Fatigability of mouse muscles during constant length, shortening, and lengthening contractions: interactions between fiber types and duty cycles

John A. Faulkner and Susan V. Brooks

Department of Physiology and Bioengineering Program, University of Michigan Medical School, Ann Arbor, MI 48109-0622, USA

Abstract

Our working hypothesis is that slow and fast fiber types have evolved for the performance of specific tasks: slow fibers for sustained force during isometric contractions and low velocity shortening and lengthening contractions and fast fibers for maximum power during a single contraction and for sustained power during high velocity shortening contractions. We tested this hypothesis by comparing the average force, sustained force and sustained power developed by slow soleus and fast extensor digitorum longus (EDL) muscles of mice during constant length, shortening, and lengthening contractions at increasing duty cycles. The duration of the contractions, amount of displacement, and velocity of shortening and lengthening were controlled and muscles were allowed to develop an appropriate force for a given duty cycle. For both muscles and each type of contraction, the average force developed during single contractions decreased as the duty cycle was increased. During constant length contractions, soleus muscles sustained a four-fold greater force than EDL muscles. Surprisingly, soleus muscles were not more proficient than EDL muscles at sustaining force or power during shortening contractions at the optimum velocity for the development of power by soleus muscles, whereas EDL muscles developed the greater sustained power when each muscle contracted at its own optimum velocity for power. During isovelocity lengthening contractions at 0.25 L_f/s, soleus muscles produced more than two-fold the sustained force, or power, of fast muscles. In general, the results are in good agreement with our working hypothesis.

Introduction

Traditionally, muscular fatigue is defined as "a failure to maintain the required or expected force" (Edwards in Porter & Whelan, 1981, pg.1). This definition reflects the reliance of previous measurements of fatigability on protocols involving isometric contractions (Porter & Whelan, 1981). Subsequently, the NHLB Institute Workshop (1990) defined muscle fatigue as "a condition in which there is a loss in the capacity of a muscle for developing force and/or velocity, resulting from muscle activity under load and which is reversible by rest". Although the latter definition incorporates the concept that the fatigued state *impairs* the ability of the muscle to develop both force and velocity (Metzger & Moss, 1987), the approach remains that of measuring a *failure to maintain* or a *loss in* force, velocity, or both. When exercising, even highly trained athletes tend to exercise at an intensity that can be maintained, rather than an intensity at which failure occurs.

For slow soleus and fast extensor digitorum longus (EDL) muscles of mice, the highest force that could be sustained during repeated constant length contractions and the highest power the could be developed during repeated isovelocity shortening contractions at optimum velocity for power were compared (Brooks & Faulkner, 1991). The stimulation frequency, duration, and, where appropriate, displacement and velocity of shortening of all contractions were chosen to facilitate the comparisons between slow and fast muscles under comparable conditions. Under these circumstances, the muscle developed a force appropriate for a given duty cycle. At each duty cycle, the average force equilibrated within the first minute and then could remain constant for up to 40 min. The coupling between energy input and energy output was too rapid to postulate a role for decreased calcium release or calcium sensitivity under these conditions. The level of force maintained was more likely based on the concentration of inorganic phosphate (Hibberd et al. 1985), hydrogen ion concentration (Metzger & Moss, 1987), or some interaction between the two. In keeping with the concept of a *graded exercise test* (Balke & Ware, 1959), the force or power were increased by increasing the train rate of the contractions, and consequently the duty cycle. Consistent with previous observations, during repeated isometric contractions, slow soleus muscles lost less average force than fast EDL muscles. Consequently, with increasing duty cycle, slow muscles sustained a greater force than fast muscles. Similarly, during repeated isovelocity shortening contractions at the optimum velocity for power for each muscle, gradual increments in duty cycle produced a more rapid loss in force by fast than slow muscles. In spite of the more rapid loss in force, the two-fold higher values for optimum velocity for the fast muscles resulted in fast muscles developing higher values than slow muscles for sustained power (Brooks & Faulkner, 1991).

