# The biomechanics of skipping gaits: a third locomotion paradigm? 

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#### Abstract

Skipping, a gait children display when they are about four- to five-years-old, is revealed to be more than a behavioural peculiarity. By means of metabolic and biomechanical measurements at several speeds, the relevance of skipping is shown to extend from links between bipedal and quadrupedal locomotion (namely galloping) to understanding why it could be a gait of choice in low-gravity conditions, and to some aspects of locomotion evolution (ground reaction forces of skipping seem to originate from pushing the walking gait to unnaturally high speeds). When the time-courses of mechanical energy and the horizontal ground reaction force are considered, a different locomotion paradigm emerges, enabling us to separate, among the bouncing gaits, the trot from the gallop (quadrupeds) and running from skipping (bipeds). The simultaneous use of pendulum-like and elastic mechanisms in skipping gaits, as shown by the energy curve analysis, helps us to understand the low cost of transport of galloping quadrupeds.


Keywords: skipping; gallop; locomotion; paradigm; biomechanics; energetics

## 1. INTRODUCTION

There are three, apparently unrelated, issues in human locomotion.

1. A walking horse can be imitated by two humans, one in front of the other, walking $75 \%$ of the cycle out-ofphase. Similarly, a horse trotting corresponds to two humans running $50 \%$ out-of-phase. As the gait repertoire for 'usual' locomotion is limited in humans to walking and running, how can they imitate a galloping horse?
2. The vertical ground reaction force of a single limb during walking displays a double-humped pattern, the trough between the two humps being deeper the faster the progression speed (Alexander \& Jayes 1980). While this is consistent with the inverted pendulum paradigm, one might wonder which gait results from resisting to switching to a run and allowing the centrifugal force to exceed gravity, with a consequent take-off at mid-stance.
3. What is a suitable, fast locomotion style on the moon for humans? Previous investigators (Margaria \& Cavagna 1964; Margaria 1976) noted that walking and running would be impaired in reduced gravity.
Skipping (S), a gait children display at about 4.5 years of age (mainly for behavioural purposes) and dismiss in adulthood, is the answer to the previous three questions. Particularly, astronauts from Apollo Missions tried many different gaits on the moon's surface and the most preferred one was skipping, as referred to in the postflight debriefing (transcriptions are available from NASA at www.hq.nasa.gov/office/pao/History/alsj/ a17/a17.sta8.html, .../a14/a14.trvstaf.html, and .../a15/a15.elbowtrv.html): 'Ed Mitchell of

Apollo 14 and Gene Cernan on Apollo 17 favoured a skipping stride in which they kept one foot always forward, let's say the left and, as they landed, hit with the trailing foot just a fraction of a second before the leading foot, pushing off with each foot as it hit and launching into the next glide'.
S can be unilateral (left or right depending on the last foot in contact with the ground prior to the flight), but is most commonly bilateral, with alternating right and left unilateral strides: the latter is shown schematically in figure 1, together with typical foot contact patterns for walking and running. S differs from pure walking because it has a significant flight phase, and from pure running because a double support period often occurs. When performed by adults, a sense of high speed is perceived. In addition, other bipeds such as some birds (Hayes \& Alexander 1983), jerboas (Fokin 1978) and lemurs for instance, use skipping (Alexander 1995, p. 115 (Sifaka hop), p. 117 (rook) and p. 206 (rook walk and hop)).

Apart from the examples in the previous paragraphs, most of which are derived from observational data, no systematic study on the biomechanics and energetics of S has appeared in the literature. As both humans and horses, it seems, are involved in the topics mentioned, I also decided to investigate the similarities between bipedal and quadrupedal locomotion paradigms.

## 2. MATERIALS AND METHODS

A total of five healthy men (see table 1 for personal data) were asked to bilaterally skip on a motor-driven treadmill (Woodway Ergo LG70, Germany) at different speeds (range $1.7-3.3 \mathrm{~m} \mathrm{~s}^{-1}$ ). Almost all the subjects got used to that gait within a few minutes of practise on the treadmill.


