High Efficiency of Type I Muscle Fibers Improves Performance

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Abstract


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We have recently demonstrated that people with a high percentage of Type I muscle fibers display a relatively high muscular efficiency when cycling. These individuals generate a relatively high muscular power output at a given steady-state level of oxygen consumption and caloric expenditure. The purpose of this study was to directly determine the extent to which differences in muscle fiber composition and efficiency influence endurance performance in competitive cyclists. The percentage of Type I and II muscle fibers was determined from several biopsies from the vastus lateralis which were histochemically stained for ATPase activity. During a laboratory performance test, 14 endurance trained cyclists (mean:±SE; VO2max, 5.2±0.11/min; body weight, 74±1 kg) cycled an ergometer for 1 h at the highest work rate they could tolerate. VO2 and RER were simultaneously measured using open circuit spirometry for calculating caloric expenditure. Subjects were divided into two groups of seven according to their muscle fiber type composition: High % Type I Group (> 56 % Type I fibers); Normal % Type I Group (38-55 % Type I fibers). Each subject from High % Type I Group was paired with a subject from the Normal % Type I Group according to their similarity in VO2max, blood lactate threshold and average VO2 maintained during the 1 h performance test. Both groups averaged 4.5±0.11/min during the 1 h performance test (i.e., 86-88% VO2max). However, the High % Type I Group, which possessed an average of 72±3% Type I fibers, was able to maintain a 9 % higher power output (i.e., 342±9 vs 315±11 watts; p<0.001) than the Normal % Type I Group which possessed an average of 48±2% Type I fibers. Gross efficiency was thus significantly higher in the High % Type I Group compared to the Normal % Type I Group (i.e., 21.9±0.3 % vs. 20.4±0.3 %; p<0.001). We conclude that a high percentage of Type I muscle fibers improves endurance performance ability by significantly increasing the power output generated for a given rate of oxygen consumption and energy expenditure.

Key words

Endurance, bicycling, myosin type, muscular contraction, physical exertion

Introduction

It is generally recognized that people can vary greatly in cycling efficiency (8) and running economy (4,9,23). Obviously, superior economy or mechanical efficiency has potential to improve athletic performance. Indeed, running and walking economy have been correlated with endurance performance ability (4,9,15). The factors responsible for the heterogeneity in economy and mechanical efficiency during exercise have not been identified (19,20).

We have recently reported that both gross and delta mechanical efficiency while cycling at a cadence of 80 rpm is highly correlated (i.e., r = 0.75–0.85) with the percentage of Type I muscle fibers within the vastus lateralis of well-trained cyclists (8). This observation in people indicates that during relatively slow velocity muscular contractions, Type I muscle fibers (i.e., slow twitch) appear more efficient at converting chemical energy into mechanical work compared to Type II muscle fibers (i.e., fast twitch). This observation is consistent with the previous work performed in vitro using isolated muscle preparations (12,17).

The knowledge that exercise performance is greatly influenced by economy (4,9,15), together with our recent observations that mechanical efficiency is related to muscle fiber composition of the exercising musculature (8), leads to the obvious assumption that muscle fiber composition may directly influence exercise performance by improving mechanical efficiency. However, no study to date has directly determined that improved mechanical efficiency as a result of a relatively high percentage of Type I muscle fibers indeed improves endurance performance. This was the primary purpose of this investigation.
Another purpose of this investigation was to identify the functional advantage of possessing a high percentage of Type I muscle fibers during a cycling performance test lasting one hour. It has been suggested that a high percentage of Type I fibers allows for superior endurance running performance (10). However, to our knowledge, the reason for this assumed superior performance has not been well studied. Improved mechanical efficiency is just one aspect which may predispose individuals with a high percentage of Type I fibers to excel in endurance activities. Theoretically, Type I muscle fibers could possess other functional and metabolic abilities which make them superior for endurance performance, such as superior oxidative ability and reduced muscle glycogenolysis (3). Therefore, this study also sought to determine if cycling performance is enhanced in individuals with a relatively high percentage of Type I fibers, more than can be expected simply as a result of superior mechanical efficiency.

