

Experimental Physiology

Influence of muscle fibre type and fitness on the oxygen uptake/power output slope during incremental exercise in humans

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We recently reported that a higher percentage of type I fibres in vastus lateralis and a greater peak oxygen uptake (\dot{V}_{O_2}) were associated with a greater initial rise in \dot{V}_{O_2} ($\Delta\dot{V}_{O_2}/\Delta W$, where W is work rate) following the onset of heavy constant power output exercise (above the lactate threshold, LT). It was unclear if these results were true only for heavy exercise, or if the association between fibre type and/or fitness and $\Delta\dot{V}_{O_2}/\Delta W$ would also be seen for moderate (< LT) exercise. The purpose of the present study was to compare the relationships between fibre type or peak \dot{V}_{O_2} and $\Delta\dot{V}_{O_2}/\Delta W$ determined for moderate (< LT) and heavy (> LT) exercise intensities during incremental exercise. Nine healthy subjects performed an incremental ramp test on a cycle ergometer. The \dot{V}_{O_2}/W slope was calculated for the domain of power outputs up to the LT (S_1), from the LT towards peak \dot{V}_{O_2} (S_2), and over the entire linear portion of the $\Delta\dot{V}_{O_2}/\Delta W$ response (S_T), and compared to fibre type distribution determined from biopsy of the vastus lateralis, and to peak \dot{V}_{O_2} (as $\text{ml kg}^{-1} \text{min}^{-1}$). Significant correlations between $\Delta\dot{V}_{O_2}/\Delta W$ and the proportion of type I fibres were found for each exercise domain (r is 0.69, 0.71 and 0.84 for S_1 , S_2 and S_T , respectively, $P < 0.05$). S_1 ranged between about $9 \text{ ml min}^{-1} \text{W}^{-1}$ for a low proportion of type I fibres and $11 \text{ ml min}^{-1} \text{W}^{-1}$ for a high proportion of type I fibres. Similar correlations were also found between S_2 ($r = 0.70$) and S_T ($r = 0.76$) and peak \dot{V}_{O_2} . These results are consistent with our previous findings during >LT constant power output exercise, and suggest that the proportion of type I fibres, and possibly fitness as indicated by peak \dot{V}_{O_2} , is associated with greater $\Delta\dot{V}_{O_2}/\Delta W$ during the initial adjustment to < LT as well as > LT exercise. These results do not appear to be explained by classical descriptions of the kinetics of adjustment of \dot{V}_{O_2} following the onset of ramp or constant power output exercise. They might reflect enhanced motor unit recruitment in subjects with a greater percentage of type I fibres, and/or who are more aerobically fit. However, the underlying mechanism for these findings must await further study. *Experimental Physiology* (2000), **85.1**, pp.109–116.

Previously, we characterized the kinetics of \dot{V}_{O_2} during heavy exercise (above the lactate threshold LT) as a function of the percentage of type I (slow twitch) muscle fibres present in the contracting muscles (Barstow *et al.* 1996). Figure 1 presents data from our previous study which illustrates the \dot{V}_{O_2} response for the subject with the greatest proportion of type I fibres (67%) and the subject with the least (18%). To our surprise, the initial, predominant rise in \dot{V}_{O_2} , normalized to the increase in power output (i.e. $\Delta\dot{V}_{O_2}/\Delta W$, or gain G_1 in Fig. 1), was significantly related to fibre type: the greater the proportion of type I fibres, the greater was the initial rise in \dot{V}_{O_2} . Further, the gain G_1 was directly related to the relative fitness of the subjects, as indicated by peak \dot{V}_{O_2} (in

$\text{ml kg}^{-1} \text{min}^{-1}$). Interestingly, after 8 min of exercise, there was no significant influence of fibre type on \dot{V}_{O_2} (Fig. 1).

It was unclear from our previous results if the greater initial $\Delta\dot{V}_{O_2}/\Delta W$ (G_1 of Fig. 1) seen with a greater proportion of type I fibres or peak \dot{V}_{O_2} was associated only with heavy exercise (> LT), or if it would also be seen for moderate intensities of exercise (< LT). From glycogen depletion patterns, type I fibres appear to be recruited first during exercise, with type II fibres being recruited as exercise intensity or duration increases (Gollnick *et al.* 1974; Vollestad & Blom, 1985). Based on this, we predicted that the influence of fibre type distribution on exercise energetics would be most pronounced at higher exercise intensities (i.e. > LT),

