Influence of peak $\dot{V}O_2$ and muscle fiber type on the efficiency of moderate exercise

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ABSTRACT

MALLORY, L. A., B. W. SCHEUERMANN, B. D. HOELTING, M. L. WEISS, R. M. MCALLISTER, and T. J. BARSTOW. Influence of peak $\dot{V}O_2$ and muscle fiber type on the efficiency of moderate exercise. *Med. Sci. Sports Exerc.*, Vol. 34, No. 8, pp. 1279–1287, 2002. **Purpose:** The purpose of this study was to determine if %Type I fibers and/or aerobic fitness (as peak $\dot{V}O_2$) would predict Δ efficiency (ΔEff) and $\Delta\dot{V}O_2$/Δwork rate (WR) for moderate (below lactate threshold <LT) constant work rate exercise in subjects with diverse level of fitness and fiber type. **Methods:** Twenty-two subjects (15 male, 23 ± 6 yr) heterogenous for fitness (peak $\dot{V}O_2$: 43.9 ± 7.1 $mL\cdot kg^{-1}\cdot min^{-1}$) were tested. On 3 different days, each subject performed constant load exercise for 6 min at work rates corresponding to 30, 50, 70, and 90% LT, separated by 6 min of 10% LT pedaling. After a short rest, each subject then completed 8 min of exercise at a WR corresponding to 50% of the difference between LT and peak $\dot{V}O_2$ (Δ50%). The mean $\dot{V}O_2$ determined for the last 3 min of each <LT WR was regressed against the absolute WR for each subject and trial. **Results:** The group mean $\Delta\dot{V}O_2/\Delta WR$ was 10.1 $mL\cdot min^{-1}\cdot W^{-1}$ (range 8.6–11.2 $mL\cdot min^{-1}\cdot W^{-1}$), whereas the mean ΔEff was 28.0% (range 24.5–32.0%); both were significantly inversely correlated with each other ($r = 0.972$, $P < 0.0001$). ΔEff was significantly negatively, and $\Delta\dot{V}O_2/\Delta WR$ positively, correlated with peak $\dot{V}O_2$ ($r = -0.51$ and 0.57, respectively; both $P < 0.01$), but not to % Type I fibers ($r = 0.01$ and 0.11, $P > 0.05$). **Conclusion:** These results suggest that aerobic fitness affects the energetic response to changes in power output during moderate exercise, such that the more aerobically fit a subject, the greater the increase in oxygen cost ($\dot{V}O_2$) (reduced efficiency) as work rate increases. Further, $\Delta\dot{V}O_2/\Delta WR$ reflects the inverse of ΔEff for moderate-intensity exercise in healthy fed subjects. **Key Words:** EFFICIENCY, DELTA EFFICIENCY, ECONOMY, OXYGEN UPTAKE, CYCLING

Determining the efficiency of muscle contractions *in vivo*, especially in humans, is difficult, given the inherent problems in measuring energy transformations directly in the muscle. One solution has been to calculate the ratio of the mechanical work or power performed to the overall energetics (as work + heat) of the whole body. This latter term can be estimated by converting oxygen uptake ($\dot{V}O_2$), measured at the mouth as the whole-body $\dot{V}O_2$, to energy using caloric equivalents based on the respiratory quotient (RQ) (24). Various efficiency terms can then be calculated (14,37), including gross efficiency (when the entire $\dot{V}O_2$ is used), net efficiency (if the $\dot{V}O_2$ is corrected for resting metabolism), or work efficiency (when resting metabolism plus the cost of moving the limbs against no external load is subtracted). Finally, delta efficiency (ΔEff) can be calculated by expressing the change in total energy output for a given change in mechanical power output (14,37). ΔEff is considered by some (14) but not all authors (37) as the best index of muscle contraction.

Another commonly used method is to express the metabolic response (as $\dot{V}O_2$) relative to the power output, termed economy. The slope of this relationship ($\Delta\dot{V}O_2/\Delta WR$) represents approximately the reciprocal of ΔEff, without the RQ modification of the energy equivalent for the $\dot{V}O_2$. Previous studies have reported an average $\Delta\dot{V}O_2/\Delta WR$ of about 10 $mL\cdot min^{-1}\cdot W^{-1}$ for humans performing moderate exercise on a cycle ergometer, but the standard deviations often approach 1.0 (16–18). Calculations of ΔEff also show similar intersubject differences (12,14,36). This suggests the existence of a relatively large intersubject variation.

Previously, we have found that the amplitude of the initial rise in $\dot{V}O_2$ during phases I and II (i.e., over the first 2–3 min on average) of heavy constant work rate exercise (above the lactate threshold, LT) was inversely related to both fitness (as peak $\dot{V}O_2$) and to the percentage of Type I fibers of the vastus lateralis, i.e., the greater the peak $\dot{V}O_2$ or % Type I fibers, the greater the initial rise in $\dot{V}O_2$ (3). Because on average this initial or primary $\dot{V}O_2$ response (before any slow component of $\dot{V}O_2$ begins) rises linearly with increases in work rate (2,5,18,32), these results predicted that the differences in the $\dot{V}O_2$ response (and thus in efficiency) for heavy exercise associated with differences in fitness and/or fiber type distribution might also exist for moderate exercise.

Previous work that explored possible determinants of ΔEff have provided conflicting results, with some reporting no apparent influence of fiber type (26,39) or maximal oxygen uptake (38), whereas others (12) found a positive relationship between percent Type I fibers and ΔEff. However, these previous studies explored these relationships in fit to highly trained subjects. It remains currently unclear to what extent, if any, fitness and/or fiber type distribution

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0195-9131/02/3408-1279/$3.00/0
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Submitted for publication August 2001.
Accepted for publication April 2002.

TABLE 1. Summary of metabolic simulator results.

