# ORIGINAL ARTICLE

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# The resonant step frequency in human running

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Abstract At running speeds less than about 13 km h<sup>-1</sup> the freely chosen step frequency  $(f_{\text{free}})$  is lower than the frequency at which the mechanical power is minimized  $(f_{\min})$ . This dissociation between  $f_{\text{free}}$  and  $f_{\min}$  was investigated by measuring mechanical power, metabolic energy expenditure and apparent natural frequency of the body's bouncing system  $(f_{sist})$  during running at three given speeds with different step frequencies. The  $f_{\text{free}}$  requires a mechanical power greater than that at  $f_{\min}$  mainly due to a larger vertical oscillation of the body at each step. Energy expenditure is minimal and the mechanical efficiency is maximal at  $f_{\text{free}}$ . At a given speed, an increase in step frequency above  $f_{\text{free}}$  results in an increase in energy expenditure despite a decrease in mechanical power. On the other hand, a decrease in step frequency below  $f_{\text{free}}$ results in a larger increase in energy expenditure associated with an increase in mechanical power. When the step frequency is forced to values above or below  $f_{\rm free}$ ,  $f_{\rm sist}$  is forced to change similarly by adjusting the stiffness of the bouncing system. However the best match between  $f_{sist}$  and step frequency takes place only in proximity of  $f_{\text{free}}$  (2.6–2.8 Hz). It is concluded that during running at speeds less than 13 km h<sup>-1</sup> energy is saved by tuning step frequency to  $f_{sist}$ , even if this requires a mechanical power larger than necessary.

**Key words** Step frequency · Running · Muscle elasticity · Efficiency

### Introduction

It is assumed commonly that during locomotion gait parameters are adjusted for the minimization of force, work, power and/or energy expenditure. For example, in

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Unité de Réadaptation, Université Catholique de Louvain, B-1348 Louvain-la-Neuve, Belgium walking, it has been shown that the average mechanical power, i.e. the positive work done at each step divided by the step period, is minimized at a step frequency,  $f_{\rm min}$ , close to the freely chosen step frequency,  $f_{\rm free}$  [5]. Correspondingly, the oxygen consumption, which is related to the average mechanical power, is also minimized near that frequency [11, 14, 18, 21]. In running,  $f_{\rm free}$  has been found to coincide with  $f_{\rm min}$  only at about 13 km h<sup>-1</sup> [9]. Correspondingly, a minimum of oxygen consumption under aerobic conditions was found near  $f_{\rm free}$  during running at 9–16 km h<sup>-1</sup> [10, 13, 15, 19].

On the other hand, during high-speed running (above 20 km h<sup>-1</sup>)  $f_{\text{free}}$  is greater than  $f_{\min}$  and coincides with a frequency minimizing the push-average mechanical power, i.e. the work done at each step divided by the duration of positive work production [9]. This is in agreement with the observation that running speed is limited by the maximal rate of muscular work production during a contraction [7]. Between 13 and 20 km h<sup>-1</sup>,  $f_{\text{free}}$  is therefore intermediate between  $f_{\min}$  (eventually limited by the maximum aerobic power), and the frequency minimizing the push-average power (eventually limited by the maximum anaerobic power).

However, during low- to moderate-speed running (less than 13 km h<sup>-1</sup>), the mechanical power is minimized at a step frequency higher than  $f_{\text{free}}$  [9]. This indicates that at these speeds some factor other than the minimization of mechanical power determines  $f_{\text{free}}$ . Running is commonly modelled as a spring-mass system oscillating at a natural frequency that is adjustable by muscle stiffness. However, contrary to a passive spring-mass system, muscles are required to put energy into the system at each step to compensate for energy losses. It could be that at low- to moderate-running speeds the step frequency chosen is the frequency at which the muscular energy input into the bouncing system is minimal. To test this hypothesis, we measured mechanical work, oxygen consumption, and apparent natural frequency of the body's bouncing system  $f_{sist}$  [8] while running at speeds less than 13 km h<sup>-1</sup> with step frequencies lower and higher than  $f_{\text{free}}$ .