Table 1. Subject characteristics and parameters from ramp exercise test

Subject	Gender	Age yr	Weight kg	\dot{V}_{O_2} max l min ⁻¹	\dot{V}_{O_2} max ml kg ⁻¹ min ⁻¹	LT l min ⁻¹	Type I fibres %	$\Delta\dot{V}_{O_2}/\Delta W$ ml min ⁻¹ W ⁻¹		
								S ₁	S ₂	S _T
1	M	27	73	3.90	53.4	2.42	50	10.3	11.7	10.8
2	M	43	73	2.80	38.5	1.53	44	10.6	10.3	9.8
3	M	24	70	2.96	42.3	1.35	28	9.3	10.4	10.1
4	M	28	68	3.35	49.3	1.70	52	9.7	10.2	10.1
5	M	45	66	3.30	50.4	1.55	64	11.2	12.3	11.4
6	M	28	69	2.78	40.5	1.35	18	9.3	9.9	8.9
7	F	31	61	2.95	48.4	1.50	56	10.0	10.4	10.5
8	M	32	79	4.02	50.9	1.93	41	10.7	10.7	10.7
9	M	22	63	3.97	63.0	2.15	67	10.5	11.8	11.1
Mean		31	69.1	3.40	48.2	1.72	47	10.2	10.9	10.4
±SD		± 8	± 5.5	±0.52	± 7.1	±0.35	±16	±0.7	±0.9	±0.8

LT, lactate threshold, estimated from gas exchange responses. See text for definitions of S₁, S₂ and S_T.

where type II fibres are more likely to be recruited. Specifically, we hypothesized that: (a) for power outputs above the LT, where both type I and type II fibres would be recruited, the slope of $\Delta\dot{V}_{O_2}/\Delta W$ would significantly correlate with the proportion of type I fibres in the contracting muscles and with peak \dot{V}_{O_2} (as previously shown for heavy constant power output exercise; Barstow *et al.* 1996), but that (b) over the moderate power output range

(below the LT) where the primary fibre type recruited would be type I, any influence of differences in fibre type distribution or peak \dot{V}_{O_2} on the slope of $\Delta\dot{V}_{O_2}/\Delta W$ would be minimal. To test these hypotheses, we have now characterized the relationship between \dot{V}_{O_2} and power output during incremental (ramp) cycle ergometer exercise in the same nine subjects who had previously performed the constant heavy exercise bouts (Barstow *et al.* 1996). Slopes

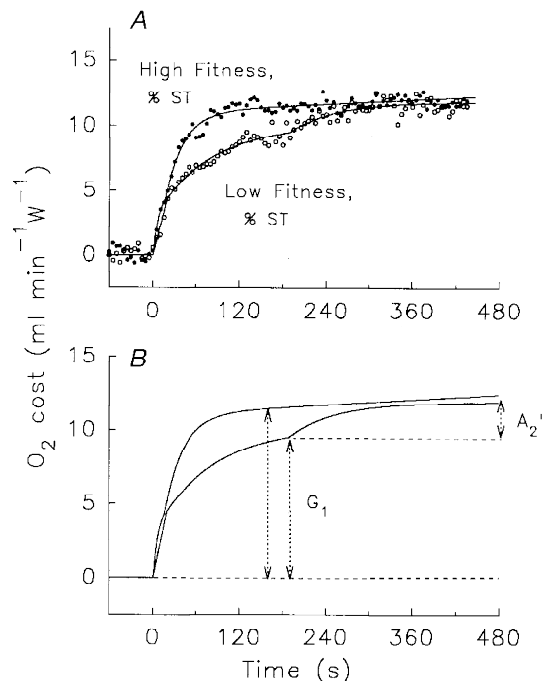


Figure 1

A, \dot{V}_{O_2} kinetics in the transition from light to heavy exercise in two subjects who differed in level of fitness and in the proportion of type I muscle fibres in their vastus lateralis, as reported previously (Barstow *et al.* 1996). B, schematic diagram summarizing differences in relative contribution of initial rise in \dot{V}_{O_2} following onset of exercise (as a gain G_1 , ml O₂ min⁻¹ W⁻¹) and relative contribution of slow component (A_2) for the two subjects in A. Modified from Barstow *et al.* (1996).

($\Delta\dot{V}_{O_2}/\Delta W$) were determined for the regions of exercise intensity corresponding to <LT, >LT and the whole response, and compared to the underlying fibre type distribution previously determined by muscle biopsy, as well as to peak \dot{V}_{O_2} .

METHODS

Subjects

Nine healthy volunteers (8 males), free of known cardiovascular, pulmonary or metabolic disease, gave written consent to participate in this study after all procedures and the possible risks and benefits of participation were explained. The experimental protocol and consent form were approved by the Human Subjects Committee of Harbor-UCLA Medical Center. This research was conducted in accordance with the Declaration of Helsinki. Subject characteristics are shown in Table 1.

