Comparison of oxygen uptake kinetics during concentric and eccentric cycle exercise

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There are conflicting results about whether the rate of adaptation of \(O_2\) uptake (\(V_{\text{O}_2}\)) at the onset of exercise is dependent on relative work rate and the type of muscular action. Although some investigators have shown adaptation of \(V_{\text{O}_2}\) to be progressively slowed as the work rate increases (11, 18, 22, 31), others have shown a constancy at least until the work rate exceeds the ventilatory threshold (VT) (15) or even above this work rate (2). In the case of high work rates above VT but below maximal \(V_{\text{O}_2}\), an additional slow component is observed, normally developing \(\approx 90\) s after the start of exercise (2, 31). There have been very few investigations of the kinetics of \(V_{\text{O}_2}\) during eccentric compared with concentric muscular actions. In their first study, Knutgen and Klausen (25) observed a very small or no \(O_2\) deficit at the onset of eccentric exercise. In a subsequent investigation, Bonde-Petersen et al. (7) found that the \(O_2\) deficit was not different from that incurred when the same absolute \(V_{\text{O}_2}\) was achieved during concentric cycling. However, these early studies were conducted with Douglas bag collections and without detailed analysis of the components of the dynamic response.

In eccentric exercise, the muscles are forcibly lengthened while activated. Walking and running downhill include large components of eccentric exercise, whereas opposing the torque transmitted from a motor to the pedals of a cycle ergometer may be a more “pure” form of eccentric exercise (32). It is possible that the kinetics of \(V_{\text{O}_2}\) might differ between cycling and running, in part because of different muscle recruitment patterns, including the proportion of eccentric vs. concentric muscle activation (10, 23). The physiological cost of eccentric muscle activation is substantially less than that of concentric muscle contraction (1, 24, 25, 32, 37), inasmuch as fewer muscle fibers are recruited to perform the same work rate during eccentric cycling (1, 5).

Electromyographic (EMG) activity has been studied in conjunction with investigations of the \(V_{\text{O}_2}\) slow component to determine whether there is an increase in integrated EMG (iEMG) or in mean power frequency (MPF). The increase in iEMG might reflect greater total muscle fiber recruitment (36) as fibers fatigue. Changes in MPF might indicate recruitment of a greater proportion of fast-twitch fibers (17, 35). Greater recruitment of fast-twitch fibers with time during heavy exercise has been suggested to accompany the onset of the \(V_{\text{O}_2}\) slow component, although the results of research are contradictory (27, 35, 36).

The purpose of the present study was to investigate the muscle activity patterns and the \(V_{\text{O}_2}\) kinetics dur-
ing concentric and eccentric cycle ergometry at the same absolute and relative work rates. We hypothesized that, for a given mechanical work rate, the increase in \( \dot{V}O_2 \) would be more rapid during eccentric exercise, because the total metabolic requirement was reduced. Comparison of the \( \dot{V}O_2 \) kinetics between eccentric and concentric exercise that had the same metabolic requirement was expected to show the same rate of increase to the steady state. We further hypothesized that a \( \dot{V}O_2 \) slow component would be observed only when there was an increase in iEMG reflecting greater motor unit recruitment as exercise continued.

**METHODS**

**Subjects.** Six healthy, well-motivated men volunteered to participate in the study after they were informed of the nature and possible inconveniences associated with the experiment. Each subject gave informed written consent on a form approved by the Office of Research Ethics at the University of Waterloo. Subjects’ age, weight, and height were (mean ± SE) 25 ± 1 yr, 74.2 ± 2.8 kg, and 180 ± 3 cm, respectively. Subjects were physically active in a variety of sports (running, cycling, and cross-country skiing) a minimum of four times per week.

