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The role of fitness on $\dot{V}O_2$ and $\dot{V}CO_2$ kinetics in response to proportional step increases in work rate

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Summary. The purpose of this study was to determine the effect of fitness and work level on the O_2 uptake and CO_2 output kinetics when the increase in work rate step is adjusted to the subject's maximum work capacity. Nine normal male subjects performed progressive incremental cycle ergometer exercise tests in 3-min steps to their maximum tolerance. The work rate step size was selected so that the symptom-limited maximum work rate would be reached in four steps at 12 min in all subjects. Oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) were calculated breath by breath. For the group, the time (mean, SEM) to reach 75% of the 3-min response ($T_{0.75}$) for $\dot{V}O_2$ increased significantly ($P<0.01$) at progressively higher work rate steps, being 53.3 (5.5) s, 63.5 (4.6) s, 79.5 (5.0) s, and 94.5 (5.8) s, respectively. In contrast, $T_{0.75}$ for $\dot{V}CO_2$ did not change significantly [74.9 (7.4) s, 75.6 (5.0) s, 85.1 (5.3) s, and 89.4 (6.3) s, respectively]. $\dot{V}CO_2$ kinetics were slower than $\dot{V}O_2$ kinetics at the low fractions of the subjects' work capacities but were the same or faster at the high fractions because of the slowing of $\dot{V}O_2$ kinetics. The first step showed the fastest rise in $\dot{V}O_2$. While $\dot{V}O_2$ kinetics slowed at each step, they were faster at each fraction of the work capacity in the fitter subjects. The step pattern in $\dot{V}O_2$ disappeared at high work rates for the less fit subjects. The heart rate response paralleled that of $\dot{V}O_2$. We conclude that $\dot{V}O_2$ and $\dot{V}CO_2$ kinetics are slower in the less fit subjects but only $\dot{V}O_2$ kinetics are significantly attenuated in response to proportional step increases in work rate.

Key words: $\dot{V}O_2$ kinetics – $\dot{V}CO_2$ kinetics – Exercise – Heart rate – Lactic acidosis threshold

Introduction

After exercise starts, the increase in O_2 uptake ($\dot{V}O_2$) reflects the changes in the rate of cellular oxidation for the generation of "high-energy" phosphate from aerobic mechanisms. Carbon dioxide output ($\dot{V}CO_2$) kinetics are proportional to $\dot{V}O_2$ kinetics except within the first minute of exercise, when CO_2 stores are increasing, and at heavy work rates, when HCO_3^- buffers metabolic (mainly lactic) acid generated from anaerobic glycolysis. The characteristics of $\dot{V}O_2$ and $\dot{V}CO_2$ kinetics in the response to a single step in work rate have been described by exponential functions with an apparent steady state being reached by 3 min for $\dot{V}O_2$ and slightly longer for $\dot{V}CO_2$ (Cerretelli et al. 1966; Diamond et al. 1977; Karlsson et al. 1975; Whipp and Wasserman 1972). At work rates above the lactic acidosis threshold (LAT), defined as the $\dot{V}O_2$ above which there is a sustained increase in blood lactate or CO_2 output secondary to HCO_3^- buffering of lactic acid, $\dot{V}O_2$ kinetics slow so that a steady-state is not reached by 3 min and may not be achieved at all before the subject stops exercise because of fatigue (Cerretelli et al. 1966; Whipp and Wasserman 1972). $\dot{V}CO_2$ kinetics have been less extensively studied, but it has been shown that they do not show similar slowing for work rates above the LAT (Casaburi et al. 1989).

Although it has been well documented that $\dot{V}O_2$ kinetics are faster in the more fit subjects (Hagberg et al. 1978; Hickson et al. 1978; Whipp and Wasserman 1972; Whipp 1971), the effect of work rate adjusted for maximum work capacity on $\dot{V}O_2$, and the extent to which the $\dot{V}CO_2$ kinetics are altered by fitness, is less well established. To determine the effect of fitness on gas exchange kinetics at proportional work intensities, we measured the dynamic changes in $\dot{V}O_2$ and $\dot{V}CO_2$ in response to four 3-min steps spanning the full range of the subject's work capacity during a single exercise test. $\dot{V}O_2$ kinetics were slowed at progressively higher work rate steps, but $\dot{V}CO_2$ kinetics were not significantly affected. Also, despite adjusting the step size so that all subjects achieved their symptom limited maximal work rate at the same time, the $\dot{V}O_2$ kinetics were slower in the less fit than in the more fit subjects at each work rate step.