During almost any total body physical activity, skeletal muscles will at various times remain at constant length, shorten, or be lengthened. The muscle performs a specific type of contraction dependent on the interaction between the force developed by the muscle and the load. If an equivalent or a fixed load is encountered, no change in length occurs; if the muscle force is greater than the load, the muscle shortens; and if the force is less than the load, the muscle is stretched. Since repeated shortening, isometric and lengthening contractions are performed habitually by skeletal muscles, our purpose was to compare the ability of slow and fast muscles to sustain force during each type of contraction during graded increases in the duty cycle. Our working hypothesis was that slow and fast fiber types have evolved for the performance of specific tasks: slow fibers for sustained force during isometric contractions and low velocity shortening and lengthening contractions and fast fibers for maximum power during a single contraction and for sustained power during high velocity shortening contractions. We recognize that although fibers may have adapted for the performance of specific types of contractions, each fiber type will under certain circumstances be recruited to perform each of the three types of contractions for varying periods of time. Such performances will on occasion result in fatigue, injury, or both (McCully & Faulkner, 1986). We tested the hypotheses that with increments in duty cycle compared with slow muscles, fast muscles will develop and sustain lower forces: a. during repeated constant length contractions, b. during isovelocity shortening contractions at the optimum velocity for power of slow fibers, and c. during isovelocity lengthening contractions with both slow and fast muscles at 0.25 L_f/s.

Experimental methods

Data were collected in situ on slow soleus and fast EDL muscles of SPF male CD-1 albino mice (Brooks & Faulkner, 1991). Mice (1 to 2 months of age) were anesthetized with sodium pentobarbitone (80 $mg \cdot kg^{-1}$). The distal tendon of the soleus, or EDL, muscle was exposed. A 5-0 suture was tied around the tendon and the tendon was severed distally. The mouse was placed on a temperature controlled (35^oC) plexiglass platform. The knee was pinned and the foot taped to the platform. The tendon was tied to the lever arm of a servomotor (Cambridge Tech, Inc., Model 300H or 305). A microcomputer interfaced with the servomotor controlled the direction, magnitude and velocity of each displacement. For both muscles, a frequency of 150 Hz appeared optimum for maintaining force and power during repeated contractions (Brooks & Faulkner, 1991). A frequency of 150 Hz produced an isometric force of 100% of maximum force (F_o) for soleus and ~85% of F_o for EDL muscles. Forces and displacements were displayed on a storage oscilloscope and sampled by a microcomputer during: a. constant length contractions which were preceded by a quick stretch, 10% of L_f and ~5 L_f/s for soleus and ~10 L_f/s for EDL muscles, designed to bring force rapidly to the level of F_o; b. shortening contractions which were through ~10% L_f at ~1.8 L_f/s, the optimum velocity for the development of power for soleus muscles; and c. lengthening contractions which were through ~10% of L_f at ~0.25 L_f/s to prevent contraction induced injury (McCully & Faulkner, 1986). The use of isovelocity shortening and lengthening contractions at the same velocities for slow and fast muscles allowed us to assess fatigue effects on force and velocity based solely in terms of the decrease in the force developed by the muscle. If fatigue caused a decrease in both force and velocity, the decrease in force during repeated isovelocity contractions reflects both aspects.