**Methods**

**Subjects and general design**

Fourteen endurance-trained male cyclists were recruited for this study. Subjects were informed of the experimental procedures and possible risks involved and each subject signed a consent form, approved by the Internal Review Board of the University of Texas at Austin. All subjects performed preliminary testing to determine maximal oxygen consumption (VO\textsubscript{2 max}), blood lactate threshold and muscle fiber type composition of the vastus lateralis. The subjects were grouped according to their muscle fiber type composition (i.e., above or below the median of 56% Type I muscle fibers). Subsequently, their endurance performance ability was evaluated during a one-hour laboratory test. Furthermore, based upon a similar average VO\textsubscript{2} during the one-hour laboratory test, each subject from one group was paired with an individual from the other group, as described below.

**Preliminary testing**

VO\textsubscript{2 max} was determined while cycling (Monark ergometer model 819) using a continuous incremental protocol, lasting 7–10 minutes. VO\textsubscript{2 max} was defined as the rate of oxygen consumption at which an increase in work rate no longer elicited an increase in VO\textsubscript{2}. Additionally, this criterion coincided with an RER value of greater than 1.1.

VO\textsubscript{2} at the blood lactate threshold (VO\textsubscript{2} at LT) was assessed using a continuous cycling protocol. The blood lactate threshold was determined by graphing venous blood lactate concentrations (13), measured after five minutes of cycling at each of five intensities, corresponding to approximately 50, 60, 70, 80 and 90% of their predetermined VO\textsubscript{2 max}. Blood lactate threshold was defined as the point at which blood lactate concentration is elevated 1 mM above baseline values (5).

**Muscle fiber type determination**

Muscle samples were obtained from the vastus lateralis using the needle biopsy technique. Incisions in the skin were made 12–20 cm above the patella. To improve the accuracy of the muscle fiber type assessment, 2 to 4 biopsies were performed at different locations in the vastus lateralis of both legs, as previously described (8), in an attempt to obtain at least 1,000 fibers for typing from each subject. Muscle samples were prepared for histochemical analysis by first transversely sectioning the samples (10\textmu m) using a Cryostat microtome. The samples were then pre-incubated at pH 4.3, 4.55 and 10.3 and stained for ATPase activity (2). Fibers were classified as Type I (i.e., slow twitch) or Type II (i.e., fast twitch) with no attempt to subclassify Type II fibers because almost all Type II fibers were Type IIa. Muscle fiber area was determined on at least 100 fibers from each biopsy using computer based digitizing pad and the % area Type I was determined.

**One-hour performance test**

Performance was assessed by measuring the minute by minute and ultimately the average power produced while the subjects cycled for one hour on a Monark cycle ergometer (Model 819) equipped with racing handle bars and seat as well as pedals for cleated shoes. Power was measured by monitoring pedal revolutions per minute (rpm) from an electric counter (±1 RPM) and resistance from a calibrated potentiometer attached to the pendulum (±1 NM). The subjects were instructed to generate the highest work rate possible throughout the one hour cycling bout. During the initial eight minutes of the exercise bout, the work rate was preset, based on a performance prediction from the results of the preliminary blood lactate threshold test (6,7). Following the initial eight minutes, the subjects were allowed to vary both pedal cadence and resistance to achieve the goal of producing the highest work rate possible for one hour. The subjects were supplied with visual feedback of pedaling cadence, power output, heart rate, and elapsed time. VO\textsubscript{2} was measured during the initial eight minutes of the exercise protocol, as well as whenever the work rate was changed. VO\textsubscript{2} measurements were made for at least three minutes following the attainment of steady state. In the event that the subject did not request for the work rate to be altered, less than seven minutes elapsed between steady state VO\textsubscript{2} measurements. The average VO\textsubscript{2} during the 1 h test was calculated from the steady-state values and the time at each work rate.