The results show that, in spite of a mechanical power greater than necessary, the metabolic energy expenditure is minimum at  $f_{\text{free}}$ , due to a maximum of mechanical efficiency. Furthermore, the difference between  $f_{\text{sist}}$  and step frequency is also minimum at  $f_{\text{free}}$ . Therefore, by analogy to mechanical forced oscillators, we conclude that at low-to-moderate running speeds, the body operates at it's resonant frequency.

### **Materials and methods**

#### Subjects

Experiments were performed on five male subjects. Three of them were untrained subjects already studied previously (C.G., T.J., W.P., see Table 1 in Cavagna et al. [9]), two were athletes of very different build: a long-distance runner (B.L., 28 years, 58.9 kg, 1.80 m), characterized by a compliant bouncing system, and a sprinter (G.L., 29 years, 66.8 kg, 1.68 m), characterized by a stiff bouncing system (see below). Informed consent of the subjects was obtained. Measurements were made during running at 5.3, 8.0 and 11.1 km h<sup>-1</sup> at  $f_{\rm free}$  and at step frequencies lower and higher than  $f_{\rm free}$ , as dictated by a metronome.

#### Mechanical power and stiffness measurements

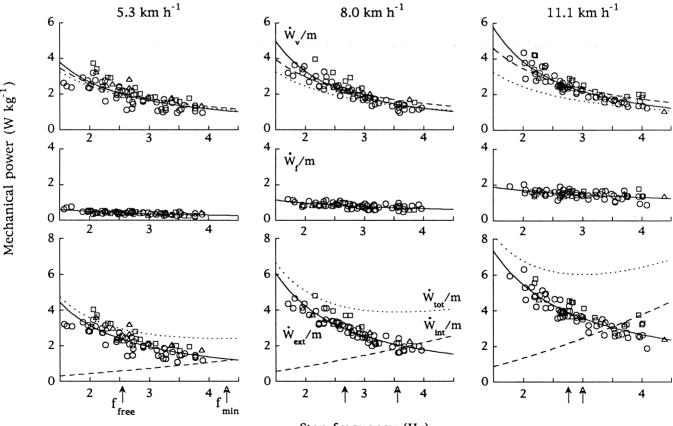
The average external mechanical power required to lift and re-accelerate the centre of mass ( $\dot{W}_{ext}$ ) was calculated from the vertical and forward component of the ground reaction force as measured by a force platform [4]. The average internal mechanical power required to accelerate the limbs relative to the centre of mass of the body was calculated for each subject, as described by Cavagna et al. [9], from an updated equation which now includes further data from Willems et al. [20]:

$$W_{\rm int}/m = 0.140 \cdot 10^{-0.200 L} \cdot V_{\rm f}^2 \cdot f_{\rm step}$$
 (1)

(*r*=0.75, *n*=220) where  $\dot{W}_{int}/m$  is the mass-specific (*m* is the body mass) average internal power (Watt per kilogram), *L* is the step length (meter),  $V_f$  is the velocity of running (meter per second), and  $f_{step}$  is the step frequency (Hertz).

The average total mechanical power, i.e. the positive work done each step divided by the step period  $(W_{tot})$ , is the sum of the  $W_{ext}$  and  $W_{int}$ .

Fig. 1 Effect of a step frequency change on the different fractions of the mechanical power necessary to maintain a given running speed. The experimental data show the positive work done per unit time (mass-specific average power) to sustain the vertical displacement of the centre of mass of the body,  $W_v/m$  (upper panels), its forward velocity changes,  $\dot{W}_{f}/m$  (middle panels) and its combined motion in the sagittal plane,  $\dot{W}_{ext}/m$  (lower panels), as a function of the step frequency during level running at the three indicated speeds. Data indicated by the circles are from [9] (Table 1), plus measurements made in the present study on a sprinter (squares) and on a long-distance runner (triangles). The continuous lines represent the best fit of the experimental data using a power function. The dotted and interrupted lines in the top panels are traced according to Eqs. 6 and 10 respectively (see text). The *interrupted* and the *dotted* lines in the *lower panels* indicate, respectively, the average power to accelerate the limbs relative to the centre of mass  $(\dot{W}_{int}/m)$ , calculated from Eq. 1 for all subjects: *cir*cles, squares and triangles), and the total average power ( $W_{tot}/m=$  $|\dot{W}_{ext}/m| + |\dot{W}_{int}/m|$ . The *filled arrows* indicate the freely chosen step frequency  $f_{\text{free}}$  and the *open arrows* indicate the frequency  $f_{\min}$  for a minimum of  $W_{\text{tot}}$ 



