

Research Article

VO₂ Kinetics during Moderate Effort in Muscles of Different Masses and Training Level

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Purpose. To examine the relative importance of central or peripheral factors in the on-transient VO₂ response dynamics to exercise with “trained” and relatively “untrained” muscles. **Methods.** Seven professional road cyclists and seven elite kayak paddlers volunteered to participate in this study. Each completed two bouts of constant-load “square-wave” rest-to-exercise transition cycling and arm-cranking exercise at a power output 50–60% of the mode-specific VO_{2peak} presented in a randomized order. **Results.** In the cyclists, the mean response time (MRT) as well as the phase II VO₂ time constant (τ_2) was significantly slower in the untrained compared with the trained muscles. The opposite was the case in the kayakers. With respect to the relatively untrained muscle groups, while both demonstrated faster VO₂ kinetics than normal (moderately fit) subjects, the kayakers evidenced faster VO₂ kinetics than the cyclists. This suggests that there is a greater stabilizing-counterforce involvement of the legs in the task of kayaking than of the arms for cycling. **Conclusions.** The results of the present study provide no support for the “transfer” of a training effect onto the VO₂ on-transient response for moderate exercise, but rather support earlier reports demonstrating that peripheral effects may be important in dictating this kinetics.

1. Introduction

The time course of the pulmonary oxygen uptake (VO₂) response to constant-load exercise of moderate intensity can be characterized by two transient phases. In Phase I, the initial, usually rapid, increase in VO₂ is mediated by an increase in cardiac output, or more properly pulmonary blood flow, whilst the gas contents of the mixed-venous blood perfusing the lungs remain similar to those at rest. Phase II transition is triggered by the gas contents of the blood perfusing the lungs being altered by the influence of active muscle metabolism; it therefore represents the blood transport delay between the active muscles and the lungs. During Phase II VO₂ reflects the decreasing mixed venous O₂ content supplementing the continuing increase in pulmonary blood flow. This is characterized by a monoexponential rise in VO₂ up to the asymptotic or steady-state level (Phase III), the time course of which closely reflects that of the increased

muscle oxygen consumption [1, 2]. However, if the work rate is appreciably above the individual's lactate threshold (LT), VO₂ may not reach a steady state, associated with a continued slower rise in VO₂ (slow component; VO_{2slow}) of a delayed onset. Opinions are divided over whether VO₂ kinetics is limited by the rate of O₂ delivery to the working muscle [3] or by peripheral factors such as oxidative enzyme activity within the muscle mitochondria or the rate at which carbohydrates are processed into the mitochondria at the pyruvate-acetyl CoA site, that is, rate limitation of O₂ utilization by working muscles despite adequate O₂ delivery [4, 5].

It has been repeatedly shown that single-legged training (relatively small muscle mass) causes significant local (peripheral) changes (such as concentration of high energy phosphate compounds, ratio of ATP to ADP, and inorganic phosphate), with only minor alterations of the cardiovascular (central) system [6]. It has also been acknowledged [6] that,

in order to induce contralateral training modifications (cross-training), larger muscle mass that produces both peripheral and central adaptations should be involved. Indeed several reports (e.g., [7]) have demonstrated that arm training did not produce significant alterations in heart rate, stroke volume, or peripheral blood flow, either at rest or during exercise performed with the nontrained muscles (legs). After leg training; however, the increase in the centrally mediated variables was approximately the same in the trained (legs) and the nontrained muscles (arms) [6, 8]. It is indeed widely accepted that there is more of a transfer effect on the central hemodynamic after training with large muscle groups, compared with training with small muscle groups. It is, therefore, suggested that arm muscles have a greater potential for local (peripheral) rather than centrally mediated improvement in function and that central circulatory changes occur in proportion to the muscle mass used during the training. In most of the studies that have examined the transfer of training phenomenon, the conclusions have been based on changes occurring in the maximal aerobic power (VO_{2max}) and its determinates. However, in recent years, the on-transient VO_2 kinetics during exercise has been considered to be a valid indicator of the integrated cardiovascular, respiratory, and muscular systems' response to meet the increased metabolic demand of the exercise [8, 9]. VO_2 kinetics has also been shown to be faster in relatively fit individuals and to be speeded by training, both in normal subjects and in those with cardiovascular and/or pulmonary disease [10, 11]. However, there are only a limited number of studies where VO_2 kinetics has been applied to trained athletes [12, 13].