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Methods

Nine sedentary male volunteers, determined to be normal by history, physical examination and electrocardiogram, gave their informed consent for this study. Some of their physical characteristics are shown in Table 1. Subject fitness was established during a preliminary exercise test in which the work rate was progressively increased in ramp pattern to determine the symptom-limited peak $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$) (Table 1). From the subject's peak $\dot{V}O_2$, a 3-min work rate step was selected so that four work rate steps would be performed by each subject, above unloaded cycling, before stopping because of fatigue. The work rate step used for each subject was calculated as follows:

$$\text{3-min step work rate} = \frac{\text{peak } \dot{V}O_2 - \text{unloaded cycling } \dot{V}O_2}{4 \times 10\ (ml \cdot min^{-1} \cdot W^{-1})}$$

where four is the number of 3-min steps to be studied and $10\ ml \cdot min^{-1} \cdot W^1$ is the approximate O_2 cost of cycle ergometer work (Wasserman et al. 1986).

During the test, the subjects breathed room air through a low-resistance breathing valve with a dead space of 90 ml attached to a turbine device (Alpha Technologies) that measured expired and inspired volume continuously. Respired air was sampled from the mouthpiece at a rate of $1\ ml \cdot s^{-1}$ from which oxygen, carbon dioxide and nitrogen were continuously measured with a mass spectrometer (Perkin-Elmer MGA 1100). These signals underwent analog-to-digital conversion for on-line, breath-by-breath computation of $\dot{V}O_2$ (STPD), $\dot{V}CO_2$ (STPD), minute expired ventilation ($\dot{V}_E$), (BTPS), Respiratory exchange ratio (R), End-tidal CO_2 partial pressure ($P_{ET}CO_2$), End-tidal O_2 partial pressure ($P_{ET}O_2$), $\dot{V}_E/\dot{V}CO_2$ and $\dot{V}_E/\dot{V}O_2$ as previously described (Beaver et al. 1973). These data were also stored on a digital disc for subsequent data analyses. ECG and heart rate (f_c) were monitored continuously.

Each subject performed the four 3-min steps in sequence, without a rest period, on an electromagnetically controlled work rate cycle ergometer (Lanooy) following 3 min of unloaded pedalling. The pedal rate was maintained at $60\ rev \cdot min^{-1}$. The work rate steps were 90, 60, and 45 W, depending on the fitness of the subject (Table 1). None of the subjects was able to perform a fifth step, as evidenced by the failure of the subjects to maintain a pedalling frequency above $45\ rev \cdot min^{-1}$.

LAT was calculated using the "V-slope" method, which consists in plotting $\dot{V}CO_2$ as a function of $\dot{V}O_2$ (Beaver et al. 1986a). This method has been shown to be well correlated with LAT directly determined by a fall in standard HCO_3^- (Beaver et al. 1986a). This was found to be a slightly higher $\dot{V}O_2$ than the lactate threshold (Beaver et al. 1986b).

For analysis, the breath-by-breath data were processed as previously described (Beaver et al. 1973). To reduce some of the inherent random breath-by-breath noise, the data were averaged and plotted for 9-s periods. The significance of the various differences was assessed by a one-way analysis of variance, the Student-Newman-Keuls test, or a paired *t*-test, depending on the comparison being performed. Linear regression analysis was used to detect correlations between responding variables and fitness. Significant differences were accepted at a $P < 0.05$.

Results

Table 1 shows the LAT and peak $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$) tolerated by each subject. The work rate step selected for each subject for the study of kinetics is also shown in Table 1. The subjects are numbered in rank order by fitness as estimated from the peak $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$). The LAT ($ml \cdot min^{-1} \cdot kg^{-1}$) measurement was closely correlated to the peak $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$) and provided a similar fitness rank order (Table 1).

The dynamic changes in $\dot{V}O_2$ and $\dot{V}CO_2$ in response to the 3-min step incremental test are shown in Fig. 1 for all nine subjects. The step response pattern of $\dot{V}O_2$ was clearly evident at the lower work rates but became blunted for all the subjects at the higher work rates. For the least fit subjects (subjects 7, 8, 9), the step pattern in $\dot{V}O_2$ disappeared at the higher work rates. The step pattern in $\dot{V}CO_2$ persisted at the higher work rates, while the $\dot{V}O_2$ step pattern was attenuated in all subjects at progressively higher work rate steps, being most marked in the least fit subjects.

Figure 2 shows the average time courses of $\dot{V}O_2$ and $\dot{V}CO_2$ in the nine subjects divided into three groups according to work rate steps (90, 60 or 45 W step) or fitness. The scales are adjusted in proportion to the size of the work rate increment to avoid making it appear that the less fit subjects have a smaller response relative to the more fit subjects. Nevertheless, the less fit subjects had a more dampened $\dot{V}O_2$ response than the more fit at each work rate step. The step pattern in $\dot{V}O_2$ was completely absent at the highest work rate step in the least fit subjects (Fig. 2, top panel). The most prominent and most abrupt step patterns were found in the most fit subjects (90 W steps). The most obvious step pattern for $\dot{V}CO_2$ was also found in the most fit subjects. However, in contrast to $\dot{V}O_2$, the step pattern for $\dot{V}CO_2$ persisted at the higher work rates (Fig. 2, bottom panel).

