Effects of exercise on maximal instantaneous muscular power of humans

GUIDO FERRETTI, MARISTELLA GUSSONI, PIETRO E. DI PRAMPERO, AND PAOLO CERRETELLI
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FERRETTI, GUIDO, MARISTELLA GUSSONI, PIETRO E. DI PRAMPERO, AND PAOLO CERRETELLI. *Effects of exercise on maximal instantaneous muscular power of humans.* J. Appl. Physiol. 62(6): 2288–2294, 1987.—The maximal instantaneous anaerobic power ($\hat{w}$), as determined during a high jump off both feet on a force platform, was measured on eight subjects starting from *1*) a resting base line; *2*) a base line of steady-state cycloergometric exercise requiring 30, 50, and 70% of individual maximum O_2 consumption ($\dot{V}O_{2\,max}$); and *3*) a base line of maximal and supramaximal exercise (100 and 120% of $\dot{V}O_{2\,max}$). In addition, *4*) $\hat{w}$ was also measured during the $\dot{V}O_2$ transients from rest to each of the above work loads. Blood lactate concentration ($[La_b]$) was determined before and 8 min after the end of each priming load. After the onset of any priming load, $\hat{w}$ decreases with time reaching in 2 min a steady level that is lower the higher the $\dot{V}O_2$. For the three lowest work rates, the steady $\hat{w}$ level is unchanged by increasing the duration of the priming exercise up to 30 min. For low work levels, the decrease of $\hat{w}$ as a function of $\dot{V}O_2$ is essentially parallel to that of estimated muscle concentration of ATP ([ATP]). For work levels >60% of $\dot{V}O_{2\,max}$ involving a substantial accumulation of lactate, the decrease of $\hat{w}$ becomes smaller than the estimated drop of muscle [ATP]. This finding is tentatively attributed to an increase of either the mechanical equivalent or of the velocity constant of ATP splitting brought about by the lowering of intracellular muscle pH after lactate accumulation. The dynamic assessment of $\hat{w}$ during the rest-to-work transients is viewed as an indicator of the changes of $\dot{V}O_2$ at the muscle level and can be approximated by an exponential with a half time on the order of 20 s.

aerobic and anaerobic metabolism; lactate accumulation; velocity constant of ATP splitting; oxygen consumption transients

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CHEMICAL MEASUREMENTS on muscle biopsies (8, 9, 14) and nuclear magnetic resonance (^{31}P-NMR) data obtained in isolated mammalian muscles (12) and in human limbs (13) show that the phosphocreatine (PCr) and, to a lesser extent, the ATP levels are reduced with increasing muscle metabolism. As a consequence, the maximal anaerobic muscular power of a subject is expected to be lower when increasing the intensity of the exercise base line on which a power test is superimposed. In fact, Margaria et al. (11) found that the maximal anaerobic power ($\hat{w}_{max}$), assessed on a time basis of 4–6 s from the body's vertical displacement during a run at top speed up a flight of stairs (10), was inversely proportional to the intensity of the steady-state stepping exercise performed immediately before the test. However, in the experiments of Margaria et al. (11), because of the relatively long time basis, a substantial fraction of the overall ATP needed for work performance was likely provided via ATP resynthesis by simultaneous PCr breakdown. Consistently, the data were interpreted by the authors as reflecting a drop of muscle PCr only.

The maximal instantaneous muscular power (peak power, $\hat{w}$), calculated from instantaneous force measurements during a maximal vertical jump off both feet on a force platform, as suggested by Davies and Rennie (3), can be assessed on a time basis of only 0.004 s, i.e., 1,000–1,500 times shorter than that for Margaria's test (10, 11). Therefore, at variance with the latter, at the moment at which $\hat{w}$ is attained, mechanical energy should derive exclusively from the splitting of ATP immediately available for muscular contraction, without interference of ATP resynthesis from PCr. The aim of the present study was to follow in a group of untrained subjects, the evolution of $\hat{w}$ as a function of base lines of submaximal, maximal, and supramaximal cycloergometric exercise both at steady state and during rest-to-work transients.

METHODS

The experiments were carried out on eight male sedentary subjects (age 27 ± 4 yr; wt = 68.4 ± 8.0 kg). The steady-state O_2 consumption was measured by standard open-circuit method. The expired air was collected in Douglas bags and analyzed for gas composition and volume using a paramagnetic O_2 meter (Sybron, Taylor), an infrared CO_2 meter (model LB-2, Beckman), and a dry gas meter. The O_2 consumption at the mouth during rest-to-work transients was measured on a breath-by-breath basis, as described by Giezendanner et al. (7). Venous blood lactate concentration ($[La_b]$) was measured by an electrometric enzymatic method (Kontron Instruments) (15).

