Apparent Efficiency and Storage of Elastic Energy in Human Muscles during Exercise

By

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Abstract


3 subjects ran on the treadmill (10 km/h) against varying horizontal impeding forces. One subject was further studied during the same kind of walking and bicycling on the treadmill, and during work consisting in lowering and lifting the body by flexing and extending the legs from a standing or sitting position at varying frequencies, with or without rebound in the deepest position. Workpower (W kcal/min), and the corresponding steady state metabolic rate (Đ kcal/min, Douglas bag method) were measured. Apparent efficiency (N) was calculated as \( \frac{AW}{\Delta E} \times 100 \) %. During load running N was 53.8, 37.6 and 41.2 %, respectively, in the 3 subjects. In the subject more extensively studied N was: running 53.8, walking 32.3, bicycling 25.1, knee-flexions (deep or half) with rebound 39.4 or 41.0, without rebound 26.1 or 21.9 %. These variations in N % were explained in accordance with the possibilities for re-using the energy, absorbed and stored in the muscles as elastic energy during a phase of negative exercise, in a subsequent phase of positive exercise. The condition of this is that the positive phase follows immediately after the negative. A calculation showed that during running 35—53 % of the energy absorbed during the negative phase was re-used. Corresponding figures for walking and rebounding knee-extensions were 23 % and 34 %, respectively, while in bicycling and knee-extensions without rebound all of the negative work degenerated into heat.

The possibility that implanted mechanical energy may be temporarily stored in the series elastic components of active muscles for re-use in a following contraction was investigated in a previous study of the vertical jump (Asmussen and Bonde-Petersen 1974). As discussed in that paper one necessary condition of such a possibility is that the muscles are being forcibly stretched while actively resisting movement, i.e. are performing eccentric contractions and doing negative work. Another is that the phase of negative work is followed immediately by a phase of positive work—i.e. a phase in which the muscles are shortening. Such conditions are realized in running,
TABLE I. Personal data of subjects.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Age</th>
<th>Height, cm</th>
<th>Weight, kg</th>
</tr>
</thead>
<tbody>
<tr>
<td>OM</td>
<td>25</td>
<td>174</td>
<td>73</td>
</tr>
<tr>
<td>MS</td>
<td>30</td>
<td>175</td>
<td>77</td>
</tr>
<tr>
<td>RH</td>
<td>33</td>
<td>170</td>
<td>79</td>
</tr>
</tbody>
</table>

as pointed out e.g. by Fenn (1930) and more recently by Cavagna et al. (1964), but also in other activities, as bouncing up and down by flexing and extending hips and knees (Thys et al. 1972).

If re-use of negative work takes place in exercise comprising alternating positive and negative work, one would expect that the amount of metabolic energy set free in the positive work phase were less than when the same amount of positive work is performed without re-use of negative work. Evidence for this has been given in experiments by Thys et al. (1972) and by Lloyd and Zacks (1972) who demonstrated that the efficiency (apparent efficiency, defined as the reciprocal of $b$ in the equation: metabolic rate = constant + $b \times$ work power, i.e. as $\Delta$ work power/$\Delta$ metabolic rate), was considerably higher in “neg.-pos.” work than in simple positive work.

It was the purpose of the present investigation to repeat and expand experiments of the same general nature as those of Lloyd and Zacks, and of Thys et al. in an attempt to add further evidence to the hypothesis. The experiments were performed as running, walking or bicycling exercise on the horizontal treadmill with loads of varying weights pulling backwards on the subjects, and as standing, respectively, sitting knee-bendings and -extensions with varying frequencies and loads on the subjects.

**Methods**

As subjects served 3 men, whose relevant data are presented in Table I. OM was of average physical fitness, a skin diver, but with no training as a runner. MS was of good fitness, an experienced middle and long distance runner, without being in top class. RH, of good fitness as a cyclist, had no recent experience in endurance running.

