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RESEARCH ARTICLE

Running, hopping and trotting: tuning step frequency to the resonant frequency of the bouncing system favors larger animals

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ABSTRACT

A long-lasting challenge in comparative physiology is to understand why the efficiency of the mechanical work done to maintain locomotion increases with body mass. It has been suggested that this is due to a more elastic step in larger animals. Here, we show in running, hopping and trotting animals, and in human running during growth, that the resonant frequency of the bouncing system decreases with increasing body mass and is, surprisingly, independent of species or gait. Step frequency roughly equals the resonant frequency in trotting and running, whereas it is about half the resonant frequency in hopping. The energy loss by elastic hysteresis during loading and unloading the bouncing system from its equilibrium position decreases with increasing body mass. Similarity to a symmetrical bounce increases with increasing body mass and, for a given body mass, seems to be maximal in hopping, intermediate in trotting and minimal in running. We conclude that: (1) tuning step frequency to the resonant frequency of the bouncing system coincides with a lower hysteresis loss in larger, more-compliant animals; (2) the mechanism of gait per se affects similarity with a symmetrical bounce, independent of hysteresis; and (3) the greater efficiency in larger animals may be due, at least in part, to a lower hysteresis loss.

KEY WORDS: Locomotion, Bouncing gaits, Efficiency, Elasticity, Hysteresis, Symmetry

INTRODUCTION

The efficiency of the mechanical work done to maintain the motion of the body in running, hopping and trotting increases with body mass in very different animal species (Heglund et al., 1982). In some cases, the efficiency exceeds the efficiency of the contractile machinery of muscle. This finding was explained by hypothesizing that some mechanical energy is conserved by elastic storage. In fact, simple spring-mass models predict several aspects of the mechanics of the bouncing step (Blickhan, 1989; McMahon and Cheng, 1990; Farley et al., 1993; Seyfarth et al., 2002). It remains to be explained why the efficiency of mechanical work production increases with body mass and if this increase is actually due to a greater elastic storage and recovery in larger animals.

To this aim, we analyze in this study the motion of the center of mass of the body in animals and humans of different body mass.

This motion results from the interaction of multiple body segments and a complete description of the whole system should clarify the link between motion of the center of mass and motion of the different body segments. However, this is not the goal of this study. Here, we merely describe some characteristics of the motion of the center of mass of the body as a function of body mass without trying to explain these characteristics by detailed mechanisms that may cause them.

We provide evidence of a more elastic step in larger animals by measuring the vertical displacement, velocity and acceleration of the center of mass of the body during its bounce on the ground. We measured in running, hopping and trotting animals of different size and in human running at different ages: (1) the resonant frequency of the bouncing system; (2) its relationship with the freely chosen step frequency; (3) the elastic hysteresis loss during the loading–unloading cycle of the resonant system; and (4) the similarity of the bounce to that of a symmetrical system.

RESULTS

Mass-specific vertical stiffness and resonant frequency

Fig. 1A shows that the mass-specific vertical stiffness k/M_b (where M_b is the mass of the body) and as a consequence, the resonant frequency of the bouncing system $f_s=(k/M_b)^{0.5}/2\pi$, decrease with increasing body mass in hopping, trotting, running animals and humans of different age according to a power function evidenced by the linear fit obtained in the log–log representation of the experimental data (inset of Fig. 1A):

$$k/M_b = 2137 M_b^{-0.42},\qquad(1)$$

where k/M_b unit is s^{-2} and M_b unit is kg ($R=0.933$; $P<0.00001$).

When the mass-specific vertical stiffness is measured as $(\pi/t_{ce})^2$ on the assumption that the effective contact time t_{ce}, i.e. the time during which the vertical force exceeds body weight, equals half-period of the resonant frequency of the oscillating system, i.e. that:

$$f_s = (k/M_b)^{0.5}/2\pi = 1/(2t_{ce}),\qquad(2)$$

a very similar equation is obtained ($R=0.927$; $P<0.00001$):

$$(\pi/t_{ce})^2 = 2121 M_b^{-0.42}.\qquad(3)$$

Average values of k/M_b and f_s are given in Tables 1,2.

Resonant frequency and step frequency

The step frequency f_{step} is plotted as a function of the resonant frequency of the bouncing system f_s in Fig. 2. The continuous line is a least-square fit of the running and trotting data points ($f_{step}= -0.434+1.073 f_s$, $R=0.983$, $P<0.00001$, f unit is s^{-1}); the dashed line is the identity line. It can be seen that step frequency f_{step} roughly

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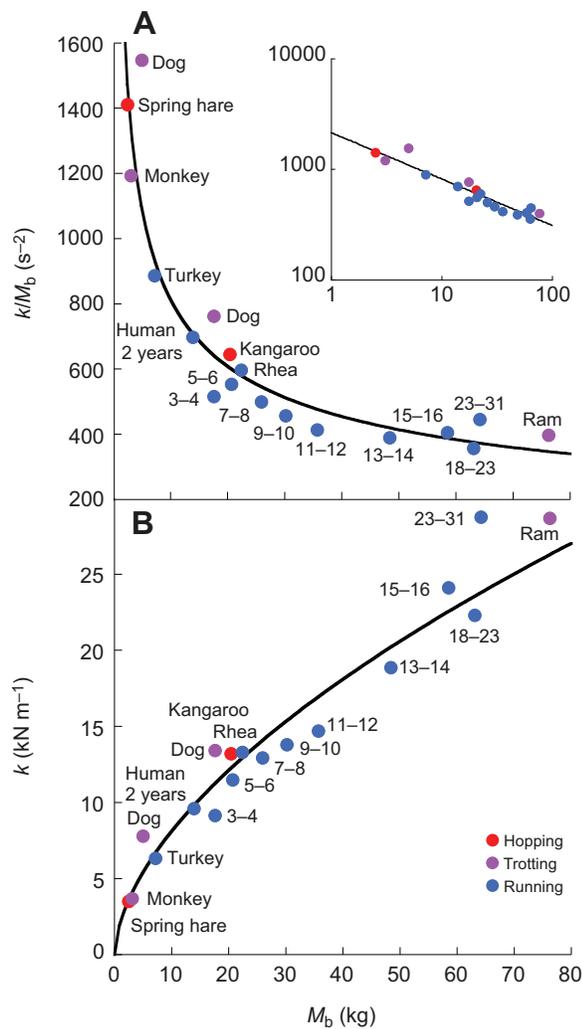*Author for correspondence (giovanni.cavagna@unimi.it)