The maximal mechanical peak power ($\hat{w}$) was determined during a maximal vertical jump off both feet performed on a force platform, as proposed by Davies and Rennie (3). A squatting starting position was chosen to minimize the unavoidable negative work done by the lower limbs' muscles at the onset of the push. The time course of the changes of the vertical forces was monitored by eight strain gauges positioned at the four corners of the platform, recorded on tape, and subsequently ana-

lyzed by a computer (MINC-11, Digital Equipment) with a dwell time of 0.004 s. The resonant frequency of the platform was 50 Hz. A typical force vs. time tracing obtained during a jump is shown in Fig. 1. $\hat{w}$ at *time t* was calculated as the product of the vertical force (F) times the vertical velocity (v)

$$\hat{w}(t) = F(t) \cdot v(t) \qquad (1)$$

where

$$F = M(g + a) \qquad (2)$$

with M being the subject's mass, g the acceleration of gravity, and a the vertical acceleration imposed by muscle contraction to the center of gravity. Rearranging *Eq. 2*

$$a = \frac{F}{M} - g \qquad (3)$$

whence, the vertical velocity of the center of gravity can be obtained by time integration

$$v(t) = \int_0^t a(t)dt = \int_0^t \left(\frac{F}{M} - g\right) dt \qquad (4)$$

The maximal calculated value of $\dot{w}(t)$ was taken as $\hat{w}$ developed during the test jump.

From $\dot{w}$, the average power throughout the whole push phase of the jump can be calculated as

$$\bar{w} = \left[\int_0^{t_1} \dot{w}(t)\, dt \right] \Big/ t_1 \qquad (5)$$

where t_1, the push phase of the jump, $\cong$0.5 s.

Experimental procedure. Ten high jumps were performed by each subject starting from a resting base line to set the control values. Subsequently, the individual maximum O_2 consumptions ($\dot{V}O_{2max}$) were measured by means of graded cycloergometric exercise. $\dot{V}O_{2max}$ was defined conventionally as the $\dot{V}O_2$ level not followed by a measurable rise (>2%) on a further 25-W increase of work rate. Five cycloergometric work rates were then chosen, corresponding to ~30, 50, 70, 100, and 120% of the individual $\dot{V}O_{2max}$, respectively. For each selected work level, a series of exercise bouts of increasing duration was performed, the shortest lasting, in all cases, 20 s. Each trial followed the preceding one with a delay of 5 min and was 20 s longer than the one immediately preceding. The longest exercise duration was 2.3 min for the heaviest work load (120% $\dot{V}O_{2max}$), 3 min for 100% $\dot{V}O_{2max}$, and 5 min for the three lower loads (70, 50, and 30% $\dot{V}O_{2max}$). In these latter cases, for exercises longer than 3 min, the duration of the bouts was increased by 30-s steps. At the end of each exercise period, two jumps were performed on the platform, allowing for a 1-s pause in between, and $\hat{w}$ was calculated. Since the force platform was placed just beside the bicycle ergometer, <3 s

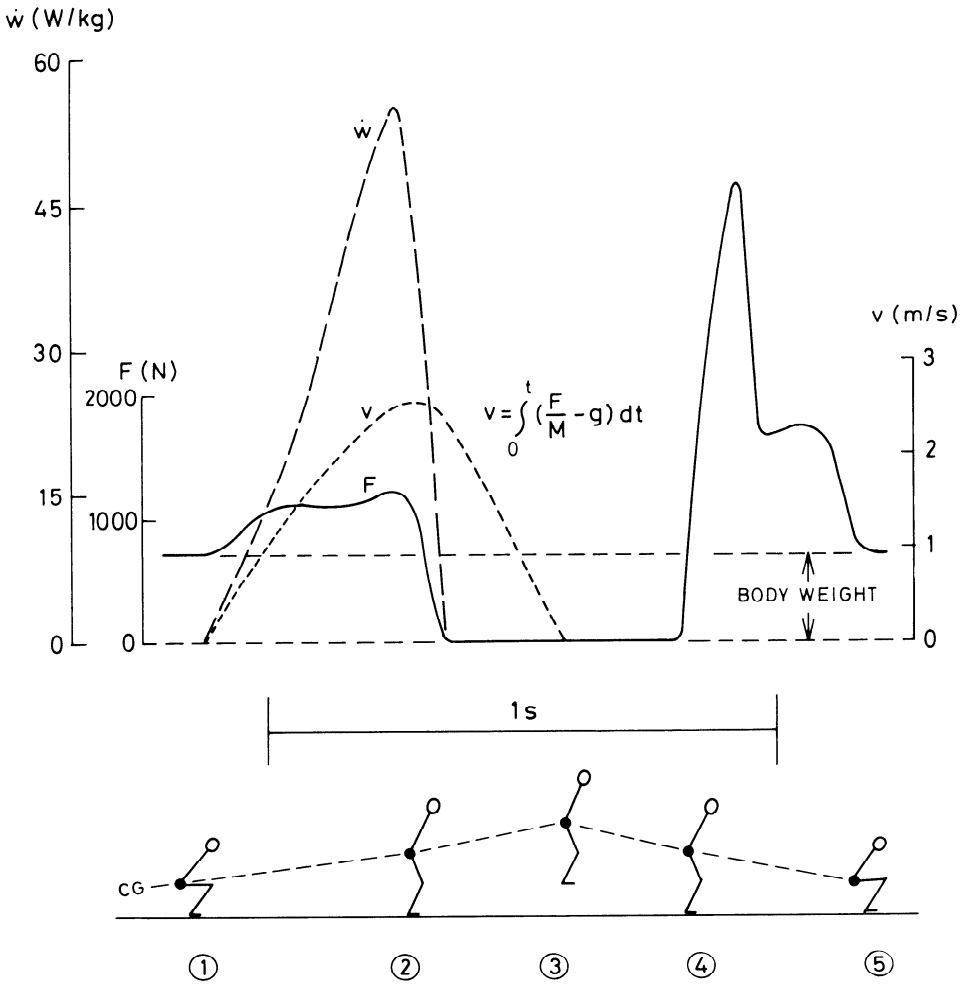

FIG. 1. Time courses of instantaneous force (F, *solid line*), velocity (v, *dotted line*), and power ($\dot{w}$, *dashed line*) during a maximal vertical jump off both feet on a force platform are given together with positions of subject's center of gravity (CG) in different phases of jump. Force vs. time tracing is obtained directly from platform. For calculation of v and $\dot{w}$, see text. Before jump (*position 1*), F is equal to subject's body weight; during push phase (*position 2*) it increases to decrease to zero during flight (*position 3*). M, mass; g, acceleration of gravity.