**Experimental protocol.** Preliminary testing of all subjects consisted of an incremental concentric exercise test to exhaustion to determine the VT and peak \( \dot{V}O_2 \). The initial work rate of 60 W was increased by 30 W/min at a cycling frequency of 60 rpm. The VT was estimated by using a five-point filter of \( \dot{V}O_2 \) and \( \dot{CO}_2 \) output (\( \dot{V}CO_2 \)) to reduce breath-to-breath variability before application of a modified V-slope method (21). \( \dot{V}CO_2 \) was examined as a function of \( \dot{V}O_2 \) under the assumption that the VT corresponds to the break point in the \( \dot{V}CO_2-\dot{V}O_2 \) relationship. The break point was selected by a computer program that determined the \( \dot{V}O_2 \) above which \( \dot{V}CO_2 \) increased faster than \( \dot{V}O_2 \), without hyperventilation. Peak \( \dot{V}O_2 \) was taken as the average of the highest five consecutive breaths attained in the last minute of exercise. The VT and peak \( \dot{V}O_2 \) were used in choosing the individual work rates for the step tests in concentric and eccentric bouts.

For the concentric bouts, the design of the study involved testing below and above the VT with step changes in work rate. On any test day, subjects completed at least two different step work rate tests. Always, the lowest intensities were performed first. Thus, on a test day, a subject might perform a moderate-intensity followed by a high-intensity concentric exercise. Data collection commenced with 4 min at 15 W to establish a baseline, then the subjects performed 6-min bouts of higher constant-load exercise. The three different work rates selected for concentric cycling were defined as light concentric (LC), moderate concentric (MC), and heavy concentric (HC) exercise. The LC intensity was selected to achieve a steady-state \( \dot{V}O_2 \) similar to that measured during the eccentric exercise. Thus it was necessary to conduct the LC tests on separate days after the eccentric tests. The MC work rate elicited \( \dot{V}O_2 \) corresponding to ~90% of the VT. No slow component rise in \( \dot{V}O_2 \) occurred at this intensity. The HC exercise was performed at a work rate estimated to require \( \dot{V}O_2 \) equal to ~70% of the difference (\( \Delta \)) between the subject’s VT and peak \( \dot{V}O_2 \), i.e., a value of \( \dot{V}O_2 + 0.7\Delta \).

The high eccentric (HE) exercise intensity was at the same absolute work rate as the HC exercise and was preceded by 4 min at baseline (15 W) pedaling. During pilot tests with three subjects, the peak work rate that could safely be achieved did not elicit a noticeable increase in \( \dot{V}CO_2 \) relative to \( \dot{V}O_2 \), so it was impossible to select the VT. At the highest exercise intensities achieved in the incremental tests (~400 W), there is a possibility of severe tissue damage and orthopedic problems with eccentric muscle actions (26). Three ≥20- to 30-min training sessions on the eccentric ergometer were completed before the HE test sessions to minimize muscle soreness.

To reduce the noise in breath-by-breath data and enhance the underlying response patterns, each subject performed several repetitions of the exercise transitions under each condition. Exercise transitions were performed three times for the concentric bouts and four times for the eccentric bouts.

The order in which the conditions were performed was randomized, except for LC exercise as noted. At least 2 days separated an eccentric test from another test, either eccentric or concentric.

Venous blood was drawn from a catheter inserted in the back of the hand into heparinized syringes at rest and before the exercise (33) and at the last minute of MC and HC exercise. The samples were then placed in ice and analyzed after a short delay. Whole blood samples were analyzed (at 37°C) for plasma lactate concentration (StatProfile 9 Plus Blood Gas-Electrolyte Analyzer, Nova Biomedical Canada). Blood was not sampled during the HE exercise in all subjects, inasmuch as samples from the first two subjects confirmed previous observations with the same ergometer (33) that lactate was unaffected at the low metabolic demand of this exercise.

At the end of each exercise step, subjects were asked to rate their perceived exertion (RPE) using the Borg scale, ranging from 0 (nothing at all) to 10 (very, very heavy) (8).

**Breath-by-breath gas exchange.** Breath-by-breath ventilation and gas exchange were measured by using a portable measurement system (Cosmed K4b², Rome, Italy). This system consists of a facemask with a low-dead-space (70 ml) and a low-resistance, bidirectional digital turbine (28-mm diameter) that was calibrated before each test with a syringe of known volume (3,007 ml). Expired gases were sampled at the mouth by an \( O_2 \) analyzer with a polarographic electrode and a \( CO_2 \) analyzer with an infrared electrode. The \( O_2 \) and \( CO_2 \) analyzers were calibrated by using ambient air and precision-measured reference gas at the beginning of each session according to procedures recommended by the manufacturer.