Fig. 1. Resonant frequency of the bouncing system decreases with body mass. The mass-specific vertical stiffness (k/M_b, A) and the vertical stiffness (k, B) are plotted as a function of the body mass M_b of hopping, trotting, running animals of different species and running humans at different ages. The mass-specific vertical stiffness and as consequence the resonant frequency of the bouncing system $f_s=(k/M_b)^{0.5}/(2\pi)$, decrease with increasing body mass with the same power function, as evidenced by the linear log–log representations (inset), independent of the different species and gaits. See also data in Tables 1,2.

equals the resonant frequency of the bouncing system f_s in running and trotting, whereas it is about half the resonant frequency in hopping. Average values of f_{step} are given in Tables 1,2.

Hysteresis

Fig. 3A shows the relationship between normalized vertical force exerted on the ground, $F_v(t)/M_b g$ (where M_b is the mass of the body and g the acceleration due to gravity) and normalized vertical displacement of the center of mass $S_v(t)/S_{v,tot}$ during hopping, trotting and running steps of larger (left) and smaller (right) animals. Fig. 3B shows the same relationship in running humans of different ages.

Hysteresis H_{ce} is measured as the difference between the areas under the curves during loading and unloading the bouncing system in the lower half of its vertical oscillation, S_{ce}. This difference is expressed here as a percentage of the energy input, i.e.

$$H_{ce}(\%) = \left[\frac{\left(\left| \int F_v(t) dS_{ce,down}(t) \right| - \left| \int F_v(t) dS_{ce,up}(t) \right| \right)}{\left| \int F_v(t) dS_{ce,down}(t) \right|} \right] 100,$$

(4)

where $S_{ce}(t)$ is the instantaneous vertical displacement of the center of mass below its equilibrium position when the vertical force equals body weight.

Since in a regular step the total negative and positive work done against gravity must be equal when moving on the level, i.e. $\int F_v(t) dS_{v,down}(t) = \int F_v(t) dS_{v,up}(t)$, an energy loss during S_{ce} must be compensated by an energy input during $S_{ae}=S_v-S_{ce}$ by active muscular contraction. This is evidenced in the tracings of Fig. 3 by the arrows showing that the F_v-S_v relation is counterclockwise (hysteresis energy loss) during S_{ce}, when F_v is greater than M_b, and clockwise (energy added by active muscular contraction) during S_{ae}, when F_v is lower than M_b.

Average values of percentage H_{ce} are given in Tables 1,2 and plotted in Fig. 4A,B as a function of M_b. It can be seen that the hysteresis decreases with increasing M_b in animals of different species and gaits and in running humans during growth with a power function ($H_{ce}=26.638\ M_b^{-0.52}$, $R=0.873$, $P=0.0046$, in animals; $H_{ce}=1364\ M_b^{-1.34}$, $R=0.911$, $P=0.0002$, in humans).

Similarity to a symmetrical bounce

Average values of the percentage similarity to a symmetrical bounce are given in Tables 1,2 and plotted in Fig. 5 for hopping, running, trotting animals and human running during growth as a function of body mass. It can be seen that similarity to a symmetrical bounce increases with M_b and that, for a given M_b, it seems to be maximal in hopping, intermediate in trotting and minimal in running.

Table 1. Step characteristics of trotting and running animals

	Hopping		Running		Trotting			
	Kangaroo	Spring hare	Rhea	Turkey	Large dog	Small dog	Ram	Monkey
N	31	26	13	12	12	16	12	14
M_b (kg)	20.4±0.1	2.5±0.03	22.4±0.1	7.2±0.1	17.6±0.04	5.0±0.04	76.2±3.3	3.1±0.05
$k/M_b=A_{v,mx,up}/S_{ce}$ (s^{-2})	644.9±30.6	1411.3±96.5	596.7±74.9	886.7±72.9	762.1±52.5	1547.4±94.6	397.2±52.9	1193.0±118.8
$f_s=(A_{v,mx,up}/S_{ce})^{0.5}/2\pi$ (Hz)	4.01±0.09	5.90±0.20	3.82±0.21	4.70±0.19	4.36±0.16	6.21±0.20	3.10±0.20	5.41±0.27
f_{step} (Hz)	2.19±0.03	3.04±0.04	3.63±0.12	4.44±0.13	4.31±0.12	6.18±0.17	3.31±0.19	5.21±0.23
Hysteresis energy loss, H_{ce} (%)	7.4±3.0	17.3±3.3	9.4±4.1(n=12)	9.9±4.8(n=9)	6.7±2.8	9.9±1.4	1.6±4.0	10.8±3.7(n=13)
Similarity to an elastic bounce (%)	95.79±1.28	91.48±1.31	84.79±1.40	76.92±1.60	89.53±0.78	83.64±1.33	97.02±2.89	90.34±2.56

Values are means±s.e.m. of data measured over the whole speed range of locomotion obtained in each animal. Data from Cavagna et al. (1977).