	Target Value[a]		Observed		Err
	Mean	SD	Mean	SD	(%)
Low metabolic rate					
$\dot{V}o_2$ (mL·min^{-1})	330	1.3	321	7	−3.0
$\dot{V}co_2$ (mL·min^{-1})	323	1.4	309	7	−4.3
Medium metabolic rate					
$\dot{V}o_2$ (mL·min^{-1})	1655	6	1617	27	−2.3
$\dot{V}co_2$ (mL·min^{-1})	1619	6	1596	23	−1.4
High metabolic rate					
$\dot{V}o_2$ (mL·min^{-1})	2899	11	2870	57	−1.0
$\dot{V}co_2$ (mL·min^{-1})	2832	11	2804	36	−1.0

[a] Target value determined using manufacturer's software; based on daily environmental conditions and tank FCO_2.

influence ΔEff in less fit or sedentary subjects. The purpose of the present study, therefore, was to test the hypothesis that individual differences in ΔEff which might exist for moderate-intensity exercise (<LT) are positively related to differences in fitness (as peak $\dot{V}O_2$) or muscle characteristics (% Type I fibers, citrate synthase activity) of the vastus lateralis (i.e., the greater the peak $\dot{V}O_2$ or % Type I fibers, the higher the ΔEff). To test this hypothesis, we evaluated ΔEff and $\Delta\dot{V}O_2/\Delta WR$ obtained from steady state moderate (<LT) exercise in a large group of subjects with varying percentages of fiber type distribution and levels of aerobic fitness, ranging from sedentary subjects to national-caliber cross-country runners.

METHODS

Subjects. Twenty-two healthy subjects (7 female, 15 male), free of known cardiovascular, respiratory, or metabolic diseases, provided verbal and written consent to participate in the study, after having all procedures and risks explained to them. The experimental protocol had been approved by the Institutional Review Board for Research Involving Human Subjects at Kansas State University. Mean (±SD) age of the subjects was 23.4 (5.9) yr, and body mass averaged 71.1 (12.0) kg.

Protocol. Subjects reported to the Human Exercise Physiology Laboratory at Kansas State University on four to five separate occasions over a 2- to 4-wk period, at approximately the same time of day for each subject. Subjects were instructed to consume only a light meal before arriving at the laboratory and to abstain from vigorous exercise for at least 12 h before the exercise testing. Seat height on the cycle ergometer (Corival 400, Lode, The Netherlands) was set so as to produce a slight bend in the knees with the heels on the pedals. Seat height and handlebar position were recorded for each subject on the first visit and replicated for all subsequent experiments.

The first visit was used to familiarize the subject with the exercise testing procedures, and for determination of peak $\dot{V}O_2$ and the lactate threshold (LT) estimated from gas exchange. Each subject performed incremental (ramp) exercise to volitional fatigue using the following protocol: unloaded cycling for 4 min, progressive exercise during which the power output rose linearly (ramp) until volitional fatigue, and 6 min of recovery at unloaded cycling. The rate of change (slope) of the ramp varied from 15 to 35 W·min^{-1}, depending on relative fitness of the subject, so as to lead to fatigue in 10–12 min. Pulmonary gas exchange and heart rate were monitored breath-by-breath throughout the test (see below). Off-line, the data were averaged over 10-s intervals, from the start of exercise, to reduce breath-by-breath variations for detection of peak $\dot{V}O_2$ and the LT. Peak $\dot{V}O_2$ was defined as the highest 10-s average during the test. The LT was estimated noninvasively from visual inspection of the gas exchange responses using plots of the V-slope, ventilatory equivalents and end-tidal gas tensions. From the results of the ramp test, five power outputs were selected which were predicted to require a $\dot{V}O_2$ equivalent to 30, 50, 70, and 90% of the LT, and 50% of the difference between the LT and peak $\dot{V}O_2$ (Δ50%).

On subsequent visits to the laboratory, each subject cycled for 6 min at work rates corresponding to 30, 50, 70, and 90% of his/her respective LT in random order separated by 6 min of cycling at 10% LT. After 5–10 min of rest off the cycle seat, the subjects exercised for 8 min at Δ50%. This protocol of four < LT and one Δ50% work rate bouts was repeated in the same order for a given subject on two other days.

Gas exchange measurements—calibration and validation. Pulmonary gas exchange ($\dot{V}O_2$ and $\dot{V}CO_2$) and minute expired ventilation ($\dot{V}E$) were measured breath-by-breath throughout the protocol using a metabolic measurement system (MedGraphics Cardio2, Medical Graphics Corp., St. Paul, MN). Heart rate was determined from the electrocardiogram using a modified V5 configuration, with the values stored in the breath-by-breath data file. The O_2 and CO_2 analyzers were calibrated using gases of known concentrations before each exercise test, whereas the volume signal was calibrated with a syringe of known volume (3.0 L). Dynamic validation of the breath-by-breath measurement system was performed on each day of testing by use of a gas exchange simulator (GESV, Medical Graphics Corp.) (21). Over the course of the present study (9 months of data collection), the average accuracy, relative to the manufacturer's target values, was −3.0%, −2.3%, and −1.0% for $\dot{V}O_2$, and −4.3%, −1.4%, and −1.0% for $\dot{V}CO_2$, for low, moderate, and high simulated metabolic rates, respectively (Table 1).

Muscle biopsy. Once all testing was completed, on a separate day, three to four muscle biopsies, approximately 50–100 mg each) were taken from one incision site on the right vastus lateralis of each subject by using standard needle-biopsy techniques. The largest sample (based on visual inspection) was mounted in embedding medium before freezing, whereas the remaining samples were combined and immediately frozen in isopentane cooled to its freezing point by liquid nitrogen. Both sets of samples were stored at −80°C until further analysis. Muscle oxidative capacity was estimated from one of the biopsy samples by using spectrophotometric techniques for measurement of activity of citrate synthase (CS). To determine muscle fiber type distribution (proportion of I vs II), serial cross-sections (8–10 μm thick) were cut in a cryostat maintained at −18 to −20°C and mounted onto microscope slides. The sections for myofibrillar ATPase histochemistry were preincubated at a pH of 10.0. According to their lability to the alkaline preincubation, the fibers were classified as either Type I or II (7). On average, 566 (range 200–1460) fibers were counted for each subject. The number of Type I and II fibers were expressed as a percentage of the total number of fibers counted.

