

Internal work and physiological responses during concentric and eccentric cycle ergometry

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Summary. Internal mechanical work during cycling, required to raise and lower the legs and change their velocities, is shown to be an important factor when interpreting physiological responses to cycle ergometer exercise. The internal work required to move the legs during concentric and eccentric cycle ergometry at different speeds and workloads was calculated from segmental energy changes determined using cinematography and directly using an eccentric ergometer. The mean internal work rates obtained at pedal frequencies of 30, 60 and 90 min⁻¹ were 11.5, 20 and 62 W respectively. When these estimates were added to the external work rates, they increased concentric and decreased eccentric work rates. The largest differences were seen at low work rates and high pedal frequencies during which concentric work rates increased by 51% and eccentric decreased 60% by the inclusion of internal work. When comparisons of concentric and eccentric cycling at equal uncorrected work rates were made, neglecting to include internal work introduced errors ranging from 12 to 97%. The calculated estimates of internal work agreed well with the power supplied by the eccentric ergometer to move the legs passively. The investigations show that the inclusion of internal work is important when comparing physiological responses during concentric and eccentric ergometry, especially when pedal frequences exceed 60 min^{-1} and when work rates are small.

Key words: Internal work — Cycling — Cycle ergometer — Concentric — Eccentric — Zeroload pedalling

Introduction

The cycle ergometer is used extensively for stressing the human body with known, repeatable work loads. Studies performed on gait have shown that it is important to account for a work component required to raise and lower the limbs and to change their velocities: This work has been termed internal work (Winter 1979a). With few exceptions the workload setting on the ergometer has been accepted as indicating the total mechanical work performed by the subject and no accounting for internal mechanical work has been made. It is however common to correct the metabolic cost of cycling by subtracting the cost of "zeroload" pedalling from the total energy required (e.g. Garry and Wishart 1931; Whipp and Wasserman 1969).

In addition, the cycle ergometer has been used to study the physiological responses to eccentric or negative work as well as to positive work (Abbott and Bigland 1953; Knuttgen et al. 1971; Hesser et al. 1977). This literature has tended to compare physiological responses at equal eccentric and concentric work rates.

Kaneko and Yamazaki (1978) were probably the first to attempt calculation of the internal mechanical work component for cycle ergometry. Unfortunately, only the kinetic energy changes of the limb segments (thigh and lower leg) were considered. To obtain an estimate that is representative of the internal mechanical work for cycle ergometry, both the kinetic and potential energy changes of all the body segments must be considered.

It is thus the purpose of this paper to measure this internal work during concentric and eccentric cycle ergometry indirectly, using cinematographic methods and directly, using an eccetric cycle er-

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gometer, and show that it is an important factor in quantifying the total work produced or absorbed by muscle.

Materials and methods

Subjects. Three healthy normal male university students volunteered to be subjects for this study. All were active but none were highly trained. Characteristics of each subject are presented in Table 1.

Test protocol. Following a detailed explanation of the design and purpose of the study, each subject signed informed consent forms. To ensure that all trials were performed utilizing primarily aerobic metabolism, the work rates chosen were those which elicited oxygen uptake values equal to 30, 60 and 90% of the ventilatory anaerobic threshold (VT) value of the subject with the lowest value. Two ramp (50 W min⁻¹) progressive power output tests at 60 min⁻¹ were used to determine the ventilatory anaerobic threshold and maximal oxygen uptake $(\dot{V}_{O_{2 \text{ max}}})$ for each subject. The VT, defined as the initial point of departure from linearity of the relationship between expired ventilation and oxygen uptake, was obtained from a computerized algorithm utilizing multisegment linear regression (Orr et al. 1982). Once $V_{O_{2mux}}$ and VT. were determined, each subject performed an incremental steady state ride. The purpose of this ride was to determine the relationship between oxygen uptake and power output. Because oxygen uptake lags behind the power output during the fast ramp progressive exercise test (Whipp et al. 1981), it was necessary to use the incremental steady state ride to determine the work rates used on subsequent trial rides.

Prior to testing sessions, a minimum of three training sessions, 20 to 30 min in duration were performed by each subject on the eccentric cycle ergometer. These sessions provided sufficient practise time on the eccentric cycle ergometer to minimize the effect of learning this novel task. In addition they overcame the muscle soreness usually associated with eccentric exercise (Davies and White 1981).