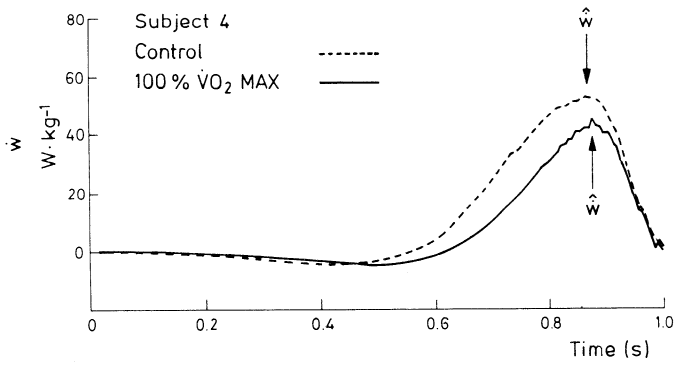

FIG. 2. Time course of instantaneous power ($\dot{w}$) developed by a typical subject during two jumps performed *1*) from a resting base line (*dashed line*) and 2) from steady state of a 100% maximum O_2 consumption ($\dot{V}O_{2max}$) priming exercise (*solid line*). *Arrows* indicate maximal instantaneous power ($\hat{w}$) achieved in two jumps.

TABLE 1. *Basic physiological data of the investigated subjects*

Subj No.	Wt, kg	Net $\dot{V}O_{2\,max}$, ml·min^{-1}·kg^{-1}	$\hat{w}_r$, W/kg
1	79.1	32.79	48.43±2.23
2	75.0	34.65	48.77±1.92
3	56.7	45.75	51.09±5.23
4	62.4	39.64	51.20±2.18
5	66.3	36.19	52.56±2.86
6	68.0	39.26	52.94±2.08
7	62.6	37.00	56.96±4.16
8	77.0	54.04	61.57±3.51
Mean ± SD	68.4±8.0	39.92±6.92	52.94±4.39

Values are means ± SD and $n = 10$ for peak anaerobic power from a resting base-line ($\hat{w}_r$) value. $\dot{V}O_{2\,max}$, maximum O_2 consumption.

elapsed before the subject could carry out the first jump. The time course of the muscular power developed by a typical subject during the push phase of a jump, performed at rest and when starting from a 100% $\dot{V}O_{2max}$ priming exercise, is shown in Fig. 2. The O_2 consumption at the steady state was measured during the last 30 s of the longest exercise period at each work load, with the exception of the heaviest one. In the latter case, the imposed mechanical power output was equal to 120% of that required for the individual $\dot{V}O_{2max}$. The above protocols allowed for all subjects ($n = 8$) *1*) the assessment of the time-dependent changes of $\hat{w}$ at the onset of exercises of the indicated loads, and *2*) the study of the relationship between $\hat{w}$ and $\dot{V}O_2$ measured at the steady state of each of the above loads. On four subjects $\dot{V}O_2$ was also determined on a breath-by-breath basis at the onset of rectangular exercises of 3-min duration requiring 30, 50, 70, and 100% of individual $\dot{V}O_{2max}$. This allowed the comparison of the time courses of the $\hat{w}$ and $\dot{V}O_2$ changes in the rest-to-work transients at the indicated power levels. In addition, in the same four subjects, at all work rates, a venous blood sample for the measurements of [La_b] was taken from the antecubital vein at rest and 6–8 min after the end of the longest exercise period.

In an additional series of experiments on five subjects, the base-line exercise was prolonged for 30 min at work intensities corresponding to 30, 50, and 70% $\dot{V}O_{2max}$ while $\hat{w}$ was determined at 5-min intervals.

RESULTS

Individual values of $\dot{V}O_{2max}$ above resting and $\hat{w}$ from a resting base line ($\hat{w}_r$, average of 10 measurements) are given in Table 1. Mean $\dot{V}O_{2max}$ was 39.9 ± 6.9 (SD) ml·min^{-1}·kg^{-1}, indicating that the present subjects were sedentary. $\hat{w}_r$ was on the average 52.9 ± 4.4 W/kg, the mean of the individual coefficients of variation amounting to 5.7 ± 2.2%. $\hat{w}_r$ was about twice the average power calculated throughout the whole push phase of the same jumps ($\bar{w}$ = 28.8 ± 5.0 (SD) W/kg).

