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MECHANICAL WORK AND EFFICIENCY IN LEVEL WALKING AND RUNNING

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SUMMARY

1. The mechanical power spent to accelerate the limbs relative to the trunk in level walking and running, $\dot{W}_{\text{int}}$, has been measured at various 'constant' speeds (3–33 km/hr) with the cinematographic procedure used by Fenn (1930*a*) at high speeds of running.

2. $\dot{W}_{\text{int}}$ increases approximately as the square of the speed of walking and running. For a given speed $\dot{W}_{\text{int}}$ is greater in walking than in running.

3. In walking above 3 km/hr, $\dot{W}_{\text{int}}$ is greater than the power spent to accelerate and lift the centre of mass of the body at each step, $\dot{W}_{\text{ext}}$ (measured by Cavagna, Thys & Zamboni, 1976*b*). In running $\dot{W}_{\text{int}} < \dot{W}_{\text{ext}}$ up to about 20 km/hr, whereas at higher speeds $\dot{W}_{\text{int}} > \dot{W}_{\text{ext}}$.

4. The total work done by the muscles was calculated as

$$W_{\text{tot}} = |W_{\text{int}}| + |W_{\text{ext}}|.$$

Except that at the highest speeds of walking, the total work done per unit distance W_{tot}/km is greater in running than in walking.

5. The efficiency of positive work was measured from the ratio W_{tot}/Net energy expenditure: this is greater than 0·25 indicating that both in walking and in running the muscles utilize, during shortening, some energy stored during a previous phase of negative work (stretching).

6. In walking the efficiency reaches a maximum (0·35–0·40) at intermediate speeds, as may be expected from the properties of the contractile component of muscle. In running the efficiency increases steadily with speed (from 0·45 to 0·70–0·80) suggesting that positive work derives mainly from the passive recoil of muscle elastic elements and to a lesser extent

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from the active shortening of the contractile machinery. These findings are consistent with the different mechanics of the two exercises.

INTRODUCTION

The function of the muscles working *in situ* can be studied by measuring the mechanical work done and the energy expended to do it. The energy consumption in exercise has been extensively studied, but the mechanical work usually measured is only a surplus the muscles must perform when a load is imposed on the unloaded movement (e.g. walking and running against a horizontal impeding force or uphill, cycling, rowing). Very few data exist of the mechanical work actually done by the muscles in natural exercises such as walking and running on the level (Fenn, 1930*a*, *b*; Cavagna, Saibene & Margaria, 1964; Ralston & Lukin, 1969): these data do not enable us to define the relationship between mechanical work and speed of locomotion. This relationship has been determined in the present study according to the procedure used by Fenn (1930*a*, *b*) for running at top speed. With this aim the work necessary to accelerate the limbs relative to the trunk has been measured at various constant speeds of level walking and running (3–33 km/hr) by cinematographic analysis. From these data and the previous determinations of the work due to the mechanical energy changes of the centre of mass (Cavagna *et al.* 1976*b*), the total positive work was calculated.

The positive work done by the muscles derives from (1) the chemical energy transformed by their contractile machinery and (2) the mechanical energy stored in their elastic elements during a preceding phase of negative work when mechanical energy is taken up from the surroundings. The maximal efficiency of the transformation of chemical energy into positive mechanical work by the muscles is about 0·25 for both frog muscle and whole human beings. The over-all efficiency of the positive work done in exercise, expressed by the ratio: positive work done by the muscles/chemical energy used up by the muscles, gives an indication of the relative importance of the contractile *vs.* the elastic behaviour of muscles; in fact a value greater than 0·25 must indicate that part of the positive work is delivered, free of cost, by elastic elements stretched by some external force during a preceding phase of negative work. This efficiency has been measured in the present study during level walking and running at different speeds. The contribution of the elastic energy turned out to be greater in running than in walking: this agrees well with the rigid *vs.* the compliant type of mechanism of these two exercises.

METHODS

Subjects and experimental procedure. Experiments were made on four male subjects: M.S. (56 kg body wt., 1·75 m tall, 22 yr old) was a national middle-distance runner, P.C. (77 kg, 1·77 m, 23 yr) was a national sprinter, A.Z. (70 kg, 1·78 m, 29 yr) and G.C. (78 kg, 1·77 m, 39 yr) were both untrained. P.C., M.S. and G.C. also served as subjects in the previous experiments (Cavagna *et al.* 1976*b*). The subjects wore gym shoes and walked or ran at different speeds in an indoor track. In each trial the subject was instructed to keep the speed as constant as possible: the length of the track in which the subject could accelerate, before reaching the place where the motion picture was taken, was 40 m; an additional distance of 19 m was left for the deceleration. The camera was set at 17 m distance from the parcours line and the motion picture covered about 6 m of the track. The average speed over this distance was measured by means of two photocells adjusted at the level of the neck to prevent interference of the moving limbs. A lattice was built along the track just behind the parcours line to determine the orientation of the limbs in respect to the horizontal; for the same purpose circular black spots (30 mm diameter) were glued on the skin over the articulations of the shoulders, elbow, wrist, hip, knee and ankle. The motion picture was taken at 64 frames/sec (Beaulieu camera, time of exposure 0·0070 sec) for slow speeds of walking and running, and at 200–600 frames/sec (Fastax camera, time of exposure 0·0010–0·0003 sec) at high speeds. With the Fastax camera the frequency of the frames in the section of the film used for the measurements was determined by means of timing marks recorded on the film every 0·01 sec.