1. **Running, walking and bicycling on the treadmill.** These experiments were planned and executed in much the same way as those of Lloyd and Zacks: The subject ran, walked or cycled on the treadmill with a string attached to a broad belt of canvas, or to the saddle of the bicycle. The string passed horizontally over a pulley at the wall behind the subject and carried a hook that could be loaded with known weights. In this way a well defined constant horizontal resistance had to be overcome by the subject, who therefore performed work in excess of unloaded running or cycling at the same speed. The increase in workpower was:

$$\text{(load in kg)} \times \text{(velocity in m/min).}$$

This extra power (W) was expressed as kcal/min (1 kcal = 427 kpm). The subject was furnished with mouthpiece and low-resistance respiratory valves, so that expired air could be collected in Douglas-bags, placed on a metal net directly over the subject. Two 150 l bags were nearly filled in direct succession after the subject had reached a steady state. This was assumed to have taken place after 6—8 min of exercise. The contents of the bags were measured by means of a large Tissot gas-meter and analyzed for CO$_2$ and O$_2$ on an infra-red CO$_2$-analyzer (Capnograph, Beckman LB-1) and a paramagnetic O$_2$ analyzer (Servomex, type DA 184). These electronic analyzers were frequently checked by
APPARENT EFFICIENCY IN MUSCLE

Fig. 1. Rate of aerobic energy liberation (\(E\)) against increase in work power (\(\Delta W\)) due to horizontal backward pull while running on the treadmill at 10 km/h. Three subjects.

Fig. 2. Increase in metabolic rate (\(\Delta E\)) against increase in work power (\(\Delta W\)) due to backward pull while bicycling (8.36 km/min) or walking (5.36 km/h) on the treadmill. Subject OM. Regression line for load running from Fig. 1 also shown. N %: apparent efficiencies.

means of the Scholander technique (micro gas-analyzer). The \(O_2\)-consumption, \(V_O_2\), measured on each of the two bags did not deviate more than \(\pm 2\%\) from the average, usually less. \(V_O_2\) was converted to kcal/min (\(E\)) by assuming 1 l \(O_2\) to equate 4.9 kcal.

In the running experiments—performed on all three subjects—the speed of the treadmill was always 167 m/min (10 km/h). The spontaneously chosen stride frequencies were 175 to 180 strides per minute. In walking—performed on one of the three subjects, OM,—the speed was 90 m/min (5.36 km/h) at 110 strides per min, and in bicycling—same subject—it was 139 m/min (8.36 km/h), performed at 65 rpm, i.e. 130 pedal strokes per minute.

2. Rebounding experiments. These were performed on only one subject (OM). They were made in 2 series: One in which the subject bent his knees to a deep squatting position, and one in which he only bent them to about 90°, as in a semisquatting position. The exercise was performed rhythmically after a metronome beating 100 times per minute. The subject was instructed to bend the knees and, by a rebound, to extend them again, counting "1—2" after the metronome, and then to stand still while counting "3", or "3—4", or "3—4—5" etc. up to "3—8", before performing the next knee-bending. In the experiments without rebound the subject sat on a stool of appropriate height, and the exercise consisted in standing up and sitting down again on counts "1—2", while the following pause was varied by counting "3", or "3—4" etc. up to "3—8". In this way the work period, negative + positive—or vice versa—lasted 0.02 min in all cases, while the pauses—standing or sitting—lasted from 0.01 to 0.06 min. The subject was fitted with mouthpiece and valves for collection of expired gas in Douglas bags suspended in front of him. A thin string was attached to the mouthpiece and guided round a 10-turn potentiometer fixed to the roof vertically over the subject. The potentiometer was fed by a 1.5 V battery and its slide contact transmitted a variable voltage, proportional to the vertical movements, to an ink-writing recorder (Brush, Mark 220). In this way the movements up and down of the subject's head could be registered. The total distance, up or down, covered in a minute, multiplied by the weight of the subject, with or without extra loads carried over the shoulders, was used as an expression of the workpower and expressed in kcal/min. The negative work was assumed to be numerically equal to the positive work. Small movements in the horizontal plane were neglected.

The collecting of expired air was started when the subject had reached a steady state of heart rate, as registered by his ecg on the Brush ink-writer. Two Douglas bags, immediately following one another, were treated as described above.
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The results were plotted in a diagram with workpower as abscissa and metabolic rate as ordinate. When it had been observed by eye that the data were distributed evenly around a straight line, the data were fed into a programmed computer and the regression equation in the form \( y = a + bx \), with correlation factor, \( r \), computed. In this equation the inverse value of \( b \) is an expression of the apparent efficiency, i.e. of \( \frac{\Delta W}{\Delta \dot{E}} \). By multiplication with 100 it was expressed as per cent (N \%).