Step frequency (Hz)

Assuming a damped harmonic motion, the frequency of the oscillations of the body's bouncing system  $f_{sist}$  can be calculated from the stiffness of the structures, on which the body may bounce, k, as:  $f_{sist}=(1/2 \pi) [(k/m)-(b/2 m)^2]^{1/2}$ , where b is the damping coefficient and *m* the mass of the body. The mass-specific vertical stiffness, k/m, was measured on the force platform. The vertical acceleration of the centre of mass  $(a_y)$  was plotted as a function of the vertical displacement of the centre of mass  $(S_v)$ . The slope of the relationship between  $a_v$  and  $S_v$  was calculated by fitting a straight line through the points during the downward deceleration and the upward acceleration using a least-squares fit method. This slope was considered to represent k/m [8]. The average k was 21.8  $\pm$  7.6 kN/m (mean  $\pm$  SD, n=167) in untrained subjects,  $20.4 \pm 8.1$  kN/m (*n*=22) in the long-distance runner and  $32.2 \pm 15.2$  kN/m (*n*=31) in the sprinter. A value for  $f_{sist}$  was then calculated using k/m measured as described above and neglecting the term  $(b/2 m)^2$  [8]. It must be pointed out that the vertical stiffness, as measured, does not represent the stiffness of the leg [17], but that of the ensemble of structures undergoing a deformation during the impact of the body against the ground [8].

In the present study, force platform experiments were done on subjects B.L. and G.L. only; for the other subjects we used the data collected by Cavagna et al. [9].

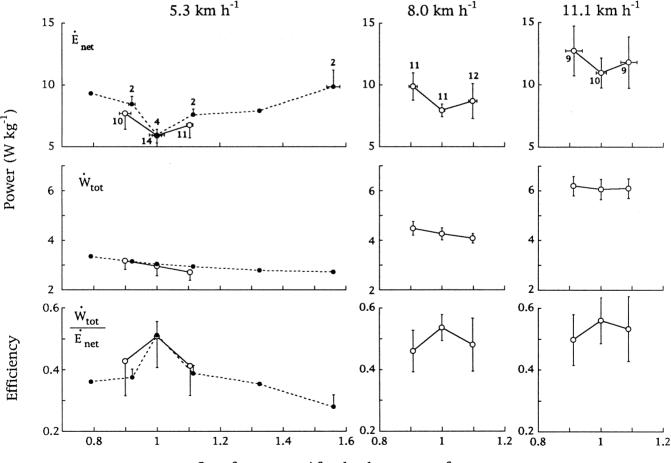
#### Oxygen consumption measurements

Oxygen consumption ( $\dot{V}O_2$ ) was determined as the subjects ran on a treadmill. A Beckman metabolic cart measured  $O_2$  uptake from the volume of expired air and the change in  $O_2$  and  $CO_2$  content, averaged over 30-s intervals, by polarographic (Beckman OM-11) and infrared (Beckman LB-2) sensors respectively. Steady state  $\dot{VO}_2$  was calculated for each run as the average of all 30-s readings after a plateau was reached; the average duration of the plateau was 442 ± 89 s (mean ± SD, *n*=101). The average  $\dot{VO}_2$  during a 512 ± 93 s (mean ± SD, *n*=33) standing period was measured prior to each set of runs and subtracted from the exercise value to obtain the net  $\dot{VO}_2$ . Measurements were made at step frequencies equal to  $f_{\rm free}$ , 1.1  $f_{\rm free}$  and 0.9  $f_{\rm free}$  and at speeds of 5.3, 8.0 and 11.1 km h<sup>-1</sup> (5.3 and 8.0 km h<sup>-1</sup> only on subject W.P.). Most of the measurements were organized in mirror pairs in order to avoid influence of test order on  $\dot{VO}_2$ . Experiments were made during a time span of 1 week to 22 months. Rate of net  $\dot{VO}_2$  was converted to rate of energy expenditure,  $\dot{E}_{\rm net}$  (Fig. 2), assuming 20.1 kJ per litre O<sub>2</sub>.