The response kinetics of $\dot{V}O_2$ and $\dot{V}CO_2$ were analyzed at each step (Fig. 3). The percentage change was calculated by considering the response from the begin-

Table 1. Subject physical characteristics, peak oxygen consumption ($\dot{V}O_2$), lactic acidosis threshold (*LAT*) and work rate step

Subject	Age (years)	Ht (m)	Mass (kg)	*LAT* ($ml \cdot min^{-1} \cdot kg^{-1}$)	peak $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$)	Work rate step ($W \cdot 3\ min^{-1}$)
1	32	1.78	70	40.3	67.0	90
2	31	1.85	86	33.7	54.5	90
3	37	1.75	66	31.1	54.2	60
4	31	1.80	66	25.6	44.4	60
5	29	1.91	97	24.7	40.7	60
6	39	1.68	73	25.5	37.7	60
7	40	1.68	70	22.1	33.7	45
8	45	1.78	71	24.2	31.0	45
9	31	1.69	60	18.3	34.7	45

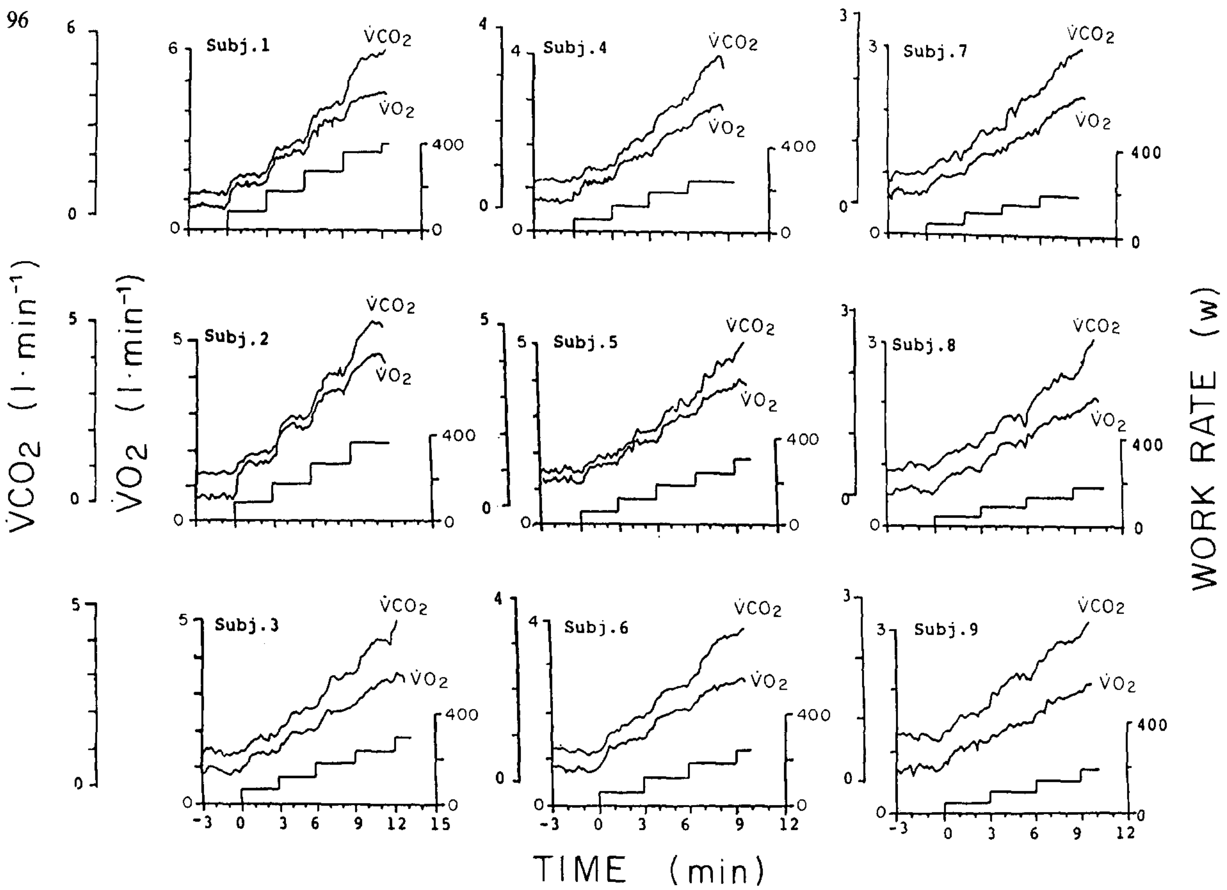

Fig. 1. A 9-s average plot of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) for a 3-min incremental step of a cycle ergometer exercise test in nine subjects. The subject numbers are in decreasing order of fitness determined by peak $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$)