Exercise protocol

Each subject performed an incremental (ramp) exercise test to volitional fatigue on an electromagnetically braked cycle ergometer (Quinton Corival model 844). The ramp protocol consisted of 2 min seated rest on the ergometer, 4 min of unloaded pedalling, the

ramp increase in power output to fatigue, then unloaded cycling recovery for 6 min (Fig. 2A). The slope of the power output increase was chosen so as to lead to fatigue in 8–12 min, and ranged from 25 to 35 W min⁻¹. Pedal frequency was kept constant at 60 r.p.m. throughout the exercise by visual feedback from a display mounted on the handlebars of the ergometer. Pulmonary ventilation (\dot{V}_E), gas exchange (\dot{V}_{O_2} and \dot{V}_{CO_2}) and heart rate were measured breath by breath throughout the exercise protocol as previously described (Barstow *et al.* 1993). Subjects were instructed to avoid the consumption of food, alcohol and caffeine for 4 h, and strenuous exercise for 24 h, preceding the test.

Muscle fibre typing

Following the completion of the exercise tests, on a separate day, a resting muscle biopsy was obtained from the left m. vastus lateralis of each subject using the needle biopsy technique of Bergstrom (1962). Muscle samples were mounted in embedding medium and frozen in isopentane previously cooled to its freezing point in liquid nitrogen. The embedded samples were stored at -80 °C until further analysis. Serial cross-sections (8–10 μ m thick) were cut in a cryostat maintained at -20 °C. The sections for myofibrillar ATPase histochemistry were preincubated at pH values of 4.6 and 9.4. According to their lability to the acid and alkaline preincubations,

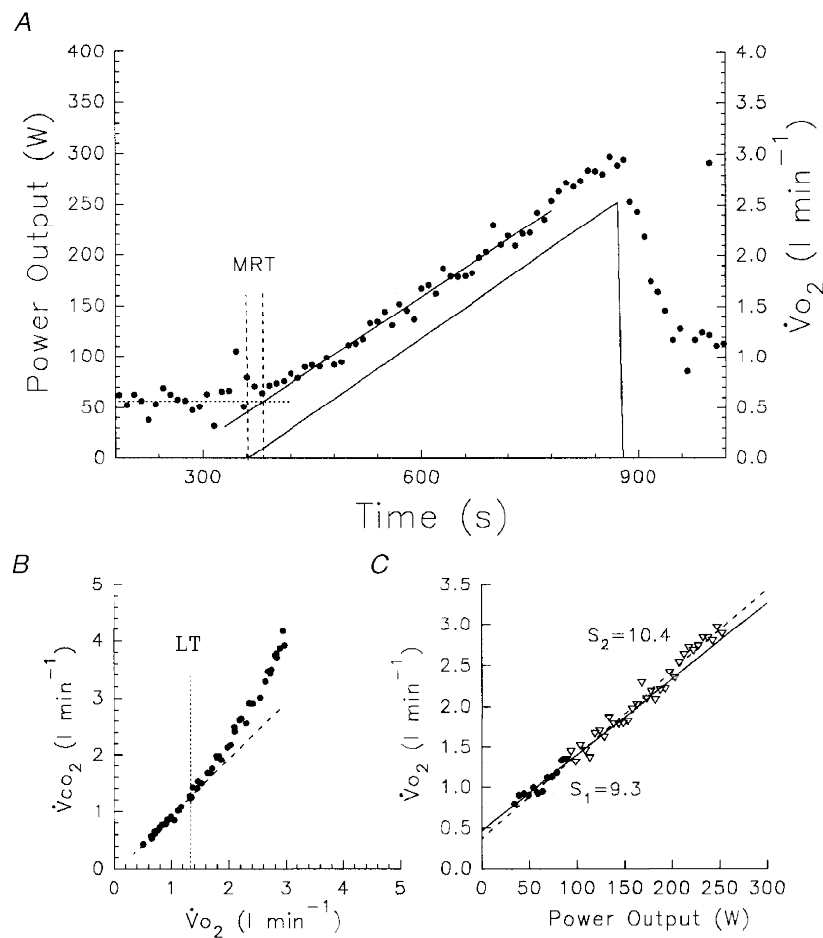


Figure 2

Data for one representative subject during ramp test. A, \dot{V}_{O_2} and power output vs. time for the exercise protocol (MRT, mean response time). B, V-slope plot of \dot{V}_{CO_2} vs. \dot{V}_{O_2} for estimation of lactate threshold (LT) from gas exchange responses. C, plot of \dot{V}_{O_2} vs. power output for determination of slope up to LT (S_1), and between LT and either peak \dot{V}_{O_2} or levelling off of \dot{V}_{O_2} (S_2). Regression line for entire slope (S_T) not shown for clarity.

the fibres were classified as either type I, IIa or IIb (Brooke & Kaiser, 1970). For each subject, 500–900 fibres were analysed. The number of each fibre type was expressed as a percentage of the total number counted.