Table 2. Step characteristics of running humans

	Age (years)									
	2	3–4	5–6	7–8	9–10	11–12	13–14	15–16	18–23*	23–31
N	81	190	183	222	215	244	264	299	229	308
M_b (kg)	13.9±0.2	17.6±0.1	20.7±0.1	25.9±0.2	30.2±0.2	35.7±0.2	48.4±0.5	58.5±0.5	63.1±0.5	64.2±0.4
$k/M_b = A_{v,mx,up}/S_{ce}$ (s^{-2})	697.1±16.9	515.7±8.8	553.3±9.9	499.7±9.6	456.9±12.4	413.9±11.4	389.4±9.6	405.3±10.3	356.8±8.4	445.5±9.2
$f_s = (A_{v,mx,up}/S_{ce})^{0.5}/2\pi$ (Hz)	4.18±0.05	3.59±0.03	3.71±0.04	3.52±0.03	3.34±0.04	3.15±0.05	3.08±0.04	3.13±0.04	2.96±0.03	3.31±0.03
f_{step} (Hz)	3.85±0.04	3.56±0.03	3.49±0.03	3.25±0.03	3.01±0.03	2.91±0.03	2.78±0.03	2.87±0.02	2.65±0.02	2.95±0.03
Hysteresis energy loss, H_{ce} (%)	47.7±5.1 (n=5)	32.4±1.3 (n=6)	13.0±3.2 (n=6)	16.4±3.3 (n=6)	17.7±4.4 (n=6)	15.4±3.8 (n=6)	8.7±4.6 (n=6)	1.3±6.1 (n=6)	6.9±3.8 (n=8)	11.8±3.8 (n=6)
Similarity to an elastic bounce (%)	67.26±1.27 (n=45)	78.00±1.06 (n=85)	81.65±0.71 (n=83)	83.72±0.73 (n=78)	79.80±0.95 (n=72)	85.47±0.63 (n=78)	88.45±0.87 (n=95)	88.40±0.75 (n=93)	87.98±0.56 (n=120)	85.75±0.45 (n=107)

Values are means±s.e.m. Mass-specific vertical stiffness, step frequency and natural frequency of the bouncing system were measured by averaging N runs obtained over the whole speed range in all subjects; hysteresis was measured on n subjects during one run at a speed approaching their average speed; similarity to an elastic bounce was measured on all runs of the subjects studied by Schepens et al. (1998) and Cavagna et al. (2008) over a speed range less than 11 km h^{-1}.
*Data from Cavagna et al. (2008).

DISCUSSION

Vertical stiffness and resonant frequency

Multiplying the mass-specific vertical stiffness k/M_b (Fig. 1A) by the body mass M_b, one obtains the stiffness k that is plotted in Fig. 1B as a function of M_b. Stiffness increases with M_b according to the equation:

$$k = 2.146 M_b^{0.58}, \qquad (5)$$

where k unit is kN m^{-1} and M_b unit is kg (R=0.970; P<0.00001).

A similar relationship between vertical stiffness and M_b in hopping and trotting animals of different size was found by Farley et al. (1993) who measured the 'effective vertical stiffness' as $F_{v,mx}/S_{vc}$, where S_{vc} is the total vertical displacement of the center of mass during contact, instead of $F_{v,mx}/S_{ce}$, where S_{ce} is the amplitude of the vertical oscillation, as in the present study. They found that

Fig. 2. Step frequency is tuned to the resonant frequency of the bouncing system. The freely chosen step frequency f_{step} is plotted as a function of the resonant frequency of the bouncing system $f_s = (k/M_b)^{0.5}/2\pi$. The continuous line is a least-square fit of the running and trotting data points; the interrupted line is the identity line. The orange filled circles indicate the step frequency in hopping multiplied by 2, other symbols as in Fig. 1. Note that $f_{step} \approx f_s$ in trotting and running and $f_{step} \approx f_s/2$ in hopping. See also data in Tables 1,2.

$F_{v,mx}/S_{vc}$ scales with body mass as $M_b^{0.61}$. The present data, showing that $k = F_{v,mx}/S_{ce}$ scales as $M_b^{0.58}$, are in reasonable agreement with their finding. In fact, using S_{vc} instead of S_{ce} does not affect appreciably scaling with M_b since we found, in the present study, that $S_{ce}/S_{vc} \approx 0.59$ independent of M_b and gait (S_{ce}=0.001+0.588 $S_{v,c}$, R=0.951, where S unit is m).

Neglecting the forward velocity changes taking place during the step, the average forward speed is $V_f = L_{step} f_{step} \approx L_{ce}/t_{ce}$, where L_{step} is the step length, f_{step} is the step frequency and L_{ce} is the forward displacement of the center of mass during t_{ce}. Substituting $1/t_{ce} = f_{step} L_{step}/L_{ce}$ into Eqn 2 one obtains:

$$k/M_b = (2\pi f_s)^2 \approx (\pi f_{step} L_{step}/L_{ce})^2. \qquad (6)$$

Eqn 6 shows that when the bounce exhibits an on-/off-ground symmetry, i.e. when L_{step}=2L_{ce} as in trotting, the step frequency equals the resonant frequency of the bouncing system $f_s = (k/M_b)^{0.5}/2\pi$. When, on the contrary L_{step}>2L_{ce}, as in hopping, two possibilities exist: (1) f_s must increase for a given step frequency f_{step}, or (2) the step frequency f_{step} must decrease to attain the same resonant frequency f_s. As shown in Fig. 1A, the second possibility is what actually takes place: the same resonant frequency of the bouncing system f_s is conserved in animals of equal mass. For example, hopping kangaroos and running rhea of similar mass exhibit a similar mass-specific vertical stiffness, and as a consequence a similar resonant frequency f_s, by compensating a different L_{step}/L_{ce} (3.6 in hopping kangaroo and 2.1 in running rhea) with a different f_{step} (2.2 Hz in hopping kangaroo and 3.6 Hz in running rhea).