Elaboration of the data. The analysis of the film was done with a standard projector for the proofs at 64 frames/sec and with a L-W Photo Kodak Analyzer for those at high speed. The procedure followed in this analysis was equal to that described by Fenn (1930*a*) and only a brief description will be given here. The position of the black spots on the joints was reproduced on a sheet of paper and the orientation of each limb (upper arm, forearm, thigh and lower leg) was determined by measuring the angle α made by the limb with the horizontal. This measurement was made for one cycle (two steps) of walking or running, i.e. over the interval of time necessary for the limbs to return to their original positions. All the frames of one cycle were analysed in the proofs at 64 frames/sec, whereas only one every fifth frame was usually analysed in the proofs at high speed. The angle α was plotted as a function of time and curves were traced by hand through the points ('displacements curves' of Fenn). The slope of these curves was measured graphically to obtain the angular velocity ω_j of the limb (usually every 0·02–0·03 sec). The kinetic energy of the motion relative to the trunk of any limb segment, E_{kj}, was then calculated as the sum of its translational and rotational energy

$$E_{kj} = \tfrac{1}{2}\, m_j\, v_j^2 + \tfrac{1}{2}\, m_j\, k_j^2\, \omega_j^2, \qquad (1)$$

where m_j is the mass of the limb, v_j is the linear velocity of its centre of mass and k_j is the radius of gyration of the limb around its centre of mass. The linear velocity of the centre of mass of the upper arm and of the thigh was determined as

$$v_j = \omega_j . s_j,$$

where s_j is the distance between the upper joint of the limb (shoulder and hip respectively) and its centre of mass. The velocity of the centre of mass of the forearm (and of the lower leg) was determined, according to the procedure described by Fenn (1930*a*), by adding graphically (*a*) the velocity of the elbow (or the knee) and (*b*) the velocity of the centre of mass relative to the elbow (or the knee). The values of m_j,

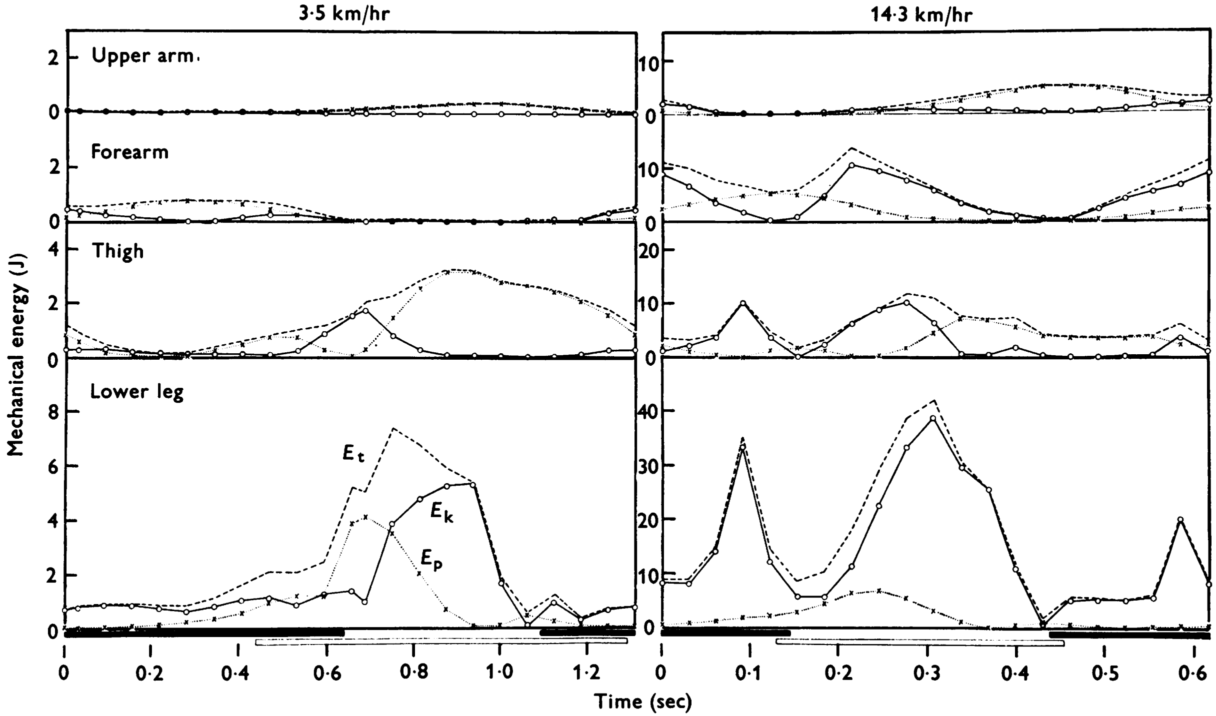

Fig. 1. The kinetic (E_k, continuous line) and the potential (E_p, dotted line) energy changes, due to the movement relative to the trunk of the limbs facing the camera, are plotted as a function of time during two steps (one complete cycle) of walking at 3·5 and 14·3 km/hr (subject M.S.). The interrupted line E_t is the sum of the E_k and E_p curves. The black bar below the tracings indicates the approximate interval of time in which the foot of the lower limb facing the camera is in contact with the ground. The open bar indicates the period of contact of the controlateral leg.

s_j and k_j were calculated from the body mass and the length of the limbs using the factors quoted by Fenn (1930*a*).

The kinetic energy E_{kj} of each limb (upper arm, forearm, thigh and lower leg) was calculated from eqn. (1) and plotted as a function of time (Fig. 1). The sum of all the increases in kinetic energy, measured from the four E_{kj} curves, was taken as the positive work necessary to accelerate the limbs of the side facing the camera. This value of positive work was multiplied by 2, to account for the movements of the controlateral limbs, and divided by the interval of time of one cycle (two steps) to determine the power $\dot{W}_{int}$ given in Fig. 2.