Data analysis

Exercise test data were averaged over 10 s periods and plotted. The lactate threshold was estimated from gas exchange responses (LT_{est}) by the V-slope method (Beaver *et al.* 1986) (i.e. the breakpoint of onset of non-linear increase in \dot{V}_{O_2} with respect to \dot{V}_{O_2}), and confirmed as the \dot{V}_{O_2} above which there was hyperventilation with respect to \dot{V}_{O_2} but not to \dot{V}_{CO_2} (Wasserman & Whipp, 1975). The slope of $\Delta\dot{V}_{O_2}/\Delta W$ was determined using linear regression analysis over three segments: S_1 , from 1 min into the ramp test up to the LT; S_2 , from the LT to either peak \dot{V}_{O_2} or where \dot{V}_{O_2} began to level off; and S_T , over the range of $S_1 + S_2$.

Finally, to test for any interaction between the kinetics of the initial \dot{V}_{O_2} adjustment during the incremental exercise and $\Delta\dot{V}_{O_2}/\Delta W$, peak \dot{V}_{O_2} or fibre type, the mean response time (MRT) was determined. This was calculated as the time from the onset of the ramp forcing function to the point of intersection between the baseline \dot{V}_{O_2} and a backwards linear extrapolation of the \dot{V}_{O_2} vs. time slope (Fig. 2A) (Glantz, 1990). This was performed in two ways, using either the region of \dot{V}_{O_2} response below the LT, S_1 (MRT₁), or the total slope S_T (MRT_T) (Whipp *et al.* 1981). The baseline was defined as the average value for \dot{V}_{O_2} during the last 2 min of unloaded cycling prior to onset of the ramp.

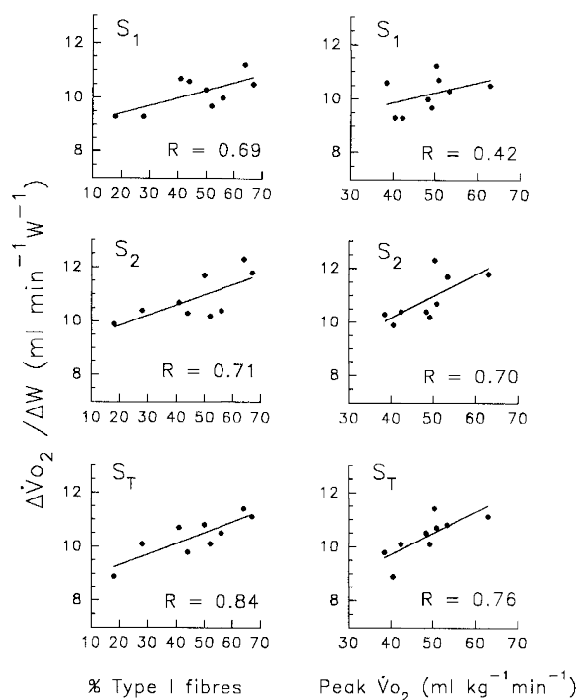


Figure 3

$\Delta\dot{V}_{O_2}/\Delta W$ during incremental exercise for the region below the estimated LT (S_1), above the estimated LT (S_2), and across the whole range (S_T), as functions of proportion of type I muscle fibres (left panels) and $\dot{V}_{O_{2,max}}$ (right panels). Correlation coefficient (R in figure) > 0.5 is significant ($P < 0.05$).

Statistical analyses

Linear correlation was used to assess the relationships between each of the three slopes of $\Delta\dot{V}_{O_2}/\Delta W$ and either the proportion of type I fibres or the peak \dot{V}_{O_2} ; significance was determined from the correlation coefficient. In addition, multiple linear correlation analysis was used to determine if there were significant independent contributions of fibre type and peak \dot{V}_{O_2} to predicting each of the $\Delta\dot{V}_{O_2}/\Delta W$ slopes. Finally, one-way ANOVA with repeated measures was used to compare the $\Delta\dot{V}_{O_2}/\Delta W$ slopes S_1 , S_2 and S_T . For all tests, significance was declared when $P < 0.05$. Dispersions about the mean are expressed \pm s.d. unless otherwise specified.