A total of twenty-four trial rides, twelve concentric and twelve eccentric (four power outputs; 0, 60, 120 and 180 W at three pedal frequencies; 30, 60 and 90 min⁻¹) were completed by each subject. During testing sessions, an average of four trials were completed (maximum seven). The order in which trial rides were completed was varied to ensure a different testing sequence for each subject. Five revolutions were filmed during the fifth minute of each trial ride. The expired gases for each trial ride were measured using an open-circuit gas exchange analysis system as described by Hughson et al. (1980).

Table 1. Subject characteristics

Sub- ject	Sex	Age	Weight kg	Height cm	₿vo₂max	Ventilatory anaerobic threshold L0 ₂ /min
A	М	23	73.5	177	3.97	2.92
В	М	25	78	182	4.58	3.09
J	М	20	71.5	182	3.85	2.4

Expired gases (expired ventilation, oxygen uptake and expired carbon dioxide) were monitored and recorded for the 6 min duration of each trial. Only the last three minutes (averaged over one minute intervals) were used for analysis.

The cycle ergometers. Eccentric trial rides and training rides were performed on a cycle ergometer (Monark) that had been modified for this study in a manner similar to that of Lichtneckert et al. (1969) and Snellen and Chang (1981). A three horse power electric motor was connected through a variable pulley system to the input shaft of an automobile differential transmission. One output shaft was connected to the ergometer crank shaft and the other to the flywheel-brake mechanism of the cycle ergometer, the original direct connection between the flywheel and cranks having been disconnected. When the load was the same on both output shafts, they would turn at equal speeds. Thus, when a known load was applied to one output shaft through the flywheel-brake mechanism and the subject was required to slow down the pedals until both output shafts of the differential were turning at the same speed, the power output at one side was equal to that at the other. The eccentric cycle ergometer was calibrated prior to each testing session and recalibrated whenever more than one pedal frequency was performed within a testing session. For concentric trials a standard cycle ergometer (Monark) with electric braking was used. For "zeroload" trials on this ergometer the minimum work load setting equalled 7 W.

Film collection and reduction. All trials were filmed using a stationary 16 mm (Locam) camera at 30 frames per second. The camera was positioned to allow filming in the sagittal plane. Seven anatomical landmarks on the legs and trunk were indicated by the placement of circular markers on the right side of the body.

The processed film was digitized. The coordinates were then transferred to a computer, scaled, corrected for parallax, and then filtered using a Butterworth fourth order, zero lag, low pass filter. The upper cut off filter frequency used to filter the marker coordinates representing each anatomical landmark was estimated using a computer program that determined the goodness of fit between the raw and the filtered data (Wells and Winter 1980). Coordinates representing the glenohumeral joint, the iliac crest and the greater trochanter were filtered at 3 Hz, while those indicating the femoral condyle, lateral malleolus, heel and fifth metatarsal-phalangeal joint were filtered at 4 Hz.

The filtered absolute coordinates were used to calculate the relative joint angles, segment and total body kinematics. Individual segment masses and the location of the centre of mass for each segment were estimated from the data compiled by Winter (1979b). Bilateral symmetry was assumed and the motion of the left leg was determined by shifting the right leg one half cycle out of phase. Segment and total body energies were calculated from the kinetmatic data and used to determine the internal work component. In this investigation, the internal work allowing transfers within and between segments (Wwb) was calculated as previously described by Winter (1979a), and Pierrynowski et al. (1980). This internal work was calculated by summing the absolute energy changes of the total body energy curve. This measure was selected to provide an estimate of internal work during cycling, as the assumption of transfer of energy between limbs is especially likely to be true in cycling given that the legs are connected by the crankshaft.

During concentric cycle ergometry, the limbs must first be actively moved at the required speed before external work can be performed, thus the muscles, in general, are performing both internal and external work. The internal work represents the work that the muscles must do in simply moving the limb segments through the desired pattern of motion and thus should be added to the ergometer work to obtain the total work performed by muscle during concentric ergometry. During eccentric cycle ergometry, the internal work represents the work that the motor must perform on the limbs to move them at the desired speed. An estimate of the required power is given by the setting on the motor driven ergometer. Based on these two observations, the positive internal work component was added algebrically to the external work component for both the concentric (positive) and eccentric (negative) trials.