The finding that k/M_b equals $(\pi/t_{ce})^2$ indicates that in the range of body mass considered in this study the bouncing motion approaches that of a harmonic oscillator in animals as in humans (see Eqn 2). Note, however, that the mass-specific vertical stiffness, as defined in this study, is not necessarily a measure of purely elastic properties as in a harmonic motion. The lengthening of muscle-tendon units that, on average, must take place as force increases and their shortening as force decreases, must in part be attributable to stretch and recoil of elastic elements but also to relative sliding of actin and myosin filaments (i.e. to the contractile elements doing negative followed by positive work). Furthermore, the vertical oscillation of the center of mass of the body, as measured in this study, results from the action of a large number of limb and trunk muscles that produce, absorb and
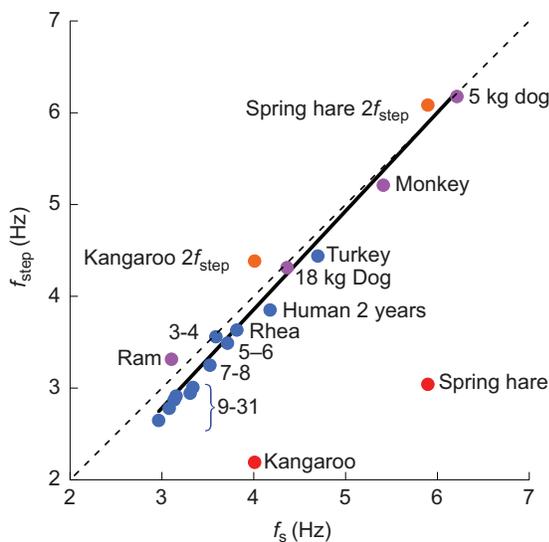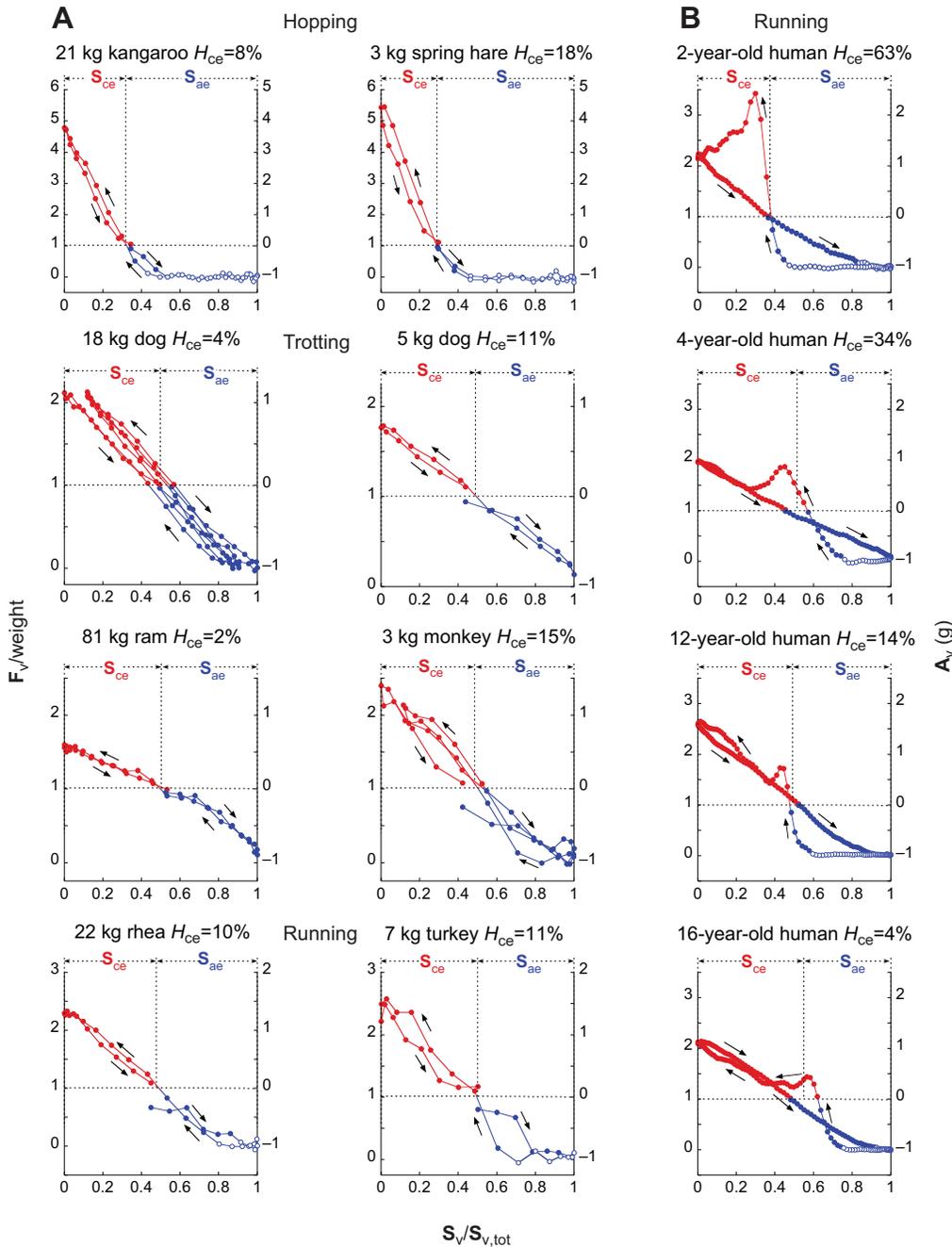
Fig. 3. Hysteresis energy loss during the lower half of the vertical oscillation of the center of mass and recovery during the upper half. Vertical force exerted on the ground plotted as a function of the vertical displacement of the center of mass of the body. Ordinates and abscissas are normalized dividing the vertical force $\mathbf{F}_v(t)$ by the body weight and the vertical displacement $\mathbf{S}_v(t)$ by the total vertical displacement. (A) Hopping, trotting and running: left column, larger animals, right column, smaller animals. (B) Human running during growth from 2 years (top) to 16 years (bottom). The vertical displacement on the abscissa is divided in $\mathbf{S}_{ce}$, force greater than body weight ($\mathbf{A}_v>0$, lower half of the oscillation, red) and $\mathbf{S}_{ae}$, force lower than body weight ($\mathbf{A}_v<0$, upper half of the oscillation, blue with open circles, indicating the aerial phase when present). The area between the loading–unloading curves during $\mathbf{S}_{ce}$ represents the mechanical energy loss because of hysteresis, H_{ce} (counterclockwise $\mathbf{F}_v$–$\mathbf{S}_v$ relation as indicated by the arrows) that must be recovered by active muscular contraction during $\mathbf{S}_{ae}$ in a perfect regular step on level locomotion (clockwise $\mathbf{F}_v$–$\mathbf{S}_v$ relation). Tracings refer to the vertical oscillation of the center of mass of the body recorded during a step except for the 18 kg trotting dog (three steps) and the 3 kg trotting monkey (two steps). It can be seen that hysteresis loss during the lower half of the oscillation (H_{ce}, red) is greater in smaller animals (A) and decreases with age during human running (B) mainly due to a decrease of the impact deceleration peak following collision of the foot on the ground, which is absent in animals. Points are taken every ≈8 ms in animals and every 2 ms in humans.