Data analysis. For each day, the last 3 min of the $\dot{V}O_2$ response to each $<$ LT work rate was averaged and plotted against the corresponding work rate. The slope ($\Delta\dot{V}O_2/\Delta WR$) was then determined from linear regression of the 4 $<$ LT points. The three daily slopes for each subject were then averaged together to derive a single value for each subject for comparison with peak $\dot{V}O_2$, fiber type distribution, and citrate synthase levels.

ΔEff was calculated for each trial for each subject as follows. The average $\dot{V}O_2$ response for each work rate for each trial was converted to W ($W = J \cdot s^{-1}$), utilizing the caloric equivalent for the $\dot{V}O_2$ determined from the measured respiratory quotient ($RQ = \dot{V}CO_2/\dot{V}O_2$) (24):

$$\dot{V}o_2(W) = [\dot{V}o_2(mL \cdot min^{-1}) * 0.001\ mL \cdot L^{-1} * Cal\ Equiv(kcal \cdot L^{-1} O_2)$$

$$* 4185\ J \cdot kcal^{-1}]/60\ s \cdot min^{-1}$$

where Cal Equiv ($kcal \cdot s^{-1}\ O_2$) $= 4.686 + (RQ - 0.707)/0.293) * 0.361$ (24). If the RQ exceeded 1.00 (reflecting small measurement variability in $\dot{V}CO_2$ and/or $\dot{V}O_2$ rather than appreciable anaerobiosis for this moderate work intensity), a value of 1.00 was used. ΔEff was then calculated as the slope of the power output (W):$\dot{V}O_2$ (W) relationship for each day.

To determine the primary amplitude of the $\dot{V}O_2$ response for the $>$LT exercise bouts, the breath-by-breath $\dot{V}O_2$ response for each transition was interpolated to produce data once per second and time aligned to the start of exercise. The pattern of response for each individual day/transition and for the average of the three responses for each subject were then determined using a three exponential plus time delay model as previously described (3), with the exception that the exponential terms have been indexed 1–3 rather than 0–2 as previously done.

$$\dot{V}o_2(t) = Vo_2(BSL) + A_1 \cdot (1 - e^{-t/\tau 1}) + A_2 \cdot (1 - e^{-(t-TD)/\tau 2})$$

$$+ A_3 \cdot (1 - e^{-(t-TD2)/\tau 3})$$

The exponential term describing phase I kinetics was truncated at the onset of phase II (i.e., at TD_1) and the relevant amplitude of phase I (A_1') calculated according to the equation,

$$A_1' = A_1 \cdot (1 - e^{-TD1/\tau 1})$$

In this way, the first exponential term is descriptive up to the value of TD_1, after which it becomes a constant. The physiologically relevant increase in $\dot{V}O_2$, that is, the amplitude of phase I and phase II (A_2') was determined as the sum of $A_1' + A_2$. For the present analysis, A_2' was used as an estimate of the initial $\Delta\dot{V}O_2/\Delta WR$ value before the onset of the slow component of the $\dot{V}O_2$ response (3).

Linear correlation analysis was performed between $\Delta\dot{V}O_2/\Delta WR$ or ΔEff as the dependent variable and each of the potential predictors or independent variables: peak $\dot{V}O_2$, % Type I fibers, and citrate synthase activity. For all statistical comparisons, the *a priori* level of significance was set for $P < 0.05$. Averaged data are reported as mean (±SD) unless otherwise noted.

RESULTS

Subject characteristics. Peak $\dot{V}O_2$ for the subjects averaged 3.11 (0.67) $L \cdot min^{-1}$ or 43.9 (range 34.3–59.2) $mL \cdot kg^{-1} \cdot min^{-1}$. Estimated lactate threshold LT averaged 1.90 (0.35) $L \cdot min^{-1}$ or 62.3 (5.7) % of peak $\dot{V}O_2$. Percentage slow-twitch fibers in the vastus lateralis averaged 39.4% (range 19–58%), whereas citrate synthase activity averaged 11.9 (range 6.4–22.7) $\mu mol \cdot min^{-1} \cdot g^{-1}$. Peak $\dot{V}O_2$ was significantly correlated with both % slow-twitch fibers ($r = 0.446$, $P < 0.05$) and with citrate synthase activity ($r = 0.72$, $P < 0.0001$).

Δ $\dot{V}O_2$/ΔWR and ΔEff. Figure 1 (top panel) shows for one subject the steady state $\dot{V}O_2$ values for each of the four $<$LT work rates for the three trials, along with the linear regression determined for each trial. On average, the steady-state $\dot{V}O_2$ values represented 27, 34, 41, and 50% of peak $\dot{V}O_2$. Group mean values for $\Delta\dot{V}O_2/\Delta WR$ for days 1–3 were 10.10 (0.87), 9.83 (0.87), and 10.11 (0.97) $mL \cdot min^{-1} \cdot W^{-1}$, respectively. The group mean value of the intrasubject averages across the 3 d was 10.01 (0.77) $mL \cdot min^{-1} \cdot W^{-1}$, with a corresponding coefficient of variation (CV) of 7.7%. The mean value of the intrasubject standard deviations for the slope was 0.43 $mL \cdot min^{-1} \cdot W^{-1}$, representing an average CV of 4.3 (2.3) % across days. Thus, the intersubject variation was greater than the day-to-day variance within a subject. Finally, the average $\Delta\dot{V}O_2/\Delta WR$ determined for each subject from the constant work rate trials was well correlated with that calculated from the ramp exercise test over a similar range of moderate work rates, but the ramp slopes tended to underestimate the constant work rate (CWR) slopes (ramp slope $= 2.74 + 0.688 \times$ CWR slope, $r = 0.65$, $P < 0.005$).