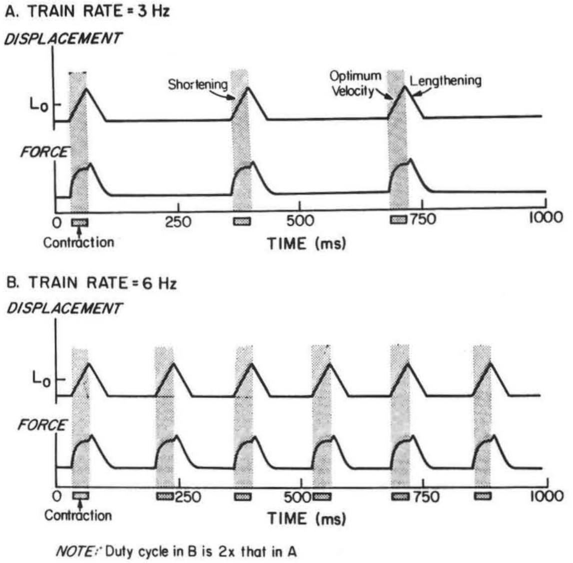

Fig. 1. Drawings of experimental records of repeated shortening contractions at two different train rates on identical time scales. Repeated contractions are at a train rate of 3 contractions/s (A) and at 6 contractions/s (B). Upper traces in both A and B show the displacements of the lever arm during isovelocity shortening and lengthening of the muscle. Displacement occurs around optimum length (L_o). Lower traces show the force developed. The stippled bars show the duration of stimulation which in this example occurs during shortening and is ~60 ms and ~30 ms for soleus and EDL muscles respectively (Modified from Faulkner et al. 1990 with permission).

The concept of a test with graded increments of force or power was achieved through gradual increases in the train rate of repeated contractions (Brooks & Faulkner, 1991). During each cycle of contraction and rest, the fraction of time occupied by the contraction, termed the duty cycle, is equal to the product of the train rate in Hz and the contraction duration in seconds. For each experiment, the duration of each contraction was constant, therefore increments in the train rate and duty cycle were proportional. During each contraction, the average force was measured. To facilitate the comparisons among muscles of different masses, all measurements of force were normalized to specific force (N/cm^2) through division by the total cross-sectional area of the fibers. The mean values for specific F_o of 23.7±0.9 N/cm^2 and 24.5±0.7 N/cm^2 and muscle masses of 8.1±0.4 mg and 8.9±0.5 mg for soleus and EDL muscles respectively are in good agreement with previous data (Brooks & Faulkner, 1991). Sustained force was calculated as the average force developed during single contractions multiplied by the duty cycle. Protocols commenced at a train rate of 0.25 Hz and then the train rate was increased every five minutes with increments such that the value for sustained force increased with the increased duty cycle until a maximum sustainable value was reached. Drawings of records are shown in Figure 1 for repeated shortening contractions at two different train rates and therefore two different duty cycles. Similar records could be drawn for constant length and lengthening contractions.

Results

For both soleus and EDL muscles, the average forces during repeated constant length, shortening, and lengthening contractions decreased as a function of the increase in duty cycle. During constant length and lengthening contractions, the rate and magnitude of the decrease in average force relative to the duty cycle was greater for EDL than soleus muscles (Figure 2A, 2C). During contractions with both muscles shortening at the optimum velocity for the development of power by soleus muscles, soleus muscles never developed higher average forces than EDL muscles. Initially, the average force of EDL muscles was higher than that of soleus muscles. Subsequently, at high duty cycles, the average forces developed by EDL and soleus muscles were not different (Figure 2B). When the EDL muscle shortened at its optimum velocity, the average force developed was lower than the other two values (Figure 2B).

During each of the three types of contractions, the sustained force developed by soleus muscles increased substantially with increased duty cycle, whereas that of EDL muscles increased substantially only during shortening contractions (Figure 2A', 2B', 2C'). The sustained forces developed by EDL muscles increased only marginally with duty cycle during constant length contractions and not at all during lengthening contractions. During constant length, shortening, and lengthening contractions, the maximum values for the sustained forces of soleus muscles were 4.6 N/cm^2, 0.48 N/cm^2, and 2.9 N/cm^2, compared with 1.38 N/cm^2, 0.43 N/cm^2, and 1.31 N/cm^2 for the EDL muscle (Figure 2A', 2B', 2C').

The sustained powers developed by soleus and EDL muscles shortening at 1.8 L_f/s (the optimum velocity for power development by soleus muscles) were not different. In contrast, when each muscle shortened at its own optimum velocity for the development of power, the two-fold higher velocity of the EDL muscles resulted in higher sustained power outputs at almost every duty cycle (Figure 3). The soleus muscles did not sustain power well above a train rate of 3 Hz or a duty cycle of 0.18, whereas EDL muscles sustained power quite well up to a train rate of 10 Hz and a duty cycle of 0.3.