Discussion of the method used to determine $\dot{W}_{int}$. It should be pointed out that by the procedure described above the velocity of the limbs was not measured in relation to the common centre of gravity of the body, as it should, but in relation to the shoulder joint for the arm and the hip joint for the leg. These joints move relatively to the centre of mass during locomotion. The error involved has been discussed by Fenn (1930*a*) who estimated that in fast running the true figure could be about 10 % larger than the calculated one. This error was neglected in the present paper.

When the movement of one limb is checked the kinetic energy may be transferred in part to another limb which, as a consequence, would accelerate without necessity of muscular contraction (as in a whip). In this case $\dot{W}_{int}$, measured as the sum of all the increases in kinetic energy, would be greater than the work done by the muscles. A transfer of kinetic energy may take place (*a*) across the trunk (e.g. from the right leg to the left leg) and (*b*) between the two segments of each limb (e.g. from the thigh to the lower leg). Fenn (1930*a*) estimated that in fast running the energy shifted according to the first mechanism may make the true value about 10 % smaller than the calculated one. The maximum possible transfer of kinetic energy according to the second mechanism was determined in the present paper by adding at each instant the kinetic energy of the two segments of each limb. By this procedure one assumes that the decrease in kinetic energy of one segment is totally used to increase the kinetic energy of the adjacent segment: the changes in opposite direction cancel out and do not appear in the resultant curve. The increases of the resultant curve, so obtained, were added together to determine the positive work done according to this assumption. The power output, $\dot{W}_{int}$, calculated in this way, is indicated in Fig. 2 by the interrupted lines.

Discussion of the method used to determine the total mechanical work done by the muscles. According to Koenig's theorem the total kinetic energy of a system of particles is given by the sum of (*a*) the kinetic energy of a point moving with the velocity of the centre of gravity, V, and having the mass of the whole system, M, i.e. $E_{ke} = \frac{1}{2}MV^2$, and (*b*) the kinetic energy associated with the velocity of the particles relative to the centre of mass v_{rj}, i.e. $E_{ki} = \frac{1}{2}\Sigma m_j v_{rj}^2$, where m_j is the mass of each of the particles. In case that the kinetic energy only is taken into account, the increment of the total kinetic energy of the system in a given time equals the work done in that time by all the forces acting on the system, external (to increase E_{ke}) and internal (to increase E_{ki}). Assuming no energy transfer between E_{ke} and E_{ki} the mechanical work done by the muscles to increase the kinetic energy of the centre of mass and of the limbs would be $\Delta E_{ke} + \Delta E_{ki}$. This procedure was followed by Fenn (1930*a*, *b*), and by Cavagna *et al.* (1964). Elftman (1944) added at each instant the curve giving E_{ke} ('...effect of external forces') and the curve giving E_{ki} ('...due to the internal forces') to obtain a curve of the total kinetic energy af the whole body during a step of walking. In this procedure a shift between external and internal kinetic energy is assumed. More recently however Elftman (1966) says that kinetic energy (E_{ke}) and potential energy of the body as a whole interchange during the step, whereas the kinetic energy due to the relative movement of the lower extremities (E_{ki}) 'must be supplied by muscle'. This second approach is in agreement with that of the present paper.

When a limb is lifted relatively to the trunk, work may be done by the muscles not only to accelerate it, i.e. to increase its kinetic energy, but also against gravity to increase its potential energy. Particularly at low speeds of walking and running, when the velocity of the limbs relative to the trunk is small, the work against gravity may be a relevant fraction of the total work done to move the limb because the kinetic energy changes are small. A vertical displacement of a limb relative to the trunk implies a vertical displacement of the centre of gravity 'within' the trunk and this may have been measured as 'external' work against gravity by means of the platform (Cavagna *et al.* 1976*b*). However if a limb is raised whereas another one is lowered, the centre of gravity may not move at all vertically, or move less than expected, with the consequence that the work done to move the limb vertically is not measured neither as 'external' work, by means of the platform, nor as 'internal' work if only the kinetic energy changes relative to the trunk are taken into account. It follows that, particularly at slow speeds of walking and running, the total work as measured in the present paper may be less than the work actually done by the muscles:

$$W_{\mathrm{tot}} = |W_{\mathrm{ext}}| + |W_{\mathrm{int}}| = |W_{\mathrm{ext}}| + \Delta E_{\mathrm{ki}} \leq \text{work done by the muscles.} \qquad (2)$$

On the other hand a shift between potential and kinetic energy of a limb may take place, as in a pendulum, without intervention of muscular activity. For example, at high speeds of walking and running, when the velocity of the limbs and then their kinetic energy relative to the trunk is high, a limb may be carried upward by its own speed, so that no work has to be done by the muscles to raise it against gravity. However the potential energy change due to this passive upward movement of the limb, may have been measured by means of the platform as active external work done by the muscles (Cavagna *et al.* 1976*b*). In this case the total work, as measured, would be greater than the work actually done by the muscles

$$W_{\mathrm{tot}} = |W_{\mathrm{ext}}| + |W_{\mathrm{int}}| = |W_{\mathrm{ext}}| + \Delta E_{\mathrm{ki}} \geq \text{work done by the muscles.} \qquad (3)$$

For this reason when measuring W_{tot} at high speed of running, Fenn neglected the work required to lift the centre of gravity within the trunk because '...the kinetic energy of the limbs is sufficient in most cases to raise the limb the requisite distance against gravity. There is therefore danger of counting the same work twice if the work of raising the limbs is included in the total'.