Figure 1. Typical contact patterns for walking, skipping and running in humans. The rhythmic transcription on the right shows the two-beat sequence of walking and running, and the three-beat pattern of skipping. $L$ and $R$ refer to left and right feet, respectively.

The motion pattern during the stride was measured by an optoelectronic device (ELITE motion analyser, BTS, Italy) consisting of four infrared cameras capable of detecting at 100 Hz the three-dimensional position of 18 reflective markers positioned on the subject's joints of interest (Minetti et al. 1993). Using for each body segment the anthropometric values (Dempster et al. 1959) of fractional mass, position of the centre of mass and radius of gyration, the coordinate data were processed by a custom program (Minetti \& Consani 1989) in order to calculate the mechanical external work $\left(W_{\mathrm{EXT}}\right)$ necessary to accelerate and lift the whole body centre of mass in the environment, and the internal work ( $W_{\text {INT }}$ ), needed to move the limbs with respect to the body centre of mass (Cavagna \& Kaneko 1977). From the same data, the stride frequency (where the stride period included left foot $(\mathrm{L}$ ), right foot ( R ) and the flight phase as shown in figure 1 ), the fraction of the stride pertaining to the single, double, and no contact phase, and the 'true' treadmill speed were obtained. 'Energy recovery', a parameter introduced by Cavagna et al. (1976) reflecting the ability of a multi-segment system to save mechanical energy through a pendulum-like mechanism, was calculated from the potential and kinetic energies of the body centre of mass.
Three of the subjects were also asked to run at the same speeds to compare the mechanics of the two gaits. In addition, the metabolic energy consumption of these three subjects was assessed both during skipping and running by an automatic oxygen uptake measuring apparatus (MedGraphics model CPX-MAX, USA). Each metabolic test started 4-5 min after the beginning of the exercise on the treadmill and lasted for $0.5-1.0 \mathrm{~min}$. To obtain the metabolic cost of locomotion, $\mathrm{Jkg}^{-1} \mathrm{~m}^{-1}$, the basal oxygen consumption was subtracted from the value obtained at the exercise steady-state and the result was divided by the progression speed and by the subject's mass. We used $20.1 \mathrm{~kJ}=11$ of $\mathrm{O}_{2}$ to convert metabolic into mechanical units. Apparent efficiency has been calculated as the ratio between the total mechanical work ( $W_{\mathrm{TOT}}=W_{\mathrm{INT}}+W_{\mathrm{EXT}}$ ) and the metabolic cost of locomotion.

Similar metabolic and mechanical analyses were made on horse locomotion in a study recently submitted by our group (Minetti et al. 1998). A total of four standard-bred horses (mass $515.0 \pm 29.1 \mathrm{~kg}$; mean $\pm$ s.d.) were studied during walking (W), trotting ( T ) and galloping ( G ) at different speeds. Inertial parameters of horse segments were taken from Buchner et al. (1997).

Table 1. Subjects' data and individual average stride frequency of skipping

|  |  |  |  |  | stride <br> subject | age <br> $(\mathrm{yr})$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| mass <br> $(\mathrm{kg})$ | stature <br> $(\mathrm{m})$ | number <br> of speeds | $\pm \mathrm{s.d}$. <br> $(\mathrm{Hz})$ | $\mathrm{Hz})$ |  |  |
| D.S. | 29 | 73.0 | 1.81 | 7 | 1.64 | 0.04 |
| L.A. | 28 | 71.5 | 1.81 | 9 | 1.71 | 0.06 |
| A.M. | 41 | 78.0 | 1.73 | 9 | 1.79 | 0.05 |
| M.L. | 29 | 63.0 | 1.73 | 7 | 1.73 | 0.08 |
| V.B. | 37 | 74.0 | 1.80 | 5 | 2.02 | 0.05 |

## 3. RESULTS

The average individual stride frequency of $\mathrm{S}( \pm$ s.d.) is reported in table 1. Figure 2 shows mechanical and metabolic results as a function of speed (only mechanical results of S at $3.7 \mathrm{~m} \mathrm{~s}^{-1}$ have been shown because no metabolic steady-state was attainable at that speed). In the same graphs, curves pertaining to walking and running humans (Cavagna et al. 1976; Minetti et al. 1993) and horses (Minetti et al. 1998) have been displayed for comparison.

