum power developed by EDL muscles, 164 ± 10 W kg⁻¹, was significantly greater than that developed by soleus muscles, 62 ± 5 W kg⁻¹. As the

duty cycle for repeated shortening contractions was increased, both the average force developed during each shortening contraction (Fig. 2C) and the sustained force (Fig. 2D) decreased in a manner similar to that seen with repeated constant length contractions. When sustained power was calculated from these data, the slower
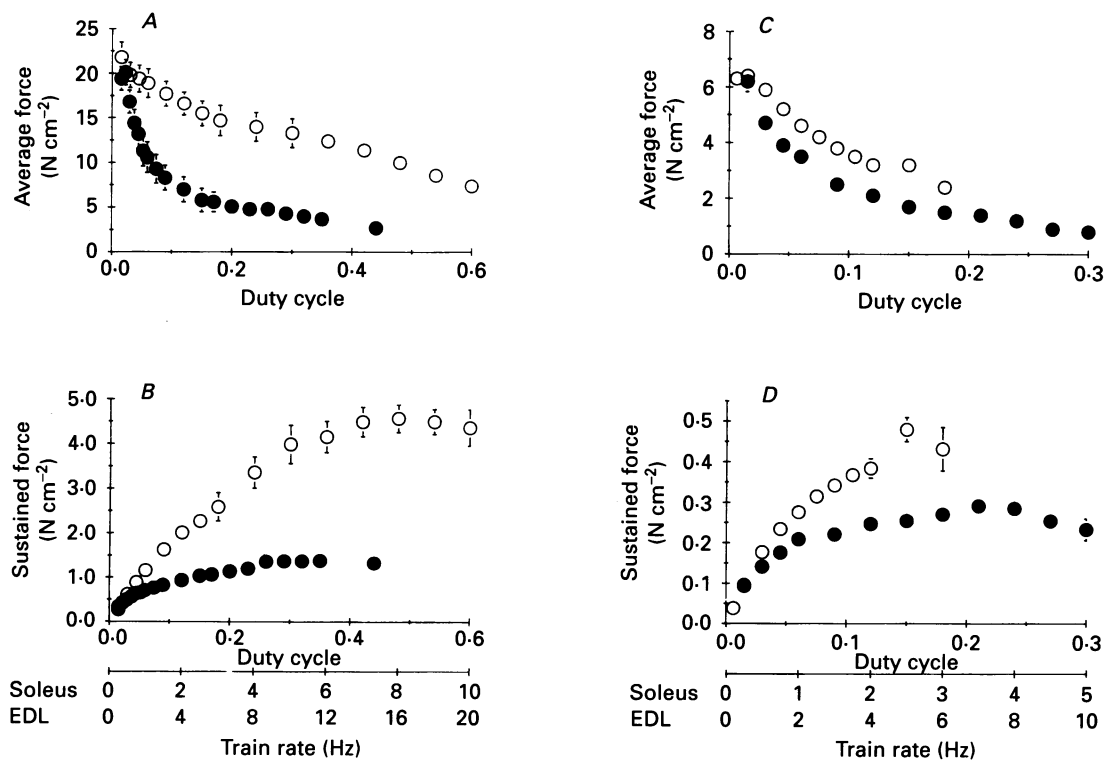

Fig. 2. The relationships of duty cycle with the average force (N cm^{-2}) developed by soleus and EDL muscles during the final (A) constant length contraction or (C) isovelocity shortening contraction after 5 min of repeated contractions at each duty cycle. The values of sustained force (N cm^{-2}) calculated from the product of average force and duty cycle are shown in panel B for constant length contractions and in panel D for shortening contractions. The train rates corresponding to duty cycles, assuming 60 and 30 ms contractions for soleus and EDL muscles, respectively, are also shown in panels B and D. Mean values are indicated for soleus muscles by $\bigcirc$ and for EDL muscles by $\bullet$. When the s.e.m. is larger than the symbol, error bars are shown. Each point includes six to ten measurements.