redistribute energy within the limbs and body during the bounce. The physiological meaning of the apparent general relationship found between resonant frequency of the bouncing system $f_s=(k/M_b)^{0.5}/2\pi=1/(2t_{ce})$ and body mass M_b, similar in different species and gaits (Fig. 1A), still remains to be explained.

Resonant frequency and step frequency

It has been shown that in human running at speeds lower than ~13 km h^{-1} efficiency is increased by tuning step frequency f_{step} with the resonant frequency of the bouncing system f_s even if this requires a mechanical power to maintain locomotion larger than necessary (Cavagna et al., 1997). Fig. 2 suggests that the same strategy also applies to different gaits in animals of different species and body mass: it can be seen that $f_{step}≈f_s$ in trotting and running, whereas $f_{step}≈f_s/2$ in hopping.

Step frequency f_{step} is defined in this study as the reciprocal of the time interval between peaks or valleys of the vertical displacement of the center of mass of the body. Stride frequency f_{stride}, however, is classically defined as the reciprocal of the time interval between ground contacts of the same limb. Two steps, i.e. two cycles of $\mathbf{S}_v(t)$, take place during one stride in running and trotting whereas one step, i.e. one cycle of $\mathbf{S}_v(t)$, takes place during one stride in hopping thanks to a greater vertical acceleration and aerial phase required to reset simultaneously both limbs. In other words, the amplitude of the oscillation $\mathbf{S}_{ce}$ is greater in hopping than in trotting and running, but the resonant frequency $f_s=1/(2t_{ce})$ is similar for a given M_b (Fig. 1A). It follows that in trotting and running, $f_{step}≈2f_{stride}≈f_s$, whereas in hopping, $f_{step}≈f_{stride}≈f_s/2$, but in both cases, the duration of the lower half of the vertical oscillation of the center of mass t_{ce} is tuned to the resonant half period of the oscillating system.
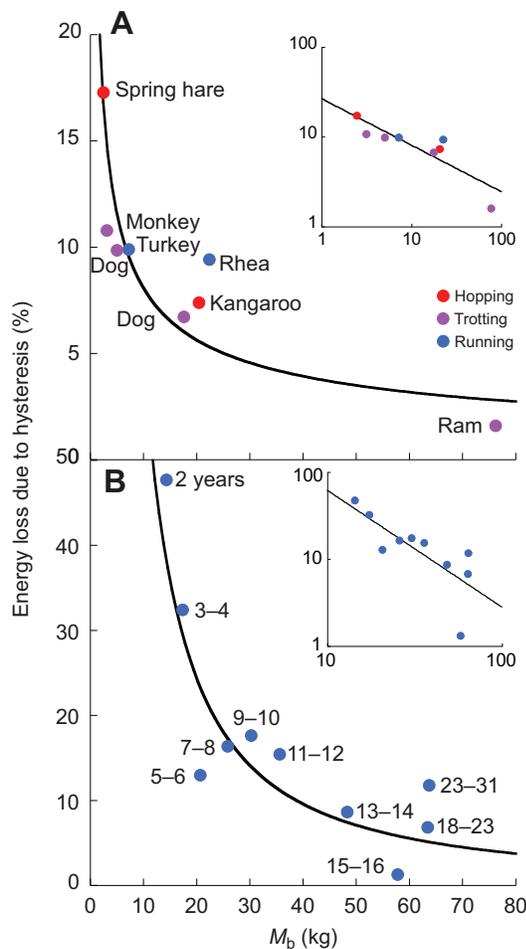
Fig. 4. Hysteresis energy loss during the lower half of the vertical oscillation of the center of mass decreases with body mass. The energy loss by hysteresis H_{ce} during the half period of the resonant oscillating system, when the vertical force loading muscle-tendon units is greater than body weight, is plotted as a function of body mass during hopping, trotting and running animals (A) and during running in humans at different ages (B). It can be seen that hysteresis decreases as the mass increases with a power function evidenced by the linear log–log representations (insets). Data are shown in Tables 1,2.

Hysteresis

In this study, deviation from a fully elastic bounce is thought to be due, at least in part, to the degradation into heat of some of the mechanical energy absorbed by body structures when the body decelerates downward and forwards (negative work). It may be pointed out that since positive and negative work done over the entire stance period must be equal in level locomotion at a constant step average speed, then there must be no hysteresis. So, how do we find different hysteresis in different animals? In a vertical spring-mass system, the oscillation takes place below and above a position of static equilibrium where the system is loaded with a force equal to body weight. In a frictionless system, the energy acquired when the mass falls below the equilibrium position (negative work) would be stored and released without losses during the lift to the equilibrium position (positive work) and hysteresis would be nil. However, if some energy were lost during negative work, less energy would be available during positive work resulting in a hysteresis loop in the force–length relation of the lower half of the oscillation. This view is in contrast with the idea that during the bouncing step the lower half of the oscillation takes place after the aerial phase during the whole
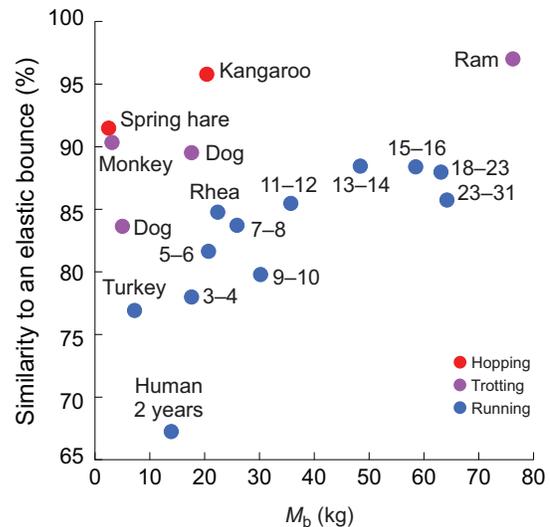