After the onset of any priming rectangular load, $\hat{w}$ decreased progressively with time to attain in ~2 min a constant value which was lower, the higher the work level (Fig. 3). Once a steady state was reached, $\hat{w}$ did not decrease further even when prolonging the exercise to 30 min (work levels corresponding to 30, 50, and 70% of $\dot{V}O_{2max}$). The time course of $\hat{w}$ can be approximated by a simple exponential function (Fig. 4) with a half time of ~20 s ($n = 4$). On the same four subjects and for the same exercise levels appearing in Fig. 4, the time course of the $\dot{V}O_2$ kinetics measured at the mouth on a breath-

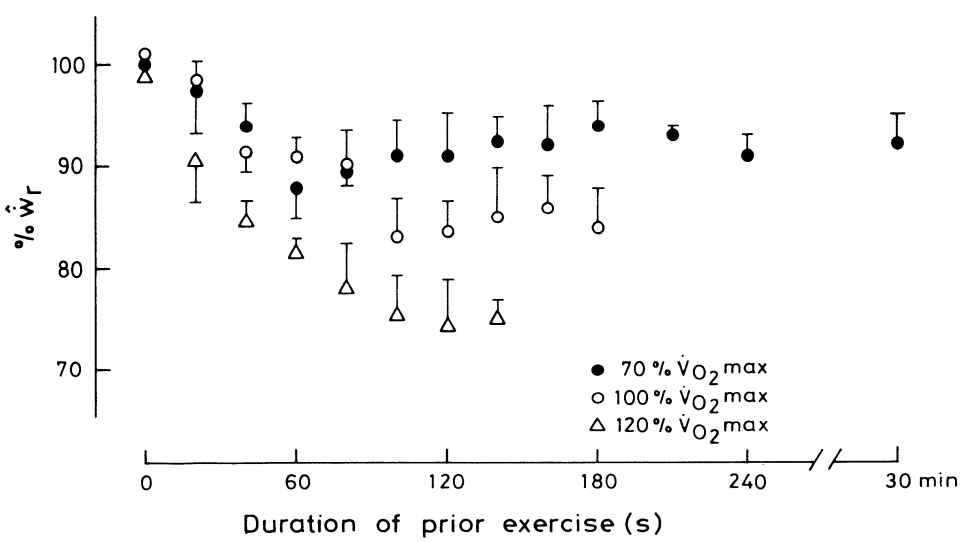

FIG. 3. Peak power ($\hat{w}$) expressed as percent of control value from a resting base line ($\hat{w}_r$), as a function of the duration of a priming exercise requiring 70% (*filled circles*), 100% (*open circles*), and 120% (*open triangles*) of individual maximum O_2 consumption ($\dot{V}O_{2max}$). For 70% $\dot{V}O_{2max}$ the $\hat{w}$ value obtained after 30 min of continuous work is also indicated. Data are mean values from all subjects. *Bars*, ±SD. For 30 and 50% $\dot{V}O_{2max}$ priming loads (not shown in figure) $\hat{w}$ reaches a higher steady-state level (Table 2), following patterns similar to those observed for heavier loads.

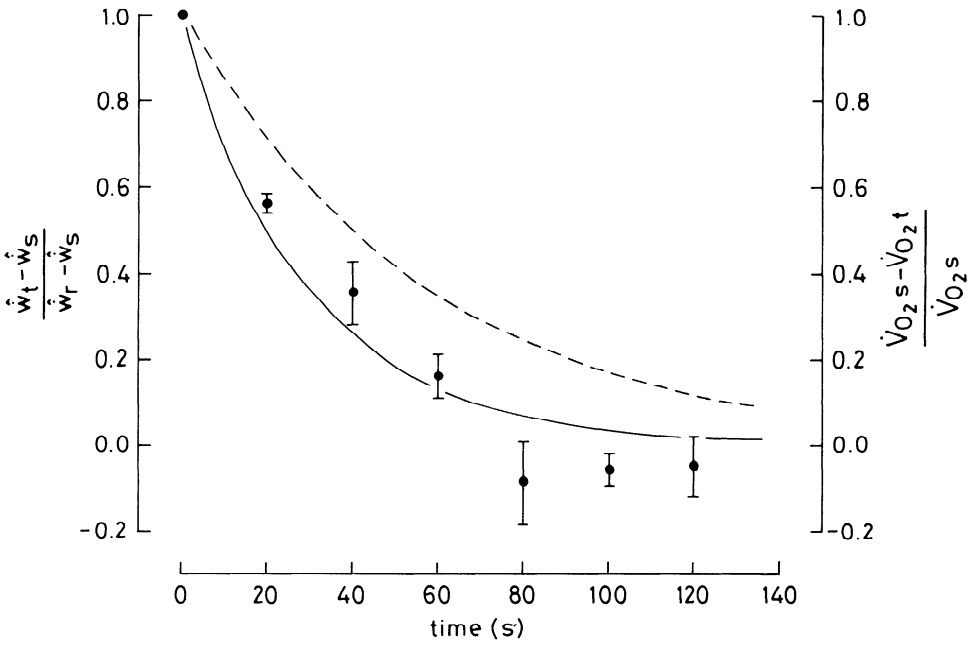

FIG. 4. Normalized values of peak power ($\hat{w}$) (resting values = 1, steady-state value = 0, *left ordinate*) during rest-to-work transients as a function of duration of priming exercise. Each *closed circle* is mean value from 4 work rates [30, 50, 70, and 100% of maximum O_2 consumption ($\dot{V}O_{2max}$)]. *Bars* indicate standard deviation of mean. *Solid line* is a monoexponential with a half time of 20 s. Data are from 4 subjects, whose mean half time of $\dot{V}O_2$ kinetics measured at the mouth at the same work levels was 40 s (*dashed line, right ordinate*). $\hat{w}_t$, $\hat{w}$ during transient; $\hat{w}_s$, $\hat{w}$ at steady state; $\hat{w}_r$, $\hat{w}$ at rest; $\dot{V}O_2s$, $\dot{V}O_2$ at steady state.