#### Measurements of $f_{step}$

The  $f_{\text{step}}$  was measured during the force plate experiments from the record of one or more complete steps. In the treadmill experiments,  $f_{\text{step}}$  was determined by averaging several measurements of 100 step periods made with a stopwatch.

**Fig. 2** Effect of a step frequency change at three given running speeds on the metabolic energy expenditure  $\dot{E}_{net}$  (*upper panels*),  $W_{tot}$  (*middle panels*) and the efficiency ( $\dot{W}_{tot}/E_{net}$ , *lower panels*). The *points* represent data obtained on all subjects (*open*) and on subject C.G. only (*filled*). Means values  $\pm$  SD when SD larger than symbol size; *n* is given by the *numbers* near the symbols of the *upper panels* 



Step frequency / freely chosen step frequency

## Results

# Effect of change in $f_{\text{step}}$ on the mechanical power

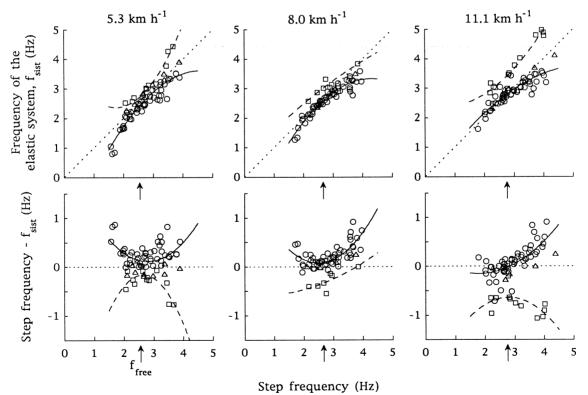
The average mechanical power required to lift the centre of mass against gravity  $(\dot{W}_v)$ , to accelerate it forwards  $(\dot{W}_{\rm f})$  and to sustain its combined motion in the sagittal plane  $(\dot{W}_{ext})$ , as well as the power required to accelerate the limbs relative to the centre of mass  $(\dot{W}_{int})$  and the total mechanical power ( $\dot{W}_{tot}$ ) are shown in Fig. 1 as a function of  $f_{\text{step}}$  for three running speeds. The filled arrow indicates  $f_{\text{free}}$ , the open arrow indicates the step frequency  $f_{\rm min}$  at which  $\dot{W}_{\rm tot}$  is minimum. It can be seen that at 5.3 and 8.0 km h<sup>-1</sup>  $\dot{W}_{\rm tot}$  is greater at  $f_{\rm free}$  than at  $f_{\rm min}$  mainly due to a greater power spent against gravity during the vertical oscillation of the centre of mass,  $\dot{W}_{v}$ . The  $\dot{W}_{tot}$ minimum occurs at a frequency which is quite independent of any conceivable errors in the  $\dot{W}_{tot}$  measurement; for example, to eliminate the difference between  $f_{\text{free}}$  and  $f_{\rm min}$  at 5.3 km h<sup>-1</sup>, a systematic error resulting in either a 3.5-fold increase in  $\dot{W}_{\rm int}$ , or a four-fold decrease in  $\dot{W}_{\rm ext}$ , would be necessary.