Figure 1 lower panel shows the corresponding ΔEff values for the same subject as in the top panel. Group mean ΔEff for days 1–3 were 27.5 (2.4), 28.2 (2.3), and 28.0 (2.6)%. The group mean of the intrasubject averages for the 3 d was 27.9 (2.2)%, with an associated CV of 7.7%. The mean of the intrasubject standard deviations was 1.3%, which represented an average 4.8 (2.8)% CV across days. Thus, as with $\Delta\dot{V}O_2/\Delta WR$, the intersubject variation for ΔEff was greater than the day-to-day variation within a subject. Finally, the intrasubject averages of ΔEff for the 3 d was highly inversely correlated with the $\Delta\dot{V}O_2/\Delta WR$ slope ($r = -0.972$, $P < 0.0001$), demonstrating that the effect of the correction for the energy equivalent of the substrate mix (from the RQ) had a minimal effect on the calculated efficiency.

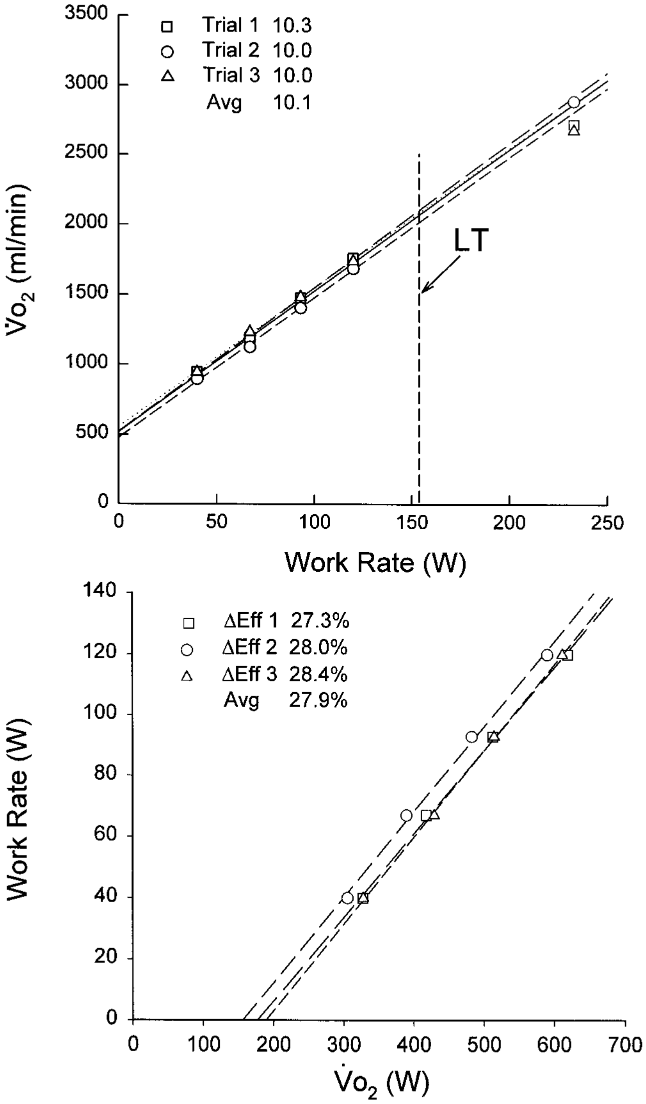

FIGURE 1—Example of the steady state $\dot{V}O_2$ (upper panel) and the associated energy equivalent (in W) (lower panel) for the 4 <LT work rates for each of the three trials, in one subject. *Lines* represent linear regressions determined from the <LT work rates for each trial. Data to the right of the LT line, in upper panel only, represent amplitude of the primary component of the $\dot{V}O_2$ response during the Δ50% work rate for each respective trial but were not included in the regression analysis nor shown in the lower panel.

Prediction of $\Delta\dot{V}O_2/\Delta WR$ or ΔEff by linear regression. Figure 2 shows the relationship between $\Delta\dot{V}O_2/\Delta WR$, and Figure 3 between ΔEff, and the three putative predictors evaluated here: peak $\dot{V}O_2$, % slow-twitch fibers, and CS activity. Only peak $\dot{V}O_2$ was significantly related to the $\Delta\dot{V}O_2/\Delta WR$ slope ($r = 0.57$, $P < 0.01$) and to ΔEff ($r = 0.51$, $P < 0.01$).

$\Delta\dot{V}O_2/\Delta WR$ and the exercise oxidative substrate mix (RQ). One source of variability in the efficiency of exercise across subjects could be differences in oxidative substrate utilization (i.e., as a difference in P:O or P:O_2 between fatty acids and carbohydrate). However, the average RQ values for the 90% LT work rate fell in the range between 0.86 and 1.04, and were not correlated with ΔEff ($r = 0.152$) or with the $\Delta\dot{V}O_2/\Delta WR$ ($r = 0.157$).