TABLE 2. *Individual data of $\hat{w}$ and $\dot{V}O_2$*

Subj No.	30% $\dot{V}O_{2\,max}$		50% $\dot{V}O_{2\,max}$		70% $\dot{V}O_{2\,max}$		100% $\dot{V}O_{2\,max}$		120% $\dot{V}O_{2\,max}$	
	$\hat{w}$	$\dot{V}O_2$	$\hat{w}$	$\dot{V}O_2$	$\hat{w}$	$\dot{V}O_2$	$\hat{w}$	$\dot{V}O_2$	$\hat{w}$	$\dot{V}O_2$
1	96.6	34.7	96.9	49.2	89.3	72.9	98.0	100.8	90.1	120
2	95.5	31.0	92.8	48.4	89.5	66.0	89.1	96.3	78.9	120
3	105.3	35.4	81.5	55.3	71.6	69.7	74.9	96.4	57.8	120
4	99.0	26.6	99.1	44.7	95.7	63.0	83.2	90.4	74.4	120
5	93.6	29.0	97.4	49.5	100.5	70.6	89.1	99.3	79.7	120
6	97.5	34.0	95.4	47.2	89.7	71.5	70.4	92.7	74.6	120
7	92.9	26.0	97.8	57.6	91.1	73.7	86.4	96.8	86.4	120
8	94.6	25.4	100.6	46.0	99.1	62.9	90.5	100.8		
Mean ± SD	96.9±4.0	30.3±4.1	95.2±6.0	49.8±4.5	90.8±9.0	68.9±4.3	85.2±8.9	96.8±3.7	75.3±9.8	

At highest work load, O_2 consumption ($\dot{V}O_2$) was obtained by extrapolation of individual $\dot{V}O_2$ vs. work rate relationships. Mean individual absolute values of maximum O_2 consumption ($\dot{V}O_{2\,max}$) and peak power from a resting base line ($\hat{w}_r$) (100% values) are indicated in Table 1. $\hat{w}$, peak anaerobic power.

by-breath basis showed an exponential increase with a half time of ~40 s. The individual $\hat{w}$ values attained at steady state are reported in Table 2 as percent of the corresponding $\hat{w}_r$ together with the $\dot{V}O_2$ levels of the priming exercise (percent of $\dot{V}O_{2max}$). A two-way analysis of variance carried out on eight subjects at 30–100% $\dot{V}O_{2max}$ and on seven subjects at all work loads showed no significant differences among subjects ($P > 0.025$), whereas a significant difference among work loads was found ($P < 0.025$). A subsequent Newman-Keuls test showed a significant difference among all work loads, with the exception of 30 vs. 50% and 50 vs. 70% $\dot{V}O_{2max}$. The mean values of $\hat{w}$, as percent of the resting values, are plotted in Fig. 5 as a function of the metabolic level of the priming load. Up to 50% $\dot{V}O_{2max}$ $\hat{w}$ appears to decrease linearly with increasing metabolism; above 50% $\dot{V}O_{2max}$, the decrease of $\hat{w}$ is progressively greater.

The $[La_b]$ values assessed on four subjects 8 min after the longest priming exercise at all tested work loads are plotted as a function of $\%\dot{V}O_{2max}$ in Fig. 6 together with the corresponding $\hat{w}$ values. $[La_b]$ starts to increase at the same $\%\dot{V}O_{2max}$ level at which the rate of decrease of $\hat{w}$ becomes greater.

DISCUSSION

Muscle involvement during cycling and jumping. The use of cycling as the priming exercise rather than walking or stepping up and down from a bench is justified by electromyographic data indicating that most muscles active during the push phase of the jump are also involved in the push phase of the cycloergometric exercise (16). As a consequence, most of the biochemical changes induced by the priming activity occur in the same muscles contracting during the subsequent test jump. For the present analysis of $\hat{w}$ it is assumed that in the jump test the activated muscle mass is the same, independent of the exercise base line from which the jump is performed, even though its metabolic history is necessarily different.

Consequences of the recoil of elastic energy on $\hat{w}$. The procedure followed for measuring $\hat{w}$, unless carefully standardized, might lead to controversial results. It is well known, in fact, that when a maximal jump off both feet on a force platform is preceded by a countermovement (flexion), the vertical displacement of the center of gravity during the flight is greater than that observed in control jumps without countermovement, thus possibly affecting the measured $\hat{w}$ value (1). This finding can be