Effect of a change in  $f_{\text{step}}$  on the metabolic power

Values of  $\dot{E}_{\rm net}$ ,  $\dot{W}_{\rm tot}$ , and the efficiency of positive work production are shown in Fig. 2 as a function of normalized  $f_{\rm step}$  during running at 5.3, 8.0 and 11.1 km h<sup>-1</sup>. The open symbols refer to average data obtained on all subjects during running at step frequencies equal to  $f_{\rm free}$ , 0.9  $f_{\rm free}$  and 1.1  $f_{\rm free}$ . The energy expenditure is at a minimum and the mechanical efficiency is at a maximum at  $f_{\rm free}$ . At 5.3 and 8.0 km h<sup>-1</sup>, a decrease of  $f_{\rm step}$  below  $f_{\rm free}$ leads to an increase in both mechanical power and energy expenditure. Conversely, an increase in  $f_{\rm step}$  above  $f_{\rm free}$ leads to a reduction in mechanical power, but in spite of this still leads to an increase in energy expenditure. As expected, the increase in energy expenditure taking place when the frequency is reduced below  $f_{\rm free}$  (and the mechanical power is increased) is greater than the increase in energy expenditure taking place when the frequency is raised above  $f_{\rm free}$  (and the mechanical power is decreased). In fact, since the efficiency is the same at 0.9  $f_{\rm free}$  as at 1.1  $f_{\rm free}$  (Fig. 2), the energy expenditure is proportional to the mechanical power and, therefore, the greater energy expenditure at 0.9  $f_{\rm free}$  can reasonably be attributed to the mechanical power being greater at 0.9  $f_{\rm free}$  than at 1.1  $f_{\rm free}$ . The filled symbols at 5.3 km h<sup>-1</sup> refer to one subject

The filled symbols at 5.3 km h<sup>-1</sup> refer to one subject running with a wider range of step frequencies: these data show clearly the contrast between the monotonic trend of the total mechanical power and that of the metabolic energy expenditure which attains a sharp minimum during running at  $f_{\text{free}}$ .

**Fig. 3** Comparison of the step frequency with the natural frequency of the body's bouncing system. The apparent natural frequency of the bouncing system  $f_{sist}$  (*upper panels*), calculated from the whole-body vertical stiffness, and the difference between measured step frequency and  $f_{sist}$  (*lower panels*), are plotted as a function of the measured step frequency during running at the indicated speeds. Experiments are the same as in Fig. 1. *Interrupted lines* refer to the sprinter (see text), *continuous lines* to the other subjects. *Lines* are fitted using a second-order polynomial regression. Symbols as in Fig. 1. The *dotted lines* are the lines of identity, the *arrows* indicate  $f_{\rm free}$ 



Step frequency and apparent natural frequency of the body's bouncing system

The apparent natural frequency of the bouncing system  $f_{\rm sist}$  (calculated from the whole-body vertical stiffness, see Materials and methods) is shown in the upper panels of Fig. 3 as a function of  $f_{\rm step}$ . It appears that, in general,  $f_{\rm sist}$  is near the identity line (dotted line) indicating that when  $f_{\rm step}$  is forced to values above and below  $f_{\rm free}$  ( $f_{\rm free}$  indicated by the arrow),  $f_{\rm sist}$  is forced to change similarly by adjusting the whole-body vertical stiffness. A closer inspection of the data, however, shows that  $f_{\rm sist}$  is nearest to the  $f_{\rm step}$  in the neighborhood of  $f_{\rm free}$ . This is better shown in the lower panels of Fig. 3: on average the difference between  $f_{\rm step}$  and  $f_{\rm sist}$  is minimal near  $f_{\rm free}$  (solid line vs. dotted line). The means (±SD) of  $f_{\rm free}$  are: 2.55 ± 0.22 (n=28) at 5.3 km h<sup>-1</sup>, 2.67 ± 0.18 (n=24) at 8.0 km h<sup>-1</sup>, and 2.75 ± 0.11 (n=27) at 11.1 km h<sup>-1</sup>.

The squares and interrupted line in Fig. 3 refer to the sprinter G.L.; his data were treated separately from those of the other subjects because he was the only subject with a vertical stiffness 1.5-fold greater than that of the other subjects (see Materials and methods), his  $f_{sist} > f_{free}$ , i.e. he had an asymmetric rebound [8], possibly leading to  $\dot{VO}_2$  during running at 8 and 11 km h<sup>-1</sup> being lower at 1.1  $f_{free}$  than at  $f_{free}$  [19].