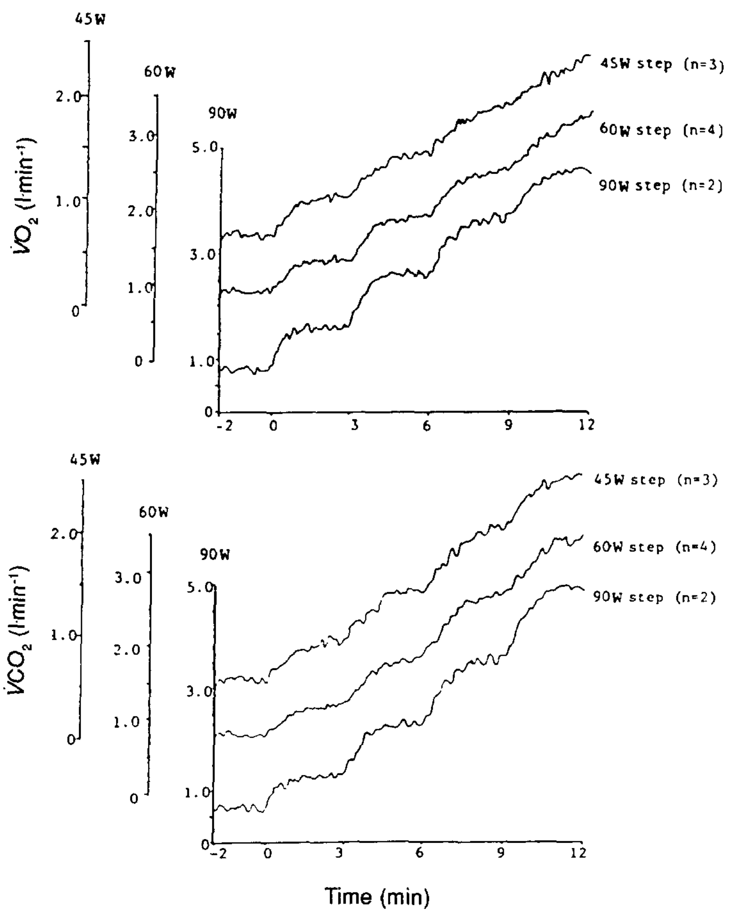

Fig. 2. The average time course of $\dot{V}O_2$ and $\dot{V}CO_2$ in response to each 3-min work rate step for three fitness levels designated by the work rate steps (90-, 60- or 45-W steps)

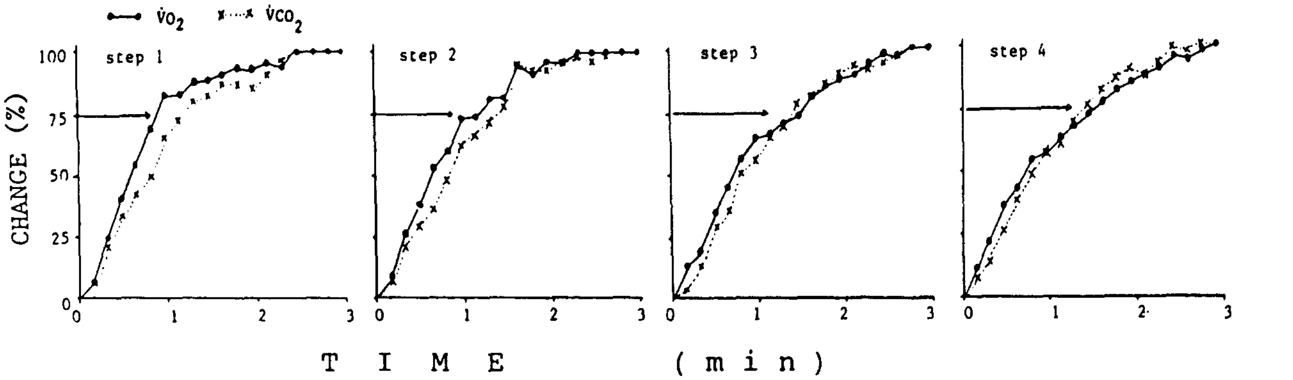

Fig. 3. The average percentage change of the 3-min response for $\dot{V}O_2$ (●—●) and $\dot{V}CO_2$ (×----×) to each step in work rate

Table 2. Time (s) to reach 75% of the response ($T_{0.75}$) for oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) response to each work rate step. The response at the end of each 3-min step was considered as 100% (mean, SE)

	Step 1	Step 2	Step 3	Step 4
$\dot{V}O_2$	53.3 (5.5)	63.5 (4.6)	79.5 (5.0)*,***	94.5 (5.8)*,**
$\dot{V}CO_2$	74.9 (7.4)*[1]	75.6 (5.0)*[2]	85.1 (5.3)	89.4 (6.3)

Comparison across steps: * $P<0.01$ compared with step 1; ** $P<0.01$ compared with step 2; *** $P<0.05$ compared with step 2; none of the other differences were significant. Comparison of variables: *[1] $P<0.002$; *[2] $P<0.02$

ning to the end of each 3-min step as 100%. The time to reach 75% of the response was measured from the plot of 10-s moving averages. For the first and second step increases in work rate, $\dot{V}O_2$ increased more rapidly than $\dot{V}CO_2$. For subsequent steps $\dot{V}CO_2$ and $\dot{V}O_2$ kinetics were more similar. Table 2 shows $T_{0.75}$ for $\dot{V}O_2$ and $\dot{V}CO_2$ for each work rate step. $T_{0.75}$ values for $\dot{V}O_2$ at the third and fourth steps were significantly increased (ANOVA) compared to steps 1 and 2. In contrast to $\dot{V}O_2$ kinetics, $\dot{V}CO_2$ kinetics were not significantly slowed at the higher steps, probably because CO_2 released from HCO_3^- buffering of lactic acid supple-