The metabolic and physiological responses to arm cranking differ markedly from those of leg cycling (see [14, 15] for reviews). At the same absolute power output, arm exercise results in higher rates of VO_2 , carbon dioxide output (VCO_2), ventilation (V_E), heart rate (HR), and greater increases in core temperature (T_{re}), plasma epinephrine, and blood lactate, than does leg exercise [14, 15]. In untrained individuals VO_{2peak} during arm cranking is approximately 60–70% of their leg-cycling VO_{2peak} [15]. When the physiological and metabolic responses to arm exercise are expressed as a percentage of the mode-specific VO_{2peak} , the differences between arm and leg exercise become less pronounced [15, 16]. The above-mentioned differences coupled with established records indicating that arm cranking results in an increased recruitment of type II muscle fibers [15, 17] and that type II muscle fibers have significantly lower metabolic efficiency than type I fibers [1] explains at least partially, why mechanical efficiency is lower in arm cranking than in leg cycling [14, 15, 17].

There is evidence that arm cranking results in slower Phase II VO_2 kinetics than leg cycling at similar absolute [8] and relative (to mode-specific maximal load) power outputs [17, 18]. Furthermore, arm muscles have been shown to have a lower capillary-to-muscle fiber ratio, reduced total capillary cross-sectional area and may induce intramuscular pressures during exercise that exceed blood perfusion pressure, when compared with leg muscles [14, 15]. It is also well documented that the proportion of type II muscle fibers is significantly higher in the muscles of the upper body compared to

those of the lower body [19]. The reduced relative perfusion of arm muscle fibers combined with findings that type II muscle fibers have slower VO_2 kinetics than type I fibers could result in slower active muscle oxygen consumption kinetics, thereby slowing Phase II VO_2 kinetics. Several other studies have already compared the on- and off-transient VO_2 responses of arms and legs [8, 17]. Our present study, however, addresses the issue of the relative importance of central or peripheral factors in the on-transient VO_2 kinetics to exercise with “trained” and “untrained” muscles in elite competitive athletes specializing in sport disciplines that require intensive and long-term training, predominantly with their arm muscles (kayakers) or leg muscles (cyclists).

2. Material and Methods

Seven professional road cyclists and seven elite flat water kayak paddlers volunteered to participate in this study during the maintenance phase of their normal training, after giving their written informed consent. All procedures were conducted in accordance with ethical standards of the Institutional Committee of the Italian National Olympic Committee and with the Helsinki Declaration of 1975.

Table 1 lists their physical characteristics. Each had trained and competed extensively at national and international levels for 5 to 10 years. Their training regimen included largely intensive and long-term aerobic activities, predominantly with their arm (kayakers) or leg (cyclists) muscles. Subjects came to the laboratory on four occasions to perform arm- and leg-cranking exercise studies. Each test was scheduled at a similar time of day in order to minimize the effect of diurnal biological fluctuation.

2.1. Measurement of Arm-Cranking and Leg-Cycling Peak Oxygen Uptake (VO_{2peak}) and Gas Exchange Threshold (GET). During the first two visits to the laboratory each subject performed two incremental exercise tests to the limit of tolerance in order to determine the arm-cranking and leg-cycling GET and VO_{2peak} . For the lower limbs, all athletes were tested on a cycle ergometer (Ergoline, Germany). For the upper limbs, the cyclists used a standard arm-cranking ergometer (Technogym, Top.XT, Italy); the kayakers used an arm paddling ergometer (Technogym, K-Race, Italy), mimicking the actual arm movement for which the kayakers' arm muscles were trained. The subjects were seated upright such that the crank axis of the ergometer was aligned with the glenohumeral joint. The height of the seat was adjusted to allow for a slight bend in the elbow when the crank handles were at their greatest distance from the subject. Additionally, the legs were not braced and the feet were placed on a footrest, mimicking the actual position in the kayak. The subjects were encouraged to use only their arms and shoulders to perform the exercise, whereas the use of lower back and legs was discouraged. For the leg-cycling test, the seat height was adjusted such that the legs were in slight flexion (170°) at the nadir of the down stroke, while the handlebars were set

TABLE 1: Physical characteristics of subjects by group.

	Age	Height	Weight
Cyclists	24.0 ± 3.7	175.0 ± 6.7	65.9 ± 5.9
Kayakers	22.0 ± 2.8	180.6 ± 5.5	79.7 ± 7.9

*Bold letters denote significant difference between groups ($P < 0.05$).

according to the individual preferences. Handle bar arm-pull was discouraged during leg cycling. During all tests the crank/cycle cadence was strictly kept between 90 and 100 strokes/revolutions per minute (SPM/RPM), respectively (typical rhythm for both activities), despite the fact that the ergometers provided speed-independent power. All three ergometers were calibrated prior to the beginning of the study using a dynamic calibration rig (Cerini, Italy).

After a 15-minute standardized warm-up, consisting of either pedaling or cranking at 60 RPM or SPM at a work rate of 100 and 50 W, respectively, and following a 5-min rest, the subject then commenced the leg-cycling or arm-cranking task. The power output was increased progressively every minute from an initial work rate for the cyclists of 100 and 50 W for the legs and arms, respectively, and 75 and 100 for the kayakers in order to bring the subject to the limit of tolerance in 8–12 minutes. This was achieved by increasing the power output in increments of 25 watts·min⁻¹ for leg cycling and 20 watts·min⁻¹ for arm cranking until the subject was unable to keep the pedaling (or stroke) rate above 50 per minute.