The relevance of these errors (eqns. (2) and (3)) has been estimated as follows. The vertical displacement relative to the trunk of the common centre of gravity of the body, S_{vrj}, due to the movement relative to the trunk of each limb, was determined according to Fisher's method (reported by Fenn, 1930*b*, Fig. 1 of his paper) for three speeds of walking (3·5, 6·7 and 14·3 km/hr) and of running (9·1, 19·5 and 32 km/hr). S_{vrj} times the body weight P gives the potential energy change relative to the trunk due to the limb movement: $E_{\mathrm{pj}} = S_{\mathrm{vrj}} . P$; this is plotted as a function of time in Fig. 1 of this paper together with the kinetic energy of the limb, E_{kj}, and their sum, $E_{\mathrm{pj}} + E_{\mathrm{kj}} = E_{\mathrm{tj}}$. The sum of the increases of all the E_{tj} curves during a cycle, ΔE_{ti}, was compared with the sum of the increases of all the E_{kj} curves, ΔE_{ki}, which is taken in the present paper as W_{int}. At high speeds of running (32 km/hr) $\Delta E_{\mathrm{ti}} < \Delta E_{\mathrm{ki}}$ (12 %) indicating that gravity may help the movement of the limbs relative to the trunk, at intermediate speeds (19·5 km/hr) $\Delta E_{\mathrm{ti}} \simeq \Delta E_{\mathrm{ki}}$ indicating that gravity plays a neutral role and at low speeds (9·1 km/hr) $\Delta E_{\mathrm{ti}} > \Delta E_{\mathrm{ki}}$ (29 %) indicating that gravity may hinder the movement of the limb relative to the trunk. In walking at 14·3 and 6·7 km/hr $\Delta E_{\mathrm{ti}} \simeq \Delta E_{\mathrm{ki}}$, whereas at 3·5 km/hr $\Delta E_{\mathrm{ti}} > \Delta E_{\mathrm{ki}}$ (28 %).

As expected the error indicated by eqn. (2) is done at low speeds of walking and running. As a consequence W_{int} may be underestimated by about 28 % in walking and 29 % in running: when referred to the total work, W_{tot}, these figures reduce to 17·5 % for walking and 12·5 % for running. However at low speeds of walking, an appreciable part of this work done against gravity, mainly to lift the lower leg (Fig. 1), is already measured in the W_{ext} fraction (Cavagna *et al.* 1976*b*): it follows that the error made in walking must be smaller than 17·5 %.

The error indicated by eqn. (3) is done at high speeds of running and overestimates W_{int}, as measured, by about 12 % which reduces to 7·5 % when referred to W_{tot}.

At high speeds of running, as at low speeds of walking, the vertical displacement of the centre of gravity within the trunk S_{vr} is more or less in phase with the vertical displacement of the trunk S_{vt} (Fenn, 1930*b*; Cavagna *et al.* 1976*b*): in this case the external work done against gravity, $P\ (S_{vr}+S_{vt})$, already measured by means of the force plate, is increased by the vertical movement of the limbs relative to the trunk. As mentioned above this decreases the error made at low walking speeds (eqn. (2)), but it increases the error made at high running speeds (eqn. (3)). Fortunately, according to Fenn's (1930*a*) and our measurements, $P.S_{vr}$ is only 3–5 % of the total positive work done at high running speeds: at low running speeds S_{vr} is smaller and no longer in phase with S_{vt} with the consequence that this error is no longer made. In conclusion: at high speeds of running the total work measured as

$$W_{tot} = |W_{ext}| + |W_{int}|$$

may be over-estimated by 11·5 % because: (*a*) W_{int} is 12 % greater than ΔE_{ti}: this makes W_{tot} 7·5 % too large, and (*b*) $P.S_{vr}$ is possibly measured twice: this makes W_{tot} 4 % too large.

All the errors estimated above were neglected because they would not alter substantially the conclusions reached in this paper: the total work done by the muscles was taken as $W_{ext}+\Delta E_{ki}$.

RESULTS

The mechanical power spent to accelerate the limbs relative to the trunk during walking and running, $\dot{W}_{int}$, is plotted as a function of the speed in Fig. 2. The experimental points and the continuous lines give a maximal figure of $\dot{W}_{int}$ measured, as described in the Methods, assuming no energy transfer between the limbs. The interrupted lines fit values of power, $\dot{W}'_{int}$, calculated assuming a complete transfer of kinetic energy between the upper and the lower segment of each limb. Both in walking and in running the kinetic energy of the lower limb shows the largest oscillations (Fig. 1) being responsible for about 80–90 % of $\dot{W}_{int}$.

In a log-log diagram, linear relationships with slope $\simeq$ 2 are obtained. The straight lines in Fig. 2 were traced according to constants calculated by the least squares method.

On a linear scale the equations are (for all the data obtained in the four subjects):

$$\dot{W}_{int}\ (\text{cal/kg.min}) = 0{\cdot}389\ \overline{V}_f\ (\text{km/hr})^{2{\cdot}051} \quad \text{for walking } (r = 0{\cdot}988);$$

$$\dot{W}_{int} = 0{\cdot}266\ \overline{V}_f^{1{\cdot}993} \quad \text{for running } (r = 0{\cdot}976);$$

$$\dot{W}'_{int} = 0{\cdot}291\ \overline{V}_f^{2{\cdot}14} \quad \text{for walking } (r = 0{\cdot}987);$$

and

$$\dot{W}'_{int} = 0{\cdot}278\ \overline{V}_f^{1{\cdot}931} \quad \text{for running } (r = 0{\cdot}967).$$