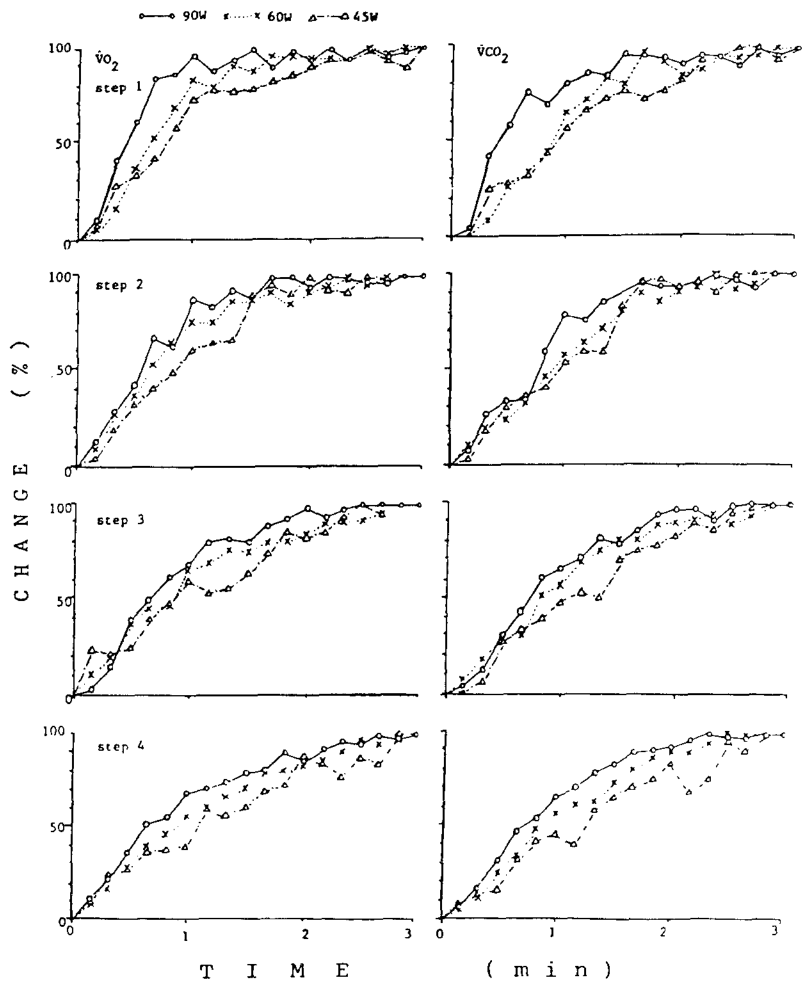

Fig. 4. The time course of the percentage change in $\dot{V}O_2$ and $\dot{V}CO_2$ to each 25% step of the work rate range as related to size of step or fitness. 90 W ○—○, 60 W ×----× and 45 W △—·—△