## 4. DISCUSSION

One of the most interesting features of S is the constancy of stride frequency at the different speeds. Table 1 shows a very low variability for that parameter on an intra-individual basis. The linear regression between frequency and speed on pooled data (see figure 2) provided a slope not significantly different from zero (a side experiment on unilateral skipping led to the same conclusion, although the average frequency was about $10 \%$ lower than in bilateral S).
When comparing S results in figure 2 to other bipedal ( W , walking; R, running) and quadrupedal (W, walking; T, trotting; G, galloping) gaits, analogies and differences emerge. Being a bouncing gait, because of the flight phase, S should be compared with $\mathrm{R}, \mathrm{T}$ and G . In fact, this is the case when $W_{\text {INT }}, W_{\text {EXT }}$ and frequency are considered. Rather, the energy recovery and the


Figure 2. Summary of mechanical and metabolic measurements of skipping (open circles) compared with other gaits in humans (thin curves, labelled as W and R (Cavagna et al. 1976; Minetti et al. 1993), and cross symbols present subjects running) and horses (thick curves, labelled as W, T and G (Minetti et al. 1998). Closed circles refer to previous data on skipping (Thomas 1978).
'apparent' efficiency of skipping are similar to those in W, whereas the energy expenditure is much higher than in all the other displayed gaits. At closer inspection, both stride frequency (because of its speed independence) and energy recovery (high values for a bouncing gait) suggest the similarity between S and G . The differences and analogies in the mechanical parameters can be better understood by examining the time-courses of energies in S and comparing them with the time-courses of energies for other gaits, namely R and G. Figure 3 shows other peculiar features of $S$ : (i) the trajectory of the body centre of mass, calculated from the three-dimensional positions of the different segments and reflected by the potential energy range ( $E_{\mathrm{p}}$ curve), shows much higher (about $200 \%$ ) vertical displacement than in running at the same speeds; and (ii) the time-courses of the potential energy and kinetic energy of the body centre of mass (3b) resemble an intermediate pattern with respect to W (not shown) and $\mathrm{R}(3 a)$ : similarly to the former, the forward kinetic energy ( $E_{\mathrm{Kx}}$ ) and the potential energy are out-ofphase (they are in-phase during pure running, ( $3 a$ ) ), and, as in running, there is a flight phase. This helps to explain why $W_{\text {EXT }}$ is similar in S and R despite the great difference in $E_{\mathrm{p}}$ range. $W_{\text {EXT }}$ is defined as the sum of the increases of the total energy curve $\left(E_{\mathrm{T}}\right)$, which is affected by the shapes of $E_{\mathrm{p}}, E_{\mathrm{Kx}}$ and $E_{\mathrm{Ky}}$ The $E_{\mathrm{Kx}}$ peak occurring in the middle of the (compound) stance phase in S helps mitigate the effect on $E_{\mathrm{T}}$ of such a high $E_{\mathrm{p}}$ range. Energy
recovery, previously introduced (Cavagna et al. 1976) to account for the pendulum-like mechanism in locomotion, is high for a bouncing gait. As I will discuss, only a component of the energy recovery in S is based on the pendulum-like mechanism, the other being generated by elastic energy release (at a non-symmetrical phase of the stance with respect to the storage).