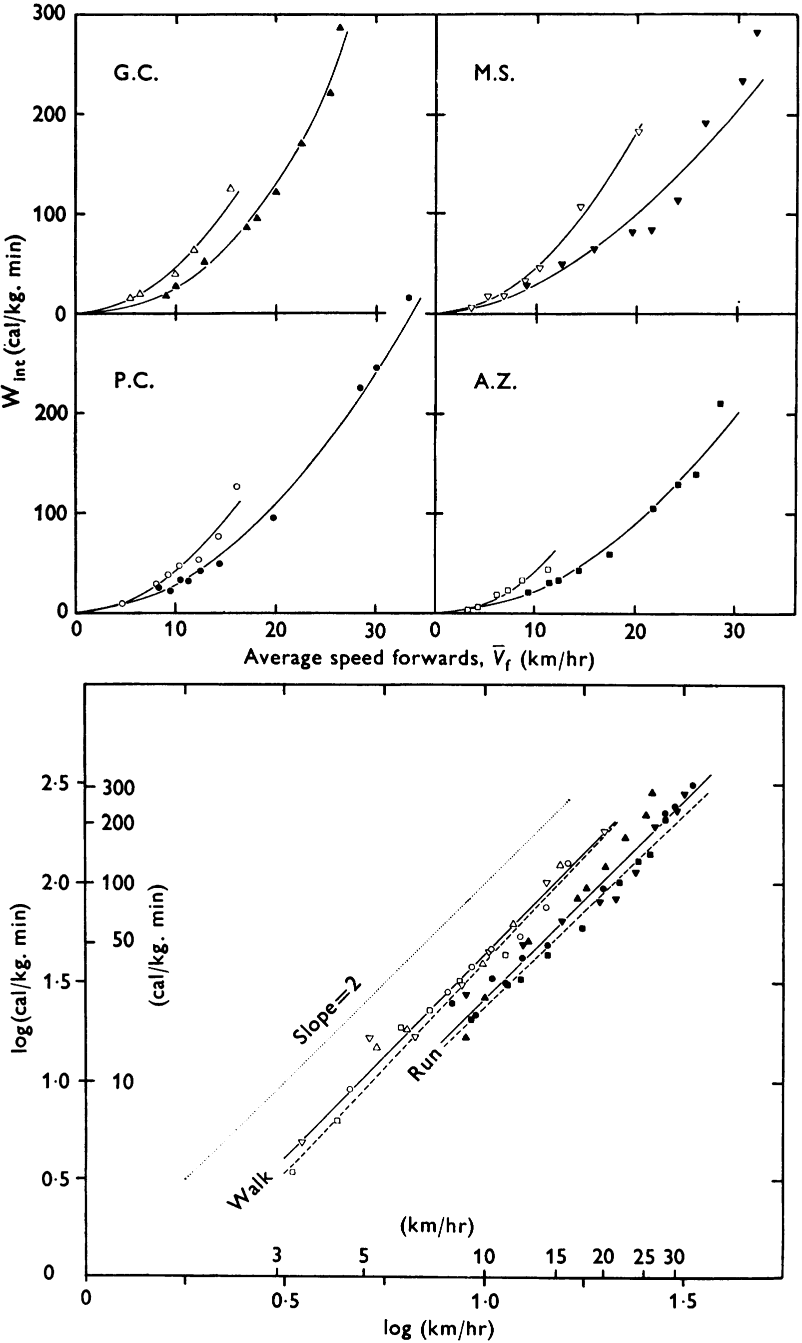

Fig. 2. Legend on facing page.

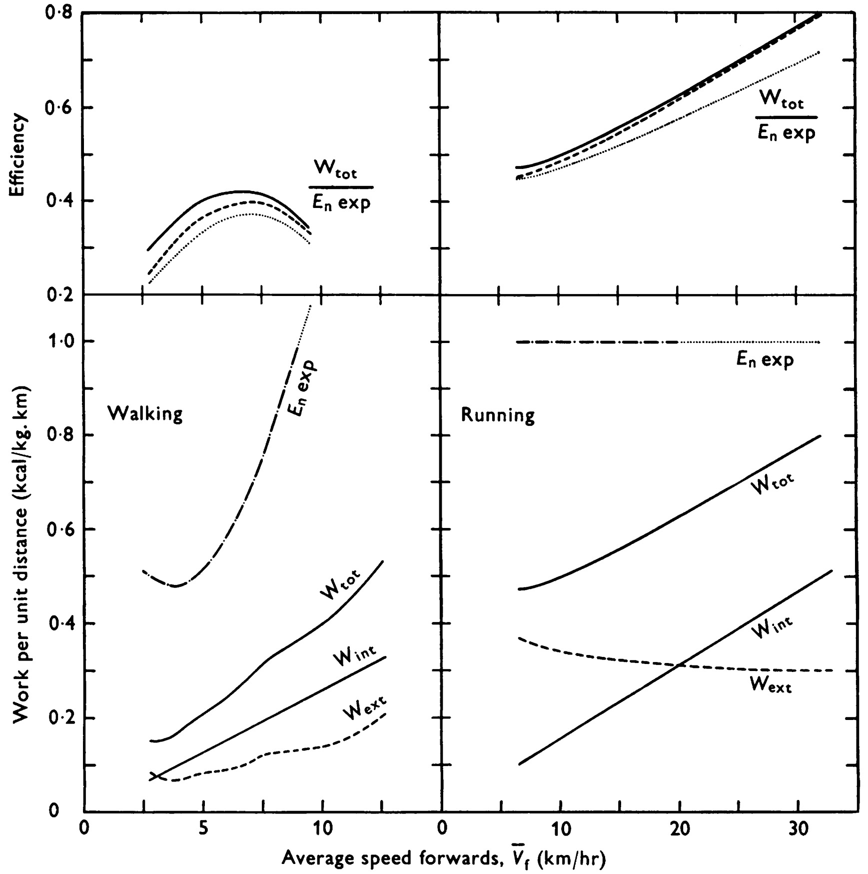

Fig. 3. *Below*: the internal, W_{int}, external, W_{ext}, and total

$$W_{\text{tot}} = |W_{\text{int}}| + |W_{\text{ext}}|,$$

mechanical work done per unit distance during level walking (left hand) and running (right hand) is given as a function of speed. The net energy expenditure (total minus standing) is also given. *Above*: efficiency of positive work measured as W_{tot}/(total minus standing energy expenditure), continuous line, and as W_{tot}/(total minus basal metabolic rate), interrupted line. The dotted line gives minimal efficiency values obtained when a shift of kinetic energy between the limbs is admitted (interrupted lines of Fig. 2) and the energy expenditure is taken as (total minus basal metabolic rate).