All trials were digitized for one subject to test any unexpected concentric/eccentric or workload effects on internal work. In addition, multiple revolutions at 30 and 90 min⁻¹ were digitized to examine revolution to revolution variability.

Results

Internal work

The internal work rate components for each trial performed by subject J are shown in Table 2.

These estimates each represent a single pedal revolution. Analysis of variance procedures indicated that there was no significant external work rate or concentric/eccentric effect but that a pedal frequency effect was present (p < 0.001, df=2, F=98.72). To investigate the source of the variations in internal work rate across workloads five revolutions were analysed at two pedal frequencies, 30 and 90 min⁻¹. These data appear in Table 3.

One is led to the conclusion that the variability across workloads and concentric/eccentric cycling is a result of revolution to revolution variability of the cyclist or the measurement techniques; cf. Grainger et al. (1983). As no eccentric/ concentric or workload effects were found in the internal work rates for subject J the internal work rates for subjects A and B were obtained from concentric trials at a single workload. The mean of at least two revolutions was used for each speed. These values are seen in Table 4.

Total mechanical work

Table 5 illustrates the effect of combining the two work rate components to obtain an estimate of the total mechanical work rate.

Inclusion of the internal work rate component resulted in greater estimates of total mechanical work rate, especially for the trials performed at pedal frequencies of 90 min⁻¹. For eccentric cycle ergometry, the signs of the terms (the internal and external work components) were opposite. The total work estimate therefore decreased significantly when the internal component was considered. Again, the effect was largest for the trials performed at pedal frequences of 90 min⁻¹. The effect of including internal work rate on total work rate was most dramatic at the low power outputs and high pedal frequencies. The effect of including internal work rates was, however, important at all pedal frequencies and workloads tested. Especially noteworthy are the large differences in total work when comparing concentric and eccentric cycling at the same uncorrected work rate.

The "zeroload" eccentric trials show that inclusion of the internal work rate brings the total

Table 2. Internal workrates for subject J (W)

Concentrio	ergomet	er workrat	e — (W)		Mean
Pedal	·0'	60	120	180	\pm SD
Fre-					
quency					
(\min^{-1})					
30	14	12	11	16	13 ± 2
60	16	19	9	18	15 ± 4
90	84	55	66	68	68 ± 10
Eccentric	ergometer	r workrate	— (W)		Mean
Pedal	٠́0'	- 60	-120	- 180	\pm SD
Fre-					
quency					
(\min^{-1})					
30	15	11	10	13	12 ± 2
60	17	21	9	18	16± 4
90	47	53	73	57	58 ± 10

Table 3. Variability of internal work rate values

Pedal Fre- quency (min ⁻¹)	Inter 5 rev	Mean work rates ± SD (W)				
30	15	9	13	14	13	12 ± 2
90	42	45	48	57	58	50 ± 7

Table 4. Mean internal work rate (W) at the three pedal frequencies. Mean of 2 trials except subject A; mean of 5 trials

Pedal fre- quency (min ⁻¹)	Subject A	Subject B	Subject J	Mean
30	12	10	12.5	11.5
60	19	26	15.5	20
90	50	72	63	62

Table 5. Internal and ergometer work rate (W) components: Mean of all subjects. ¹Lowest setting of cycle ergometer, ²Change defined as (internal workrate)/(Total workrate), ³Difference defined as (concentric workrate — eccentric workrate)/(concentric workrate)