**Results**

The results from horizontal, loaded running on the 3 subjects are presented in Fig. 1. The data from the regression equation are presented in Table II as constants in the equation \( y = a + bx \), correlation factor \( r \), and apparent efficiency, the reciprocal of \( b \).

It appears from Table II that the 3 subjects differ with respect to horizontal running economy (the constant \( a \)) and also to apparent efficiency. The differences in \( a \) are only partly explained by the different body weights of the subject (Table I). Thus, eliminating body weight and expressing running economy as kcal x kg\(^{-1}\) x km\(^{-1}\), it comes out that the difference still exists as OM uses 1.22, MS 0.95 and RH 1.18 kcal x kg\(^{-1}\) x km\(^{-1}\).

Apparent efficiency in loaded running—i.e. the efficiency of the extra work performed by the runner on the attached weight—is high in all 3 subjects, highest in OM, who according to his energy output per kg and km is the least efficient runner. The value from subject MS—who was the best trained and most efficient runner—is lowest, 37.6 %, a value that comes close to the average values found by Lloyd and Zacks (1972) on 3 experienced and welltrained athletes.

Subject OM—who had the highest apparent efficiency (53.8 %) in loaded running—was also studied during loaded walking and loaded bicycling on the treadmill. The data are shown in Fig. 2 (with the regression line from the running experiments of Fig. 1 for comparison), and the calculated constants of the regression equations in Table III.

It appears from Table III that the \( a \) values—i.e. the energy liberation during unloaded bicycling or walking—are quite normal as compared to data from the literature. The apparent efficiency for bicycling is also within the limits usually found in bicycling, but the efficiency in performing the extra work while walking is remarkably high, although less than during running (Table II).

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**Table II.** Data for the regression equations of the results on load-running plotted in Fig. 1. The constants in the equation \( y = a + bx \), the correlation factor \( r \) and the apparent efficiency N %, calculated as 100/b.

<table>
<thead>
<tr>
<th>Subject</th>
<th>( n )</th>
<th>( a ) (kcal/min)</th>
<th>( b )</th>
<th>( r )</th>
<th>N %, apparent efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>OM</td>
<td>21</td>
<td>14.81</td>
<td>1.86</td>
<td>0.94</td>
<td>53.8</td>
</tr>
<tr>
<td>MS</td>
<td>9</td>
<td>12.22</td>
<td>2.66</td>
<td>0.99</td>
<td>37.6</td>
</tr>
<tr>
<td>RH</td>
<td>8</td>
<td>15.50</td>
<td>2.43</td>
<td>0.98</td>
<td>41.2</td>
</tr>
</tbody>
</table>
Fig. 3. Metabolic rate ($\dot{E}$) against work power ($\dot{W}$) in rhythmic deep leg flexions and extensions at varying frequencies, with (closed circles) and without (open circles) rebound. A larger circle around a point signifies experiments in which the subject carried an extra load weighing 10 kg on the shoulders. Dotted lines indicate that a maximum value for oxygen uptake has been reached.

**Table III.** Data for the regression equations of the results plotted in Fig. 2 for subject OM studied during load-walking and -bicycling. The constants in the equation $y = a + bx$, the correlation factor $r$ and the apparent efficiency $N \%$, calculated as $100/b$.

<table>
<thead>
<tr>
<th>Subject OM</th>
<th>$n$</th>
<th>$a$ (kcal/min)</th>
<th>$b$</th>
<th>$r$</th>
<th>$N %$, apparent efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>walking</td>
<td>9</td>
<td>5.28</td>
<td>3.10</td>
<td>0.99</td>
<td>32.3</td>
</tr>
<tr>
<td>bicycling</td>
<td>10</td>
<td>2.85</td>
<td>3.99</td>
<td>0.99</td>
<td>25.1</td>
</tr>
</tbody>
</table>

**Table IV.** Data for the regression equations of the results plotted in Fig. 3 for subject OM studied during knee-bending with or without rebound. The constants in the equation $y = a + bx$, the correlation factor $r$ and the apparent efficiency $N \%$, calculated as $100/b$.