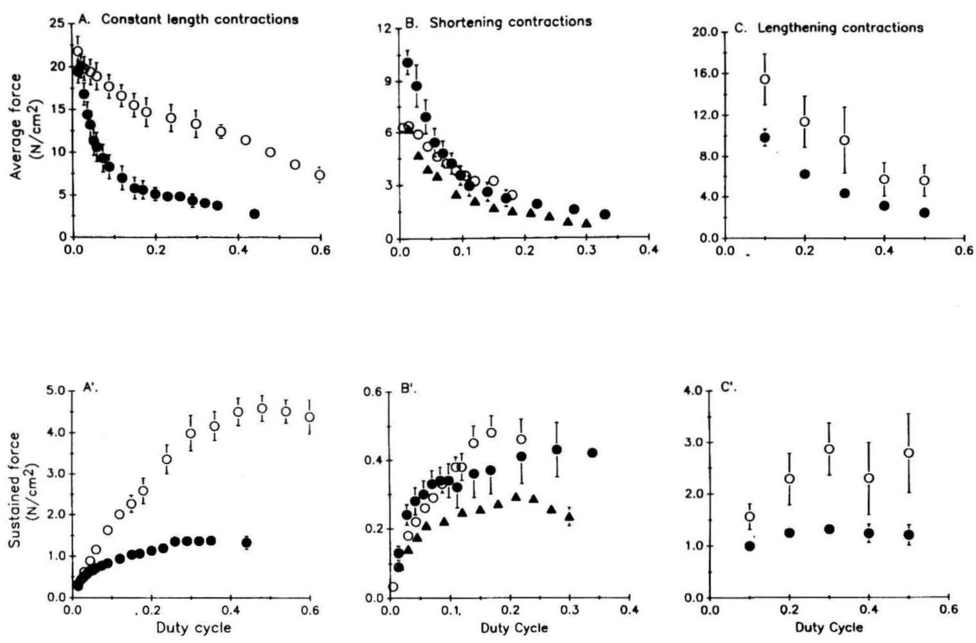

Fig. 2. The relationship of duty cycle with the average force (A, B, C) developed by slow (open symbols) and fast (filled symbols) muscles during the final (A) constant length contraction, (B) shortening contraction, and (C) lengthening contraction at each duty cycle. At each duty cycle, contractions are repeated for 5 min. The values for sustained force (A', B', C') were calculated from the product of average force and duty cycle. Each symbol represents the mean for 3 to 10 measurements. In panels B and B', circles indicate shortening at 1.8 L_f/s and triangles indicate 3.5 L_f/s. Error bars shown when 1 SEM is larger than the symbol (Modified from Brooks & Faulkner, 1991 with permission).

Discussion

Our observation that during repeated constant length contractions slow soleus muscles maintain higher average and sustained forces than fast EDL muscles is consistent with a number of previous reports that with repeated isometric contractions slow whole muscles (Segal et al. 1986) and motor units (Burke et al. 1973) are less fatigable than fast muscles or motor units. Our observation extends the range of duty cycles over which slow muscles demonstrate a superiority over fast muscles in developing force with less evidence of fatigue. The average specific force of fast muscles decreased rapidly as the duty cycle was increased above 0.025. At high (0.4 to 0.6) duty cycles, slow muscles had a four-fold greater average and sustained force than fast muscles. Presumably, the magnitude of the difference results from slow muscles having a greater oxidative capacity (Rigault & Blanchaer, 1970) and a lower energy requirement for the maintenance of a given force than fast muscles (Crow & Kushmerick, 1982). The data support the supremacy of slow over fast fibers for the performance of constant length contractions. The more rapid loss of average force by EDL muscles than by soleus muscles indicates that, compared with soleus muscles, EDL muscles experience a greater decrease in the number of attached cross-bridges, less force developed by each cross-bridge, or some combination of these two mechanisms. The present experiment does not permit the resolution of these options, nor the mechanism responsible for the change. In spite of these limitations, our data are consistent with the observations of Metzger & Moss (1990) that during isometric contractions at low pH, only fast fibers show a reduction in number of attached cross-bridges, whereas both slow and fast fibers show a decreased force per attached bridge.