$\frac{\operatorname{requency}{(\min^{-1})} \stackrel{\circ 0^{\circ}}{\circ} 60 120 180}{\operatorname{req}}$ $\frac{\operatorname{Internal workrate}(W) 11.5 11.5 11.5 11.5 11.5 \\ \text{External workrate}(W) 18.5 71.5 131.5 191.5 \\ \frac{2}{\operatorname{Change} in workrate} 62\% 16\% 9\% 66\% \\ \frac{2}{\operatorname{Concentric/eccentric}} - 32\% 18\% 12\% \\ 0 10\% 9\% 66\% 120 180 \\ 10\% 9\% 66\% 120 180 \\ 10\% 9\% 66\% 120 180 \\ 10\% 9\% 66\% 120 180 \\ 10\% 9\% 12\% 18\% 12\% 12\% 18\% 12\% 12\% 18\% 12\% 12\% 11\% 11\% 11\% 11\% 12\% 12\% 11\% 12\% 12\% 11\% 12\% 11\% 12\% 12\% 11\% 12\% 11\% 12\% 11\% 12\% 11\% 11\% 11\% 11\% 11\% 11\% 11\% 11\% 11\% 11\% 11\% 11\% 11\% 11\% 10\% 10\% 11\% $		Pedal frequency (min ⁻¹)		Ergometer work rate (W)				
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$ \begin{array}{c cccc} & Internal workrate (W) & 62 & 62 & 62 & 62 \\ External workrate (W) & 7 & 60 & 120 & 180 \\ Total workrate (W) & 69 & 122 & 182 & 242 \\ Change in workrate & 90\% & 51\% & 34\% & 26\% \\ Concentric/eccentric \\ Difference & - & 97\% & 68\% & 52\% \\ \hline \\ & Internal workrate (W) & 11.5 & 11.5 & 11.5 & 11.5 \\ Sternal workrate (W) & -6 & -60 & -120 & -180 \\ \hline \\ & Sternal workrate (W) & 5.5 & -48.5 & -108.5 & -168.5 \\ Change in workrate & 200\% & 24\% & 11\% & 7\% \\ \hline \\ & Internal workrate (W) & -18 & -60 & -120 & -180 \\ \hline \\ & Internal workrate (W) & 2 & 20 & 20 \\ \hline \\ & Internal workrate (W) & 20 & 20 & 20 \\ \hline \\ & Internal workrate (W) & -18 & -60 & -120 & -180 \\ \hline \\ & Internal workrate (W) & 2 & -40 & -100 & -160 \\ \hline \\ & Change in workrate & 1000\% & 50\% & 20\% & 12\% \\ \hline \\ & 90 & Total workrate (W) & -75 & -60 & -120 & -180 \\ \hline \\ & 90 & Total workrate (W) & -13 & 2 & -58 & -118 \\ \hline \\ & Change in workrate & 480\% & 3100\% & 110\% & 54\% \\ \hline \end{array}$			Difference	_	50%	28%	20%	
$ \begin{array}{c cccc} & & & & & & & & & & & & & & & & & $			Internal workrate (W)	62	62	62	62	
$\begin{array}{c cccc} 90 & Total workrate (W) & 69 & 122 & 182 & 242 \\ Change in workrate & 90\% & 51\% & 34\% & 26\% \\ Concentric/eccentric \\ Difference & - & 97\% & 68\% & 52\% \\ \hline \\ & Internal workrate (W) & 11.5 & 11.5 & 11.5 & 11.5 \\ External workrate (W) & -6 & -60 & -120 & -180 \\ 30 & Total workrate (W) & 5.5 & -48.5 & -108.5 & -168.5 \\ Change in workrate & 200\% & 24\% & 11\% & 7\% \\ \hline \\ & Internal workrate (W) & 20 & 20 & 20 & 20 \\ External workrate (W) & -18 & -60 & -120 & -180 \\ \hline \\ & Internal workrate (W) & 2 & -40 & -100 & -160 \\ tric & Change in workrate & 1000\% & 50\% & 20\% & 12\% \\ \hline \\ & 90 & Total workrate (W) & -75 & -60 & -120 & -180 \\ 90 & Total workrate (W) & -13 & 2 & -58 & -118 \\ Change in workrate & 480\% & 3100\% & 110\% & 54\% \\ \hline \end{array}$			External workrate (W)	7	60	120	180	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		90	Total workrate (W)	69	122	182	242	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $			Change in workrate	90%	51%	34%	26%	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $			Concentric/eccentric					
$ \begin{array}{c cccc} & Internal workrate (W) & 11.5 & 11.5 & 11.5 & 11.5 \\ External workrate (W) & -6 & -60 & -120 & -180 \\ & Total workrate (W) & 5.5 & -48.5 & -108.5 & -168.5 \\ Change in workrate & 200\% & 24\% & 11\% & 7\% \\ \hline & Internal workrate (W) & 20 & 20 & 20 & 20 \\ & External workrate (W) & -18 & -60 & -120 & -180 \\ & External workrate (W) & 2 & -40 & -100 & -160 \\ & Total workrate (W) & 2 & -40 & -100 & -160 \\ & Change in workrate & 1000\% & 50\% & 20\% & 12\% \\ \hline & Internal workrate (W) & -75 & -60 & -120 & -180 \\ & Sternal workrate (W) & -13 & 2 & -58 & -118 \\ & Change in workrate & 480\% & 3100\% & 110\% & 54\% \\ \hline \end{array} $			Difference		97%	68%	52%	
$ \begin{array}{c cccc} & & & & & & & & & & & & & & & & & $			Internal workrate (W)	11.5	11.5	11.5	11.5	
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			External workrate (W)	- 6	- 60	- 120	- 180	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		30	Total workrate (W)	5.5	-48.5	- 108.5	- 168.5	
$ \begin{array}{c cccc} Eccen- \\ fic \\ \hline 90 \\ \hline 90 \\ \hline \\ $			Change in workrate	200%	24%	11%	7%	
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		· <u> </u>	Internal workrate (W)	20	20	20	20	
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			External workrate (W)	- 18	-60	- 120	-180	
tric Change in workrate 1000% 50% 20% 12% Internal workrate (W) 62 6	Eccen-	60	Total workrate (W)	2	- 40	- 100	- 160	
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	tric		Change in workrate	1000%	50%	20%	12%	
90External workrate (W)-75-60-120-18090Total workrate (W)-132-58-118Change in workrate480%3100%110%54%			Internal workrate (W)	62	62	62	62	
90 Total workrate (W) -13 2 -58 -118 Change in workrate 480% 3100% 110% 54%			External workrate (W)	-75	60	-120	- 180	
Change in workrate 480% 3100% 110% 54%		90	Total workrate (W)	- 13	2	- 58	-118	
			Change in workrate	480%	3100%	110%	54%	