Fig. 2. The mechanical power W_{int} spent to accelerate the limbs relative to the trunk (measured from the increments of the E_k curve in Fig. 1), is plotted as a function of the speed of walking (open symbols) and of running (filled symbols). In a log-log plot straight lines with slope $\simeq$ 2 are obtained (below). The continuous lines indicate the power calculated assuming no transfer of energy between the limbs, the interrupted lines fit the data obtained by assuming a complete transfer of kinetic energy between the upper and the lower segment of each limb.

The internal work done per unit distance, $\dot{W}_{\text{int}}/\bar{V}_f$, is given in Fig. 3 together with the external work done per unit distance to sustain the mechanical energy changes of the centre of mass of the body (interrupted lines: from an average of the data of Cavagna *et al.* 1976*b*). It can be seen that in walking W_{int} is greater than W_{ext} except that at speeds lower than about 3 km/hr; in running $W_{\text{int}} < W_{\text{ext}}$ up to about 20 km/hr, whereas at higher speeds $W_{\text{int}} > W_{\text{ext}}$.

The total power output was calculated as $\dot{W}_{\text{tot}} = |\dot{W}_{\text{ext}}| + |\dot{W}_{\text{int}}|$: in level running it is related to the speed by the equation

$$\dot{W}_{\text{tot}} = 9{\cdot}42 + 4{\cdot}73\,\bar{V}_f + 0{\cdot}266\,\bar{V}_f^{1{\cdot}993}, \tag{4}$$

where $\dot{W}_{\text{tot}}$ is given in cal/(kg.min) and $\bar{V}_f$ in km/hr. No simple relationship fits the data obtained in walking. Except that at very high speeds of walking the total work done per unit distance is greater in running than in walking, but it increases with speed more than two times faster in walking than in running.

The efficiency of positive work production by muscles was measured as W_{tot}/Net energy expenditure (this includes the cost of negative work), and plotted as a function of speed in Fig. 3. It appears that (1) it is always greater than the maximal efficiency of the transformation of chemical energy into mechanical work by muscle (0·25), (2) it is greater in running than in walking, (3) in running it increases almost linearly with speed and (4) in walking it reaches a maximum at intermediate speeds.

DISCUSSION

Mechanical work. Walking. Ralston & Lukin (1969) developed a technique, completely different from that used in the present study, to measure W_{tot} during walking at moderate speeds. According to these authors the work done per unit distance at 4·4 km/hr is 0·174 kcal/(kg.km) (average for two 19 yr old girls). This figure is similar to that found at the same speed in the present study (0·185 kcal/(kg.km), Fig. 3): taking into account the work to swing the arms and the rotational energy changes of the lower limbs, neglected by these authors, their work figure would increase about 29 % (according to our measurements). Curves of the energy levels of the whole body and its subsystems, and of the work done by the muscles at each joint during walking, have been determined by Elftman (1944, 1966) and by Cappozzo, Figura, Marchetti & Pedotti (1976); these authors however do not give a final figure of the total work done during walking at a given speed. *Running.* Our average figure of total positive work during running at top speed (0·814 kcal/(kg.km) at 33 km/hr) is in agreement with that determined by Fenn (1930*a*) on students running at their maximal speed for a short sprint: about 0·83 kcal/(kg.km) at 27 km/hr (0·58 kcal/(kg.km) as W_{ext} to accelerate and lift the centre of mass and 0·25 kcal/(kg.km) as W_{int} to accelerate the limbs relatively to the trunk). Elftman (1940) calculated the work done by the muscles in sprint running from Fenn's measurements, but with a different approach: it arrived at a figure of 0·89 kcal/(kg.km) which is not very different from that found in the present study. The top speed attained by subjects P.C. and M.S. (respectively 33 and 32 km/hr) is greater than that attained by subject G.C. and by Fenn's students while exerting their maximal effort, in spite of the fact that the total mechanical power output is about the same: this suggests a greater skill of subjects P.C. and M.S. (trained runners) in transforming the mechanical power into useful forward speed of the body. From the few data obtained by Cavagna *et al.* (1964) the work done per unit distance in running appeared to be independent of speed: the present more numerous and precise data leave little doubt that it increases with speed.

Energy expenditure. The lines indicating the net energy expenditure (total minus standing) in Fig. 3 are in agreement with the oxygen consumption data of Atzler & Herbst (1927), Margaria (1938), Ralston (1958), Cotes & Meade (1960) and Dill (1965) on normal subjects. The dotted part of these curves indicates that an oyxgen debt may be necessary to meet the mechanical power output.

In walking the limit for a purely aerobic exercise is arbitrarily set for a fit subject at 9 km/hr. Olympic walkers, studied by Menier & Pugh (1968), consumed appreciably less oxygen at high speed: the mechanics of walking at high speeds of these subjects is presumably very different from that of our untrained subjects.