Heart rate (HR) was continuously calculated with each ventilatory data point via a wireless Polar monitoring system.

**Concentric and eccentric ergometers.** The concentric exercise was performed on an electrically braked cycle ergometer (Excalibur Sport, Lode, Groningen, The Netherlands). Seat and handlebar positions were kept constant for individual subjects during the study.

The eccentric test and training exercises were performed on a standard Monark cycle ergometer modified for eccentric exercise (33, 37). The pedals were driven in a reverse direction from normal cycling by an electric motor. The subjects were instructed to keep the pedaling rate at 60 rpm and thus to resist the tendency of the ergometer to increase the pedal axle from 60 rpm. For this type of ergometer, the transition from the baseline level to step work rate levels was fairly rapid (typically ~3 s) and was followed by a fine tuning. Because eccentric exercise on a cycle ergometer is not without risk due to high force development, an investigator was constantly prepared to activate a brake and press an emergency stop button. There were no emergencies.

To minimize any extra energy expenditure required during eccentric cycling as a function of movements to balance and
fix the body, we chose to use a rigid chair, rather than a standard bicycle saddle, to support the subjects. The chair was equipped with a firm back support, allowing maximum relaxation of all nonworking muscles. This enabled the subjects to resist the heavy exercise loads more easily. The subjects were seated with a hip angle of 125°. The subjects’ feet were positioned with adjustable rubber straps on pedals placed so that the center of rotation of the ankle joint was close to the axis of the pedal shaft. This minimized contractions of the gastrocnemius (GA) muscles.

**EMG on leg muscles.** EMG data of the rectus femoris (RF), vastus medialis (VM), biceps femoris, and GA muscles were collected twice for each condition on the right leg by using bipolar surface Ag-AgCl electrodes with a surface cup diameter of 10 mm (200 Medi-Trace Mini, Graphics Control, Buffalo, NY), with an intrapair distance of 35 mm. A common reference electrode was placed on the tibial tuberosity of the same leg. Before electrode placement, the skin areas were shaved and cleaned with isopropyl alcohol swabs to reduce skin impedance. Electrodes were always placed on the most prominent site of the muscle belly as noted by visualization and palpation by the same investigator. They were placed in the same direction as the muscle fibers. Electrode wires then were taped to the skin to reduce movement artifacts.

The myoelectrical signal was band-pass filtered (20–500 Hz), differentially amplified (gain 1,000 times, input impedance 90 dB), and sampled at 1,024 Hz with a 12-bit analog-to-digital conversion board (DAS-16, MetraByte, Taunton, MA) for the last 12 s of each minute during exercise. After removal of any bias, raw EMG signals were full-wave rectified and low-pass filtered with a second-order Butterworth filter (cutoff frequency = 3 Hz) (39), producing a linear envelope. The resulting smooth EMG signal was integrated (iEMG) over 10 s, generating an indication of the total muscle activity of the exercising muscle at each minute of exercise.

The digitized EMG was also processed by using a Hammering window function and 2,048-point fast Fourier transform to obtain mean power frequency (MPF) over 10 s. Surface EMG signals present extensive interindividual variance because of electrode position or impedance of underlying tissues. Therefore, iEMG and MPF were expressed relative to the value corresponding to the 1st min of exercise (nonfatigued state). This technique does not allow for comparison between test sessions but does allow for reliable tracking of changes within a test.

**Data analysis.** Breath-by-breath data for $\dot{V}_O_2$ from at least three repetitions of an identical test condition were linearly interpolated at 1-s intervals, time aligned, and ensemble averaged to provide a single response for each subject. Two mathematical models were employed to characterize the average-response curves using least-squares nonlinear regression techniques, in which the best fit was defined by minimization of the residual sum of squares. The model utilized to describe the kinetic response provides an estimate of the mean response time (MRT), which is calculated from a weighted sum of TD and $\tau$ for each component (28). MRT is equivalent to the time required to achieve ~63% of the difference between $A_0$ and the final $\dot{V}_O_2$.