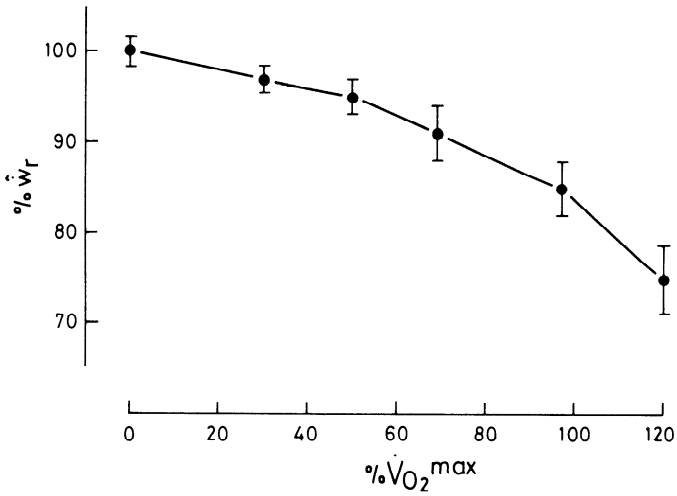

FIG. 5. Peak power at steady state, [% of control value from a resting base line ($\hat{w}_r$)] as a function of the net $\dot{V}O_2$ level of priming exercise [% of individual maximum O_2 consumption ($\dot{V}O_{2max}$)]. Data are mean values from all subjects. *Bars* indicate standard deviation of mean.

attributed to a substantial contribution of the mechanical energy stored in the previously stretched series elastic elements of the muscle to the energy output throughout the jump. In the present experiments a squatting starting position was therefore imposed to the subjects who were carefully instructed to avoid any flexion before the jump. In spite of this, a small but measurable flexion leading to negative work (w_n) performance immediately before the push phase of the jump was nearly unavoidable. To evaluate whether and to which extent $\hat{w}$ is affected by w_n, the latter was calculated for each subject by time integration of the negative instantaneous power values during the series of control jumps ($n = 10$). No relationship was found between $\hat{w}$ and w_n for any of the eight investigated subjects, the average r^2 amounting to 0.167 ± 0.146 (SD). Thus it can be concluded that, in spite of its effect on the vertical displacement of the center of gravity during the flight (1), the flexion immediately preceding the jump had no effects on the observed values of $\hat{w}$.

Average power and peak power. The method employed in the present experiments allowed calculation of two sets of maximal power data: *1*) the peak values ($\hat{w}$) calculated on a time basis of 4 ms; and *2*) the average values ($\bar{w}$), obtained through the whole push phase of the maximal vertical jump (0.5 s), the value of the latter being about half that of the former (see METHODS and RESULTS). Because of the much longer time basis on which $\bar{w}$ is calculated (500 vs. 4 ms), a substantial contribution of PCr splitting cannot be ruled out. We therefore focused our attention only on the peak power which we consider, at present, the only realistic estimate of the maximal ATP splitting rate in human muscle in vivo.

$\hat{w}$, alactic energy sources, and muscle acidosis. The found average value of $\hat{w}_r$ of 52.9 W/kg body wt, i.e., of ~200 W/kg of activated muscle mass, can be compared with similar data obtained in humans and in the isolated perfused dog gastrocnemius. Wilkie (17), during maximal concentric contractions of the biceps brachii of humans, found a $\hat{w}$ of 200 W/kg, a figure recalculated for an assumed working muscle mass of 400 g. On the other hand, in the isolated-perfused muscle of the dog (5, 6) the calculated values appear to be somewhat less (100–150 W/kg of muscle). In the latter case, however, allowance must be made for the conditions of the preparation and for the set up utilized which may not have allowed the development of maximal power.

Since the role played by the mechanical energy stored in the series elastic elements of the muscle in determining the observed $\hat{w}$ values is negligible, the energy required to develop $\hat{w}$ as measured in the present study can be supplied only by the splitting of the ATP already available in the muscle before the jump. In fact, since $\hat{w}$ refers to a time not longer than 8 ms (see the dwell time used for the calculations), energy can neither originate from ATP resynthesized by aerobic or anaerobic glycolysis nor from PCr breakdown. Therefore $\hat{w}$ can be assumed to be

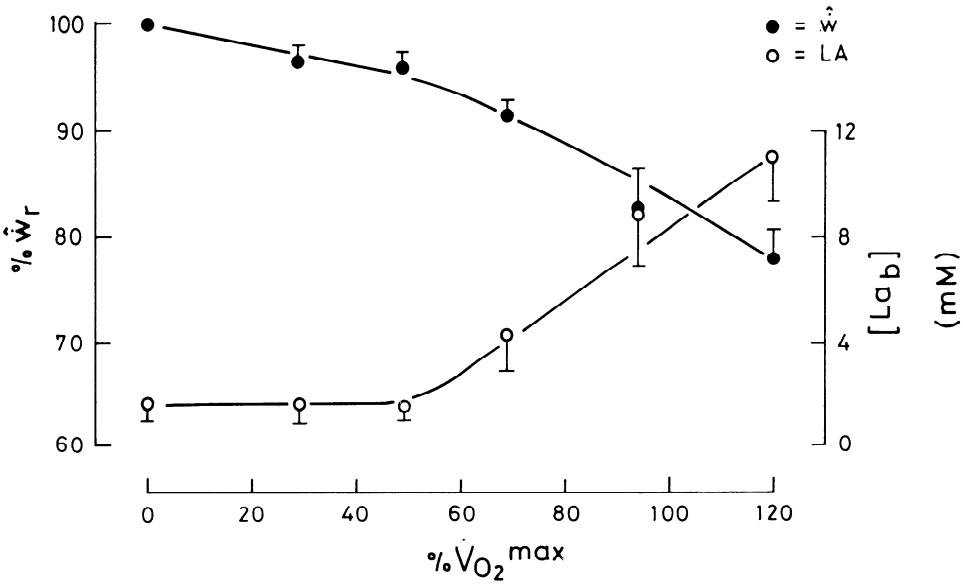

FIG. 6. Peak power ($\hat{w}$) at steady state as percent of control value from resting base line (*filled circles, left ordinate*) and corresponding blood lactate concentration (in mM) ([La_b], *open circles, right ordinate*) determined 8 min after end of priming exercise on 4 subjects, as a function of O_2 consumption preceding exercise [% of the individual maximum O_2 consumption ($\dot{V}O_{2max}$)].