During both incremental exercise tests, HR, VO₂, VCO₂, and V_E were measured breath by breath via standard open-circuit spirometry techniques using computerized metabolic cart (Quark b2, Cosmed, Italy). Daily calibration of volume (with 3-L syringe) and pretest calibration of carbon dioxide and oxygen gas analyzers (with precision gas mixers) were carried out. Heart rate was continuously monitored by means of a telemetric system (Polar, Electro, Finland).

Peak oxygen uptake (VO_{2max}) was defined as the highest average VO₂ during a 30-second period of the last 90 seconds of the test. The criteria for the noninvasive determination of the gas exchange threshold (GET) were as follows. (1) The modified V-slope method [20], in which VCO₂ is plotted against VO₂. The GET was defined as the last value prior to the departing of VCO₂ versus VO₂ slope from linearity. (2) A systematic increase in the ventilatory equivalent for O₂ (V_E/VO₂) without an increase in the ventilatory equivalent for CO₂ (V_E/VCO₂), when plotted against exercise time [20]. The GET was determined by inspection in a blinded manner by two investigators. A third investigator was consulted to adjudicate between the two when the two investigators did not agree on threshold placement.

2.2. Oxygen Kinetics during Moderate-Intensity Constant-Load Exercise. On the two following visits, each subject performed one arm-cranking and one leg-cycling 4-5-minute constant-load test, in a randomized order. Following 10 minutes at rest, the work rate, equal to that which elicited 50% of VO_{2max} during the incremental test, was applied

instantaneously (from absolute rest) without prior warning given to the subject. During both tests the crank/cycle cadence was strictly kept between 90 and 100 SPM and RPM, respectively. Gas exchange was measured breath-by-breath using the same apparatus as for the incremental tests. Heart rate was monitored and recorded continuously during all constant-load exercise tests by means of a telemetric system (Polar, Electro, Finland).

2.3. Calculation of Oxygen Uptake Kinetics. Individual responses during the rest-to-exercise transitions were linearly interpolated to give 1-s values. For each subject and each exercise protocol, data were time-aligned to the start of exercise, superimposed, and averaged to reduce the breath-to-breath noise and enhance the underlying physiological response characteristics. The baseline VO₂ (VO_{2bs}) was defined as the average VO₂ measured during the last two minutes before the start of exercise (rest period). The VO₂ mean response time (MRT) was fitted by combining the first and the second exponential terms. The MRT was then used to indicate the overall rate of change of the VO₂ toward its new steady state. The MRT for a single-term exponential model is equivalent to $\tau + T_D$ and therefore provides response information including not only the time constant (τ) but also the time delay (T_D). At the MRT, this response has attained 63% of its final value. To estimate the phase II time constant for the VO₂ kinetics (τ_2) we used a nonlinear least-squares monoexponential fit to the data as previously described [17, 21]. However, in order to maximize the amount of transient data available for the characterization (an important determinant of the goodness of fit [22]) we chose to discard the first 15 sec rather than the more common 20 sec—reasoning that the more rapid cardiac output kinetics in our fit subjects would reduce the limb-to-lung transit time and hence the duration of Phase I.

VO₂ kinetics tends to be slower at higher work rates even when the work rates are not associated with a sustained increase in blood lactate [23]. Therefore, and in order to facilitate comparison across subjects exercising at different absolute work rates, the relative gain of the response ($G = A/\text{work rate}$) and the exercise specific relative oxygen deficit were computed using the following equation:

$$\text{O}_2\text{D}/\text{W} = G (\text{VO}_2/\text{W}) \times \text{MRT} (\text{sec}) = \text{mL O}_2/\text{min}/\text{W}. \quad (1)$$

2.4. Data Analysis. Group data are reported as means and standard deviation. A two-way ANOVA with repeated measures for training status (trained or nontrained) and for muscle group (upper or lower extremity) (independent variables) was used to determine differences and relationships in and among the various dependent (O₂ kinetics parameters) and independent parameters between arm cranking and leg cycling and between the trained and nontrained muscles. Tukey's post hoc test was utilized to determine where significant differences existed. Statistical significance was accepted at $P < 0.05$.

TABLE 2: Peak and sub-maximal responses to arm and leg exercise by each group (mean \pm SD).