### Discussion

The first section of the following gives the literature background indicating (1) a minimum in energy expenditure near  $f_{\text{free}}$ , but not the reasons for it, and (2) previous experimental evidence suggesting the 'elastic' mechanism of running. The second section shows that the relationship between  $f_{\text{step}}$  and  $\dot{W}_v$  is predicted by the elastic model. In the third section, the changes in vertical stiffness of the bouncing system with frequency provide a possible explanation for the minimum energy expenditure near  $f_{\text{free}}$ .

#### Relation to previous studies

As mentioned above, a minimum  $\dot{VO}_2$  in the proximity of  $f_{\rm free}$  has been reported for running in aerobic conditions at speeds of 9–16 km h<sup>-1</sup> [10, 13, 15, 19]. A minimum of metabolic energy expenditure may be due to a minimum of mechanical power and/or to a maximum of efficiency. To distinguish between these possibilities it is necessary to measure both metabolic energy expenditure and mechanical work in the same subject. Kaneko et al. have measured both the  $\dot{VO}_2$  and the total average mechanical power  $\dot{W}_{\rm tot}$  during running at 9, 13 and 16 km h<sup>-1</sup> [15] and report a minimum energy expenditure at an  $f_{\rm step}$  of 2.9 Hz, a maximum efficiency at 2.8–3.0 Hz, and a minimum  $\dot{W}_{\rm tot}$  at 3.0 Hz; all very close to  $f_{\rm free}$  (2.8 Hz). This is similar to the findings in the present study at 11.1 km h<sup>-1</sup>, but not at 8.0 and 5.3 km h<sup>-1</sup>, where the minimum

energy expenditure rate during running at  $f_{\text{free}}$  is associated with a  $\dot{W}_{\text{tot}}$  larger than the minimum value (Fig. 2). The physiological mechanisms leading to a minimum cost during running at the  $f_{\text{free}}$  are unknown.

A "bouncing ball" model of running has been proposed by Cavagna et al. [6] to explain, through an elastic recovery of energy, efficiency values about 2 times greater than the maximum efficiency of muscular contraction. These values are similar to those measured in the present study (Fig. 2). It must be pointed out that the mechanical positive work, as measured, derives not only from the transformation of chemical energy, but also from the mechanical energy stored during negative work within tendons and sarcomeres. The efficiency of positive work production, as a consequence, does not refer to the efficiency of the transformation of chemical energy into mechanical work, but rather represents the end result of all possible losses (e.g. friction, isometric contractions) and energy saving mechanisms mentioned above.

Landing on one leg with the calf muscles in sustained contraction leads to damped oscillations of the body with a frequency (2.9 Hz) compatible with the values of  $f_{\text{free}}$  found here [3]. Cavagna et al. [8] have found that  $f_{\text{free}}$  equals  $f_{\text{sist}}$  up to about 11 km h<sup>-1</sup> (i.e. in the speed range of the present study).

Does a spring-mass model agree with the present experimental results?

As shown below, the relation between step frequency and work against gravity (Fig. 1) provides further evidence that the vertical oscillation of the centre of mass during each running step agrees substantially with a linear spring-mass model. According to this model, an increase in  $f_{\text{step}}$  at a given speed leads to a decrease in the external mechanical power spent against gravity similar to that observed experimentally.