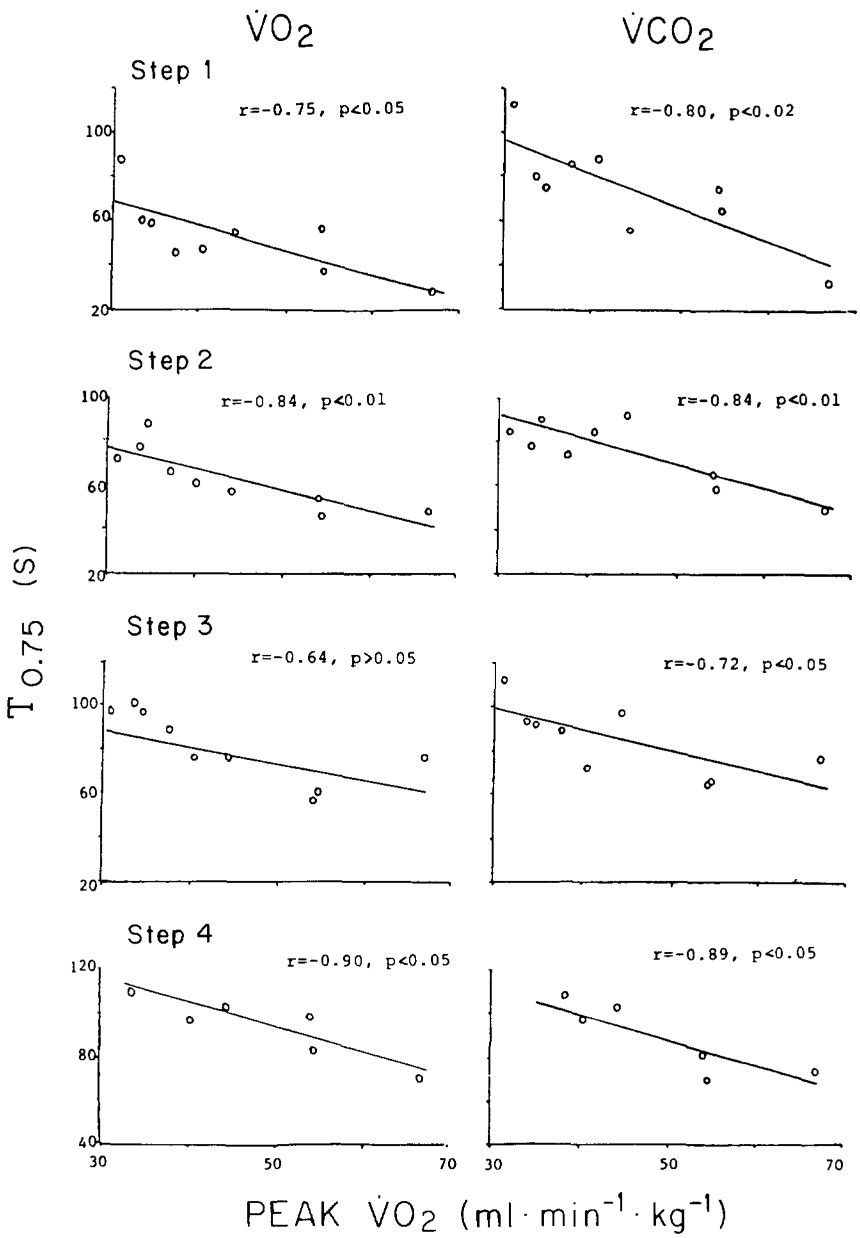

Fig. 5. The relationship between time to reach 75% of 3-min response ($T_{0.75}$) for $\dot{V}O_2$ or $\dot{V}CO_2$ and fitness determined by the peak $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$) for all four work rate steps. $T_{0.75}$ for $\dot{V}O_2$ as a function of peak $\dot{V}O_2$ in step 1 ($r = -0.75$, $P < 0.05$, $Y = -1.04X + 99.30$); step 2 ($r = -0.84$, $P < 0.01$, $Y = -0.97X + 106.44$); step 3 ($r = -0.64$, $P > 0.05$, $Y = -0.80X + 114.91$) and step 4 ($r = -0.90$, $P < 0.05$, $Y = -1.07X + 147.23$). $T_{0.75}$ for $\dot{V}CO_2$ as a function of peak $\dot{V}O_2$ in step 1 ($r = -0.80$, $P < 0.02$, $Y = -1.49X + 140.65$); step 2 ($r = -0.84$, $P < 0.01$, $Y = -1.03X + 121.25$); step 3 ($r = -0.72$, $P < 0.05$, $Y = -0.95X + 127.20$), and step 4 ($r = -0.89$, $P < 0.05$, $Y = -1.16X + 146.14$)

mented the slowed CO_2 production from aerobic metabolism. Thus the difference between $T_{0.75}$ for $\dot{V}O_2$ and $\dot{V}CO_2$ was not significant at the higher work rate steps.

Figure 4 presents the time course of $\dot{V}O_2$ and $\dot{V}CO_2$ as related to fitness at each work step. $\dot{V}O_2$ and $\dot{V}CO_2$ increase more rapidly in the more fit than in less fit subjects, despite the comparisons being made at comparable fractions of the subjects' work capacities.

Figure 5 shows the relationships between $T_{0.75}$ for $\dot{V}O_2$ or $\dot{V}CO_2$ and fitness as estimated by the peak $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$) for every work rate step. Significant correlations were found except for $\dot{V}O_2$ in the third step. However, if the point for the third step of the most fit subject (peak $\dot{V}O_2 = 63$ $ml \cdot min^{-1} \cdot kg^{-1}$) is omitted, a close relationship becomes apparent ($r = -0.84$, $P < 0.02$). Faster kinetics are evident in the fitter subjects at each proportion of the subjects' work capacities.

The pattern of change in f_c was similar to that for $\dot{V}O_2$ (Fig. 6). Since $\dot{V}O_2$ increase depends on increasing cardiac output and O_2 extraction [$C(a\text{-}\bar{v})O_2$], when stroke volume has become constant and $C(a\text{-}\bar{v})O_2$ change is minimal, changes in $\dot{V}O_2$ and f_c must be closely related.

The O_2 pulse [$\dot{V}O_2/f_c$ or stroke volume × $C(a\text{-}\bar{v})O_2$] in response to the step increases in work rate is shown in Fig. 7. The step pattern is small and evident only at the lowest work steps for the three least fit subjects (45-W step). For the most fit subjects (90 W step), the O_2-pulse increase is abrupt and about the same size for the first two steps. For the subjects with intermediate fitness (60-W step), the size of the second step is reduced and lost for the third and fourth steps.