$O_2$ deficit ($O_2$Def) was calculated for exercise without evidence of a slow component as follows: $O_2$Def = $(A_1 + A_2)\cdot$MRT (38).

HR response was estimated during HE and LC exercise as the equivalent to MRT from the time to achieve 63% of the difference between the baseline and the steady-state or end-exercise HR. In HE exercise, there was often an overshoot before steady state.

**Statistics.** A one-way repeated-measures analysis of variance with multiple comparisons (Student-Newman-Keuls post hoc test) was used to compare the differences in variables among conditions. A one-way repeated-measures analysis of variance was also used to determine the overall effect of time on iEMG data with respect to the normalized baseline at $t = 1$. The Friedman rank test was used for variables with nonnormal distribution or unequal variance. Statistical significance was set at $P < 0.05$, and values are means $\pm$ SE.

**RESULTS**

The peak $\dot{V}_O_2$ achieved by the subjects during the preliminary incremental exercise test was 59.7 $\pm$ 1.4 ml·kg$^{-1}$·min$^{-1}$. The work rates utilized during the constant-load tests were 207 $\pm$ 11 W for MC exercise and 317 $\pm$ 14 W for HC and HE exercise. The work rate required in LC exercise to achieve approximately the same metabolic cost as in HE exercise was 62 $\pm$ 7 W (range 40–88 W). Steady-state $\dot{V}_O_2$ was not different between LC and HE exercise (1,212 $\pm$ 79 and 1,169 $\pm$ 103 ml/min, respectively).

$\dot{V}_O_2$ kinetics. The principal results of $\dot{V}_O_2$ kinetics for the concentric and eccentric exercises are presented in Table 1, with an example of the $\dot{V}_O_2$ response for a single subject during each condition in Fig. 1. For eccentric exercise, the $\dot{V}_O_2$ response was best described with two exponential terms because of an absence of the slow component rise in $\dot{V}_O_2$. During the baseline period, $\dot{V}_O_2$ ($A_0$) was significantly lower in HE than in the three concentric exercises ($P < 0.05$). The onset of phase 2 (TD2) was significantly earlier in HC than in any other exercise, whereas TD2 in HE exercise occurred earlier than in LC exercise (Table 1). The phase 2 time constant ($\tau_2$) was slower in HC than in HE and LC exercise but was not different from MC exercise. HC exercise resulted in higher amplitudes ($A_1$ and $A_2$) than the other exercises, as did MC exercise compared with LC and HE exercises. $A_2$ was smaller in LC than in HE exercise. HC exercise was characterized by a $\dot{V}_O_2$ slow component at 123.7 $\pm$ 3.5 s after exercise onset (TD3, Table 1). Hence, HC exercise resulted in a slower
not a steady end-exercise value. HC exercise are not presented, inasmuch as there was than during LC exercise (Table 2). HR kinetics data for HR above baseline was significantly less during HE (Table 2). The time to achieve 63% of the increase in min) in the first seconds after the onset of exercise (Fig. 1). Toledo. O2 uptake (V˙O2) for 1 subject during final 2 min of baseline exercise at 15 W and during 6 min of LC (○) and HE exercise (▲). Values are averages of 6 subjects; see Table 2 for SE. bpm, Beats/min.

**EMG data.** The normalized iEMG was constant across time periods for all muscles during each of the MC and HE exercise tests (data for VM and RF muscles are shown in Fig. 3). In the HC tests, iEMG increased significantly at minutes 5 and 6 from the values at minutes 1, 2, and 3 in the VM and RF muscles (Fig. 3), but not in the biceps femoris and GA, muscles. The increase in iEMG between minutes 3 and 6 of the HE exercise tests averaged 20 and 30% in VM and RF muscles, respectively. There were no changes in MPF as a function of time for any muscle during any of the exercise tests (data not shown).