optimum velocity for power of soleus compared with EDL muscles (Table 1) resulted in a maximum value of 9.1 ± 0.4 W kg^{-1} for EDL muscles that was significantly greater than the value of 7.4 ± 0.5 W kg^{-1} for soleus muscles (Fig. 3). Even at lower duty cycles, the level of sustained power that could be maintained by EDL muscles was significantly greater than that of soleus muscles (Fig. 3).
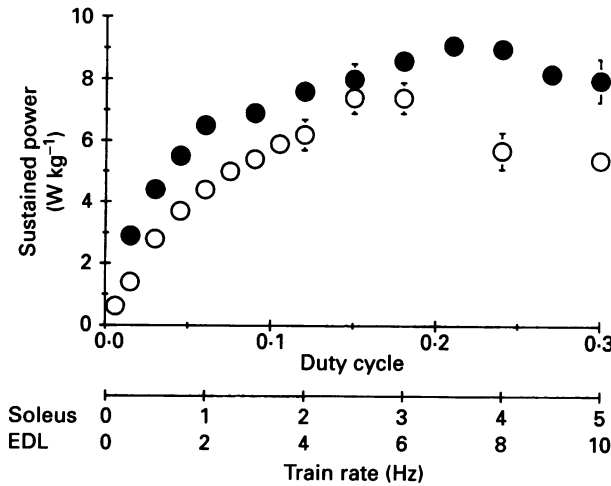
Fig. 3. The power developed during each of a series of contractions was averaged over the entire cycle of activity and rest by multiplying the power developed during the final isovelocity shortening contraction of a 5 min period of repeated contractions by the duty cycle. Relationship of duty cycle with sustained power (W kg^{-1}) measured during repeated isovelocity shortening contractions for soleus and EDL muscles is shown. The train rates corresponding to duty cycles, assuming 60 and 30 ms contractions for soleus and EDL muscles, respectively, are also shown. Mean values for sustained power are indicated for soleus muscles by ○ and for EDL muscles by ●. When the s.e.m. is larger than the symbol, error bars are shown. Each point includes six to ten measurements.

DISCUSSION

The observation that during repeated fixed length contractions fast EDL muscles of mice maintain lower values for sustained force than slow soleus muscles is in agreement with previous reports of more rapid fatigue in fast than slow muscles in rats (Segal *et al.* 1986) and cats (Hammarberg & Kellerth, 1975) and in fast than slow motor units in cats (Burke *et al.* 1973). The concept of a greater fatigability for fast muscles, motor units and fibres than slow muscles, motor units and fibres is consistent with histochemical, biochemical and metabolic characteristics. Compared with slow muscles, fast muscles have a lower oxidative capacity (Rigault & Blanchaer, 1970) and a higher energy requirement for maintaining a given isometric force (Crow & Kushmerick, 1982).

We now report that EDL muscles are also inferior to soleus muscles in maintaining force development during repeated isovelocity shortening contractions at their respective optimum velocities for power development. During shortening, compared with soleus muscles, EDL muscles have higher optimum velocities for power output, presumably as a consequence of their high actomyosin turnover rates (Bárány, 1967). For a given muscle, either EDL or soleus, the same factors are likely to influence the metabolic cost during shortening and isometric contractions.

In spite of the lower ability of EDL than soleus muscles to sustain force during shortening contractions, EDL muscles maintained higher values of sustained power

than soleus muscles for periods of up to 30 min. The different abilities of soleus and
EDL muscles to sustain power arise at least in part from the differences in their
relative abilities to develop power during single contractions. The fast–slow ratio of
maximum power during a single contraction is 2·5 for whole EDL and soleus muscles
of mice and 4·0 for bundles of fast and slow fibre segments of human muscles
(Faulkner et al. 1986). Rather than a species difference, this difference probably
results from the proportions of fibre types present in the whole muscles. EDL muscles
in mice are 95 % fast (Crow & Kushmerick, 1982; Florini & Ewton, 1989) and soleus
muscles are composed of ∼ 60 % slow and ∼ 40 % fast fibres (Florini & Ewton,
1989), whereas bundles of human fibre segments are composed exclusively of either
fast or slow fibres. A greater ability to develop power during a single contraction does
not guarantee superiority in sustaining power during repeated contractions. During
a single contraction, EDL muscles of adult mice generate a 20 % greater power than
young mice, yet during repeated contractions, muscles in young mice produce nearly
a 2-fold greater value for sustained power and tolerate higher duty cycles (Brooks &
Faulkner, 1990).