	Kayakers		Cyclists	
	Leg ^a	Arm ^b	Leg ^c	Arm ^d
Peak work rate (W)	298 \pm 42 ^{cd}	279 \pm 20 ^{cd}	390 \pm 52 ^{abd}	157 \pm 17 ^{abc}
Peak VO ₂ (mL/min)	4268 \pm 656 ^{cd}	4087 \pm 499 ^{cd}	4921 \pm 380 ^{abd}	3147 \pm 436 ^{abc}
Peak HR (b/min)	183 \pm 3	183 \pm 8	192 \pm 11 ^d	178 \pm 11 ^c
VO _{2ss} (mL/min)	2015 \pm 368 ^{cd}	1943 \pm 404 ^{cd}	2952 \pm 195 ^{abd}	1501 \pm 384 ^{abc}
Work rate _{ss} (W)	108 \pm 31 ^{cd}	106 \pm 15 ^{cd}	170 \pm 16 ^{abd}	69 \pm 12 ^{abc}
Work rate _{ss} (% VO _{2peak}) ^{**}	39 \pm 3	40 \pm 4	44 \pm 4	43 \pm 3
VO _{2ss} (% VO _{2peak}) ^{**}	47 \pm 6 ^c	47 \pm 6 ^c	58 \pm 4 ^{abd}	50 \pm 8 ^c
VO ₂ at GET (L/min)	2.84 \pm 0.39 ^c	3.31 \pm 0.25 ^{cd}	3.86 \pm 0.33 ^{abc}	2.50 \pm 0.33 ^{abc}
VO _{2ss} /VO ₂ at GET (%)	72.3 \pm 21 ^{bd}	62.5 \pm 15 ^{ac}	74.1 \pm 11 ^{bd}	61.6 \pm 17 ^{ac}
HR _{ss} (% VO _{2peak}) ^{**}	66 \pm 7	63 \pm 6	67 \pm 5	62 \pm 6

Like letters denote significant difference ($P < 0.05$).

^{**} Values are percentages of their respective peak values.

Peak work rate: work rate achieved at exhaustion; Peak VO₂: rate of oxygen uptake at exhaustion; Peak HR: heart rate at exhaustion; VO_{2ss}: rate of oxygen uptake at steady state level; Work rate_{ss}: work rate at steady state level; VO₂ at GET: rate of oxygen uptake at the gas exchange threshold; VO_{2ss}/VO₂ at GET: ratio of oxygen uptake at steady state level to oxygen uptake at the gas exchange threshold; HR_{ss}: heart rate at steady state level.

3. Results

3.1. Peak and Related Values. Table 2 presents data obtained during and at the end of all incremental and submaximal constant-load tests performed with the trained and untrained-muscle groups.

3.1.1. Cyclists. As expected for cyclists, all peak mechanical and cardiovascular-related responses (central) were significantly higher in the trained (legs) compared with the nontrained (arms) muscles. The exception was the peak respiratory exchange ratio values (RERs), which were similar in the two muscle groups (1.16 \pm 0.05 versus 1.16 \pm 0.06), and of a magnitude, which was consistent with maximal effort in both. The arms-to-legs ratio of VO_{2peak} in this group was 64% (Table 2).

3.1.2. Kayakers. For these athletes the results were considerably different, demonstrating similar peak responses (mechanical and physiological) in both the trained and the nontrained muscles (Table 2). The arms to legs ratio of VO_{2peak} in this group was 96%.

Also presented in Table 2 are values representing relative physiologic stress and strain during the constant submaximal load exercise challenges. Work rates, VO₂, and HR achieved during the steady-state phase of the respective submaximal constant-load exercise, in percent of their respective peak values, as well as the ratio between the measured VO₂ during the constant-load exercise challenges, and the respective VO₂ of the muscle group-specific GETs, were not significantly different within and between groups (Table 2).

3.2. VO₂ Kinetics. Figures 1–4 compare the groups' mean Phase II of the VO₂ response kinetics (excluding Phase I in each response), during the transition from rest to constant moderate exercise level between and within groups and muscles, along with the best exponential fit to each mean

response. Visual inspection of these plots reveals that phase II of the VO₂ response rose in biphasic fashion toward phase III (the exercise steady state levels). It seems that the relative load selected for this study (50–60% mode-specific VO_{2peak}) was not only physiologically similar (in relative terms) (see Table 2), but also sufficiently low for both the lower and upper body musculatures for an attainment of a steady-state VO₂ (after 2–3 min) without a development of VO_{2slow} component, in the trained and untrained muscles alike.

A more quantitative assessment of the relative speed of VO₂ response as a function of muscle group and training status is presented in Table 3 (means \pm SD).

3.2.1. Within-Group Comparisons

Trained versus Untrained Muscles

(1) Cyclists. Onset of lower and upper extremity exercise at 50 to 60% of the mode-specific VO_{2max} was associated with significantly higher amplitude-related values (VO_{2ss} and A), and with faster overall (MRT) and Phase II response time (τ_2) in the trained muscles (legs) compared with the nontrained muscles (arms) (Figure 1 and Table 3).

It should be pointed out that when normalized for work rate attained by each muscle group (170 versus 79 W for the legs and arms, resp.), the “relative” rise (amplitude) in VO₂ per unit load (G) was similar in the two muscle groups. In contrast, relative oxygen deficit (O₂D/W) remained significantly larger in the untrained (arm) muscles compared with the trained (leg) muscles (594.5 versus 370.3 mL/min/W) (Table 3).