**RPE and lactate.** Significant differences in RPE were noted among exercise conditions (Table 3), with the highest RPE observed during HC exercise followed by HE, MC, and LC exercise (each different from one another, P < 0.05). Blood lactate concentration increased more at the end of HC than MC exercise (Table 3).

**DISCUSSION**

We have found that the time course for the increase in V˙O2 at the onset of eccentric exercise (HE), indicated by t2, is similar to that for concentric exercise at the same metabolic demand (LC). On the other hand, t2 for V˙O2 was slower for HC than for HE or LC exercise. Measurements of muscle activation patterns by nor-

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**Table 1. V˙O2 kinetic parameters during concentric and eccentric exercise**

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Concentric</th>
<th>Eccentric</th>
</tr>
</thead>
<tbody>
<tr>
<td>A0, ml/min</td>
<td>837 ± 40</td>
<td>418 ± 21†‡</td>
</tr>
<tr>
<td>A1, ml/min</td>
<td>704 ± 70</td>
<td>223 ± 43†</td>
</tr>
<tr>
<td>TD1, s</td>
<td>1.1 ± 0.5</td>
<td>0.9 ± 0.3§‡</td>
</tr>
<tr>
<td>t1, s</td>
<td>5.8 ± 1.0</td>
<td>6.7 ± 0.9</td>
</tr>
<tr>
<td>A2, ml/min</td>
<td>2,055 ± 158</td>
<td>528 ± 70†</td>
</tr>
<tr>
<td>TD2, s</td>
<td>16.4 ± 0.7</td>
<td>19.3 ± 1.3‡</td>
</tr>
<tr>
<td>t2, s</td>
<td>24.0 ± 1.7</td>
<td>14.7 ± 2.8§</td>
</tr>
<tr>
<td>A3, ml/min</td>
<td>525 ± 76</td>
<td></td>
</tr>
<tr>
<td>TD3, s</td>
<td>123.7 ± 3.5</td>
<td></td>
</tr>
<tr>
<td>t3, s</td>
<td>103.1 ± 10.8</td>
<td></td>
</tr>
<tr>
<td>O2Def, liters</td>
<td>NA 1.03 ± 0.07</td>
<td>0.32 ± 0.05†</td>
</tr>
<tr>
<td>MRT, s</td>
<td>63.2 ± 4.5</td>
<td>26.4 ± 2.8§</td>
</tr>
</tbody>
</table>

Values are means ± SE; n = 6 subjects. V˙O2, O2 uptake; A, amplitudes of response; t, time constants; TD, time delay; MRT, mean response time; O2Def, O2 deficit; NA, not available. *Significantly different from light concentric, P < 0.05. †Significantly different from moderate concentric, P < 0.05. ‡Significantly different from heavy concentric, P < 0.05.

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**Fig. 2.** Heart rate during final 2 min of baseline exercise at 15 W and during 6 min of LC (○) and HE exercise (▲). Values are averages of 6 subjects; see Table 2 for SE. bpm, Beats/min.

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**Table 2. Selected parameters for kinetic analysis of HR during HE and LC exercises**

<table>
<thead>
<tr>
<th>Measurement</th>
<th>LC</th>
<th>HE</th>
</tr>
</thead>
<tbody>
<tr>
<td>HR baseline, beats/min</td>
<td>77.9 ± 2.6</td>
<td>70.1 ± 2.0*a</td>
</tr>
<tr>
<td>Overshoot, beats/min</td>
<td>None</td>
<td>6.1 ± 2.4</td>
</tr>
<tr>
<td>HR increase, beats/min</td>
<td>14.6 ± 2.4</td>
<td>32.5 ± 2.0*a</td>
</tr>
<tr>
<td>Time to 63%, s</td>
<td>24.9 ± 2.2</td>
<td>13.8 ± 1.3*a</td>
</tr>
</tbody>
</table>