The comparison between S and G leads to the observation that the canter stride can be considered to comprise two skipping strides, the first performed by the hind limbs and the second by the fore limbs, with about $25 \%$ of the stride period being out-of-phase between each other (at the overall illustrated speed). In fact, both in the middle of the 'hind' stride ( $\mathrm{RH}-\mathrm{LH}$ ) and the 'fore' stride (RF-LF) a $E_{\mathrm{Kx}}$ peak occurs (see figure $3(c)$ ). Such a similarity helps to answer question 3: S in humans and galloping (or cantering, at low speeds) in quadrupeds are related. Also, during galloping the stride frequency changes little with speed, the vertical displacement of the body centre of mass is doubled with respect to trotting, and the mechanical energy recovery and the average vertical ground reaction force (for S , see next paragraph) are higher than in trotting (Minetti et al. 1998). Thus, cantering horses could be imitated by two humans performing (unilateral) S with $25 \%$ of the stride period being out-of-phase. At higher speeds the only difference would be the phase between the two humans, which would approach $50 \%$ and include a second flight period.


Figure 3. Time-course of potential $\left(E_{\mathrm{p}}\right)$, horizontal kinetic $\left(E_{\mathrm{Kx}}\right)$, vertical kinetic ( $E_{\mathrm{Ky}}$ ), and total energy ( $E_{\mathrm{T}}$ ) for running, skipping (both for a human with $m=72 \mathrm{~kg}$ ) and slow galloping (horse canter, $m=538 \mathrm{~kg}$ ). For each gait, several identical patterns have been joined to illustrate the energy patterns before and after the single stride, limited by the two vertical lines (except for S where the symmetrical stride is limited and the dashed line represents the single stride). Symbols below the first skipping stride (b) indicate the mechanical energy transformation within each phase of the contact period: $y, x$ and $e$ are the (potential + kinetic) vertical,
(kinetic) horizontal and elastic energy, respectively. Upper symbols refer to the energy source, while the lower ones are the energy destination (upper $y$ followed by a lower $e$ indicates a storage of vertical energy into the elastic one). See text for details.

mechanical energy flow during ground contact


Figure 4. Mechanical energy fluctuations of the body centre of mass (com) using a single pogo stick (b) and (part of) a rimless wheel with springy spokes (actually, two linked pogo sticks in sequence; $(c)$ ), as obtained from simulation models. The springs are constrained not to extend beyond their resting length. A model of a pogo stick with very high spring stiffness, used as an inverted pendulum, simulated walking and is shown in $(a) . E_{\mathrm{p}}$ and $E_{\mathrm{Ky}}$ have been grouped in a single trace to explain better the role of pendulum-like (non-elastic) horizontal $\left(E_{\mathrm{h}}: E_{\mathrm{Kx}}\right)$ and vertical $\left(E_{\mathrm{v}}: E_{\mathrm{p}}+E_{\mathrm{Ky}}\right)$ energy transfer. $E_{\mathrm{T}}$ represents the total energy of com, obtained by summing $E_{\mathrm{v}}$ and $E_{\mathrm{h}}$ curves. Such a curve does not take into account the energy stored and released by the elastic structures, here plotted as spring tension in the graphs below. The lower part of the picture schematically shows the differences in the energy flow during the contact time (numbers refer to equally spaced phases) in the three categories of terrestrial locomotion. The two basic energy-saving mechanisms, indicated by yellow (pendulum-like) and red-blue (elastic) arrows, concurrently operate in skipping gaits.

The resulting gait is named 'transverse gallop' or 'rotary gallop', depending on whether the two bipeds adopt the same (e.g. left-left) or different (e.g. left-right) unilateral skipping.