**Selection of subject pairs**

Subjects were divided into two groups according to their percentage of Type I muscle fibers. Each subject with a relatively high percentage of Type I muscle fibers (High % Type I) (i.e., greater than 56% Type I) was paired with an individual with a relatively average or normal distribution of Type I muscle fibers (Normal % Type I) (i.e., less than 56% Type I, with a range of 38–55% Type I). The Normal % Type I group displayed a fiber type distribution typical of healthy young people (23). The pairing of subjects was based upon the following criteria: 1) less than 2% difference in VO\textsubscript{2 max}, 2) less than 4% difference in VO\textsubscript{2} at lactate threshold, 3) muscle fiber composition which differed by more than 10% Type I fibers of the total, and 4) less than 0.1 liter/min difference in mean VO\textsubscript{2} during the performance test.

**Measurement of gas exchange**

All measurements of oxygen consumption (VO\textsubscript{2}) and respiratory exchange ratio (RER) were performed using indirect calorimetry. While the subjects inhaled through a Daniels valve, the volume of inspired air was measured using a Parkinson-Cowan CD4 dry gas meter. The expired gases were continuously sampled from a mixing chamber and analyzed for O\textsubscript{2} (Applied Electrochemistry SA3) and CO\textsubscript{2} (Beckman LB-2).
These instruments were interfaced with an Apple IIe computer for calculations of \( \text{VO}_2 \) and RER. Gross efficiency was calculated as the ratio of the energy produced by the cyclist on the ergometer (i.e., power output) to the rate of caloric expenditure (i.e., indirect calorimetry) as previously described (8).

**Statistics**

Statistical differences were determined between the matched subject pairs using Student’s t-test for paired comparisons. Additionally, the subjects were ranked according to their individual gross efficiency, divided into two equal groups, and the % Type I fibers of the groups were compared using Student’s t-test for unpaired comparisons. The Pearson product moment formula was used to calculate the correlation coefficient. Statistically significant differences are reported at \( p<0.05 \).

**Results**

**Subject pairs according to differences in muscle fiber type composition**

The population of subjects was fairly homogeneous and possessed the following mean (± SE) characteristics: age, 25 ± 1 yr; weight, 74 ± 1 kg; \( \text{VO}_{2} \text{max} \), 5.2 ± 0.11/l min; and \( \text{VO}_{2} \) at LT, 3.97 ± 0.16/l/min. However, these subjects exhibited a high degree of heterogeneity in muscle fiber type composition of the vastus lateralis. The percent of Type I muscle fibers ranged from 38% to 83% (Table 1). As shown in Table 1, the subjects were divided into two groups according to their percentage of Type I fibers (i.e., above and below 56% Type I fibers) and then paired (i.e., 1 + 8, 2 + 9, 3 + 10, etc.). The High % Type I group (i.e., subjects 1–7, Table 1) possessed an average of 73±3% Type I fibers whereas the Normal % Type I group (i.e., subjects 8–14, Table 1) possessed an average of 48±2% Type I fibers. The percentage of muscle fiber area composed of Type I fibers reflected a similar pattern (i.e., 72±3% Type I area and 45±4% Type I area for the High and Normal groups, respectively). However, the respective High and Normal % Type I groups were very similar regarding \( \text{VO}_{2} \text{max} \) (i.e., 5.2±0.1 vs 5.1±0.2/l/min), \( \text{VO}_{2} \) at LT (i.e., 4.0±0.1 vs 3.9±0.2/l/min) and years of bicycle training (i.e., 6±1 vs 4±1 yrs).