Values are means ± SE; n = 6 subjects. HR, heart rate; LC, light concentric; HE, high eccentric. *Significantly different from LC, P < 0.05.
malized iEMG demonstrated a significant increase with time only for HC exercise where there was also the appearance of a phase 3 response in $\dot{V}O_2$. There was no change in iEMG with time during HE exercise, and there was a phase 3 component of $\dot{V}O_2$, even though the absolute work rate was the same as in HC exercise. These results provide new information about the kinetics of $\dot{V}O_2$ during eccentric patterns of muscle activation. In an early study of eccentric cycling, Knuttgen and Klausen (25) described a very rapid increase in $\dot{V}O_2$ that appeared to proceed immediately to steady state without development of an $O_2$ deficit. A subsequent study from that group (7) in which $O_2$ deficit measured during HE exercise did not differ from that of an equivalent concentric workload. The considerably lower baseline values and the smaller increase in $\dot{V}O_2$ for a given change in applied work rate during HE exercise than during any of the concentric exercise tests indicate the greater efficiency of eccentric exercise. The gain calculated as the change in $\dot{V}O_2$ per change in work rate was $2.4 \text{ ml} \cdot \text{min}^{-1} \cdot W^{-1}$ for the eccentric exercise compared with $9–10 \text{ ml} \cdot \text{min}^{-1} \cdot W^{-1}$ for the concentric exercise. The reduced effort to accomplish the same absolute work rate with eccentric exercise was reflected in the lower scores for RPE with HE than with HC exercise. However, the higher RPE and HR (see below) at the same metabolic rate for HE than for LC exercise probably indicates the greater stimulation of peripheral mechanoreceptors during eccentric exercise (20).

Incremental eccentric exercise was performed by three of our subjects. The peak $\dot{V}O_2$ attained during these tests was only 26–45% of peak during concentric cycling to exhaustion, and none of the subjects displayed evidence of reaching VT. Safety considerations and the ability to generate muscular power, rather than metabolic demand is in agreement with some studies (15, 31) but in contrast with others that reported no difference in $\tau_2$ across a wide range of work rates (2, 35).

Eccentric exercise. Resisting the lengthening of a muscle as force is applied is a common part of daily activities such as normal walking, but it is especially important during downhill walking or running (32). In this study, we were able to focus on the eccentric muscle action by application of force to the muscle as a motor-driven cycle ergometer pedals backward. However, the maximum force that can be generated during eccentric contractions is sufficiently high that muscle damage can occur (26). Indeed, even moderate intensities of eccentric exercise will cause muscle soreness in subjects unaccustomed to this type of exercise. Thus we introduced training sessions to allow our subjects to adapt and to avoid subsequent pain. It is possible that the reason we observed no progressive increase in $\dot{V}O_2$ (the $\dot{V}O_2$ slow component, see below) during the HE tests was that our subjects did not experience any fatigue. The constant iEMG and MPF with time during HE exercise are consistent with the absence of fatigue during HE exercise. Eccentric exercise is accomplished with lower muscle activation (5, 30) and a pattern of activation (16) that is different from that of an equivalent concentric workload. The considerably lower baseline values and the smaller increase in $\dot{V}O_2$ for a given change in applied work rate during HE exercise than during any of the concentric exercise tests indicate the greater efficiency of eccentric exercise. The gain calculated as the change in $\dot{V}O_2$ per change in work rate was $2.4 \text{ ml} \cdot \text{min}^{-1} \cdot W^{-1}$ for the eccentric exercise compared with $9–10 \text{ ml} \cdot \text{min}^{-1} \cdot W^{-1}$ for the concentric exercise. The reduced effort to accomplish the same absolute work rate with eccentric exercise was reflected in the lower scores for RPE with HE than with HC exercise. However, the higher RPE and HR (see below) at the same metabolic rate for HE than for LC exercise probably indicates the greater stimulation of peripheral mechanoreceptors during eccentric exercise (20).