The more vertical position of the first limb to land, the speed-independent frequency and the different timecourses of mechanical energies in S with respect to running
raise the argument for a new locomotion paradigm. In the past both the pogo stick (Blickhan 1989) and the bouncing ball (Margaria 1976) have been proposed, sometimes interchangeably, as paradigms for the explanation of fast gaits (running, trotting, hopping, galloping). The present data support the hypothesis that the pogo stick is a convenient simplification for $\mathrm{R}, \mathrm{T}$ and hopping, whereas G and S are
better represented by a 'would-be' bouncing ball, i.e. a rimless wheel with springy spokes (two for S , four for G ). In fact, an ideal elastic ball lands with a vertical contacti.e. its centre of mass is always on the same vertical line of the part of the sphere touching the ground at landingand keeps on bouncing (with the same vertical excursion) at the same frequency regardless of the horizontal speed. To investigate the likelihood of such a hypothesis a simulation package (Interactive Physics, Knowledge Revolution, USA) was used. A passive model of a pogo stick (figure $4 b$ ) and of a (part of a) rimless wheel (figure $4 c$ ), where each 'limb' is made by a simple constrained spring, shows that the mechanical energy fluctuations during a bounce are similar to those found experimentally for bipedal R and S , respectively (figure 3). An inverted-pendulum model is also shown (figure 4a) to accommodate in the same diagram the paradigm for W . In the graphs, potential energy $\left(E_{\mathrm{p}}\right)$ and vertical kinetic energy $\left(E_{\mathrm{v}}\right)$ have been grouped in a single trace to allow simple considerations about the transfer among the different types of energy (horizontal $\left(E_{\mathrm{h}}\right), E_{\mathrm{Kx}}$; vertical ( $E_{\mathrm{v}}$ ), $E_{\mathrm{p}}+E_{\mathrm{Ky}}$; and elastic $\left(E_{\mathrm{EL}}\right)$, spring tension). It is confirmed that the paradigms of R and S differ in the $E_{\mathrm{Kx}}$ pattern during the contact phase; thus, they cannot be used interchangeably for describing bouncing gaits. The two, basic, energy-saving mechanisms, i.e. the potential-kinetic energy interchange (W) and the elastic energy storage-release ( R and T ), seem to be simultaneously operating during S and G , as is also indicated by the intermediate values of 'energy recovery' (this has already been reported for G in a paper by Cavagna et al. (1977)). The asymmetry between the $E_{\mathrm{v}}$ decrease and the $E_{\mathrm{h}}$ increase during the contact time in S (different from W) is a sign of the combined energy-saving mechanism. The greater $E_{\mathrm{v}}$ decrease occurring at the beginning of ground contact can only be explained by a concurrent energy transfer towards elastic storage and horizontal energy, as witnessed by the $E_{\mathrm{h}}$ increase when the first (posterior) spring is fully loaded. The lower part of figure 4 schematically shows the energy flow of the three gait categories of terrestrial locomotion (see figure legend for details). S gaits seem to use $E_{\mathrm{Kx}}$ as an intermediate buffer in which to store energy. This energy is successively reused to load a distant spring (the front limb), allowing energy transfer in a (spatially) widened contact phase.

Figure 5 shows an attempt to explain the mechanical energy fluctuations during G by combining the dynamics of two (bipedal) S strides with the phase shift between the hind and forelimbs which occurs during cantering (the second hindlimb hits the ground simultaneously with the first forelimb). While it is certainly too simplistic to add energy curves to find out how a quadruped works as a combination of two bipeds, the result can help us to interpret the experimental data, at least qualitatively. The thicker curves, being the 'straight' sum of the thinner ones, resemble the energy curves experimentally obtained during G (see figure $3 c$ ), as far as peaks and valleys are concerned.

In contrast to man, where S is metabolically more demanding than R at the same speed (about $150 \%$, see figure 2; Thomas 1978), horse galloping (at high speeds) shows the same cost of transport of T (Hoyt \& Taylor 1981; Minetti et al. 1998). The reason why the same mechanical principle is associated with such different


Figure 5. An attempt to explain the energy fluctuations of the body centre of mass during the canter (slow gallop, figure $3 c$ ) by combining two skipping strides (figure $4 c$ ), with a delay between them corresponding to half the contact time of the single stride (so as to reproduce the typical footfall sequence of a canter). As in figure 4, $E_{\mathrm{p}}$ and $E_{\mathrm{Ky}}$ have been grouped in a single trace to allow the distinction between horizontal and vertical energies. The thicker continuous curves represent the combined overall energy of the 'quadruped', obtained by summing the contribution of the two 'bipeds'.
metabolic energy expenditures (in humans and horses) probably lies in the number of limbs and in the type and amount of elastic structures involved (quadrupeds use also the bending of the spine ligaments to store and release elastic energy (Alexander 1988; Minetti et al. 1998); horses, in particular, have very long tendons in their limb extensor muscles).