work rate to near zero. This is to be expected as the subjects were instructed to allow the ergometer to drive their legs with no muscular resistance. The mechanical work required to move the limbs was very similar to the estimate of internal mechanical work obtained from the cinematographic analysis. Figure 1 demonstrates the relationship between these two measures. Based on this relationship, the internal mechanical work rate measure (\hat{W}_{wb}) provides a good estimate of the mechanical work rate required to passively move the limbs during cycle ergometry in the absence of a suitable ergometer.

Physiological responses

Oxygen cost. Statistical analysis of oxygen uptake data (see Fig. 2) revealed a significant (p < 0.01)

three way interaction between work type, pedal frequency and the uncorrected power output.

For eccentric cycle ergometry, the metabolic cost of pedalling at the 30 min^{-1} was greater than at 60 and 90 min⁻¹.

Figure 3 demonstrates the effect of including the internal work component to estimate the oxygen uptake vs. total power output relationship.

Heart rate

Examination of the results presented in Fig. 4 indicates that for concentric cycle ergometry, as the uncorrected power output increases, heart rate also increases. The heart rate responses to increases in power output for eccentric cycle ergometry were not of the same magnitude as those found for concentric cycle ergometry. In addition,



Fig. 1. Relationship of calculated internal mechanical work rate (\dot{W}_{wb}) to directly measured power to rotate the legs on the eccentric cycle ergometer. Three pedal frequencies for each of three subjects. The equation of the line is y = 6.624 + 0.8177 x, r = 0.9876



Fig. 2. Oxygen cost versus uncorrected power output for eccentric and concentric cycle ergometry at three pedal frequencies. Significantly different responses between pedal frequencies are indicated. Mean of all subjects. Key O - O = pedal frequency 90 min⁻¹, + · · · · · + 60 min⁻¹ and \bullet ---- \bullet 30 min⁻¹

in some cases heart rate did not increase as the uncorrected power output increased, and in six instances actually decreased or remained the same.

Figure 5 demonstrates the relationship between heart rate and total power output. As with the oxygen uptake, the inclusion of the internal work rate component in estimating the power developed by the subjects results in a rather dramatic change in the relationship between heart rate and power at the different pedal frequencies for both concentric and eccentric work. Attention is drawn to the 90 min⁻¹ trials, where the inclusion of the internal work component had the largest effect.



Fig. 3. Oxygen cost vs. total power output for eccentric and concentric cycle ergometry. The total power is obtained by adding the internal mechanical work rate to the ergometer work rate. Mean of all subjects (convention as Fig. 2)



Fig. 4. Heartrate vs. uncorrected power output for eccentric and concentric cycle ergometry at three pedal frequencies. Mean of all subjects (convention as Fig. 2)



Fig. 5. Heartrate vs. total power output for eccentric and concentric cycle ergometry. The total power is obtained by adding the internal mechanical work rate to their ergometer work rate. Mean of all subjects (convention as Fig. 2).