Table 3. RPE and increase in lactate during concentric and eccentric exercise

<table>
<thead>
<tr>
<th></th>
<th>Concentric</th>
<th>Eccentric</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HC</td>
<td>MC</td>
</tr>
<tr>
<td>RPE</td>
<td>9.0 ± 0.8†</td>
<td>3.8 ± 0.6†</td>
</tr>
<tr>
<td>ΔLac, mmol/l</td>
<td>8.2 ± 1.2</td>
<td>2.1 ± 0.4†</td>
</tr>
</tbody>
</table>

Values are means ± SE; n = 6 subjects. RPE, rating of perceived exertion; ΔLac, increase in lactate. †Significantly different from HC, $P < 0.05$. **Significantly different from each other $P < 0.05$.
than a cardiovascular limitation, determined the end points in the tests.

During exercise, such as running, that involves eccentric and concentric muscle actions, it appears that the magnitude of the VO₂ slow component is reduced when the proportion of concentric exercise is reduced (6, 23). Our results that showed no VO₂ slow component during HE compared with HC cycling exercise might provide a partial explanation for these observations during running, as previously suggested (10, 23).

VO₂ and HR kinetics in concentric and eccentric exercise. The two-component model adequately described VO₂ kinetics, except for the HC exercise, where a third component was necessary. The amplitude of the phase 1 component was graded according to the total metabolic cost of the exercise. The onset of phase 2 (TD₂) occurred first in HC exercise, but phase 2 for HE exercise also occurred before that for LC exercise. Thus it appears that the magnitude of the muscle tension influenced the return of deoxygenated blood to the lungs. In the case of HE compared with LC exercise, not only was there greater muscle tension and, therefore, the potential to cause a greater mechanical displacement of blood back to the heart, but also the HR adapted more rapidly. Although we do not have information on cardiac stroke volume in the transition to exercise, it is likely that stroke volume was maintained at or even above baseline levels at the start of HE exercise. Thus the more rapid increase in HR, where there was even an overshoot during HE exercise, probably reduced the time required for blood to go to and return from the working muscle, facilitating a shorter time to the onset of phase 2. Because of the nonlinear nature of HR control across the range of work rates investigated, we did not attempt to fit exponential curves to these data. The absolute HR was higher during HE than during LC exercise, even though the metabolic demand was similar. Similar results were reported for downhill vs. uphill treadmill walking (14).

Greater muscle tension during HE than during LC exercise might be expected to provide greater stimulus to control of HR through activation of the motor cortex as well as peripheral mechanoreceptor feedback.

The observation that TD₂ of the VO₂ response was significantly faster in HE and LC exercise than in the HC test provides some interesting new data for a long-standing debate about the effect of work rate on VO₂ kinetics. Progressive slowing of VO₂ kinetics has been reported across a range of work rates from very light to near maximal (11, 18). However, these studies reported results on the basis of a one-component model rather than allowing for separate isolation of phases 1, 2, and 3 as required. When Casaburi et al. (11) explored the effect of different fitting models on their results, they concluded that the early-phase response did not differ substantially between low- and high-intensity exercise. There are other studies in which significant differences were reported for TD₂ across a range of work rates, especially below vs. above VT (15, 31), as we found. As part of this experiment, which was designed to focus on HE vs. HC and HE vs. LC exercise, our subjects also completed MC tests. The rationale for this was that the MC work rate was more typical of the demand investigated in many other studies, and the TD₂ and MRT values were consistent with previous findings (15, 28). There was clearly a trend for TD₂ to increase from LC (16.7 ± 2.2 s) to MC (20.6 ± 2.1 s) and HC (24.0 ± 1.7 s) exercise. The lack of significant difference between each of these mean values might have consequences of insufficient sample size to isolate the effect. Engelen et al. (15) also suggested that a small sample size might explain why some investigators reported slower VO₂ kinetics above than below VT (31), whereas others did not (2). In recent investigations, values for TD₂ that were 24 (10) and 40% (35) slower in above-VT than in below-VT exercise were reported as not statistically significant. The small sample size (n = 7 in each study) and some between-subject variation probably precluded detection of significance. The differences between studies highlight the need for future investigations to be conducted carefully and with sufficient statistical power to isolate physiologically significant differences in the time course of adaptation of VO₂ at the onset of exercise.