Initial amplitude (A_2') for heavy exercise (Δ50%). The power output for the Δ50% transitions averaged 191 (37) W. The initial amplitude for the $\dot{V}O_2$ response (A_2') during these transitions for days 1–3 averaged 95.5 (6.5), 100.0 (8.6), and 99.1 (8.0) % of that predicted from extrapolation of the <LT $\Delta\dot{V}O_2/\Delta WR$ for that day. The group mean value for the 3-d average for each subject was 97.2 (4.5)% of the predicted level, not significantly different from 100% ($P > 0.05$). Thus, on average, the initial rise in $\dot{V}O_2$ during the first 2–3 min of >LT exercise was well predicted by the $\Delta\dot{V}O_2/\Delta WR$ slope determined from <LT exercise. However, when the individual responses were examined (Fig. 4), there was a significant inverse relationship between the observed A_2' as a percentage of the value predicted from the <LT slope and the $\Delta\dot{V}O_2/\Delta WR$, i.e., subjects with a higher $\Delta\dot{V}O_2/\Delta WR$ slope tended to slightly undershoot the predicted A_2' value for the Δ50% work rate. A similar inverse, but marginally insignificant, relationship was found between A_2' as a % predicted and peak $\dot{V}O_2$ ($r = 0.351$, $P = 0.07$).

DISCUSSION

The observation of a linear relationship between $\dot{V}O_2$ and light to moderate work rates is not new (e.g., (5,16,17,32,39)). However, despite the awareness of appreciable intersubject variability in the slope of this relationship, there appears to have been little previous systematic evaluation of the potential sources of this variability across fitness levels. This is the first study, to our knowledge, that has systematically examined the extent of the intersubject variability in ΔEff and $\Delta\dot{V}O_2/\Delta WR$ of truly moderate (<LT) constant work rate exercise in a moderately large group of subjects heterogeneous for aerobic fitness. Several new findings emerged from our study. First, day-to-day variability in ΔEff and $\Delta\dot{V}O_2/\Delta WR$ within a subject were less than the differences observed across subjects, suggesting that the intersubject differences in ΔEff and $\Delta\dot{V}O_2/\Delta WR$ reflect real physiological differences. Second, ΔEff was inversely, and $\Delta\dot{V}O_2/\Delta WR$ positively, related to fitness as peak $\dot{V}O_2$. However, neither ΔEff nor $\Delta\dot{V}O_2/\Delta WR$ were related to % slow-twitch (Type I) fibers, nor to the activity of citrate synthase, in the vastus lateralis muscle. In addition, the $\Delta\dot{V}O_2/\Delta WR$ determined from the moderate exercise intensities predicted well the initial rise in $\dot{V}O_2$ (A_2') during heavy exercise (>LT). Finally, the $\Delta\dot{V}O_2/\Delta WR$ for moderate constant work rate exercise was significantly correlated with, but underestimated by, that determined from ramp exercise. These results demonstrate that the individual differences we previously reported for $\Delta\dot{V}O_2/\Delta WR$ for >LT exercise (3) are also present for moderate work rates (<LT).

Previous cross-sectional studies that have examined the relationship between fitness and measures of efficiency or $\Delta\dot{V}O_2/\Delta WR$ have produced equivocal results. Marsh et al. (25) found no difference in ΔEff across a range of pedal frequencies from 50 to 110 rpm among cyclists, runners, and less-trained subjects. However, at the higher power outputs

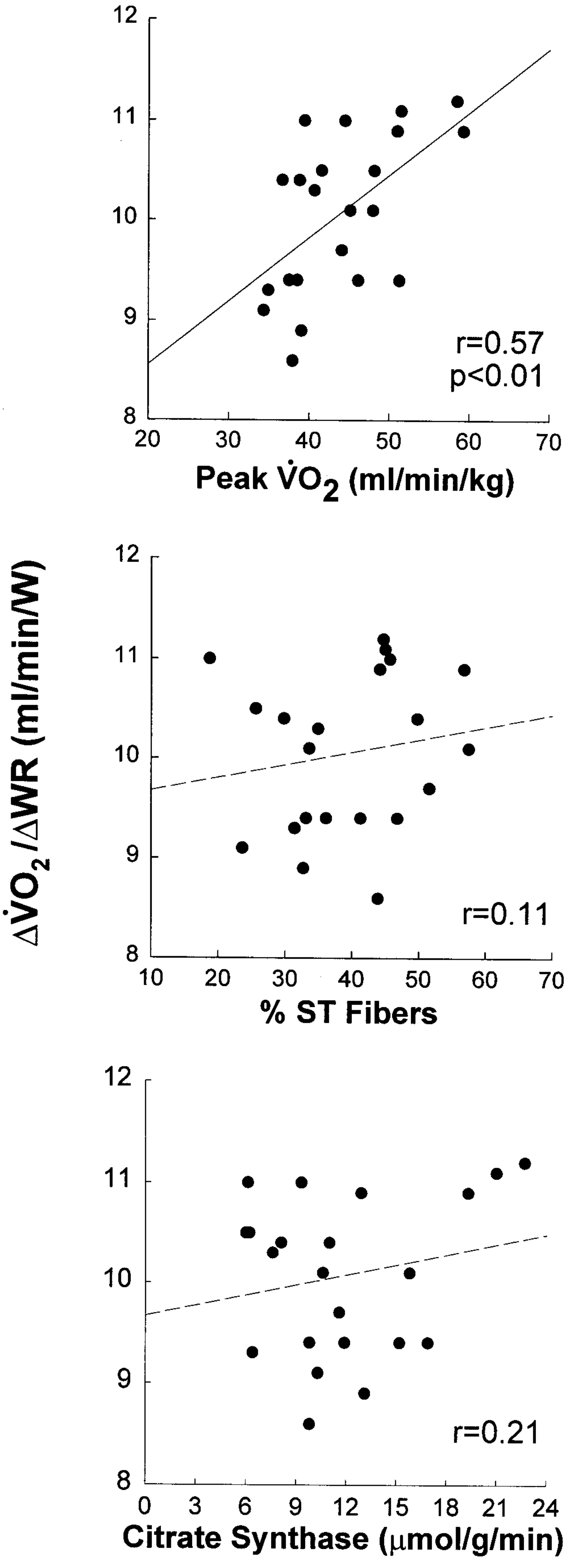

FIGURE 2—Relationships between $\Delta\dot{V}O_2/\Delta WR$ and peak $\dot{V}O_2$, % slow-twitch (ST) fibers, and citrate synthase of the vastus lateralis, in 22 subjects. Only the relationship with peak $\dot{V}O_2$ was significant.