(2) Kayakers. Although arm training (kayakers) did not bring about superiority in any of the upper body musculature VO₂ amplitude- or response-related parameters at the onset of a below threshold square-wave exercise, such training promoted the VO₂ response-related parameters to a level approaching that of their legs (Table 3).

TABLE 3: Parameters of oxygen uptake response during moderate exercise as a function of exercise modality (muscle group involved) (mean \pm SD).

Variable	Kayakers		Cyclists	
	Legs ^a	Arms ^b	Leg ^c	Arm ^d
VO _{2bs} (L/min)	0.46 \pm 0.04	0.46 \pm 0.09	0.41 \pm 0.07	0.40 \pm 0.10
VO _{2ss} (L/min)	1.99 \pm 0.34 ^{cd}	1.94 \pm 0.40 ^{cd}	2.85 \pm 0.33 ^{abd}	1.50 \pm 0.38 ^{ac}
A (L/min)	1.54 \pm 0.34 ^{cd}	1.45 \pm 0.36 ^{cd}	2.45 \pm 0.38 ^{abd}	1.03 \pm 0.26 ^{abc}
G (mL O ₂ /min/W)	14.35 \pm 1.11	13.6 \pm 2.21	14.38 \pm 0.84	14.5 \pm 3.83
τ_2 (sec)	16.50 \pm 2.6 ^{bd}	18.81 \pm 3.7 ^{ac}	14.90 \pm 2.7 ^{bd}	19.70 \pm 3.6 ^{ac}
MRT (sec)	22.62 \pm 3.1 ^{bcd}	26.73 \pm 8.9 ^{ad}	25.76 \pm 4.9 ^d	40.90 \pm 5.6 ^{abc}
O ₂ D (mL)	34.6 \pm 11.9 ^c	39.4 \pm 11.5 ^c	61.2 \pm 17.4 ^{abd}	40.7 \pm 15.3 ^c
Relative O ₂ D (mL O ₂ /min/W)	323.2 \pm 97 ^d	363.2 \pm 92 ^d	370.3 \pm 90 ^d	594.5 \pm 155 ^{abc}

Like letters denote significant difference ($P < 0.05$).

VO_{2bs}: average value over the two min of resting baseline; VO_{2ss}: rate of oxygen uptake at steady state level; A: the asymptotic amplitude for the exponential term; τ_2 : time constant of primary phase; MRT: mean VO₂ response time; O₂D: calculated oxygen deficit; G: relative (to work rate) gain of the VO₂ response; Relative O₂D: O₂ deficit normalized to work rate.

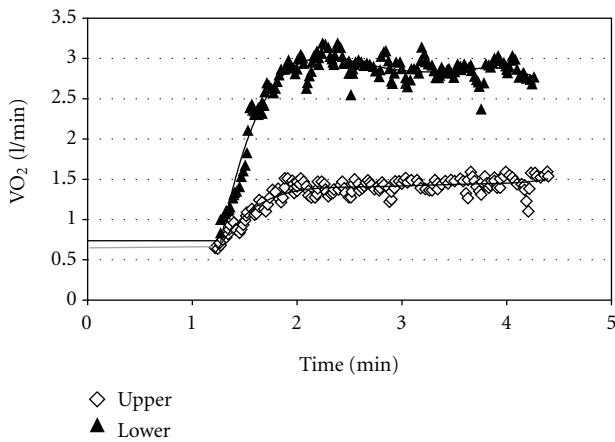


FIGURE 1: Average phase II of the VO₂ response during transition from rest to moderate exercise using untrained arms (\diamond) and trained legs (\blacktriangle) by the cyclists.

3.2.2. Between-Groups Comparisons

Trained Muscles (Leg (Cyclists) versus Arm (Kayakers) Muscles). As expected, and partially due to the differences in muscle mass and consequently in work rate, VO_{2ss} and A, were significantly higher in the trained lower limbs than in the trained upper limbs (Figure 3 and Table 3). Similarly, the Phase II time constant (τ_2), was faster in the trained lower than the trained upper limbs. Nevertheless, the overall VO₂ transient during the square wave exercise (MRT) and the relative O₂D did not differ significantly between the large and the relatively small trained-muscle groups (Table 3).

Nontrained Muscles (Leg (Kayakers) versus Arm (Cyclists) Muscles). Except for VO_{2bs} and G, all other VO₂ response kinetic parameters (A, MRT, and τ_2) were higher (or faster) in the untrained lower limbs compared with the untrained upper limbs (Table 3). Similarly, relative O₂D showed significantly smaller volume when exercising with the legs compared with arm exercise (323.2 versus 594.5 mL O₂/min/W, resp.).