VO₂ slow component in HC. During HC exercise, a three-component exponential model was required to achieve a satisfactory description of the VO₂ kinetics. This observation is consistent with the concept of the VO₂ slow component, in which there appears to be an additional metabolic cost in addition to the expected VO₂ or that work rate (2, 31). The present experiments show that this added cost is not a function of the work rate per se, because there was no slow component in the HE exercise. A potential explanation for the VO₂ slow component is the metabolic cost of recruiting additional muscle fibers to accomplish the work task as some of the fibers initially recruited to complete the exercise task fatigue. This explanation differs from the proposal that recruitment of fast-twitch fibers to accomplish the greater work rate caused a higher metabolic cost (3), inasmuch as the newly recruited fibers could be slow or fast twitch. Although many authors suggest that it must be additional fast-twitch fibers that contribute to the VO₂ slow component, the rationale for this is not clear. The study of Crow and Kushmerick (13), in which it was shown that mouse fast-twitch fibers had a greater metabolic requirement than slow-twitch fibers, is frequently cited as rationale for the VO₂ slow component (4, 9, 34). However, differences in metabolic cost for tension development in human fast- vs. slow-twitch muscle are not clear. Recent in vitro studies of human muscle indicated a greater metabolic cost for tension development in fast-twitch fibers (19). Coyle et al. (12) reported greater efficiency during cycling across a range of constant loads in trained cyclists with a higher percentage of slow-twitch fibers. In contrast, Barstow et al. (4) found during ramp incremental cycling that the metabolic cost might actually be less in subjects with a high percentage of fast-twitch fibers than in those with a high percentage of slow-twitch fibers (9 vs. 11 ml·min⁻¹·W⁻¹). The same researchers reported that
individuals with a high percentage of fast-twitch fibers also had a larger VO$_2$ slow component (3).

Changes in MPF have been investigated as a possible indicator of the proportion of fast-twitch fibers contributing to muscle contraction (17). Recent evidence on changes in MPF during heavy exercise is conflicting. Although an increase in MPF of the vastus lateralis muscle that coincided with the slow component has been observed (34), other studies found no change (27, 35). Our results from four different muscles also suggest a no change in the proportion of fast-twitch fibers contributing, but the relatively high fitness level of our subjects might have reduced the likelihood of recruiting fast-twitch fibers (27). Furthermore, caution should always be applied to interpretation of surface EMG results.

The progressive increase in iEMG for the RF and VM muscles paralleling the increase in VO$_2$ during HC exercise supports the hypothesis that more fibers are being recruited. In previous investigations of EMG during high-intensity exercise, progressive increases (34, 36) or no change (27, 35) in EMG was found, coinciding with the appearance of the VO$_2$ slow component. It is possible that examination of different muscles (typically only the vastus lateralis in many investigations) or selection of exercise intensity as a percentage of the difference between VT and peak VO$_2$ might be responsible for some of the between-study discrepancies. A recent investigation (34) confirmed the greater muscle fiber recruitment from the transverse relaxation time (T$_2$) of magnetic resonance imaging. The concept of recruiting additional fibers and/or increasing motor unit firing rate to maintain the work rate is consistent with previous investigations of fatigue during sustained contractions (29). This can explain the greater metabolic cost, inasmuch as it is necessary to maintain cellular homeostasis after an action potential, even when there is not normal contractile activity.

**Conclusion.** The kinetics of VO$_2$ during the onset of high-intensity eccentric cycling exercise were described by a two-component exponential model similar to that required to describe the responses during low-to-moderate-intensity concentric cycling. Consistent with our hypothesis, the rate of increase in VO$_2$ was faster for HE and LC exercise, where the metabolic demand was reduced, than for the higher-intensity (HC) concentric exercise. Previous investigations that employed Douglas bag techniques to study the VO$_2$ kinetics at the onset of eccentric exercise could not clearly extract this information on the time course of the response (7, 25). In our comparison of muscle activation between HE and HC exercise, it became apparent that the VO$_2$ slow component was not a function of absolute work rate, but that it increased only when the iEMG of the VM and RF muscles increased. This latter observation suggests that fatigue of individual motor units forced recruitment of additional motor units to achieve the same work rate, increasing the total VO$_2$.

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