Assuming that:

1. the work done against gravity at each step equals the release of elastic energy by a linear spring, i.e.

$$mgS_{v} = (kS_{vc}^{2}) / 2$$
 (2)

where *m* is the mass of the body, *g* the acceleration of gravity,  $S_v$  is the total vertical lift of the centre of mass at each step, *k* the vertical stiffness, and  $S_{v,c}$  the vertical component of the deformation of the spring from maximum to zero vertical force;

2.  $S_v$  takes place only during contact of the foot on the ground, with no lift during the aerial phase, i.e.  $S_{v,c}=S_v$ , so that Eq. 2 can be rewritten as

$$k/m = 2g/S_{\rm v} \tag{3}$$

3. The  $f_{\text{step}}$  equals  $f_{\text{sist}} = (1/2 \pi)(k/m)^{1/2}$  (see Materials and methods) also when it is forced to be lower or higher than  $f_{\text{free}}$ ; i.e.

$$k/m = 4 \pi^2 f_{\text{step}}^2$$
. (4)

From Eqs. 5 and 4  

$$S_v = (g/2 \pi^2) f_{step}^{-2}$$
 (5)

Multiplying both parts of Eq. 5 by  $mgf_{step}$  and rearranging yields the mass specific average power against gravity as a function of the step frequency:

$$\dot{W}_{\rm v}/m = (g^2/2 \ \pi^2) f_{\rm step}^{-1}$$
 (6)

(dotted lines in Fig. 1 top).

Should  $S_v > S_{v,c}$ , as when a vertical lift occurs during the aerial phase of the step, assumption (2) is no longer valid. In this case  $S_{v,c}$  can be calculated assuming that the maximal vertical force exerted on the ground is proportional to the length change of the spring from maximum compression to zero load, i.e.

$$m(g + a_{\rm y max}) = kS_{\rm yc} \tag{7}$$

where  $a_{v,max}$  is the maximal vertical acceleration of the centre of mass during the rebound. Substituting  $S_{v,c}=(m/k)$   $(g + a_{v,max})$  into Eq. 2

$$S_{\rm v} = (1/2 g) (m/k) (g + a_{\rm v,max})^2$$
 (8)

and, from Eq. 4,

$$S_{\rm v} = ((g + a_{\rm v,max})^2 / (8g\pi^2)) f_{\rm step}^{-2}.$$
 (9)

Equation 9 reduces to Eq. 5 when  $a_{v,max}=g$ . Multiplying both sides of Eq. 9 by  $mgf_{step}$  and rearranging

$$\dot{W}_{v}/m = ((g + a_{v,max})^{2}/(8 \pi^{2}))f_{step}^{-1} = A f_{step}^{-1}$$
 (10)

(interrupted lines Fig. 1 top). From the *A* values obtained by fitting the  $\dot{W}_{v}/m$  data to Eq. 10,  $a_{v,max}$  can be calculated to be 10.5, 11.8 and 13.5 m s<sup>-2</sup> at 5.3, 8.0 and 11.1 km h<sup>-1</sup>, respectively A, compared with the means (± SD) of 10.5 ± 3.4 (*n*=74), 11.7 ± 3.0 (*n*=71) and 14.9 ± 3.9 m s<sup>-2</sup> (*n*=74), measured directly from the individual acceleration records at the instant at which the vertical motion of the centre of mass reverses from downwards to upwards (see Fig. 1 in [8]).

At 5.3 km h<sup>-1</sup> and at high frequencies at 8.0 and 11.1 km h<sup>-1</sup> the close fit of the  $\dot{W}_{v}/m$  data to Eq. 6 (dotted line in Fig. 1 top) suggests that all three assumptions are tenable. This is because the vertical displacement of the centre of mass  $S_{v}$  may be compared to the total vertical displacement  $S_{v,c}$  during the oscillation of an elastic system only when the aerial phase is nil and the vertical acceleration approaches during the oscillation a maximum of 1 g and a minimum of -1 g [8]. This condition is essentially met at 5.3 km h<sup>-1</sup> and at high frequencies at 8.0 and 11.1 km h<sup>-1</sup> when most of the lift takes place during contact.

The divergence of the dotted line from the low-frequency data at 8.0 and 11.1 km h<sup>-1</sup> is due to an increase in the vertical push leading to a significant aerial phase, so that  $S_v$  becomes greater than  $S_{v,c}$ . Consequently, a rough fit of the data is obtained for  $a_{v,max}$  in Eq. 10 greater than 1 g (interrupted lines Fig. 1 top): the fit is best in a range of frequencies near  $f_{free}$  (filled arrow). Similarly, assumption (3), though not far from reality over the whole frequency range (Fig. 3 top), is best fulfilled only near  $f_{free}$  (Fig. 3 bottom).