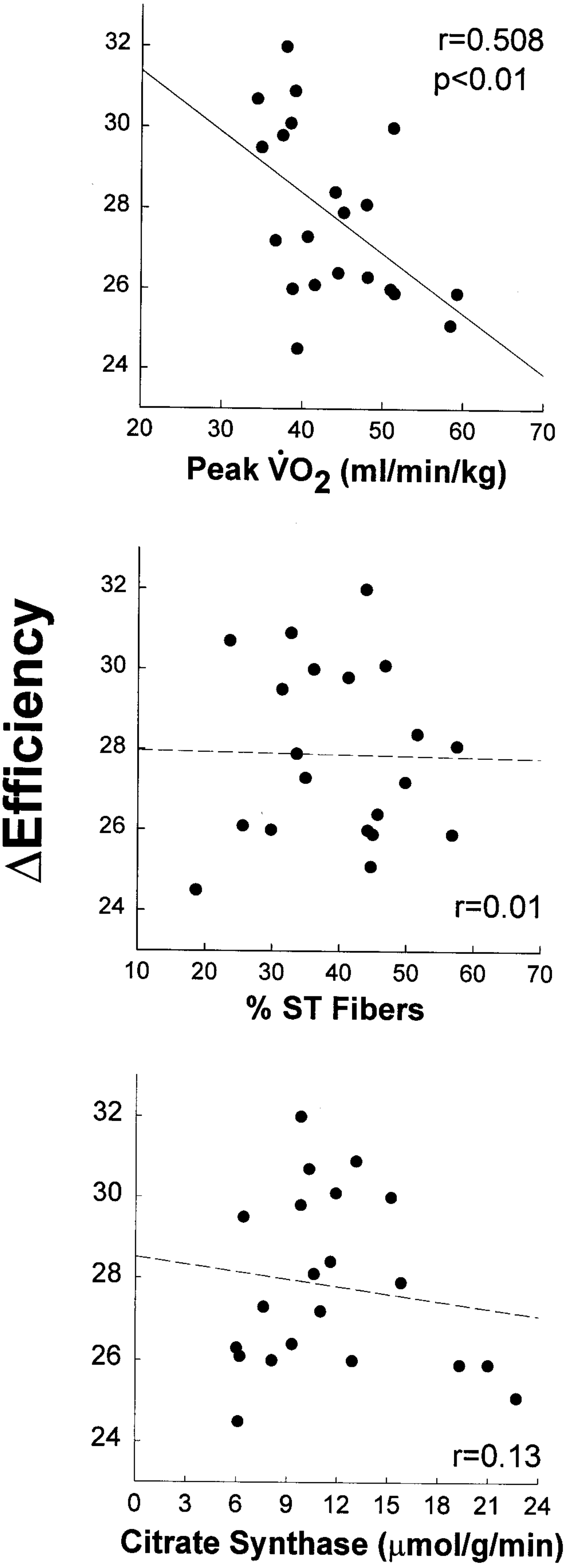

FIGURE 3—Relationships between ΔEff and peak $\dot{V}O_2$, % slow-twitch (ST) fibers, and citrate synthase of the vastus lateralis, in 22 subjects. Only the relationship with peak $\dot{V}O_2$ was significant.

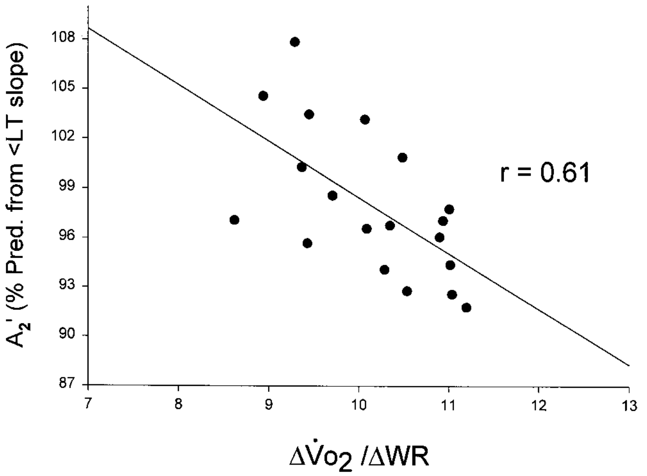

FIGURE 4—Measured amplitude of the primary rise in $\dot{V}O_2$ (A_2') for the Δ50% work rate as a percent of the value predicted from the $\Delta\dot{V}O_2/\Delta WR$ for the <LT work rates, plotted as a function of the $\Delta\dot{V}O_2/\Delta WR$ slope.

and pedal rates, the selected work rates for the less-trained subjects very likely exceeded their lactate thresholds. Thus, in the less fit subjects, the $\dot{V}O_2$ may have been artificially elevated (and the resulting ΔEff lower) due to the additional contribution of the slow component to the overall $\dot{V}O_2$ response known to occur for >LT exercise. If true, then a real difference in ΔEff between trained and untrained subjects over a range of moderate work rates, as implied by our data, would have been masked in the untrained subjects by a lower ΔEff due to additional $\dot{V}O_2$ of the slow component at the higher metabolic rates. Suzuki (39) also noted no difference in ΔEff between three subjects with high $\dot{V}O_{2max}$ (mean 61 $mL \cdot kg^{-1} \cdot min^{-1}$) and three with lower max values (44 $mL \cdot kg^{-1} \cdot min^{-1}$) at 60 rpm, but at 100 rpm the ΔEff was lower for the more fit group, consistent with the present findings. On the other hand, Boning et al. (6) found slightly higher $\dot{V}O_2$ values for untrained subjects, compared with trained cyclists, for several different work rates and pedal frequencies, although visual inspection of their data suggests the differences were primarily at the frequency extremes (40 and 100 rpm). Finally, Stuart et al. (38) found both ΔEff and instantaneous efficiency for light to moderate work rates to be similar between distance runners and sprinters, although both measures decreased more with increasing work rate in the distance runners, suggesting progressively less efficient responses in the aerobically fitter subjects as work rate increased, also consistent with the present results.