Discussion

Kaneko and Yamazaki (1978) calculated internal work values ranging from 11.7 W to 23.2 W for pedal frequencies of 53.3 to 56.5 min^{-1} during concentric cycling only. Although potential energy changes were not included in their calculations, the mean internal work value for pedal frequencies between 48 and 56.5 min⁻¹ was 15.2 W (standard deviation ± 5.86 W). This value is slightly lower than the values calculated for subjects A and B but very close to that found for subject J at a pedal frequency of 60 min^{-1} . The complex cancellations which occur between the potential and kinetic energies of a segment however, means that neglect of potential energies will tend to give erroneous internal work values at lower pedal frequencies where the potential and kinetic energy variations are of the same magnitude.

The excellent agreement between the calculated internal work rate and the power the ergometer required to passively rotate the limbs (Fig. 1) empirically supports the use of the cinematographic method to estimate internal work during cycling in the absence of a suitable ergometer. During cycling the total energy of the trunk and legs varies. The absolute sum of this variation is used to estimate the internal mechanical work. In a frictionless pendulum (or other conservative system) the total energy of the system is constant and it will, ideally, continue in its motion without work being performed upon it. The total energy of the body is not constant during cycling and the legs, even if frictionless, would not therefore continue indefinitely under their own momentum once brought up to speed: Work would be required to maintain their speed. The calculation of internal work used in this paper assumes the skeleton to be made up segments joined by frictionless joints. Given that human joints exhibit velocity dependant friction (Hayes and Hatze 1977) one would expect that the calculation of internal work would underestimate the work required to move the legs at a given pedal frequency. This was not the case in this investigation. To these authors knowledge, this is the only direct comparison of the internal work rate (\dot{W}_{wb}) with a directly measured power making comparisons with the literature impossible. Two possibilities present themselves: 1) friction in moving joints and the inactive muscles is negligable or 2) that it is nonnegligable and the calculated internal work rate under-predicts the work to move the limbs and change their velocities. The explanation of choice is at present, however, unclear.

The study strongly supports the notion of accounting for the work required to move the limbs. This is especially important at high pedal speeds and when concentric and eccentric work rates are to be compared; the errors introduced by not including internal work ranged from 12% to 97%. The effect of internal work rate is to reduce the estimate of the power output for eccentric cycle ergometry and to increase this estimate for concentric cycle ergometry. This phenomenon was most pronounced for the 90 min⁻¹ conditions. For example, the trials performed at an external work rate of -180 W and 180 W became -118 W and 242 W respectively. In addition, the minimum of the oxygen uptake vs. power relationship is at zero when the total power is used.

In accordance with previous studies a ratio to compare the cost of concentric to eccentric cycle ergometry was calculated. From Figure 2, the largest differences occurred at the higher work rates for pedal frequencies of 60 and 90 min⁻¹. For pedalling at 60 min^{-1} the cost of concentric cycle ergometry at uncorrected power outputs of 120 W and 180 W was 2.6 and 2.8 times that of eccentric cycle ergometry at the same uncorrected work rate settings. These values are close to the ratios of three and less than four presented by Bonde-Peterson et al. (1972) and Knuttgen et al. (1971). By using the total power, the difference between the metabolic cost for these two types of cycle ergometry is reduced. Calculation of this ratio for a power output of 120 W (oxygen uptake ratios interpolated) resulted in values of approximately 1.25:, 2:1 and 1.5:1 for pedal frequencies of 30, 60 and 90 min⁻¹ respectively. An alternative explanation as to why previous researchers have obtained large differences in the oxygen cost for seemingly equal amount of positive and negative work can be put forward: Investigators have over-estimated the amount of negative work and under-estimated the amount of positive work that was done by the musculature.

In summary, the inclusion of the internal work term to estimate the mechanical work performed, resulted in a change in the relationship between the physiological responses and power output. Three important effects were noted; the minimum of the response curves appeared at a true zero workload; the differences between eccentric and concentric work were reduced, and lastly, the relationship between the responses at the various pedal frequences was also altered. This last effect was largest for the 90 min⁻¹ trials.

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