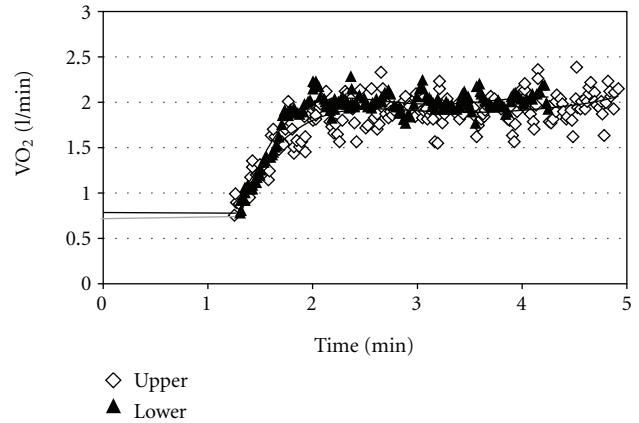


FIGURE 2: Average phase II of the VO₂ response during transition from rest to moderate exercise using trained arms (\diamond) and untrained legs (\blacktriangle) by the kayakers.

Trained versus Nontrained Muscles

(1) *Lower Limbs.* Whereas load- or muscle mass-associated variables (VO_{2ss} and A) were significantly higher in the trained legs compared with the nontrained legs, variables related to the rate of VO₂ response during moderate constant load exercise (τ_2 and MRT) showed *no* significant differences between the trained and the untrained legs (Table 3). Similar trend was also evident in the load-normalized rise in oxygen uptake (G) and oxygen deficit (O₂D) being statistically similar in the trained and the nontrained leg muscles (Table 3).

(2) *Upper Body.* Except for the τ_2 (statistically similar in the trained and untrained upper body muscles), and unlike in the lower limbs, the trained arms demonstrated significantly higher (A, VO_{2ss}) and faster (MRT) O₂ kinetics-related values than the untrained arms (Figure 4 and Table 3). Relative O₂D showed significantly smaller volume in the trained muscles

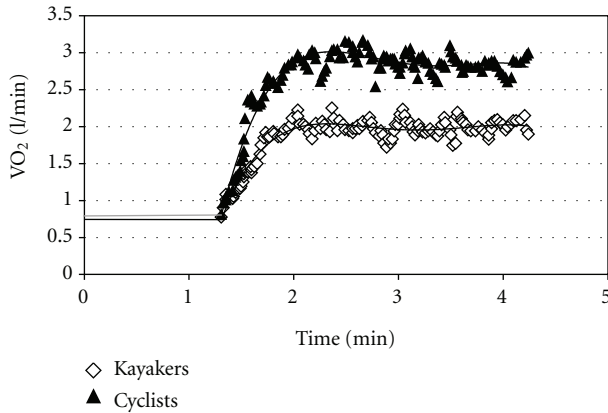


FIGURE 3: Average phase II of the VO_2 response during transition from rest to moderate exercise using lower limbs muscles by the cyclists (trained) (\blacktriangle) and the kayakers (untrained) (\diamond).

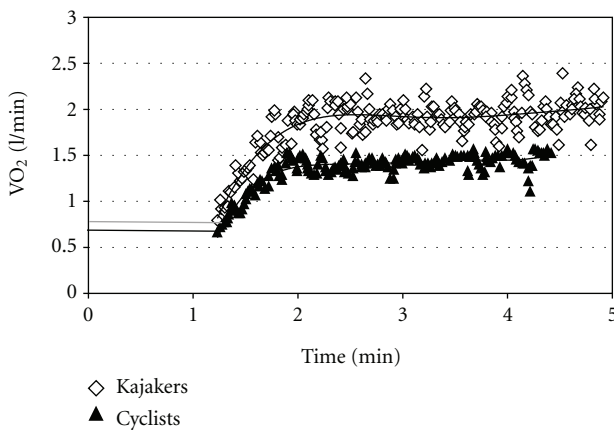


FIGURE 4: Average phase II of the VO_2 response during transition from rest to moderate exercise using upper limbs muscles by the cyclists (untrained) (\blacktriangle) and the kayakers (trained) (\diamond).

compared with that of the untrained upper body muscles (Table 3).

4. Discussion

To our knowledge, this is the first study to consider the kinetics of the VO_2 response to dynamic muscular exercise in highly trained athletes who compete in events predominantly utilizing the lower or upper extremities, that is, cyclists and kayakers.

As expected, both VO_{2peak} and peak power output were higher for the trained than for the untrained muscles in each group. However, to make a valid comparison of VO_2 kinetics across exercise modes, we chose to normalize the exercise intensity to 50–60% of the mode-specific VO_{2peak} (i.e., below the GET in this trained subjects). In this exercise intensity domain, it is believed that a metabolic inertia within the muscle cells themselves is the principal limitation to the acceleration of oxidative metabolism after the onset of exercise [4, 24, 25].