In running the limit is set at 20 km/hr according to the determinations of Margaria, Cerretelli, Aghemo & Sassi (1963) on runners (such as subjects P.C. and M.S.). The dotted line above this limit was drawn according to Margaria's opinion that the energy expenditure remains about 1 kcal/(kg.km) even when an oxygen debt is contracted (Margaria *et al.* 1963).

Is it correct to take the total minus standing energy expenditure as the energy requirement for the mechanical work done in walking and running? During standing some muscles are active and spend energy to maintain posture: suppose the same energy is used during walking to maintain muscular activity, in substitution of the energy spent, during standing, to maintain posture. In this case the total minus standing energy expenditure could not be correctly used to calculate efficiency: the cost to maintain posture should also be included in the calculation. In walking at slow speeds the error can be appreciable: we estimated the energy expenditure during standing as 1·23 kcal/(kg.hr) (average of the data reported by Benedict & Murschhauser, 1915, p. 74, Margaria, 1938, and Ralston, 1958) and the basal metabolic rate of our subjects as 0·966 kcal/(kg.hr). When the difference (0·264 kcal/(kg.hr)) is added to the total minus standing energy expenditure to calculate efficiency, appreciably lower values are obtained at low walking speeds (interrupted lines in Fig. 3).

Efficiency. In spite of the fact that the present mechanical work measurements are in good agreement with those of Ralston & Lukin (1969) for walking and of Fenn (1930*a*) for running, the efficiency values herein reported (Fig. 3) are appreciably greater than those measured by Ralston & Lukin (0·21–0·24) and by Fenn (0·23). Evidently the discrepancy is due to a different figure of energy expenditure used to calculate efficiency. Ralston *et al.* (1969) used the total metabolic expenditure instead of total minus standing or the total minus basal as we did. During walking at low speeds the basal metabolic rate may be as much as 30–50 % of the total: this large fraction, not directly related to muscular activity, explains the difference between Ralston's and our results. Fenn (1930*a*) used 13 h.p. as total excess energy consumed divided by the time of a short sprint at top speed: as pointed out by Margaria (e.g. Margaria *et al.* 1963), this figure is probably affected by a considerable positive error involved in the method of measuring the oxygen debt. Anyway, Cavagna *et al.* (1964) found efficiency values in running as high as 0·4–0·5 over the speed range (10–15 km/hr) in which running can be a completely aerobic process. Since the maximal accepted efficiency of the contractile machinery is about 0·25, this finding was taken as evidence of a substantial recovery of elastic energy in running.

Elftman (1944, Fig. 8) put in evidence that both in walking and in running the muscles continuously undergo a stretch-shorten cycle in which they receive and release mechanical energy; however he thought that the muscle '...is unable to keep but dissipates as heat' the energy received and that '...the consequent loss of energy from the system is aggravated by the fact that the muscle must actually contribute chemical energy during the process'. The high efficiency values in Fig. 3 indicate, on the contrary, that the stretch-shorten cycle is a highly profitable process; this in spite of the fact that the cost of negative work is included in the calculation.

The present data show that the efficiency is greater in running than in walking. This finding is in agreement with the different mechanics of the two exercises: in walking potential and kinetic energy of the body interchange (as in a 'rolling egg') whereas in running they both enter the muscles to be restored immediately after during subsequent shortening (as in a 'bouncing ball': cf. Fig. 1 and 5 of Cavagna *et al.* 1976*b*). Clearly this second mechanism is more suitable for the storage and release of energy by muscles than the first one. In sprint running, i.e. when the body is on the average accelerated forward, the contribution of elastic energy to W_{ext} is negligible at speeds less than about 20 km/hr because up to this speed practically no external negative work is done (Cavagna, Komarek & Mazzoleni, 1971); during running at a 'constant' speed, on the contrary, external negative work is done, and consequently elastic energy can be stored, also at the lowest speeds. It may be thought that the forces involved in walking are too small to stretch appreciably the tendons thus storing elastic energy. However elastic energy can be stored also within the contractile component (Huxley & Simmons, 1971): the elastic energy stored within each active fibre, when it is forcibly stretched, is independent of the total force, i.e. of the number of fibres brought into activity.

An apparent efficiency has been measured during running, walking and bicycling against a horizontal impeding force: the values obtained are 0·39–0·54 in running (Lloyd & Zacks, 1972; Zacks, 1973; Asmussen & Bonde-Petersen, 1974), 0·32 in walking (Asmussen & Bonde-Petersen, 1974) and 0·25–0·26 in cycling (Zacks, 1973; Asmussen & Bonde-Petersen, 1974). Even if the apparent efficiency is not necessarily expression of the efficiency of positive work production by muscles, it is indicative that also in these experiments the apparent efficiency in running was greater than in walking and in walking was greater than 0·25: this last value is approached only by that measured in cycling, an exercise during which the muscles contract without a preceding phase of negative work, i.e. without a chance to store mechanical energy immediately before shortening.

Efficiency changes with the speed of locomotion. In walking the efficiency changes with speed as may be expected from the known properties of the contractile component of muscle. A maximum (0·35–0·4) is attained at intermediate speeds according to the force–velocity relation and the measurements of the 'initial efficiency' of muscle (Hill, 1964). Also in cycling the efficiency attains a maximum (0·22) at intermediate speeds of movement (Dickinson, 1929), but the absolute values are lower than in walking. These findings suggest that in walking, as in cycling, the role played by the contractile machinery prevails over that of the elastic component: this last however cannot be neglected in walking.

In running the efficiency increases continuously with speed: this trend, together with the high values attained, suggests that the role played by elasticity prevails over that of the contractile machinery. Cavagna, Dusman & Margaria (1968, figs. 6 and 7) found that the useful effect of stretching increases with the speed of stretching and shortening and Cavagna & Citterio (1974) put in evidence the transient character of muscle elasticity. Also in sprint running the contribution of elasticity turned out to increase with speed (Cavagna *et al.* 1971).