Fig. 5. Similarity to a symmetrical bounce as a function of body mass. It can be seen that, on average, similarity seems to increase with body mass, and, for a given body mass, seems to be maximal in hopping, intermediate in trotting and minimal in running. Data are shown in Tables 1,2.

stance phase of the step. However, as pointed out in several previous studies (e.g. McMahon and Cheng, 1990), the aerial phase may not occur at all in bouncing gaits (e.g. trotting ram in Fig. 6). With or without an aerial phase, the lower half of the vertical oscillation of the center of mass takes place during stance below a vertical force equal to body weight (Blickhan, 1989).

As described in the Results section, the hysteresis energy loss in the lower half of the vertical oscillation of the center of mass (counterclockwise $\mathbf{F_v}–\mathbf{S_v}$ relation in Fig. 3, red), must be compensated by an energy input in the upper half of the oscillation (clockwise $\mathbf{F_v}–\mathbf{S_v}$ relation in Fig. 3, blue) when running on the level. This compensation, being carried out by active muscular contraction results in a lower similarity to a symmetrical bounce: the maximal vertical velocity attained during the lift is lower than that attained during the fall and the push duration is greater than brake duration. Assuming constant muscle activation, both discrepancies could be a consequence of the lower force that muscle can exert during shortening relative to that it can exert during forcible stretching according to the force–velocity relation.

The present results suggest that the greater efficiency found in larger animals (Heglund et al., 1982) may be due, at least in part, to their lower energy loss by hysteresis during the bounce of the body (Fig. 4). A possible explanation for the lower hysteresis found in larger animals may be given by anatomical studies showing that in the stretch-shortening cycle of muscle-tendon units the role of the more elastic tendons (Ker, 1981; Alexander, 2002) relative to that of the less-elastic muscles is greater in larger animals (Maloiy et al., 1979; Alexander et al., 1981; Biewener et al., 1981; Pollock and Shadwick, 1994; Bennett and Taylor, 1995; McGowan et al., 2008). It must be pointed out, however, that the data of the present study are based on force and displacement of the center of mass of the whole body, not on the underlying action of muscle-tendon units. As mentioned above, the present results do not refer to muscle-tendon units of specific muscles or muscle groups, but rather to the final effect of a complex ensemble of muscle groups with different activation patterns and tendon lengths.

During human running, the decrease in hysteresis with M_b (Fig. 3B) is mainly due to a decrease of the energy loss caused by
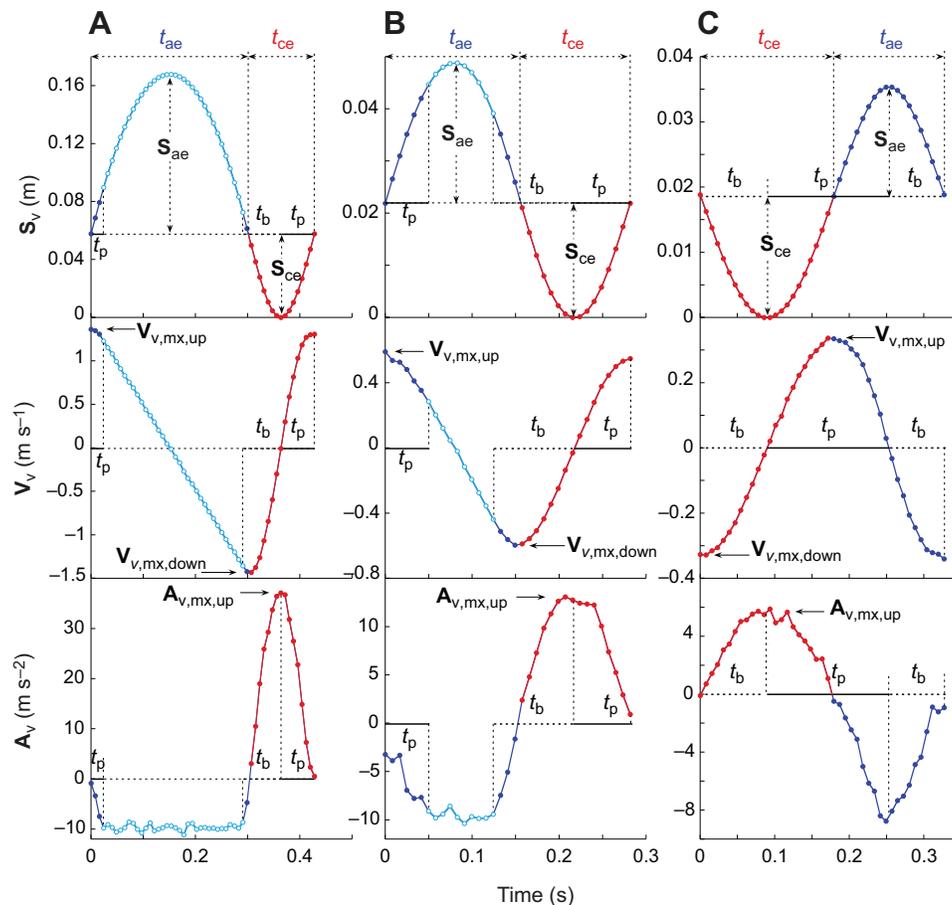
Fig. 6. Examples of experimental gait recordings used. Vertical displacement S_v (top row), velocity V_v (middle row) and acceleration A_v (bottom row) of the center of mass of the body during one step of a 21 kg hopping kangaroo (A), a 22 kg running rhea (B) and an 81 kg trotting ram (C). The step is divided into effective aerial time t_{ae}, with vertical displacement S_{ae}, when the vertical force on the ground is less than body weight (blue with open circles indicating the aerial phase when present) and effective contact time t_{ce}, with vertical displacement S_{ce}, when the vertical force is greater than body weight (red). Note that t_{ce} represents half of the resonant period and S_{ce} represents the amplitude of the resonant oscillation of the bouncing system. The maximal upward velocity $V_{v,mx,up}$, downward velocity $V_{v,mx,down}$ and upward vertical acceleration $A_{v,mx,up}$ are indicated. The horizontal black lines represent the push duration (t_p, continuous) and the brake duration (t_b, interrupted). Graphs of hopping kangaroo, trotting ram and running rhea refer to the same steps illustrated in Fig. 3.