**One-hour performance bout**

Table 1 indicates that the average \( \text{VO}_2 \) for each pair of subjects during the one-hour performance bout was indeed within 0.1/l/min of each other and thus the High and Normal % Type I groups were identical regarding their average rate of energy expenditure. This represented approximately 86–88% of \( \text{VO}_{2} \text{max} \). However, despite the similarity of energy expenditure during the one-hour performance bout, the average power output of the High % Type I group was 9% (\( p<0.05 \)) higher than the Normal % Type I group (i.e., 342±9 vs 315±11 watts; Table 1). When comparing each pair of subjects, in all cases the subject belonging to the High % Type I group was more powerful (Table 1). As shown in Fig. 1, gross cycling efficiency during the one-hour performance bout was positively correlated with % Type I muscle fibers (i.e., \( r = 0.75 \); \( p<0.001 \)). The average pedalling cadences during the 1 h performance bout were nearly identical for the two groups (i.e., 91±1 vs 89±1 RPM for the Normal and High % Type I groups, respectively). These pedalling rates are typical for endurance cycling events (14).

**Table 1** Comparison of the % Type I muscle fiber composition, average oxygen consumption (\( \text{VO}_2 \)) and average power (watts) during the 1 h performance bout for the individual subjects and pairs.

<table>
<thead>
<tr>
<th>Subject Pair</th>
<th>Muscle Fiber Composition (% Type I)</th>
<th>Performance ( \text{VO}_2 ) (l/min)</th>
<th>Performance Power (Watts)</th>
<th>Performance Power (Watts)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High % Type I</td>
<td>Normal % Type I</td>
<td>High % Type I</td>
<td>Normal % Type I</td>
</tr>
<tr>
<td>1 + 8</td>
<td>83</td>
<td>46</td>
<td>4.62</td>
<td>4.67</td>
</tr>
<tr>
<td>2 + 9</td>
<td>77</td>
<td>54</td>
<td>4.39</td>
<td>4.38</td>
</tr>
<tr>
<td>3 + 10</td>
<td>76</td>
<td>49</td>
<td>4.59</td>
<td>4.54</td>
</tr>
<tr>
<td>4 + 11</td>
<td>76</td>
<td>55</td>
<td>4.12</td>
<td>4.06</td>
</tr>
<tr>
<td>5 + 12</td>
<td>70</td>
<td>38</td>
<td>4.61</td>
<td>4.66</td>
</tr>
<tr>
<td>6 + 13</td>
<td>64</td>
<td>45</td>
<td>4.00</td>
<td>4.01</td>
</tr>
<tr>
<td>7 + 14</td>
<td>62</td>
<td>52</td>
<td>5.00</td>
<td>4.91</td>
</tr>
<tr>
<td><strong>Mean ± SE</strong></td>
<td><strong>73±3</strong></td>
<td><strong>48±2</strong></td>
<td><strong>4.48±0.13</strong></td>
<td><strong>4.46±0.13</strong></td>
</tr>
</tbody>
</table>

High % Type I Group (subjects 1–7) possessed more than 56% Type I fibers whereas the Normal % Type I Group possessed 38–55% Type I fibers (subjects 8–14). The subjects were paired according to the criteria in methods section.

*Significantly greater than Normal % Type I Group (\( p<0.002 \)).

(Statistical differences are determined between the matched subject pairs using Student’s t-test, and the groups differed in % Type I muscle fibers, with the High % Type I group having more than 56% Type I fibers and the Normal % Type I group having 38–55% Type I fibers. The Pearson product moment formula was used to calculate the correlation coefficient. Statistically significant differences are reported at \( p<0.05 \).)
Subjects grouped according to gross efficiency

In order to examine these data devoid of potential investigator bias when selecting subject pairs, subjects were ranked based upon their gross efficiency during the 1 h performance bout and then were formed into two equal groups of seven subjects each. When this was done the gross efficiency of one group was 22.10±0.21% (i.e., High Efficiency) whereas the gross efficiency of the other group was 20.26±0.20% (i.e., Low Efficiency). These two groups displayed a significant (p<0.05) difference in muscle fiber type composition with the High Efficiency group possessing 70±4% Type I fibers compared to 51±4% Type I fibers for the Low Efficiency group. These two groups maintained an identical average VO₂ during the one hour performance bout (i.e., 4.47±0.131/min), while the High Efficiency group generated 10% more power than the Low Efficiency group (i.e., 34±8 vs 31±10 watts).