<table>
<thead>
<tr>
<th>n</th>
<th>$a$ (kcal/min)</th>
<th>$b$</th>
<th>$r$</th>
<th>$N %$, apparent efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>deep knee-bending rebound</td>
<td>10</td>
<td>3.29</td>
<td>2.54</td>
<td>0.96</td>
</tr>
<tr>
<td>no rebound</td>
<td>11</td>
<td>2.75</td>
<td>3.84</td>
<td>0.97</td>
</tr>
<tr>
<td>half knee-bending rebound</td>
<td>10</td>
<td>3.11</td>
<td>2.44</td>
<td>0.97</td>
</tr>
<tr>
<td>no rebound</td>
<td>12</td>
<td>0.85</td>
<td>4.56</td>
<td>0.96</td>
</tr>
</tbody>
</table>
The results from the rebounding experiments (on subject OM only) are presented as individual data in Fig. 3 (deep knee-bendings) and as regression constants etc. from the straight part of the graphs, in Table IV. The apparent efficiency was 21.9—26.1 % without rebound—i.e. within the normal range of efficiencies found e.g. in stair-climbing, uphill-walking and bicycling—whereas the "apparent efficiency" in the work with rebound was 39.4—41.0 %—considerably higher than the usually accepted values in muscular work. At work loads higher than about 3.5 kcal/min, the metabolic rate did not increase further. This is probably because the subject had reached his maximal oxygen uptake for this kind of exercise.

The activity of one of the principal active leg muscles during this kind of exercise is illustrated by the emg's from the vastus lateralis, presented as Fig. 4. It demonstrates the uninterrupted activity during the down-up movements (rebound) and the short period of inactivity at the change of direction in the up-down movements.

Discussion

Our results from loaded running on apparent efficiency are similar to those of Lloyd and Zacks (1972) in that they show very high efficiencies, higher than could be expected from biochemical and thermodynamical data (see discussions by Lloyd and Zacks (1972) and Whipp and Wasserman (1969)). Also our data on loaded horizontal walking are surprisingly high, whereas loaded horizontal bicycling gave "normal" values. One important difference between the mechanical activity of the leg muscles in running and bicycling is that in running the extensors of the legs perform alternating negative and positive work during the contact period with the ground, being stretched during contraction as the body's center of gravity moves...
forward-downward, and shortening and performing work as the center of gravity moves up again. This was pointed out e.g. by Fenn (1930) and by Cavagna et al. (1964). These 2 phases—negative to positive—follow immediately upon one another, without an intermediate period of muscle relaxation. In contrast, during bicycling, the extensors of the legs are performing positive work during the down-stroke, but are relaxed during the up-stroke (cf. Carlsöö and Molbech 1966). It is, therefore, quite possible that work performed on the muscles in the negative phase of running, may be stored as elastic energy for re-use in the following positive phase. This possibility was discussed also by Fenn (1930), who, however, believed that the saving of energy would be very limited, because the muscles to act as springs should maintain tension, i.e. remain in the “active state” where the elastic stiffness of the fibers is great—and this would cost metabolic energy. In running, with a stride frequency of 180 strides per minute, as in the present experiments, each stride lasts 333 ms at 10 km/h. About 80 % of this time is spent in contact with the ground (Höberg 1952), i.e. about 260 ms. Of these 260 ms about half are spent doing negative work, i.e. 130 ms. Buchthal and Schmalbruch (1970) found that the “time to peak” in single twitches in human calf muscles was on an average 74 ms. The “active state” probably lasts close to twice this time. It follows that the period of negative work during which elastic energy can be stored is short enough for the active motor units to carry this elastic energy over into the subsequent period of positive work without extra liberation of metabolic energy.

The energy implanted in the muscles during the negative phase of the running movements is partly potential gravitational energy and partly kinetic energy. In loaded running it is probably only that part of the implanted energy that involves the center of gravity that can be assumed to assist in holding the extra load. The work done on the limbs was in the present experiments the same as in unloaded running as the stride frequency was unaltered. The work done on the center of gravity is the sum of the vertical lift and the work done in horizontal accelerations of the center of gravity. Both Fenn (1930) and Cavagna et al. (1964) state that these two are in phase during running (as opposed to walking), and, therefore, can be summated. Consequently the same magnitude of negative work power will be available for re-use in the positive work phase of running. In loaded running the same conditions probably obtain, i.e. a certain amount of negative work must be available for re-use.