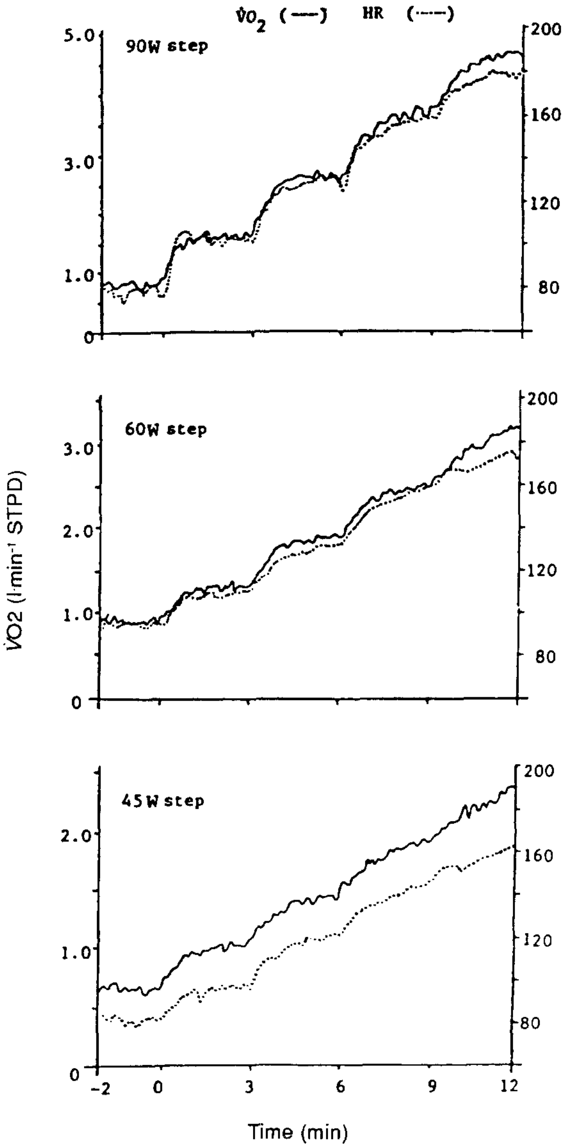

Fig. 6. The average time of $\dot{V}O_2$ (——) and heart rate (......) in response to each 3-min work rate step for three fitness levels designated by the work rate steps (90-, 60- or 45-W step)

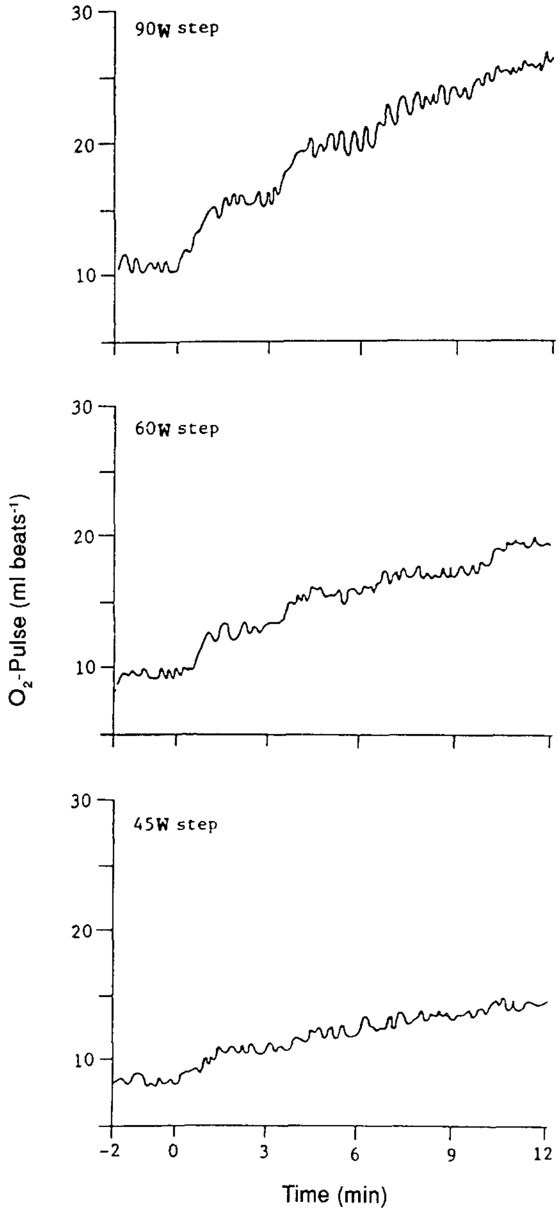

Fig. 7. O_2-pulse ($\dot{V}O_2$/heart rate) response to each 3-min work rate step according to the size of the work rate or fitness