RESULTS

Figure 2 illustrates the exercise protocol and gas exchange responses for one subject (Subject 3 in Table 1). \dot{V}_{O_2} and power output are shown as functions of time in panel A, panel B shows the estimation of the LT by the V-slope method, while panel C shows \dot{V}_{O_2} as a function of instantaneous power output over the regions of linear regression analysis (only the regression lines for S_1 and S_2 are shown for clarity). The values for peak \dot{V}_{O_2} , estimated LT, proportion of type I fibres, and slopes S_1 , S_2 and S_T for each individual are given in Table 1. Peak \dot{V}_{O_2} averaged 3.40 ± 0.52 l min⁻¹ (48.2 ± 7.1 ml kg⁻¹ min⁻¹), while the estimated LT was 1.72 ± 0.35 l min⁻¹, or approximately 50% $\dot{V}_{O_{2,max}}$. The proportion of type I fibres averaged $47 \pm 16\%$, with a wide range among subjects (18–67%). Of the remaining fibres, most were type IIa ($50 \pm 17\%$);

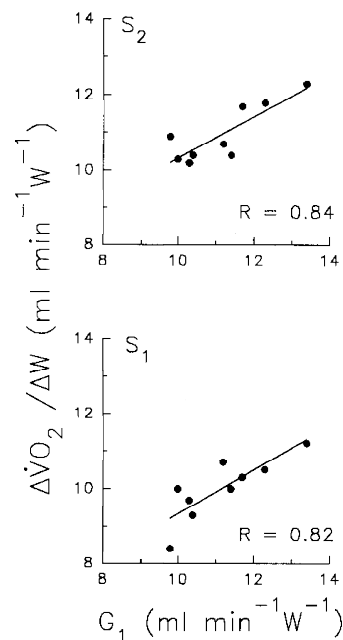


Figure 4

$\Delta\dot{V}_{O_2}/\Delta W$ during incremental exercise for data above (S_2) and below (S_1) the estimated LT, compared to the gain (G_1) for the primary rise in \dot{V}_{O_2} during heavy constant power output exercise ($> LT$). Values for G_1 have been reported previously (Barstow *et al.* 1996). Both relationships are significant ($P < 0.005$).

there were few discernable type IIb fibres ($3 \pm 3\%$). S_1 averaged $10.2 \pm 0.7 \text{ ml min}^{-1} \text{ W}^{-1}$, S_2 was $10.9 \pm 0.9 \text{ ml min}^{-1} \text{ W}^{-1}$, and S_T averaged $10.4 \pm 0.8 \text{ ml min}^{-1} \text{ W}^{-1}$. S_2 was significantly greater than S_1 ($P < 0.01$).

Figure 3 shows the relationships between S_1 , S_2 and S_T , as functions of proportion of type I fibres (left panels) and peak \dot{V}_{O_2} (right panels). All three slopes were significantly correlated with proportion of type I muscle fibres, while S_2 and S_T were also significantly correlated with peak \dot{V}_{O_2} (all $P < 0.05$). However, multiple linear regression analysis failed to show a significant improvement in prediction of any of the $\Delta\dot{V}_{O_2}/\Delta W$ slopes when the peak \dot{V}_{O_2} values were added to the proportion of type I fibre information (all $P > 0.05$).

MRT_1 averaged $43.1 \pm 19.4 \text{ s}$, while MRT_T was $43.9 \pm 16.5 \text{ s}$. Neither MRT_1 nor MRT_T was significantly related to peak \dot{V}_{O_2} , proportion of type I fibres, or the respective $\Delta\dot{V}_{O_2}/\Delta W$ (S_1 or S_T) (r ranged from 0.16 to 0.47, all $P > 0.05$).

DISCUSSION

Consistent with our first hypothesis, the slope of the \dot{V}_{O_2}/W relationship during incremental cycle ergometer exercise for the power output domain above LT (S_2) significantly correlated with both the proportion of type I fibres and the peak \dot{V}_{O_2} . However, in contrast to our second hypothesis, the slope for the region of power outputs below the LT (S_1) also was significantly correlated to the proportion of type I fibres. Further, the slope over the entire linear portion (S_T) was significantly related to the proportion of type I fibres and to peak \dot{V}_{O_2} . The finding that S_2 was proportional to both the underlying proportion of type I fibres and peak \dot{V}_{O_2} is consistent with our previous findings for the gain of the primary rise in \dot{V}_{O_2} (G_1 in Fig. 1) during heavy constant power output exercise in the same subjects (Barstow *et al.* 1996). The current results for S_1 extend these observations and suggest that muscle fibre type and/or fitness also affects the gain of the \dot{V}_{O_2} response to moderate exercise.