the deceleration peak following the impact of the foot on the ground (Legramandi et al., 2013). The present results, however, show that a decrease in hysteresis loss with M_b also takes place in the hopping spring hare and kangaroo, trotting dog, monkey and ram, and running turkey and rhea, even if no impact peak is observed after landing in all the steps we recorded (Fig. 3A).

Similarity to a symmetrical bounce

Fig. 5 shows that similarity to a symmetrical bounce increases with M_b, but also that, for a given M_b, it seems to be maximal in hopping, intermediate in trotting and minimal in running. This finding suggests that gait, in addition to hysteresis, affects similarity to an ideal symmetrical bounce. For example, similarity to a symmetrical bounce is greater in the spring hare than in turkeys (Fig. 5), despite a greater hysteresis in the spring hare (Fig. 4). In fact, asymmetrical lever arms in the lower limb of running humans were found to cause a divergence from the purely symmetrical model, resulting in a landing–take-off asymmetry, i.e. in a lower similarity to a symmetrical bounce (Maykranz and Seyfarth, 2014). The present results suggest that the hopping gait is better than the running gait: kangaroos exploit the same resonant frequency better than rhea (Fig. 1A and Fig. 5). This is consistent with the finding that the efficiency of the transformation of chemical energy into external mechanical work is greater in hopping kangaroos and the spring hare than in running turkeys and rhea (Cavagna et al., 1977).

MATERIALS AND METHODS

The results described in this study were obtained by analyzing records of vertical velocity changes during running, hopping and trotting animals (Cavagna et al., 1977) and running humans (Schepens et al., 1998; Cavagna

et al., 2008) during one or more steps made on a force platform sensitive to the force exerted by the feet on its surface. The characteristics of the platform and the principle of the method used to process the platform's signals are described in detail in previous studies (Schepens et al., 1998; Cavagna et al., 2008). The section below briefly describes the experimental procedure used previously. The following sections describe the additional measurements made in the present study.

Subjects

The mass of the body prior to each run experiment, the mass-specific vertical stiffness, the resonant frequency of the bouncing system, the step frequency, the hysteresis and the similarity to a symmetrical bounce were measured from records obtained by Cavagna et al. (1977) on two kangaroos (*Megaleia rufa*) and one spring hare (*Pedetes cafer*) during hopping; on two wild turkeys (*Meleagris gallopavo*) and one rhea (*Rhea americana*) during running; on two dogs (*Canis familiaris*), one monkey (*Macaca speciosa*) and two rams (*Ovis musimon*) during trotting (Table 1).

For human running, we used records obtained by Schepens et al. (1998) during growth and by Cavagna et al. (2008) on young adults (Table 2).

In this study, the effect of M_b on the variables mentioned above was analyzed regardless of the effect of the speed of locomotion. The average values reported in Table 1 represent the mean of data measured over the whole speed range of locomotion obtained in each animal. In Table 2, step frequency and natural frequency of the bouncing system were measured by averaging N runs obtained over the whole speed range in all subjects; hysteresis was measured on n subjects during one run at a speed approaching their average speed; similarity to an elastic bounce was measured on all runs of the subjects studied by Legramandi et al. (2013) and Cavagna et al. (2008) over a speed range less than 11 km h^{-1} where the freely chosen step frequency equals the resonant frequency of the system (on-/off-ground symmetrical rebound) (Schepens et al., 1998) and the deviation from similarity to a symmetrical bounce (landing–take-off asymmetry) is largest (Cavagna, 2009).

Vertical velocity, displacement and acceleration of the center of mass

Records of the vertical velocity changes of the center of mass were obtained in previous studies by integrating the force platform signals (Cavagna et al., 1977, 2008; Schepens et al., 1998). These records are analyzed in this study by means of custom LabView software (v7.1; National Instruments, Austin, TX, USA) to measure the instantaneous vertical velocity $V_v(t)$, the vertical displacement of the center of mass $S_v(t)$, obtained by integration of the vertical velocity [LabView, Integral $x(t)$.vi, trapezoidal rule] and the vertical acceleration $A_v(t)$ obtained by differentiation of $V_v(t)$ [LabView, Derivative $x(t)$.vi] (Fig. 6). When $V_v(t)$ is at a maximum or at a minimum, the vertical acceleration is nil and the vertical force equals body weight. The vertical displacement of the center of mass taking place below the points where the vertical force equals body weight was measured both during the downward deceleration $S_{ce,down}$ (i.e. during the brake t_b, see Fig. 6) and during the upward acceleration, $S_{ce,up}$ (i.e. during the push t_p, see Fig. 6). In this study, the amplitude of the oscillation of the center of mass taking place during the fraction of the contact period in which the acceleration is above zero was taken as their average $S_{ce}=(S_{ce,up}+S_{ce,down})/2$.