TABLE 3. *Comparison of present $\hat{w}$ data with $\dot{w}_{max}$ data*

Net $\dot{V}O_2$, % $\dot{V}O_{2\,max}$	$\hat{w}$		$\dot{w}_{max}$	
	W/kg	%	W/kg	%
0	52.9	100	14.2	100
30	51.3	97	13.6	96
50	50.4	95	13.2	93
70	48.1	91	12.8	90
100	45.1	85	12.2	86
120	39.9	75		

$\dot{w}_{max}$, maximum anaerobic power [data obtained by Margaria et al. (11)]. See Table 2 for further definitions.

proportional to the muscle [ATP] according to the equation

$$\hat{w} = k\, w^*_{\sim p}\, [ATP] \qquad (6)$$

where k is the velocity constant of ATP splitting and $w^*_{\sim p}$ is the amount of mechanical work performed per mole of ATP split. In humans, $w^*_{\sim p}$, as calculated from the molar enthalpy change of O_2 ($\overline{\Delta H}_{O_2}$ = 469 kJ/mol), from the efficiency of muscle contraction (0.25), and from the P/O_2 ratio (6.2), turns out to be (4)

$$w^*_{\sim p} = 0.25\, \frac{\overline{\Delta H}_{O_2}}{P/O_2} = 0.25 \cdot 469/6.2 = 19 \text{ kJ/mol} \qquad (7)$$

Inserting this value into *Eq. 6*, for an average $\hat{w}$ = 52.9 W/kg body wt as found in the present study starting from rest, and assuming that *1*) resting [ATP] is 4.6 mmol/kg of wet muscle at rest (8, 9, 12, 14) and *2*) only 0.66 of the muscle mass is maximally activated, k turns out to be on the order of 2.3 s^{-1}. This value is about four times greater than that (0.6 s^{-1}) calculated by di Prampero (4) from the maximal power ($\dot{w}_{max}$ = 14.2 W/kg) developed by human subjects when running at top speed up a flight of stairs (11). This difference reflects the fact that $\hat{w}$ is the highest instantaneous value during a simultaneous contraction of the extensor muscles of the two legs, whereas $\dot{w}_{max}$ is the average maximal power developed by the push of one leg contracting alternatively over a period of 4–6 s. In addition, given the average power observed by Margaria et al. (Ref. 11; see Table 3) and assuming that the splitting of 1 mol ATP yields 19 kJ of mechanical work (Table 4), it can be calculated that the overall amount of ATP needed for a 6-s run amounted to 17 mmol/kg wet muscle wt, a figure about four times greater than the resting muscle [ATP]. As a consequence, a substantial fraction of $\dot{w}_{max}$ is necessarily due to the splitting of ATP resynthesized from PCr breakdown. Thus, the present value of k (2.3 s^{-1}) is a closer estimate of the "maximal" absolute rate of ATP splitting in human muscle in physiological conditions than that calculated by di Prampero from $\dot{w}_{max}$ (4). It is noteworthy that in spite of the described differences, the decrease of $\hat{w}$ as a function of the base-line $\dot{V}O_2$ found in the present study is essentially the same as that found by Margaria et al. for $\dot{w}_{max}$ (Table 3).

A comparison between the $\hat{w}$ data as a function of $\dot{V}O_2$ as measured in the present experiments (see Table 2) and the average [ATP] values found for humans and for the dog in muscle biopsies (8, 9, 14) and from ^{31}P-NMR spectra (12, 13) at increasing $\dot{V}O_2$ levels is attempted in Fig. 7. Both $\hat{w}$ and [ATP] are given as percent of their maximal levels. Based on *Eq. 6*, if k and $w^*_{\sim p}$ were constant, independent of the intensity of the priming exercise, the above two curves should coincide. Evidently, this is not the case, as the $\hat{w}$ values are consistently higher than expected. This implies that either $w^*_{\sim p}$ and/or k increase with increasing the intensity of the priming load. Since the difference between the two curves becomes appreciable as La begins accumulating in the tissues and appears to be proportional to [La], we propose that the above described changes may be the consequence of the increase of muscle [H^+] due to lactate accumulation that occurs at work loads exceeding 60% $\dot{V}O_{2\,max}$. In fact, an increase of the mechanical efficiency of the contraction and of $w^*_{\sim p}$ has been found to occur in the isolated-perfused dog gastrocnemius in the course of repeated short tetani, simultaneously with La accumulation and depletion of the high-energy phosphate stores