Discussion

The subject's work capacity was divided into four equal parts (from unloaded cycling to 25%, 25% to 50%, 50% to 75% and 75% to 100% of the maximum work capacity), and the gas exchange response for each part was studied. The $\dot{V}O_2$ response to the first step increase (lowest 25% of subject's work capacity) appeared to reach a constant value by 3 min for all subjects. However, $\dot{V}O_2$ was progressively more dampened for each of the subsequent steps. This was particularly evident for the less fit subjects (Figs. 1, 2). Relative to the $\dot{V}O_2$ changes, the $\dot{V}CO_2$ changes in response to the low work rate step were slower (Figs. 1, 2). However, over the upper range in work rates $\dot{V}O_2$ kinetics became more attenuated relative to the changes in $\dot{V}CO_2$ kinetics, which remained unchanged (Fig. 3, Table 2). The kinetics of both $\dot{V}O_2$ and $\dot{V}CO_2$ are affected by fitness (Fig. 5).

In the response to moderate constant work rate exercise, $\dot{V}O_2$ increases with a time constant of some 30–40 s, whereas the time constant for $\dot{V}CO_2$ is considerable longer at 50–60 s (Hughson and Morrissey 1982; Linnarsson 1974; Whipp et al. 1980). The kinetic dissociation, primarily at the first step, most probably reflects the relatively high CO_2 solubility in the tissues and increasing CO_2 stores at the beginning of exercise. This contrasts with the second step during which the kinetics of $\dot{V}O_2$ and $\dot{V}CO_2$ are more similar (Fig. 3). This suggests that increasing tissue PCO_2 occurs primarily with the first work rate step. For steps three and four, $\dot{V}O_2$ kinetics are slowed, but CO_2 is evolved from the stores presumably as a result of HCO_3^- buffering of lactic acid.

The disappearance of the step pattern for $\dot{V}O_2$ in response to the step increase in work rate in the less fit subjects, at the work rates starting at 50% and 75% of the subjects' work capacities, indicates that $\dot{V}O_2$ kinetics were markedly slowed in this group. This must reflect slowing of regeneration of ATP by aerobic metabolism and increase of anaerobically produced ATP. $\dot{V}O_2$ kinetics were faster in the more fit subjects than the less fit subjects over the same range in work rate (Fig. 4). There is a significant negative relationship between $T_{0.75}$ for $\dot{V}O_2$ and $\dot{V}CO_2$ when correlated to peak $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$) (Fig. 5).

Although $\dot{V}O_2$ kinetics were slowed as the work rate steps increased, $T_{0.75}$ for $\dot{V}CO_2$ remained relatively constant (Table 2). Casaburi et al. (1989) also reported that the mean response time for $\dot{V}CO_2$ did not change for work rates of different intensities, using a different work rate protocol. It is likely that the slowing of the $\dot{V}O_2$ response time without a change in $\dot{V}CO_2$ response time at progressively higher work intensities results from the coincident influence of increased CO_2 production related to the buffering of lactic acid and decreased CO_2 production resulting from slowed aerobic metabolism.

In this study, the sizes of the work rate steps were designed so that all subjects would reach exhaustion at the same time. Endurance training can substantially decrease blood lactate levels during heavy exercise (Karlsson et al. 1972; Winder et al. 1979). In this study, we have shown the differences in the aerobic contribution of energy generation at identical proportions of each subject's maximum work rate, as related to fitness. The more rapid $\dot{V}O_2$ kinetics seen in the more fit subjects at a comparable proportion of the maximal work rate indicate that the kinetics of aerobically produced ATP flux relative to the anaerobic ATP flux are relatively greater in the more fit subjects.

The f_c response is similar to the step pattern in $\dot{V}O_2$ including the attenuation at high work rates (Fig. 6). However, the size of the f_c step is smaller than the $\dot{V}O_2$ step. This results in step increases in O_2 pulse for the low work rate steps. This implies that the product of stroke volume × arterial-venous O_2 difference increases in step pattern for the low work rate steps. At high work rates, the step increases in O_2 pulse, at the time of work rate increase, disappear. This is explained by the only slight further change in stroke volume and/or arterial-venous O_2 difference with increasing work rates. The loss of the step increase occurs at a proportionately lower fraction of the work capacity for the less fit subjects (Fig. 7).

In summary, these findings demonstrate that the kinetics of $\dot{V}O_2$ become slower over the higher range of a subject's work capacity, while $\dot{V}CO_2$ kinetics remain unchanged. But at each level of work, the kinetics of $\dot{V}O_2$ and $\dot{V}CO_2$ are faster in the more fit subjects. The step pattern in $\dot{V}O_2$ is lost in the less fit subjects over the upper 50% of the subject's work capacity. This contrasts with the persistence of the step pattern in $\dot{V}CO_2$. The f_c response paralleled that of $\dot{V}O_2$. We have found that a progressive test of four 3-min steps, each over progressively high fractions of the subject's work capacity, is a practical and rapid method to assess $\dot{V}O_2$ and $\dot{V}CO_2$ kinetics. $\dot{V}O_2$ kinetics were slower, the higher the fraction of the subject's maximum work capacity and the slowing was more marked in the less fit subjects.

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