The reduction of  $S_v$  with frequency during hopping in place at maximum height has been predicted by Blickhan [2] using the same spring-mass system.

Why does the energy expenditure during running at slow-to-moderate speeds reach a minimum near  $f_{\text{free}}$ ?

Despite the close agreement between the experimental results and the linear spring-mass model, running is not a purely elastic phenomenon; energy must be added by the muscles each stretch-shorten cycle to compensate for energy losses due to damping. The resulting muscle work loop can simulate a stress-strain loop obtained during the stretch and release of a passive spring. This does not mean that elasticity plays no role in the muscle work loop: the energy added will be less the greater the elastic recovery. In a force-driven oscillator, the frequency requiring the minimum energy to maintain oscillation is called the resonant frequency of the system. The present results suggest that, below 11 km h<sup>-1</sup>,  $f_{\text{free}}$  is equal to the resonant frequency since the energy expenditure is minimal and the muscular efficiency is maximal (Fig. 2). Furthermore, the difference between  $f_{sist}$  and  $f_{step}$  is minimum near  $f_{\text{free}}$  (Fig. 3).

It was hitherto believed that stiffness could be adjusted to step and hopping frequency by controlling muscle activation [2, 12]. In this case it would not be appropriate to define one resonant frequency. In fact, many resonant frequencies would exist according to the degree of muscle stiffening. However, contrary to this line of thought, this study shows that vertical stiffness is not adjusted to all step frequencies by muscle control. As illustrated in Fig. 3, a change in stiffness is often not sufficient to match  $f_{sist}$  to  $f_{step}$  at step frequencies different from  $f_{free}$ . When  $f_{\text{step}}$  is forced to increase above  $f_{\text{free}}$ , the stiffness of the system increases in an attempt to match the new frequency, but the match is lost and energy expenditure increases despite a reduction in mechanical work. When  $f_{\text{step}}$  is forced to decrease below  $f_{\text{free}}$ , the stiffness of the system decreases, but again the match is lost; in this case, however, the mechanical work increases with the consequence that the increase in energy expenditure is greater. A close match between frequency of the system and  $f_{\text{step}}$  seems to occur on the average only at one frequency (2.6-2.8 Hz). In addition, the experiments show that energy expenditure  $(VO_2)$  is minimum just at this frequency which coincides with the  $f_{\text{free}}$  (arrows in Fig. 3). These findings lead us to the conclusion that, of all the possible frequencies obtained by adjusting the stiffness of the bouncing system, only one, the resonant step frequency, allows the best recovery of mechanical energy.

It has been suggested that energy expenditure during running is due to the cost of generating force, not due to the work done; if the foot-ground contact time is made shorter, faster fibres would be used leading to an higher rate of energy consumption [1, 16]. The same argument has been used to explain the preferred hopping and running frequencies in humans [12]. The present experiments provide a test for this hypothesis. Frequencies higher than  $f_{\text{free}}$  should involve a greater cost of generating force due to the shorter time of contact, but require less mechanical work; and vice versa for frequencies lower than  $f_{\text{free}}$ . The finding that during running at 5.3 and 8.0 km h<sup>-1</sup> the energy expenditure measured at 0.9  $f_{\text{free}}$  is greater than the energy expenditure at 1.1  $f_{\text{free}}$  shows that an increase in work leads to an increase in energy expenditure despite a longer contact time.

In conclusion, at running speeds up to about 11 km h<sup>-1</sup>, where a  $f_{step}$  shift from  $f_{min}$  has a small effect on  $\dot{W}_{tot}$  (dotted lines in Fig. 1 bottom), tuning  $f_{free}$  to  $f_{sist}$  leads to a lower energy cost than forcing  $f_{free}$  to approach  $f_{min}$ . At higher speeds the  $f_{free}$  becomes progressively lower than  $f_{sist}$  to contain the increase in  $\dot{W}_{tot}$  [8].

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