Fundamental to the interpretation of these data is the extent to which the $\Delta\dot{V}_{O_2}$ approximates the true increase in ATP turnover rate associated with the increase in power output (ΔW). One implicit assumption in the analysis of the $\Delta\dot{V}_{O_2}/\Delta W$ data obtained from ramp exercise is that the slope represents the equivalent steady-state ($< \text{LT}$) or initial ($> \text{LT}$) \dot{V}_{O_2} response. This appears to be a reasonable assumption for the $< \text{LT}$ exercise domain, as both Whipp *et al.* (1981) and Henson *et al.* (1989) found good agreement between the $\Delta\dot{V}_{O_2}/\Delta W$ determined from ramp tests (S_1) and that measured for constant power output exercise. For exercise above the LT, the relationship is less clear. In this intensity domain, the \dot{V}_{O_2} response does not represent the total rate of ATP resynthesis, as there is generally considered to be concomitant anaerobiosis which contributes to the overall energetics (note that, quantitatively, this is likely to be small; Medbo, 1996). However, somewhat

paradoxically, during sustained heavy exercise where there is apparently increased anaerobiosis, pulmonary \dot{V}_{O_2} is also greater than predicted from moderate exercise (Whipp & Mahler, 1980; Roston *et al.* 1987). The observation that S_2 is greater than S_1 during ramp exercise, as seen here and in previous studies (Hansen *et al.* 1988; Zoladz *et al.* 1995), probably reflects the contribution of additional \dot{V}_{O_2} from mechanism(s) similar to those responsible for the slow component seen during $> \text{LT}$ constant power output exercise (for review, see Poole *et al.* 1994).

One interpretation of the significant relationship in the present study between $\Delta\dot{V}_{O_2}/\Delta W$ and the percentage of type I fibres is that these differences are due to inherent energetic differences between type I and type II fibres. However, when the efficiency of contraction has been examined in isolated muscles differing in fibre type composition, conflicting results have been obtained. The metabolic cost of producing tension during brief tetanic (isometric) contractions is 3–5 times greater in the fast-twitch extensor digitorum longus (EDL) muscle of the mouse than in the slow-twitch soleus (Crow & Kushmerick, 1982; Barclay *et al.* 1993), although this difference becomes only 1.5 times when the contraction is sustained for more than 12 s (Crow & Kushmerick, 1982). However, during isotonic contractions where the muscle is allowed to shorten (more relevant to the human cycling condition studied here), maximum mechanical efficiency for slow twitch muscle has been reported to be greater than (Barclay, 1994), similar to (Gibbs & Gibson, 1972; Wendt & Gibbs, 1973; Barclay *et al.* 1993), or less than (Heglund & Cavagna, 1987) that for fast twitch muscle. Further, fast twitch muscle appears to be able to sustain a high mechanical efficiency over a greater range of contraction velocities than slow twitch muscle (Heglund & Cavagna, 1987; Barclay *et al.* 1993, but also see Barclay, 1994). Thus, there appears to be no consensus to date in the isolated muscle literature regarding the manner in which differences in muscle fibre type might translate into differences in mechanical efficiency of contraction.

Studies of the relationship between muscle fibre type and the oxygen cost of performing exercise in humans have produced similarly equivocal findings. Mechanical or delta efficiency for cycle exercise (defined as $\Delta W/\Delta\dot{V}_{O_2}$, the reciprocal to that used here) has been reported to be similar between sprinters and distance runners (Stuart *et al.* 1981) and between subjects with low and high percentages of fast twitch fibres (Suzuki, 1979; Medbo, 1990). Also, the mechanical efficiency of performing purely positive leg extension exercise on a sledge ergometer is similar among subjects who differ in the percentage of fast twitch fibres (Aura & Komi, 1987). On the other hand, Coyle and coworkers (1992) found that trained cyclists with predominantly type I fibres had a greater gross efficiency (W/\dot{V}_{O_2}) while performing exhaustive heavy ($> \text{LT}$) exercise for 1 h (Horowitz *et al.* 1994) or 5 min of two-legged knee extension exercise, and a greater delta efficiency for

presumably moderate intensity (<LT) cycle ergometer exercise (Coyle *et al.* 1992). Subjects with mostly type I fibres are also reported to be more efficient when performing positive leg extension work following active prestretch (Aura & Komi, 1987), and while running on a treadmill at a fixed speed or performing jumping activities (Bosco *et al.* 1987). Here, too, there currently does not appear to be a simple explanation for the reported differences in the association between mechanical efficiency and predominant muscle fibre type for exercising humans.