An estimate of how large a proportion of the extra negative work that can be re-used, can be made in the following way (cf. Fig. 1, subject OM): For an increase in aerobic metabolic rate from 14.75 to 18.50 kcal/min—3.75 kcal/min—extra mechanical power corresponding to 2.0 kcal/min is developed. Assuming an efficiency for positive work (as on the bicycle, Table III) of 25 %, the increase in metabolism of 3.75 kcal/min would have led to the performance of only \(3.75 \times 0.25 = 0.94\) kcal/min. The difference, 2.0—0.94 = 1.06 kcal/min is then so to speak gratis. It amounts to 53 % of the work on the load. For the 2 other subjects it was 35 % (MS) and 37 % (RH), respectively.
These figures are not very different from the estimated value of about 50% elastic energy re-used in horizontal unloaded running as calculated by Cavagna et al. (1964).

In walking the work done on the center of gravity also can be divided into work against gravity (vertical lifts) and work performed in changing the kinetic energy of the center of gravity in a horizontal, forward-backward direction. Cavagna and Margaria (1966) who registered and measured this work, found that potential work and kinetic energy are opposed in direction, the one being positive as the other becomes negative. The changes in total energy of the body are, therefore, small, and the negative work that may be available for storing elastic energy is correspondingly small. This may explain the lower apparent efficiency of loaded walking as compared to loaded running in the same subject (Fig. 2 and Table III). Only about 23% of the work on the load was gratis in loaded walking (as estimated from Fig. 2).

The bicycle-experiments, with extra loads attached, need no long explanations. The apparent efficiency of 25% is equal to that found under similar conditions (Bannister and Jackson (1967), Asmussen (1953), Zacks (1973)) and easily explainable in biochemical terms (cf. Lloyd and Zacks 1972).

The rebounding experiments support the experiments on loaded running in that they show that when rebound is possible, the efficiency is considerably higher (N% = 39—41%) than when no rebound takes place (N% = 22—26%). A re-use of mechanical, potential energy, temporarily stored as elastic energy in the active muscles apparently takes place. The degree to which this is performed can be estimated from Fig. 3 or Table IV as follows: (Example from deep knee-bending).

With rebound \( y = 3.29 + 2.54x \) a positive workpower of, say, 3 kcal/min will demand extra metabolic energy liberation at the rate of \( 2.54 \times 3 = 7.62 \) kcal/min. An extra energy liberation of this size would correspond to a mechanical workpower without rebound \( y = 2.75 + 3.84x \) of only \( 7.62/3.84 = 1.98 \) kcal/min (plus the same numerical amount of negative work, which, however, will degenerate into heat in the interval between the negative and the positive phase). The performing of 3 kcal/min of positive work with a rebound after negative work of the same numerical value thus has given the difference \( (3.00 - 1.98) \) kcal/min = 1.02 kcal/min without any extra metabolic cost. In other words, 3.00 kcal/min negative work will turn up, after elastic recoil, as 1.02 kcal/min positive (and same amount of negative) work. 1.02 out of 3.00 kcal represent 34% of the negative work performed with rebound was saved for the subsequent positive work.

There are, apparently, differences in the subjects' ability to re-use negative work in running. OM seems to be best in this respect, in spite of the fact that he was the clumsiest runner. It may even be this lack of skill in running that causes this difference, maybe because his work against gravity is unnecessarily large. On the other hand, it may also be due to inherent differences in the structure of the muscles.

The present experiments—as those of Cavagna et al., Thys et al., Lloyd and Zacks—strongly emphasize the role of muscle elasticity in the economy of muscular
exercise as running, jumping etc. A recent report by Dawson and Taylor (1973) points to the same energy saving function of the elastic components in the legs of jumping kangaroos. Where this elastic component is located—except that it must be in active muscles at least in man—cannot be decided from the present experiments. Several reports (Joyce et al. (1969), Huxley and Simmons (1971), Wise et al. (1973) a.o.) point to the cross-bridges between filaments in the muscle fibers as the most likely location.

References

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HUXLEY, A. F. and R. M. SIMMONS, Mechanical properties of the crossbridges of frog striated muscle. J. Physiol. (Lond.) 1971. 218. 59P—60P.