Vertical stiffness, resonant frequency and step frequency

The mass-specific vertical stiffness, k/M_b, has been measured as the ratio between the maximal upward acceleration, $A_{v,mx,up}$, and the vertical displacement of the center of mass from its equilibrium position (vertical force=body weight) to the lowest point attained, S_{ce}, during animal locomotion (Cavagna et al., 1977) and in the experiments of human running made by Cavagna et al. (2008), whereas it was calculated from the slope of the A_v–S_{ce} relation by Schepens et al. (1998). $A_{v,mx,up}$ was measured as the value of vertical acceleration at the lowest point attained by the vertical displacement of the center of mass. The resonant frequency of the bouncing system was calculated as $f_s=(A_{v,mx,up}/S_{ce})^{0.5}/2\pi$.

Resonant frequency of the bouncing system was also calculated as $f_s{}'=1/(2t_{ce})$ on the assumption that $A_{v,mx,up}/S_{ce}=(\pi/t_{ce})^2$, i.e. that the duration of the lower half of the vertical oscillation of the center of mass, t_{ce}, measured when the system is loaded by a force greater than body weight, corresponds to half period of the resonant oscillation of the bouncing system. Step frequency was calculated as the reciprocal of the time interval measured between repeating peaks or valleys of $S_v(t)$.

Hysteresis

The hysteresis area of the stretch–shortening cycle H_{ce} was measured as the difference between the areas under the curves obtained by plotting the vertical force exerted on the ground versus the vertical displacement of the center of mass during the lower half of the vertical oscillation of the center of mass. As mentioned above, during this time interval, t_{ce}, the height of the center of mass shifts from its equilibrium position, when the vertical force on the ground F_v equals body weight, down to the maximal amplitude of the oscillation S_{ce} during loading, and vice versa during unloading.

Body structures are loaded beyond the equilibrium position by a combination of fore–aft breaking/propulsion forces F_f and vertical forces F_v. In this study, the forward component of the force loading the spring-mass system during the half period of the oscillating system t_{ce} was neglected because its contribution is small relative to that of the vertical component. In fact, half of the angle swept by the 'leg spring' is about 34 deg during the whole contact time t_c, independent of body mass and mechanisms of locomotion, and reduces to 21 deg during half of the resonant period of the oscillation t_{ce} because $t_{ce}/t_c=0.61$ (Farley et al., 1993, their fig. 4A and fig. 5). The projections of F_v and F_f on the line connecting the center of mass of the body with the point of contact on the ground, i.e. the projections on the 'leg spring', will then be $F_v{}^*=F_v\cos 21$ deg and $F_f{}^*=F_f \cos (90-21$ deg), respectively. The maximum value of F_f is attained during the brake after the beginning of t_{ce}, when F_v increases above body weight, resulting in a ratio $F_f/F_v=0.28$, as measured by averaging the data in Fig. 5 of Cavagna et al. (1977). It follows that the ratio between the components of F_f and F_v that are loading the spring will be: $F_f{}^*/F_v{}^* = F_f/F_v[\cos(90 - 21$ deg)/$\cos 21$ deg] $= F_f/F_v(0.36/0.93) = 0.28 \times 0.39 = 0.11$.

This is a maximum value because: (1) half of the angle swept by the spring is lower than 21 deg when the maximum of F_f is attained, and (2) the ratio F_f/F_v decreases to zero when the maximum value of F_v is attained, to increase again to $F_f{}^*/F_v{}^*=0.07$ when F_f reaches a maximum during the push before the end of t_{ce}. It is therefore reasonable to assume that loading and unloading of the spring mass system is sufficiently described by taking into account the vertical component of the ground reaction force only.

In a symmetrical bounce, the vertical position and acceleration at the beginning of the step would equal those at the end of the step. Whereas the upward and downward vertical displacements are assumed to be equal on level locomotion in the analysis of the force platform records, the vertical acceleration at the beginning and at the end of the step may differ due to the noise of the $A_v(t)$ records (Fig. 6). This results in a large error in the measure of the hysteresis loops. For this reason, hysteresis was measured only in the runs where the difference between initial and final acceleration in the steps recorded for the analysis was less than 33% of the maximal acceleration attained during the step. This condition was satisfied in all hopping runs and trotting dogs, but was not satisfied in one trotting run of the monkey, one run of the rhea and three runs of the turkeys (see n in Table 1). In order to improve the accuracy in the measure of the hysteresis loops (Fig. 3), all records obtained in animals by Cavagna et al. (1977) were linearly interpolated in 10 intervals between experimental points acquired every 8–9 ms (Fig. 3A). This procedure was not required for the records of Schepens et al. (1998) and Cavagna et al. (2008), which were acquired every 2 ms (Fig. 3B).

Similarity to a symmetrical bounce

Fig. 6 shows the vertical acceleration, velocity and displacement of the center of mass of the body during one step of a hopping kangaroo, a running rhea and a trotting ram. Brake duration, t_b, push duration, t_p, are indicated together with the maximal upward and downward velocities attained by the center of mass during the lift and the fall, $V_{v,mx,up}$ and $V_{v,mx,down}$, and with the times t_{ae} (blue) and t_{ce} (red) during which the vertical force exerted on the ground is less, respectively greater, than body weight.

In a previous paper (Legramandi et al., 2013), the similarity to a symmetrical bounce during human growth was assessed for each running step by the ratios between: (1) brake and push durations (t_b/t_p) and (2) maximal upward and downward vertical velocities attained by the center of mass during the rebound ($V_{v,mx,up}/V_{v,mx,down}$), both of which would attain unity in an ideal symmetrical bounce. Since both ratios change similarly with body mass (Legramandi et al., 2013), the percentage similarity to an elastic bounce was determined for simplicity in this study by their average, i.e. $[(t_b/t_p)+(V_{v,mx,up}/V_{v,mx,down})]50$ (Tables 1,2).

Competing interests
The authors declare no competing or financial interests.

Author contributions
G.A.C. conceived of the study, made literature search and wrote the paper. M.A.L. made the analysis of the data and helped in the final version of the MS. Both authors gave final approval for publication.

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