Similar ambiguity exists for longitudinal studies. Barbeau et al. (1) found that gross efficiency did not change in elite cyclists over a 9 months cycling season for exercise at 150 or 200 W for pedal rates ranging from 50 to 120 rpm, but at 250-W gross efficiency increased during the season, suggesting reduced $\dot{V}O_2$ response. In contrast, Hoogeveen (19) found a significant increase in $\dot{V}O_2$ for work rates from 200 to 400 W in elite cyclists over 6 months of training. In neither of these studies was ΔEff determined. It should be recognized that the $\dot{V}O_2$ response for the work rates in these two studies likely encroached upon (1) or exceeded (19) the lactate threshold for the subjects, which as noted above may have introduced an additional ("slow") component to the metabolic response (5) and, thus, reduced the apparent efficiency. If true, one would have predicted improved efficiency (reduced $\dot{V}O_2$ response) over time with training, due to a presumed decrease in the amplitude and relative contribution of the slow component to the overall response (9,10). This mechanism is consistent with the results of Barbeau et al. (1) but would not explain the findings of Hoogeveen (19).

Previously, we had reported significant relationships between percent Type I fibers in the vastus lateralis and both $\Delta\dot{V}O_2/\Delta WR$ determined from ramp exercise (4), and the gain (A_1'/W) for the primary component of the $\dot{V}O_2$ response during heavy (>LT) constant work rate exercise (3). (Note that A_1' in the previous study is identical to A_2' in the present study). In the present study, this finding was not supported in a larger heterogeneous group of subjects. It is presently unclear to what extent differences in fiber composition might translate into differences in ΔEff for humans performing moderate-intensity exercise. We have previously reviewed the differences between fast- and slow-twitch fibers which might affect the efficiency of contraction, and the literature regarding human subjects in which fiber composition was related to the energetics of muscle contractions (3,4,29). To summarize those reviews, although many of the studies in both isolated muscles and exercising humans suggest that Type I fibers are more efficient than Type II fibers, there are notable exceptions. Further complicating the interpretation of the results in isolated muscles is the fact that many of those studies were performed under near or maximal stimulation conditions (eliciting near maximal force production and motor unit recruitment), which may not be relevant to the low force and power outputs utilized in the present study.

Relevant to this discussion is whether or not Type II fibers might be recruited during light-to-moderate exercise as examined here, and whether or not any Type II fibers that are recruited would be discernibly different in their metabolic response, and specifically the efficiency (as ΔEff) or economy (as $\Delta\dot{V}O_2/\Delta WR$) of contractions. Regarding the first point, given the light to moderate intensity of the exercise utilized in the present study, and the relatively short duration of each bout of exercise (6 min), it is likely that Type I fibers were the predominant fiber type recruited, with at most a small contribution from Type II(a) fibers (15,23,40). Further, given the hierarchical order of recruitment of motor units (27), there is a likely dissociation between the fiber type distribution estimated from muscle biopsies, which represents the distribution of the whole population of fibers within the sampled muscle, and the relative distribution of fibers which are recruited for a given light-to-moderate intensity exercise task. A related factor that contributes to this uncertainty is the variability in the estimate of fiber type distribution due to sampling variability; one sample from one biopsy site in the quadriceps (as in the present study) may have a coefficient of variation approaching 9% (13).

Regarding the second point, although we have utilized a common strategy of dividing fibers into two to three general "types" based on the sensitivity of the myosin ATPase to pH, in fact, muscle fibers exhibit a spectrum, or continuum, of metabolic characteristics (23,28). Thus, fibers classified as Type II (or IIa) by the current approach may be very similar metabolically and structurally (e.g., mitochondrial and capillary densities, enzyme activities, oxidative capacity) to Type I fibers in the same mixed muscle. Consistent with this is the observation that, for the heavy exercise intensity (Δ50%) performed here, where recruitment of Type II fibers is likely, the initial amplitude of the $\dot{V}O_2$ response (A_2') was well predicted by the $\Delta\dot{V}O_2/\Delta WR$ slope determined from the moderate exercise intensities. If Type II fibers were recruited from the onset of exercise for the Δ50% work rate, these results suggest that the efficiency of these fibers was similar to those recruited to perform the moderate exercise (26). This interpretation is also consistent with our recent observation that similar heavy-intensity exercise for 8 min does not lead to recruitment of fibers that are discernibly different by EMG from those utilized for moderate (<LT) exercise (35). Alternatively, as suggested by Sargeant and Rademaker (33), even if the efficiency of Type I and II fibers differs in humans, at the rpm utilized in the present study (70 rpm), the difference may be relatively small (efficiency of about 18% for Type II and 23% for Type I fibers, based on their Fig. 2), and not readily discernible (their Fig. 3). Thus, upon further consideration, it does not seem probable that the intersubject differences in ΔEff or $\Delta\dot{V}O_2/\Delta WR$ observed for moderate exercise would be associated with differences in total fiber type distribution *per se*.

In addition to muscle fiber characteristics, biomechanical factors may affect peak power and/or the efficiency of cycle exercise, including seat height and cycle frame dimensions (31) and crank length (20). Although a detailed biomechanical analysis of body position was beyond the scope of this study, seat height was set so as to produce a similar leg extension (with slight bend at the knee) at bottom dead center for all subjects. We did not record leg length to ascertain its relationship to crank length; however, there was no significant correlation between seat height (as a surrogate for leg length) and ΔEff ($r = 0.30$, $P > 0.05$), suggesting that in this study, variation between leg length, and a constant crank length did not measurably contribute to the intersubject variability in ΔEff.