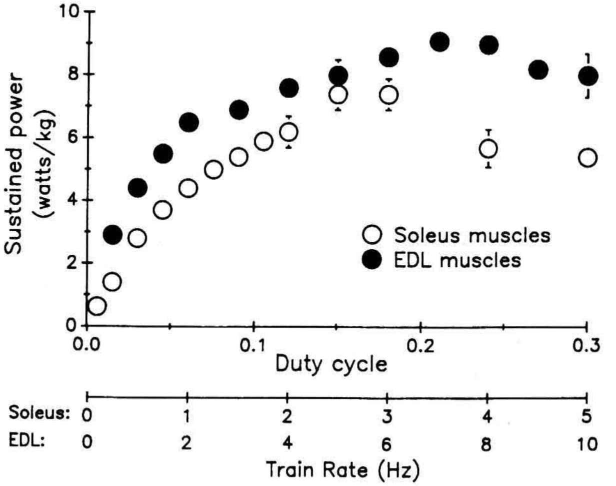

Fig. 3. The relationship between the sustained power and the duty cycle/train rate for slow soleus and fast EDL muscles. The power developed during each 5 min period at a given duty cycle was represented by the final cycle of activity and rest. The power sustained at each duty cycle was determined by multiplying the power developed during the final isovelocity shortening contraction by the duty cycle. The correspondence of the train rates and duty cycles assume a 60 ms and 30 ms contractions for soleus and EDL muscles respectively. Power (W) was normalized to wet muscle mass. Each symbol represents the mean for 6 to 10 measurements. Error bars shown when 1 SEM is larger than the symbol (Modified from Brooks & Faulkner, 1991 with permission).

In contrast to the differences in the average and sustained forces developed by slow and fast muscles during constant length contractions, slow muscles were not superior to fast muscles in developing and sustaining force when the shortening velocity for both was optimum for power development by the slow muscles. The lower than optimum velocity of shortening for the fast EDL muscles increased the average and sustained force developed, but reduced the power output compared to that developed at optimum velocity for a fast muscle (Brooks & Faulkner, 1991). In spite of the low velocity for the EDL muscles, during shortening contractions, the maximum sustained power outputs were not different for soleus and EDL muscles. The equivalence in the maximum sustained power output of slow and fast fibers at low velocities would enable muscles composed of slow and fast motor units to perform a variety of low velocity tasks with equal contributions of power from slow and fast motor units. In addition, fast oxidative motor units would be capable of performing high power tasks beyond the sustained power capabilities of slow motor units.

During stretches of activated single frog fibers, measurements of stiffness indicate that the number of attached cross-bridges is only about 10% to 20% greater than during an isometric contraction, indicating that the high forces observed during lengthening are due predominantly to increased strain of cross-bridges (Lombardi & Piazzesi, 1990). During lengthening contractions at low velocities, the two-fold greater average forces developed by soleus compared with EDL muscles likely reflects to some degree the two-fold higher elastic modulus of slow fibers (Metzger & Moss, 1990). The larger drop for fast muscles in the magnitude of average force with duty cycle indicates differences in the rate of fatigue between slow and fast muscles during lengthening contractions. Not only do the slow muscles sustain force better than fast muscles during lengthening contractions, but when the lengthening extends through greater displacements, the slow fibers are less likely to be injured than fast fibers (Jones et al. 1986).

The duty cycles that can be achieved with specific types of contractions reflect complex interactions between stimulation frequency, displacement, velocity, load, contraction duration and train rate. In addition, the duty cycle that can be sustained is dependent on the contractile history of the muscle. Only the lowest duty cycles could be sustained successfully from the resting state. Muscles that had been at rest had to progress through several increments of low duty cycles before the higher duty cycles could be sustained. Once muscles had achieved energy balance through several lower level duty cycles, subsequent duty cycles could be sustained for up to 40 min. In terms of the duty cycle achieved, the soleus muscles were superior to the EDL muscles during constant length contractions, whereas during shortening contractions, EDL muscles achieved higher duty cycles and train rates. Consequently, the duty cycles and train rates that can be tolerated place constraints on the tasks that muscles or motor units can perform. The tolerable levels have implications for stride, stroke, or pedalling frequency during various physical activities.

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