Hence, despite differences in the absolute VO_2 , the relative intensity of each square-wave transition was successfully matched across exercise modes: the $\% \Delta VO_2$, the % of the mode-specific peak power output, and the % of mode-specific of maximal heart rate were not significantly different (Table 2). Therefore, our study allows a comparison of the fundamental components of the VO_2 kinetics between cycling and arm cranking within the same intensity domain.

Unsurprisingly, the VO_2 response to moderate exercise in the cyclists revealed different patterns for the trained (legs) and the untrained (arms) muscles (Figure 2; Table 3). The higher absolute work rate in the trained-muscle group naturally resulted in a higher steady-state amplitude of the VO_2 response than for the untrained-muscle group. However, the phase II time constant (a functional correlate of the muscle VO_2 time constant) [2, 9, 24] as well as the VO_2 mean response time (MRS) reflecting, in addition, the utilization of oxygen from the oxygen stores [26] was significantly faster in the trained than the untrained muscles. Consequently, the oxygen deficit per unit power output (O_2D/W) was significantly larger in the tests with the untrained muscles than with the trained muscles (Table 3).

While the VO_2 kinetics for the cyclists' arms ($\tau_2 = 19.7$ sec; MRT = 40.9 sec) were slower than those of their leg ($\tau_2 = 14.9$ sec; MRT = 25.8 sec), they were appreciably faster than those previously reported for arm-cranking exercise in normal untrained males (60–80 s) [8, 18]. In fact, the VO_2 time constant for the cyclists' arms was similar to, and sometimes even faster than, those previously reported for normal nontrained legs (30–40 s) [8, 27]. This suggests that the muscles used by the cyclists for the arm-cranking exercise ought not be considered “untrained,” that is, reflecting the additional compensatory component arising from dynamic stabilization of the body during cycling and even periods of active “pulling” on the handlebars. Support for the above contention comes from studies by Baker et al. [28, 29] who reported that power generated during sprint cycling was significantly higher in a protocol that allowed for the gripping of the handle bars than in another protocol without the gripping of handle bars. Their results demonstrated that the arms and the upper body were involved in stabilizing the entire body so that the lower limbs could exert forces downwards onto the cycle pedals to generate the mechanical power and that the contribution of muscle groups not directly involved during sprint cycling toward power generation cannot be discounted.

Alternatively, of course, a “transfer effect” on the VO_2 kinetics may have been contributory, resulting from an increased amount of blood and, therefore, oxygen, available to the cyclists' arms as a result of a “central” training effect consequent to the leg training. However, for this to be contributory, the VO_2 kinetics would need to be limited by oxygen delivery at this work intensity. However, there is no convincing evidence that increases in maximum VO_2 and, hence, maximum cardiac output induced by training alter the steady-state cardiac output response to a moderate-intensity work rate, at least for leg exercise (i.e., [26]). Furthermore, the VO_2 time constant for moderate exercise has been demonstrated not to be speeded by: experimentally-induced

increases in muscle blood flow [4], beginning the exercise when blood flow has remained high following a prior bout of higher intensity exercise [30], and even by increased inspired O_2 fractions [31]. Hence, any improvement in central indices of cardiovascular function is unlikely to be contributory.

The VO_2 response to moderate exercise in the kayakers, in contrast, revealed similar patterns (amplitude, kinetics, and O_2D) for the arm and the leg exercise, both in absolute and relative terms (Figure 2; Table 3). These results suggest either that the long-term intensive training with the relative small muscle mass of the arms did not cause any appreciable cross-training effect on the VO_2 kinetics and/or that there is a significant leg contribution to kayaking [32]. The fact that the values for the VO_2 time constant (16.5 sec) and MRT (22.6 sec) for leg exercise in the kayakers are appreciably faster than for normal untrained cycle ergometry [2, 8] suggests that the latter explanation is more likely.

Our finding that the VO_2 kinetics for the kayakers' arms are not significantly different from those of the cyclists' arms, despite the "central" capacity (as reflected by the leg VO_{2peak}) being appreciably lower in the kayakers, suggests that the VO_2 kinetics at the onset of subthreshold square-wave exercise depend primarily on peripheral factors (muscle mass, distribution of muscle fiber type, number of mitochondria, activity levels of oxidative enzymes, and possibly muscle vascularization) and not on central factors (cardiac output, pulmonary ventilation, etc.). These results are in line with previous reports suggesting that on-transient VO_2 kinetics for moderate square-wave exercise is mainly reflective of and dictated by peripheral (local) rather than central attributes [4, 5, 33].