The observation that $\Delta\dot{V}O_2/\Delta WR$ is lower (and ΔEff is greater) for subjects with reduced peak $\dot{V}O_2$ is illustrated further in Figure 5. Shown are the individual subject data from the current study (solid circles) and the associated linear regression for these data, as well as individual subject data determined from ramp exercise in our preliminary report (upright open triangles) (3). In addition are plotted mean data for elderly subjects performing constant work rate exercise (open square) (34), obese subjects performing constant work rate exercise (solid diamond) (30), and mean values for healthy controls, and patients with class I and II heart failure (down open triangles, reading right to left) performing ramp exercise (22). Finally, the estimated mean value for ΔEff in trained cyclists from Coyle et al. (12) is shown (solid triangle), where the ΔEff for each subject was converted to $\Delta\dot{V}O_2/\Delta WR$ by using the regression from the present study. It is readily apparent that these data from other research labs on different subject groups follow the general trend in the relationship between $\Delta\dot{V}O_2/\Delta WR$ and peak $\dot{V}O_2$ seen in the present study.

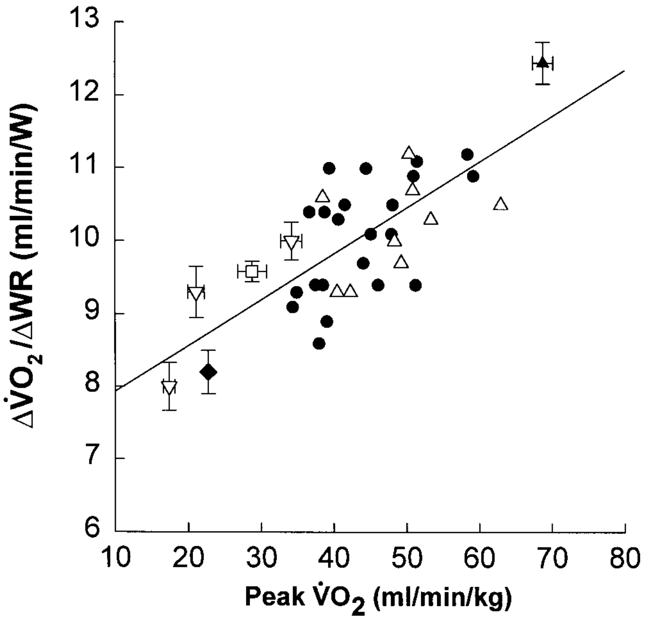

FIGURE 5—$\Delta\dot{V}O_2/\Delta WR$ as a function of peak $\dot{V}O_2$. ***Solid circles*** **represent the present study.** ***Open upright triangles*** **represent individual healthy subjects from our preliminary data (4).** ***Solid diamond*** **represents group mean data for obese women in ref. (30).** ***Open square*** **represents mean data for older subjects (34).** ***Upside-down triangles*** **represent mean data for (left to right) class II heart failure patients, class I heart failure patients, and age-matched controls from (22).** ***Solid triangle*** **represents data for trained cyclists (12).** ***Line*** **is the best-fit regression for the data in the current study.**

Another factor that may contribute to the intersubject variation in the ΔEff is the P:O ratio of oxidative phosphorylation, reflecting differences in substrate utilization. However, for this to be a primary mechanism for the observed differences in ΔEff, the fitter subjects would have had to start with predominantly carbohydrate oxidation at very light exercise intensities and shift to greater fatty acid oxidation as work intensity increased (contrary to the "crossover concept" (8)), whereas the less fit subjects would show the opposite trend (from greater fatty acid to greater carbohydrate oxidation) as work rate increased. In fact, all subjects demonstrated high carbohydrate oxidation during the 90% LT work rate, as evidenced by whole-body RQs above 0.92 with one exception (RQ = 0.86), which were not correlated with ΔEff. Thus, the differences in ΔEff across subjects could not be explained by the small differences in whole-body RQ.

Lastly, another potential mechanism for the observed differences in ΔEff and $\Delta\dot{V}O_2/\Delta WR$ among subjects could be differences in the stability of baseline metabolism as work rate is increased (37). For example, the "true" intramuscular efficiency could be relatively similar across all subjects. However, those subjects with a higher ΔEff could have had a reduction in baseline metabolism (e.g., fall in metabolism of the splanchnic and renal tissues and/or resting skeletal muscle) as work rate increased, compared with subjects with a lower ΔEff. Although previous studies have implied that splanchnic and renal blood flows decline similarly in trained and untrained subjects when expressed as a function of $\%\dot{V}O_{2max}$ (11), the precision of the data, specifically for work rates clearly below each subject's lactate threshold, is currently insufficient to address this hypothesis.

In conclusion, we found that intersubject differences in ΔEff and $\Delta\dot{V}O_2/\Delta WR$ are greater than within subject day-to-day measurement variability and that these differences are observable even for intentionally moderate ($<$LT) exercise intensities. Further, these differences were significantly correlated with aerobic fitness as estimated by peak $\dot{V}O_2$ but not directly with either % Type I fibers or citrate synthase activity of the vastus lateralis. These intersubject differences are not explained by small differences in substrate utilization among the subjects. Thus, for well-fed healthy subjects performing light to moderate steady-state exercise, $\Delta\dot{V}O_2/\Delta WR$ reflects the inverse of ΔEff.

We thank the subjects for their time commitment to this project, and L. A. Lloyd and J. E. Hix for technical assistance. L. A. Mallory was a McNair Scholar. B. W. Scheuermann was supported by a Medical Research Council of Canada Post Doctoral Fellowship. This work was supported in part by the National Heart, Lung and Blood Institute grants HL46769 to T. J. Barstow, and HL57226 to R. M. McAllister.

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