In hopping kangaroo $\dot{W}_{ext}$ increases with speed very similarly to man

(Cavagna, Heglund & Taylor, 1976*a*), but, contrary to man, $\dot{W}_{\text{int}}$ is a small fraction of $\dot{W}_{\text{ext}}$ (Alexander & Vernon, 1975). As a consequence $\dot{W}_{\text{tot}}$ is much smaller than in man: however in this animal the oxygen consumption per unit time decreases slightly with speed (Dawson & Taylor, 1973) so that its mechanical efficiency increases with speed just as in man (Cavagna *et al.* 1976*a*). This confirms the present results obtained in man during running.

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REFERENCES

Alexander, R. McN. & Vernon, A. (1975). The mechanics of hopping by kangaroos (Macropoditae). *J. Zool.* **177** 265–303.

Asmussen, E. & Bonde-Petersen, F. (1974). Apparent efficiency and storage of elastic energy in human muscles during exercise. *Acta physiol. scand.* **92**, 537–545.

Atzler, E. & Herbst, R. (1927). Arbeitsphysiologische Studien. Teil III. *Pflügers Arch. ges. Physiol.* **215**, 291–328.

Benedict, F. G. & Murschhauser, H. (1915). *Energy Transformation during Horizontal Walking.* Carnegie Inst. Wash. Publ. No. 231.

Cappozzo, A., Figura, F., Marchetti, M. & Pedotti, A. (1976). The interplay of muscular and external forces in human ambulation. *J. Biomech.* **9**, 35–43.

Cavagna, G. A. & Citterio, G. (1974). Effect of stretching on the elastic characteristics and the contractile component of frog striated muscle. *J. Physiol.* **239**, 1–14.

Cavagna, G. A., Dusman, B. & Margaria, R. (1968). Positive work done by a previously stretched muscle. *J. appl. Physiol.* **24**, 21–32.

Cavagna, G. A., Heglund, N. C. & Taylor, C. R. (1976*a*). Walking, running and galloping: mechanical similarities between different animals. *In Biodynamics of Animal Locomotion*, ed. Pedley, T. J. London: Academic Press.

Cavagna, G. A., Komarek, L. & Mazzoleni, S. (1971). The mechanics of sprint running. *J. Physiol.* **217**, 709–721.

Cavagna, G. A., Saibene, F. P. & Margaria, R. (1964). Mechanical work in running. *J. appl. Physiol.* **19**, 249–256.

Cavagna, G. A., Thys, H. & Zamboni, A. (1976*b*). The sources of external work in level walking and running, *J. Physiol.* **262**, 639–657.

Cotes, J. E. & Meade, F. (1960). The energy expenditure and mechanical energy demand in walking. *Ergonomics.* **3**, 97–119.

Dawson, T. J. & Taylor, C. R. (1973). Energetics cost of locomotion in kangaroo. *Nature, Lond.* **246**, 5431, 313–314.

Dickinson, S. (1929). The efficiency of bicycle-pedalling, as affected by speed and load. *J. Physiol.* **67**, 242–255.

Dill, D. B. (1965). Oxygen used in horizontal and grade walking and running on the treadmill. *J. appl. Physiol.* **20**, 19–22.

Elftman, H. (1940). The work done by muscles in running. *Am. J. Physiol.* **129**, 672–684.

ELFTMAN, H. (1944). Skeletal and muscular systems: structure and function. In *Medical Physics 1*, ed. GLASSER, O., pp. 1420–1430. Chicago: Year Book Publishers.

ELFTMAN, H. (1966). Biomechanics of muscle with particular applications to studies of gait. *J. Bone Jt Surg.* **48**-A, 2, 363–377.

FENN, W. O. (1930*a*). Frictional and kinetic factors in the work of sprint running. *Am. J. Physiol.* **92**, 583–611.

FENN, W. O. (1930*b*). Work against gravity and work due to velocity changes in running. *Am. J. Physiol.* **93**, 433–462.

HILL, A. V. (1964). The efficiency of mechanical power development during muscular shortening and its relation to load. *Proc. R. Soc.* B **159**, 319–324.

HUXLEY, A. F. & SIMMONS, R. M. (1971). Mechanical properties of the cross-bridges of frog striated muscle. *J. Physiol.* **218**, 59–60*P*.

LLOYD, B. B. & ZACKS, R. M. (1972). The mechanical efficiency of treadmill running against a horizontal impeding force. *J. Physiol.* **223**, 355–373.

MARGARIA, R. (1938). Sulla fisiologia e specialmente sul consumo energetico della marcia e della corsa a varie velocità ed inclinazioni del terreno. *Atti Accad. naz. Lincei Memoric* 7299–368.

MARGARIA, R., CERRETELLI, P., AGHEMO, P. & SASSI, G. (1963). Energy cost of running. *J. appl. Physiol.* **18**, 367–370.

MENIER, D. R. & PUGH, L. G. C. E. (1968). The relation of oxygen intake and velocity of walking and running, in competition walkers. *J. Physiol.* **197**, 717–721.

RALSTON, H. J. (1958). Energy-speed relation and optimal speed during level walking. *Int. Z. angew. Physiol.* **17**, 277–283,

RALSTON, H. J. & LUKIN, L. (1969). Energy levels of human body segments during level walking. *Ergonomics* **12**, 1, 39–46.

ZACKS, R. M. (1973). The mechanical efficiencies of running and bicycling against a horizontal impeding force. *Int. Z. angew. Physiol.* **31**, 249–258.