It should be noted that $\Delta\dot{V}_{O_2}/\Delta W$ described here, and its reciprocal determined by others, termed delta or mechanical efficiency, does not directly reflect the efficiency of muscle contraction, but rather the increase in aerobic metabolism as muscle power output is increased. The value thus obtained may not represent the metabolic cost of contraction (either as $(\Delta\text{heat production} + \Delta\text{work}) = \Delta\text{enthalpy}$ or $\Delta\text{oxygen consumption}$), as there is energy use associated both with myosin crossbridge cycling (which is directly related to force production) and with non-crossbridge activities (termed activation heat). The activation heat is primarily thought to arise from the movement of calcium out of and back into the sarcoplasmic reticulum, the latter being ATP dependent. One uncertainty at the moment is whether the activation heat stays relatively constant across contraction schemes, or varies with muscle length, frequency of contraction and fatigue (Barclay, 1996). Thus, it is unclear to what extent the $\Delta\dot{V}_{O_2}/\Delta W$ determined here includes changes in activation heat, in addition to the expected increase in crossbridge heat, as power output increases.

In the present study, S_2 and S_T were also significantly correlated with peak \dot{V}_{O_2} . However, to our knowledge there is no evidence that fitness or training leads to an increased $\Delta\dot{V}_{O_2}/\Delta W$. Differences in level (Boning *et al.* 1984), type (Stuart *et al.* 1981) or duration (Nickleberry & Brooks, 1996) of training do not appear to have an effect on either gross or delta efficiency. Further, \dot{V}_{O_2} is unchanged for a given moderate power output after training (Hagberg *et al.* 1980), although during heavy exercise \dot{V}_{O_2} may be reduced (Karlsson *et al.* 1972), presumably due to a reduction in the slow component (Casaburi *et al.* 1987). However, there is one brief report (Jammes *et al.* 1997) which suggests enhanced motor unit recruitment in trained cyclists compared to untrained subjects, based on a greater increase in the root mean square (RMS) of the EMG of the vastus lateralis during incremental exercise. If reproducible, these findings might imply a greater rate of increase in \dot{V}_{O_2} associated with the greater increase in EMG RMS in trained subjects. However, these preliminary results must await further confirmation.

At the present time we cannot distinguish potential effects of fibre type from those of fitness on $\Delta\dot{V}_{O_2}/\Delta W$. Previously we found that the proportion of type I fibres and peak \dot{V}_{O_2} were correlated in this group of subjects ($r = 0.74$) (Barstow *et al.* 1996). Multiple correlational analysis in the present study did not reveal any significant additional contribution of fitness to improve the prediction of $\Delta\dot{V}_{O_2}/\Delta W$ based on

fibre type distribution alone. Differentiating the potential influence of fibre type from that of fitness on $\Delta\dot{V}_{O_2}/\Delta W$, must, therefore, await further study. While the correlation coefficients between the $\Delta\dot{V}_{O_2}/\Delta W$ slope and either fibre type or fitness were significant, the values for r^2 suggest that only 50–70% of the variance in the $\Delta\dot{V}_{O_2}/\Delta W$ slope can be attributed to either of these two factors, implying that other, as yet unidentified mechanisms also contribute to the intersubject differences in $\Delta\dot{V}_{O_2}/\Delta W$. Variability in these relationships may also arise from small uncertainties in the determination of the primary variables. While 500–900 muscle fibres were counted for each subject for the determination of fibre type distribution, sampling variability for the results from one biopsy site may reach 9% for the vastus lateralis (Elder *et al.* 1982). Also, the data used to determine S_1 on average contained fewer data points than for S_2 or S_T , which could decrease the precision of determination of the $\Delta\dot{V}_{O_2}/\Delta W$ slope in this region. While these factors might contribute to the variance seen in Fig. 3, statistically this variability would tend to increase the chances of a type II error.

The question arose as to what extent the $\Delta\dot{V}_{O_2}/\Delta W$ slope determined here for ramp exercise reflected the gain G_1 (in the same units of $\Delta\dot{V}_{O_2}/\Delta W$) for heavy constant power output exercise from our previous study (Barstow *et al.* 1996). To evaluate this, we plotted S_2 and S_1 as functions of G_1 for each subject. As shown in Fig. 4, there was a very good correlation between both slope terms and G_1 across the subjects. This suggests that the effect of fibre type or fitness on the $\Delta\dot{V}_{O_2}/\Delta W$ of both moderate and heavy exercise are similar across exercise modes. These results are consistent with those of Whipp *et al.* (1981) and Henson *et al.* (1989), who found good agreement between the gain for ramp exercise and that for moderate constant power output exercise, but not with those of Murphy *et al.* (1989), who found the gain for constant power output exercise to be slightly higher.