While the phase II time constant (reflective of the kinetics of muscle oxygen utilization, that is, [1, 24]) for the exercise involving the trained-muscle groups were both fast relative to normal subjects, the value in the cyclists (14.9 sec) was even (and significantly) faster than that for the kayakers (18.8 sec). However, the mean ratio of leg to arm τ_2 in our highly trained subjects was $81 \pm 5\%$, being appreciably higher than the respective ratio of 50–60% observed in healthy untrained subjects [8, 17, 27]. That is, while both muscle groups were evidently "highly trained," the cyclists were trained for longer-duration exercise (i.e., hours); the kayaker's training program, preparing for all-out races lasting 2–7 minutes, included both aerobic- and anaerobic-type activities (including resistance training) [32]. Furthermore, the energy demand for the kayakers, during both competitions and training, was frequently in excess of VO_{2peak} , which was not the case for the cyclists. These factors may have contributed to even greater improvements in aerobic enzymatic function and capillarity—thought to be important contributors to VO_2 kinetics [5, 24].

With respect to the relatively untrained-muscle groups, the kayakers evidenced faster VO_2 kinetics both with respect to τ_2 and MRT, than the cyclists (Table 3). This suggests that, while both muscle groups may be considered to be relatively trained [29, 32] with respect to normal moderately fit subjects, it seems that there is a greater stabilizing-counterforce involvement of the legs in the task of kayaking [32] than of the arms for cycling.

Another interesting and, possibly, surprising finding of the present study was the similarity of the VO_2 response kinetics for the trained (cyclists) and untrained (kayakers) leg muscles. This finding is not only surprising, but also contrary to several previous reports demonstrating a significant speeding of these kinetics following endurance training [13, 34]. One possible explanation for this unexpected outcome is that the speeding of the VO_2 kinetics with endurance training does not increase *pari passu* with the increase of VO_{2peak} , but rather effectively attains a plateau. We speculate that this "asymptotic" level of the phase II time constant is relatively "easy" to reach since even the relatively mild "whole body" training (including leg muscles) of our kayakers group appeared sufficient for their leg VO_2 kinetics to attain this assumed critical limiting level. This suggestion is further supported by the similar MRT in the trained and untrained leg muscles, despite significant differences in the respective VO_{2peak} values (73.2 versus 53.4 mL/kg/min). Furthermore, when comparing the ratio of τ_2 of the leg muscles to that of the arm muscles (τ_2 legs/ τ_2 arms) between the two elite athlete groups, it becomes evident that the kayakers arm muscles' "machinery" (as determined by the τ_2) is significantly closer to that of their leg muscles (88.3 versus 73.4% in the kayakers and cyclists, resp.). It is clear that such proximity is not due to relatively slow legs' τ_2 in the kayakers, as the latter is as fast in the kayakers as it is in the cyclists (see Table 3). Such high ratio implies that (a) arm training, as used by our kayakers, provides stronger stimulus for improving the VO_2 response kinetics during constant and moderate exercise task, and (b) for achieving high level in kayak competition, one needs to promote his arm muscle functioning to a level very close to that of his legs. It should be pointed out that the difference in the MRT legs-to-arms ratio between the two groups was even greater (86.7 versus 63.2% for the kayakers and cyclists, resp.).

Limitations of Study Design. Probably, the most powerful way to test the hypothesis of this study would be to conduct a "classic" training study (pre- versus posttraining comparisons). However, legalistically and logistically, such "classic" approach will not allow a long and intensive training regimen, such as that pursued by our subjects. Further, the design of this study does not allow to exclude the possibility of genetic predisposition influence on the observed results and hence on the final conclusions of the study.

Also, in the present study we used differing testing modes of arm exercise between groups. The logic for using different exercise modalities to test and compare arm exercise between cyclists and kayakers was intended to allow subjects in each group to perform exercise (in their respective trained muscles) similar to those they were most accustomed to and trained for.

Notwithstanding the above-mentioned limitations, the results of the present study provide no support for the "transfer" of a training effect onto the VO_2 on-transient response for moderate exercise, but rather support earlier reports demonstrating that peripheral (local) and not central (hemodynamic) effects may be important in dictating these kinetics. As a consequence, we suggest that predominantly

local and/or specific training is required to speed the muscle O_2 consumption response to moderate exercise. This consequently reduces the associated oxygen deficit and hence the reliance on stored energy resources, predominantly phosphocreatine and O_2 , and anaerobic lactate production.

Finally and in line with the above-mentioned limitations, further effort should be attempted to validate the study's findings.

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B. Whipp, who passed away in 2011, was a pioneer and a highly prolific and respected researcher at the forefront of physiology in general and exercise physiology in particular. His work benefited countless scientists, physicians, coaches, and students. On top of all that he was a gifted educator, a unique lecturer, and above all, a warm, humble, and sincere human being. The authors are highly fortunate to have worked under his supervision and as his colleagues throughout various stages of his distinguished career and are indebted to the invaluable guidance, mentorship, and inspiration he bestowed upon them. Whipp was profoundly involved in writing this paper but did not live to see it published. His judgment and perspectives of future works will be greatly missed by many. The authors wish to dedicate this study to his legacy and cherished memory. This study was financed, in part, by the Italian National Olympic Committee (CONI). Many grateful thanks to the athletes for their participation in the study.

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