S is also the answer to the second question formulated in § 1. Figure 6 schematically shows patterns of vertical $\left(F_{\mathrm{y}}\right)$ and horizontal $\left(F_{\mathrm{x}}\right)$ ground reaction forces of single limbs


Figure 6. Single limb (thin and thick curves) ground reaction force ( $F_{y}$, vertical; $F_{x}$, horizontal) for walking (W), skipping (S) and running (R). Simulations were obtained for a mass of 70 kg using equations (1)-(4) of the locomotion model by Alexander (1992), which derives horizontal force from the vertical force by assuming that the resultant force vector is always in line with the body centre of mass. W and R curves were calculated using average experimental stride duration, duty (the fraction of the stride at which a foot is on the ground) and shape (vertical force pattern) factors at the indicated speeds. S was simulated by imposing, at the same speed of R, extrapolated values of walking duty and shape factors.
 Plus and minus labels represent acceleration and braking in the forward direction, while T and L refer to trail and leading limbs, respectively. (a) Typical $F_{\mathrm{y}}$ and $F_{\mathrm{x}}$ patterns for human running and skipping, obtained in our laboratory. (b) $F_{\mathrm{x}}$ tracings of each limb of a horse cantering at a speed of about $5.2 \mathrm{~m} \mathrm{~s}^{-1}$ (Niki et al. 1984, adapted from their Fig. 2); hind- and forelimb signals have been aligned with respect to the time axis so as to maintain the real footfall sequence during the stride.
at different gaits, obtained using a model of bipedal locomotion (Alexander 1992). As speed increases, the trough in the $F_{\mathrm{y}}$ pattern gets deeper according to the inverted pendulum mechanics, where gravity progressively fails to contrast the centrifugal acceleration (proportional to the (squared) limb angular speed). The simulation shows that when the trough at mid-stance reaches zero, and a double contact between the two limbs persists, the resulting overall pattern resembles the $S$ gait (see figure $7 a$ ). The first emerging difference with respect to $R$ is that in $S$ the 'stance' is made by the compound contribution of two consecutive supporting limbs before the flight, rather than only one at a time. In addition, even more interestingly, the (compound) horizontal force pattern before the flight shows an initial acceleration (first limb) and a successive deceleration (second limb), an opposite sequence to R. The
main reason for this is the more vertical and anterior position (with respect to the body centre of mass) of the first and second limb, respectively, of the 'compound' step at touchdown. Experimental records of $F_{\mathrm{y}}$ and $F_{\mathrm{x}}$ in skipping adults, obtained in our laboratory, were consistent with the simulation (see figure $7 a$ ). Figure $7 b$ shows $F_{\mathrm{x}}$ records (Niki et al. 1984) from the four limbs of a galloping horse (mass $=540 \mathrm{~kg}$, speed $=5.2 \mathrm{~m} \mathrm{~s}^{-1}$ ) where the pattern for the hindlimbs resembles the one for skipping humans. (Actually, a paper by Bryant et al. (1976) shows that foreaft ground reaction forces in the galloping dog are different from the ones measured in horses (Niki et al. 1984; Merkens et al. 1991), with the braking phase preceding the acceleration phase in all limbs. The authors, however, comment that the dog could be accelerating when galloping over the platforms. Whereas the paper
by Niki et al. (1984) showed traces for only one stride, the average force patterns measured on seven horses by others (Merkens et al. 1991) confirm the presently described curve shapes.) Thus, S appears as a gait originating from the pattern of W, when the speed increases beyond a certain value. This suggestion could be of some relevance when dealing with the structure and function of the central pattern generator, the neuronal assembly devoted to impart activation sequences to limb muscles in periodic movements. Referring back to quadrupeds, there is evidence that some of them never use T (Pennycuick 1975), strengthening the rationale about the gallop ( S ) as an evolution of walking at high speeds. Electromyographic studies, investigating the similarities in the activation pattern between S and W , could also help us understand why children adopt such a gait, albeit for short distances.