Intersubject variability for the slope of $\Delta\dot{V}_{O_2}/\Delta W$, determined over the full power output range encountered in the ramp exercise test, has ranged in other studies from about 4 to 13% coefficient of variation (CV) (Whipp *et al.* 1981; Poole & Henson, 1988; Swanson & Hughson, 1988; Hansen *et al.* 1988; Murphy *et al.* 1989; Koike *et al.* 1990). It is interesting to note that in the present study, the CV for S_T was 7.7%, similar to that found in these other studies. This analysis suggests that the subtle intersubject variability in S_T noted in previous studies may have had physiological origins (e.g. differences in fitness or fibre type distribution), rather than being the result of random or measurement noise.

The influences of several factors on $\Delta\dot{V}_{O_2}/\Delta W$ during incremental exercise have been investigated. Factors such as age, gender, or caloric intake (Hansen *et al.* 1987; Poole & Henson, 1988; Itoh *et al.* 1990) do not significantly affect the slope in healthy subjects. However, several factors which ultimately impair O_2 delivery to the mitochondria of the exercising muscles are associated with reduced $\Delta\dot{V}_{O_2}/\Delta W$.

These factors include acute perturbations in healthy subjects, such as reductions in arterial O_2 content with either hypoxia (Murphy *et al.* 1989; Ibanez *et al.* 1993) or carboxyhaemoglobinaemia (Koike *et al.* 1990), and chronic conditions such as cardiac or cardiovascular disease (Hansen *et al.* 1987; Itoh, 1992; Itoh & Kato, 1996). Interestingly, the reduction in slope is most observable above the LT (Murphy *et al.* 1989; Koike *et al.* 1990; Ibanez *et al.* 1993). Under these conditions, a reduced $\Delta\dot{V}_{O_2}/\Delta W$ has been interpreted to represent a dynamic impairment in O_2 delivery with resulting reduced \dot{V}_{O_2} compared to the corresponding O_2 requirement. Consistent with this, exercise training in cardiac patients is associated with an increase in the $\Delta\dot{V}_{O_2}/\Delta W$ back towards values found in healthy subjects (Itoh & Kato, 1996). It is thus possible that aerobic training in healthy subjects might also cause a further increase in the $\Delta\dot{V}_{O_2}/\Delta W$ slope, leading to the relationship found here between fitness and the $\Delta\dot{V}_{O_2}/\Delta W$ slope.

Since G_1 in our previous study (Barstow *et al.* 1996) and the slopes S_1 , S_2 and S_T in the present work were determined under non-steady-state conditions, the question arises if our results could be partially explained by intersubject differences in the kinetic adjustments of \dot{V}_{O_2} during these two exercise conditions. To this point, the time constants for adjustments in muscle phosphocreatine and/or \dot{V}_{O_2} (Crow & Kushmerick, 1982; Kushmerick *et al.* 1992) are faster for isolated muscles with predominantly type I fibres, compared to those with primarily type II fibres. Also, training is associated with faster \dot{V}_{O_2} kinetics (Hagberg *et al.* 1978, 1980). However, \dot{V}_{O_2} kinetics, expressed either as the MRT for ramp exercise in the present study or the time constant for the primary exponential term for \dot{V}_{O_2} rise during constant power output exercise (τ_1) in our previous study (Barstow *et al.* 1996), were not significantly related to the percentage of type I fibres. However, it should be noted that the coefficient of variation for MRT determined from one ramp test for a given subject averaged 31% in the present study. This is very similar to the coefficients of variation calculated from repeated determinations of MRT from replicate ramp tests (19–29%) reported by Hughson & Inman (1986). Thus, while the observed relationships between fibre type, fitness and $\Delta\dot{V}_{O_2}/\Delta W$ found in both the present and our previous study do not appear to be explained by intersubject variability in the speed of adjustment (kinetics) of \dot{V}_{O_2} , a definitive test of this must await more rigorous evaluation.

In conclusion, these results confirm our previous findings that the initial \dot{V}_{O_2} response to exercise ($\Delta\dot{V}_{O_2}/\Delta W$ for either incremental or constant power output exercise) is correlated with muscle fibre type and possibly level of fitness. A greater proportion of type I fibres and/or a higher peak \dot{V}_{O_2} are both associated with a greater $\Delta\dot{V}_{O_2}/\Delta W$ in exercise intensity domains both below and above LT. These results do not appear to be explained by differences in the kinetics of adjustment of \dot{V}_{O_2} among subjects. It is possible that they might reflect a greater rate of motor unit recruitment in

subjects with a greater proportion of type I fibres and/or who are more aerobically conditioned. However, elucidation of the underlying mechanisms which relate changes in \dot{V}_{O_2} to changes in power output during moderate (and heavy) intensity exercise must await further study.

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