Discussion

The observation that mechanical efficiency while cycling is highly correlated with the percentage of Type I muscle fibers within the vastus lateralis muscle (i.e., r = 0.75, p<0.001; Fig. 1) is in agreement with the data from our previous work (8). The present investigation was specifically designed to examine how this relationship influences cycling performance. Clearly, superior mechanical efficiency while cycling would be expected to provide a performance advantage. However, no study has directly determined that high mechanical efficiency, associated with having a relatively high percentage of Type I muscle fibers, results in greater cycling performance.

Having access to a population of competitive cyclists with homogeneous characteristics and training, we were able to create two groups that were identical regarding VO₂max and VO₂ at LT, yet who differed greatly in their muscle fiber composition within their vastus lateralis. Interestingly, during the one-hour laboratory performance test, the subject pairs, and therefore the High and Normal % Type I groups, maintained a very similar average VO₂ and thus similar rates of energy expenditure. Therefore, the 9% greater average power output during the performance test displayed by the High % Type I group, compared to the Normal % Type I group, was due to greater gross efficiency when cycling. It should be realized that a 9% mean difference in performance power among homogeneously trained groups of competitive cyclists is quite large, with potential for much impact on their athletic standing. Even more remarkable, some of the subject pairs differed by as much as 13–15% in one-hour power performance despite comparable rates of oxygen consumption over the one hour period (i.e., Table 1, subject 2 vs 9; subject 4 vs 11).

These data can be grouped and analyzed in several different ways, all with the same basic findings. For example, to avoid grouping subjects according to their muscle fiber type, subjects were ranked and grouped according to their gross efficiency during the performance test. In this case, the High Efficiency and Low Efficiency groups were significantly different regarding their % Type I muscle fibers (i.e., 70±4% vs 51±4% Type I fibers; p<0.05). This indicates that the direct positive relationship between % Type I fibers and performance ability is robust in this population and not an artifact of the method used for data analysis and presentation.

The relationship between muscular efficiency and muscle fiber type is dependent upon the velocity of contraction (12,17). Peak muscular efficiency occurs when the contraction velocity is approximately one-third of the maximal velocity of contraction (Vmax) of the specific muscle fiber (17). Since the Vmax of the Type II muscle fibers in humans is three to five times higher than the Vmax of a Type I fiber (11), the absolute velocity at peak efficiency is also three to five times higher in a Type II muscle fiber when compared to a Type I muscle fiber. In mammalian muscle, the velocity of contraction at peak efficiency for Type I and Type II muscle fibers have been reported to be about 1 and 5 fiber lengths/sec, respectively (11,12).

We have recently reported that while cycling at similar pedalling rates as employed in the present study (i.e., 80–90 rpm), the vastus lateralis shortens at a rate between 1 and 1.5 fiber lengths/sec (8,11). Clearly, this contraction velocity is closer to the velocity of peak efficiency of a Type I fiber than a Type II fiber. It is likely that the subjects in the High % Type I group were more efficient during the 1 h performance bout than those in the Normal % Type I group because while cycling, a greater percentage of their active musculature was contracting at a velocity close to the velocity of peak efficiency of Type I muscle fibers.