The final intriguing aspect of S biomechanics is the potential use of this gait in low gravity. Margaria \& Cavagna (1964) demonstrated that in gravity conditions such as those that exist on the moon ( 0.16 g ), W should be impaired and R could be adopted in a limited range of speeds (up to $1.4 \mathrm{~m} \mathrm{~s}^{-1}$ and up to $3.6 \mathrm{~m} \mathrm{~s}^{-1}$ for realistic (dust) and ideal conditions of the surface, respectively). The reason for the impairment of W was mainly ascribed to the uneven interchange between $E_{\mathrm{Kx}}$ and $E_{\mathrm{p}}$, the last being affected by the reduced gravity. As far as running is concerned, 'the vertical component of the force may be too low to maintain the adherence of the foot to the ground and prevent skidding' (Margaria \& Cavagna 1964). They concluded that generic jumping could be the gait of choice on the moon. This is where S is involved. On Earth, S produces higher vertical ground reaction forces than R at the same speed because a greater fraction of the stride and of the body is off the ground ( $t_{\mathrm{f}}$, compare open circles and the stippled range in figure 8). As the average vertical force during the whole stride must match the body weight $(B W)$, the average force during the contact phase is computable as $B W /\left(1-t_{\mathrm{f}}\right)$. At a speed of about $2.5 \mathrm{~m} \mathrm{~s}^{-1}$, running $t_{\mathrm{f}}$ was equal (Nilsson \& Thorstensson 1989) to $16.1 \%$, whereas it was $31.8 \%$ ( $\pm 8.2$ s.d., $n=5$ ) for S , with an increase in the average vertical force from 1.19 to 1.47 BW (see right-hand side ordinate in figure 8). In addition, in case of slippery surfaces, $S$ can benefit from having the trailing foot (the first to touch the ground after a flight) in a more vertical position at landing, and it is immediately followed by the leading foot, increasing therefore the stability of the combined push. Thus, it seems that we do not need to invent a new gait to move quickly in sub-gravity, we simply have to recall a dismissed pattern. (It is quite common to spot people skipping down stairs and while manoeuvring around sharp corners. Despite this, some adults cannot skip smoothly on a treadmill at the first attempt, and therefore a little practise is required before the experimental session begins. This has to be kept in mind when preparing a sojourn in low-gravity environments.) The drawback associated with the high metabolic cost of S is overridden by the need for less work against gravity.
In conclusion, the metabolic and biomechanical analyses of $S$ have been used to obtain insights into many, apparently unrelated, fields. It was shown that children,


Figure 8. Fractional duration of the flight phase of skipping, compared with running (stippled area; Nilsson \&
Thorstensson 1989; Minetti et al. 1994), at different speeds. The ordinate on the right-hand side shows the average vertical ground reaction force associated with the flight duration, calculated as $1 /\left(1-t_{\mathrm{f}}\right)$ (in $B W$ units).
astronauts and horses share a gait with a mechanical paradigm different from W and $\mathrm{R}(\mathrm{T})$. Such a gait is suitable for high speeds, as the two basic strategies for mechanical energy saving are simultaneously operating. Other aspects related to the S gaits remain to be investigated; for example, the reasons why children display such a gait after they have learned to run, and why adults keep on (unilaterally) skipping when descending stairs and turning corners. This last topic can be transposed to quadrupeds by asking whether the trot-gallop spontaneous transition speed, which is expected to be set by several constraints, is different for linear and circular motions. The asymmetry of G (and of unilateral S) may be the key to such a difference.