   The observation that the values of sustained power during repeated contractions
by soleus and EDL muscles are 8 and 4 % of the power produced during a single
contraction is consistent with data on human beings (Wilkie, 1960). The difference
between single and repeated contractions is due to the averaging of force over both
the duty and rest cycles and to the decrease in the development of force during each
contraction when contractions are performed repetitively. If the force developed by
muscles during each contraction remained constant, a linear increase in values of
sustained power would be predicted as duty cycle increased. During repeated
isovelocity shortening contractions, the values for sustained power for both soleus
and EDL muscles did increase with increases in duty cycle, but the discrepancy
between measured and predicted values also increased with duty cycle. At maximum
values of sustained power, the measured values were 66 and 26 % of the values
predicted for power in the absence of any loss of force, for soleus and EDL muscles
respectively. In spite of the greater decrease in force by EDL muscles, the sustained
power of EDL muscles was greater than that of soleus muscles.

   The higher maximum sustained power for EDL muscles than for soleus muscles is
consistent with the hypothesis proposed by Faulkner et al. (1986) that for any given
period of time fast-oxidative fibres are able to maintain a higher level of power
output than slow fibres. Presumably, the difference in the power developed by soleus
and EDL muscles is due to the difference in the types of fibres present. Therefore,
because neither muscle consists of only one type of fibre, the difference between the
single slow and fast fibres or motor units would be greater than that between these
muscles of mixed fibre types.

   During graded increments in duty cycle, the increase and eventual plateau in
sustained force and sustained power for in situ soleus muscles in mice are similar to
the responses observed for oxygen uptake (Balke & Ware, 1959; Tabakin, Hanson,
Merriam & Caldwell, 1964) and cardiac output (Tabakin et al. 1964) of human beings
during graded exercise tests. The flatter curves of the EDL muscles are likely to
reflect the decreasing contribution of fast-fatigable fibres to the development of force
and power as the duty cycle is increased (Burke et al. 1973). Human beings make

more rapid metabolic adjustments to gradual increases in exercise intensity compared with a step increment from rest to an exercise intensity that requires a near maximum oxygen consumption (Whipp & Ward, 1990). The different responses to gradual increases in exercise intensity compared with a step increment from rest to near maximum intensity appear to involve higher rate constants for oxygen consumption kinetics during gradual increments than occur with a step increment (Mahler, 1985; Whipp & Ward, 1990). The inability of soleus and EDL muscles to achieve maximum values for sustained force or sustained power when exposed to a step increment from rest to the duty cycle at which sustained force or power was maximum is consistent with these observations.

Our observation that with both repeated constant length contractions and repeated shortening contractions the ability of fast muscles to develop force decreases more rapidly than that of slow muscles is consistent with the generalized concept of a greater fatigability of fast compared with slow motor units (Burke *et al.* 1973) and whole muscles (Hammarberg & Kellerth, 1975; Porter & Whelan, 1981; Segal *et al.* 1986). Based on the present results, the difference in the relative fatigability of slow and fast muscles is much less during shortening contractions than during constant length contractions. In spite of a greater fatigability in each type of contraction, during shortening contractions, fast muscles, and presumably fast-oxidative motor units (Faulkner *et al.* 1986), sustain a greater power than slow muscles or motor units because of their higher optimum velocity of shortening. The finding has implications for the training of skeletal muscles for the development of sustained power.

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