A high percentage of Type I muscle fibers has been associated with superior 10 km running performance (10). In general, this observation has been assumed to indicate that possessing a relatively high percentage of Type I muscle fibers predisposes those individuals to have a greater aerobic capacity, possibly as a consequence of Type I muscle fibers having more mitochondria and thus higher oxidative ability than Type II fibers. Indeed, in untrained individuals, mitochondrial enzyme activity in Type I muscle fibers is roughly two-fold greater than that of Type II muscle fibers (3,18). However, this is not the case in well-trained endurance athletes who have been training intensely for several years (3,6,16), such as the subjects of the present study. Endurance athletes performing high intensity training for prolonged periods display almost equal mitochondrial activity of the Krebs cycle enzymes in Type I and Type II fibers (3,18), although enzymes related to fat oxidation and glycolysis are respectively higher and lower in Type I compared to Type II fibers (3).

In agreement with the idea that Type I and Type II fibers in well-trained endurance athletes do not differ in overall oxidative ability (i.e., to oxidize pyruvate), we found that the Normal and High % Type I groups were similar in both VO₂max and the percentage of VO₂max maintained for the 1 h performance bout (i.e., 86–88% VO₂max). Therefore, we have found no compelling evidence or strong support for the concept that Type I fibers in well-trained endurance athletes improve performance by allowing higher rates of energy expenditure. It should be realized, however, that the present study was not optimally designed to detect functional differences in the oxidative ability of Type I and Type II fibers of endurance athletes because the present subjects were paired based upon a similar VO₂max and VO₂ during the 1 h performance bout. These observations serve only to indicate that differences between Type I and Type II fibers in well-trained endurance athletes do not endow these athletes with markedly different oxidative function as reflected in VO₂max, blood lactate threshold or the percentage of VO₂max maintained for 1 hour. Therefore, well-trained
endurance athletes with a greater percentage of Type I muscle fibers are able to generate more power during high intensity endurance performance lasting about one hour compared to well-trained endurance athletes with a normal percentage of Type I muscle fibers, not because of a greater ability to resynthesize ATP aerobically, but apparently due to superior efficiency in converting the chemical energy from ATP hydrolysis during contraction, into mechanical work.

Regarding athletic performance, gross efficiency is the most practical and functional measure because it reflects whole body oxygen consumption. Gross efficiency reflects energy expenditure from all bodily processes. It has been recently shown that during intense exercise the vast majority of oxygen is consumed by the exercising muscles for power production and that VO$_2$ measurements at the mouth provide a valid reflection of changes within the exercising leg muscles (21,22).

The potential importance of mechanical and muscular efficiency to endurance performance is well recognized, especially in sports such as running, racewalking, and swimming. Since calculation of the actual physical work accomplished during these activities is not practical, it is common to simply determine the VO$_2$ required for movement at a given velocity, and term this “economy”. For a long time we have recognized that running and racewalking performance is significantly related to the economy of motion (9,15). Using a similar approach to our present study, Conley and Krahenbuhl (4) assembled a group of competitive runners who were very similar in training and VO$_2$-max. In this homogeneous population of runners they found that most of the variation in 10 km running performance was accounted for by differences in running economy. This is similar to our present findings that cycling performance is largely determined by gross cycling efficiency in our group of homogeneous cyclists.

However, despite extensive research, investigators have failed to identify the biomechanical or physiological factors that are primarily responsible for determining running economy (19,20). We think it is quite possible that muscle fiber type also influences running economy, although we recognize that the mechanics of running are more complex than cycling and thus prone to the variable influence of other factors. Bosco et al. (1) reported a significant positive correlation between economy and percentage of Type I muscle fibers (r = 0.75, p<0.001). Therefore, although energy expenditure during the 1 h performance test was similar, the group of cyclists with a higher than normal percentage of Type I muscle fibers were able to generate 9% (p<0.002) more power throughout the 1 h performance bout. In competitive endurance-trained cyclists, it seems clear that gross efficiency is positively related to % Type I muscle fibers and that cyclists with a relatively high percentage of Type I muscle fibers display at least a 9% greater performance ability than equally well-trained cyclists possessing a normal muscle fiber type composition.

References