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## REFERENCES

Alexander, R. McN. 1988 Why mammals gallop. Am. Zool. 28, 237-245.
Alexander R. McN. 1992 A model of bipedal locomotion on compliant legs. Phil. Trans. R. Soc. Lond. B 338, 189-198.
Alexander, R. McN. 1995 How animals move. CD-ROM. The Discovery Channel and Maris Multimedia.
Alexander, R. McN. \& Jayes A. S. 1980 Fourier analysis of forces exerted in walking and running. F. Biomech. 13, 383-390.
Blickhan, R. 1989 The spring-mass model for running and hopping. J. Biomech. 22, 1217-1227.
Bryant, J. D., Bennett, M. B., Brust, J. \& Alexander, R. McN. 1976 Forces exerted on the ground by galloping dogs (Canis familiaris). F. Physiol. 262, 639-657.
Buchner, H. H. F., Savelberg, H. H. C. M., Schamhardt, H. C. \& Barneveld, A. 1997 Inertial properties of Dutch Warmblood horses. F. Biomech. 30, 653-658.

Cavagna, G. A. \& Kaneko, M. 1977 Mechanical work and efficiency in level walking and running. 7. Physiol. 268, 467-481.
Cavagna, G. A., Thys, H. \& Zamboni, A. 1976 The sources of external work in level walking and running. 7. Physiol. 262, 639-657.
Cavagna, G. A., Heglund, N. C. \& Taylor, C. R. 1977 Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. Am. $\mathcal{F}$. Physiol. 233, R243-261.
Dempster, W. T., Gabel, W. C. \& Felts, W. J. L. 1959 The anthropometry of manual work space for the seated subject. Am. $\mathcal{F}$. Physiol. Anthrop. 17, 289-317.
Fokin, I. M. 1978 Locomotion and the morphology of the organs of motion in the Jerboa. Leningrad: Nauka. (In Russian.)
Hayes G. \& Alexander, R. McN. 1983 The hopping gait of crows (Corvidae) and other bipeds. 7. Zool. 200, 205-213.
Hoyt, D. F. \& Taylor, C. R. 1981 Gait and the energetics of locomotion in horses. Nature 292, 239-240.
Margaria, R. 1976 Biomechanics and energetics of muscular exercise. Oxford: Clarendon Press.
Margaria, R. \& Cavagna, G. 1964 Human locomotion in subgravity. Aerosp. Med. 35, 1140-1146.
Merkens, H. W., Schamhardt, H. C., Van Osch, G. J. V. M. \& Van Den Bogert, A. J. 1991 Ground reaction force analysis of Dutch Warmblood horses at canter and jumping. Equine Ererc. Physiol. 3, 128-135.

Minetti, A. E. \& Consani, I. R. 1989 A computational method for the mechanical work estimation of locomotion. C.N.R. patent no. 21564 A/89 (28/8/1989) and software registered (SIAE).
Minetti, A. E., Ardigò, L. P. \& Saibene, F. 1993 Mechanical determinants of grade walking energetics in man. 7. Physiol. 472, 725-735.
Minetti, A. E., Ardigò, L. P. \& Saibene, F. 1994 Mechanical determinants of the minimum energy cost of gradient running in humans. 7. Exp. Biol. 195, 211-225.
Minetti, A. E., Ardigò, L. P., Reinach, E. \& Saibene, F. 1998 The relationship between the mechanical work and energy expenditure of locomotion in horses. (In preparation.)
Niki, Y., Ueda, Y. \& Masumitsu, H. 1984 A force plate study in equine biomechanics. 3. The vertical and fore-aft components of floor reaction forces and motion of equine limbs at canter. Bull. Equine Res. Inst. 21, 8-18.
Nilsson, J. \& Thorstensson, A. 1989 Ground reaction forces at different speeds of human walking and running. Acta Physiol. Scand. 136, 217-227.
Pennycuick, C. J. 1975 On the running of the gnu (Connochaetes taurinus) and other animals. J. Exp. Biol. 63, 775-799.
Thomas, C. 1978 The efficiency of running and skipping. Report number 1. School of Physical Education, University of Otago, Dunedin.

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