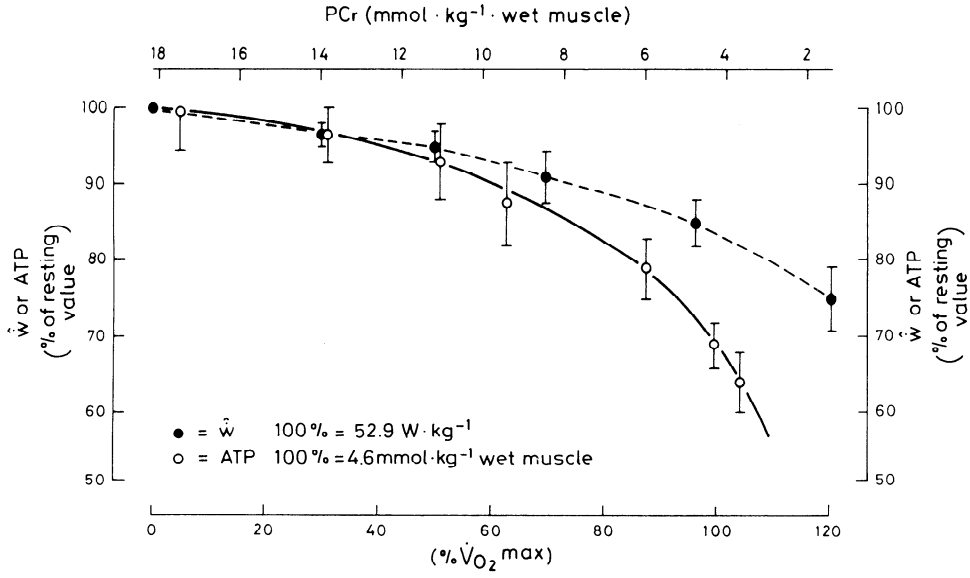

FIG. 7. Peak power ($\hat{w}$) (*closed circles* and *dashed line*, data from Fig. 5) and ATP concentration ([ATP]) (*open circles, solid line*, data from Refs. 8, 9, 12–14) both expressed as percent of their resting values are given as a function of net O_2 consumption of priming load [% of maximum O_2 consumption ($\dot{V}O_{2\,max}$)]. Phosphocreatine ([PCr]) scale, as calculated from Ref. 8, is also given.

TABLE 4. *Work performed per mole ATP split and velocity constant of ATP splitting*

Net $\dot{V}O_2$, % of $\dot{V}O_{2\,max}$	$\hat{w}$, W/kg	[ATP], mmol/kg muscle	k = constant = 2.3 $s^{-1}w^*_p$, (kJ/mol)	w^*_p = constant = 18.9 kJ·mol^{-1}·k^{-1}, s^{-1}
0	52.9	4.60	18.9	2.30
30	51.3	4.44	19.0	2.32
50	50.4	4.30	19.3	2.35
70	48.1	3.98	19.9	2.42
100	45.1	3.34	22.2	2.71

Calculated from *Eq. 6*, assuming either k = constant or w^*_p = constant for indicated peak power ($\hat{w}$) and ATP concentration ([ATP]) values as in Fig. 7. w^*_p, work performed per mole ATP split; k, velocity constant of ATP splitting. See Table 2 for further definitions.

(6). The solutions of *Eq. 6* using the data of Fig. 7 and keeping either k or w^*_p constant appear in Table 4. The experimental data can be explained with a change of either the mechanical work per mole ATP split or the maximal rate of ATP splitting, on the order of 20% compared with the reference resting levels for the priming load range from 0 to 100% of net $\dot{V}O_{2\,max}$.

$\hat{w}$ during the rest-to-work transients. During the transient between rest and a given work load, $\hat{w}$ appears to decrease with time, reaching within 2 min a steady value whose absolute level depends on the intensity of the priming load (Fig. 3). Once the steady-state $\dot{V}O_2$ is attained, the duration of the priming exercise has no effect on $\hat{w}$, at least up to 30 min. Hence of the two considered variables, i.e., time and $\dot{V}O_2$, only the latter affects $\hat{w}$. Therefore, during a rest-to-exercise transient, the time course of $\hat{w}$ can be expected to be the mirror image of the $\dot{V}O_2$ changes at the muscle level. From Fig. 4, the kinetics of the $\hat{w}$ transients appear to be roughly exponential, with a half time of ~20 s. This value is similar to that directly measured for $\dot{V}O_2$ in the isolated-perfused gastrocnemius muscle of the dog (14) and to the figure estimated on humans by Cerretelli et al. (2). The $\dot{V}O_2$ measured at the mouth on a breath-by-breath basis (7) on the same subjects, at the same exercise levels as for $\hat{w}$ (Fig. 4), increases exponentially as a function of exercise duration with a half time of ~40 s. This finding provides evidence supporting the hypothesis that the changes of $\dot{V}O_2$ at the muscle level at the onset of exercise are faster than at the mouth (4).

CONCLUSIONS

In conclusion, $\hat{w}$, during an all out effort, decreases with increasing the intensity of the priming exercise. This decrease takes place during the first 2 min of exercise and is not affected by the duration of submaximal base-line loads, at least up to 30 min. For priming levels <60% $\dot{V}O_{2\,max}$, the decrease of $\hat{w}$ essentially parallels the decrease of the muscle [ATP], as estimated from the literature data. For work levels >60% $\dot{V}O_{2\,max}$ and involving a substantial accumulation of lactate, the decrease of $\hat{w}$ is smaller than the estimated drop of muscle ATP. This finding is tentatively attributed to an increase of either the work performed per mole of ATP split and/or the maximal rate of ATP splitting brought about by the increased $[H^+]$.

Moreover, the dynamic assessment of $\hat{w}$ in the rest-to-work transient can provide a noninvasive estimate of the $\dot{V}O_2$ kinetics at the muscle level. This can be approximated by a single exponential with a half time on the order of 20 s.

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