Skipping vs. Running as the bipedal gait of choice in hypogravity

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Running Head: locomotion in hypogravity

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Abstract

Hypogravity challenges bipedal locomotion in its common forms. However as previously theoretically and empirically suggested, humans can rely on 'skipping', a less common gait available as a functional analogue (perhaps a vestigium) of quadrupedal gallop, to confidently move when gravity is much lower than on Earth. We set up a 17 m tall cavaedium (skylight shaft) with a bungee rubber body-suspension system and a treadmill to investigate the metabolic cost and the biomechanics of low-gravity (Mars, Moon) locomotion. Although skipping is never more metabolically economical than running, the difference becomes marginal at lunar gravities, with both bouncing gaits approaching values of walking on Earth (cost ≈ 2 J/(kg m)). Non-metabolic factors may thus be allowed to dominate the choice of skipping on the Moon. Based on centre of pressure measurements and body segments kinetics, we can speculate that these factors may include a further reduction of mechanical work to move the limbs when wearing space suits and a more effective motor control during the ground (regoliths)-boot interaction.

Keywords: Locomotion, low gravity, cost of transport, work, efficiency

Introduction

Despite of the apparently slow timescale of space exploration, evolutionary changes genetically adapting our body to different gravitational environments take much longer, and humans (and, eventually, their legged pets) will have to rely on the actual musculo-skeletal system when trying to locomote on other planets.

The usual gait repertoire is challenged by a change in gravity. Walking, the mechanics of which is based on the exchange of potential and kinetic energy of the body centre of mass (BCoM), as occurring in a pendulum (7), is impaired in low gravity (8, 9). The theory of dynamic similarity (2)
states that when pendulum-like dynamics is involved, the speed of movement has to scale with the ratio between the planet and Earth's gravity raised to the power of 0.5. Thus, despite the 'facilitating' lower body weight experienced in low gravity, the operative speed range of walking is very much reduced (40% on the Moon). The change in dynamically similar speeds, experimentally simulated at different gravities, has been shown to follow that theory (13, 18). Even running, which mechanically resembles a pogo-stick where BCoM (kinetic + potential) energy exchanges with elastic energy (tendon length changes) at each bounce, has also been predicted as an impaired locomotion when the body weight reduces, assuming the same ratio as on Earth between vertical and horizontal force components at foot push off, with a top speed of only 3.3 m/s on the Moon (15).

Skipping is the third, almost neglected, human gait characterized by the two feet getting in contact with the ground one after the other, followed by the flight phase. Kids use it for fun, adults adopt it sometimes when descending stairs or during cornering, and its mechanical paradigm is a combination of the pendulum and the pogo-stick (17). From the footfall perspective, a biped performing unilateral skipping (e.g. Right-Left-Flight) moves exactly as the fore or hind pairs of limbs of a galloping quadruped. The first investigation on this gait pointed out that the ratio between contact phase and stride time, lower on Earth than in running at the same speed, was associated to a higher vertical ground reaction force (hence higher friction with the slippery terrain) and this could partly explain the observation of Apollo astronauts adopting skipping while searching for the most appropriate Lunar gait (see the movie in Supplementary material). That study also showed that, differently from horses where galloping is as economical as trotting (corresponding to bipedal running (20)), the metabolic cost of transport on Earth was up to 40% higher in skipping than in running, requiring a high aerobic power even at slow speed (17, 21).

Ackermann and Van Den Bogert (1) recently designed a musculoskeletal model, with seven body segments, searching for the least effort, or least fatiguing, locomotion type depending on the gravity
conditions based on the activity of eight muscle groups for each lower limb. They found that at
speeds of 1.1 and 2.0 m/s skipping is the preferable gait on the Moon, while on Mars the least effort
is associated to walking at slow speeds and mainly to running at high speeds.

Although quite encouraging, all the previous results do not help to assess the metabolic
sustainability of running and skipping in low gravity, a task needing steady-state measurements of
oxygen consumption that could not be achieved in 30 s lasting experimental sessions of parabolic
flights reproducing given levels of gravity. Also, the gravity dependence of mechanical energy
saving strategies for the three gaits (17), partially responsible for their metabolic ranking on Earth
(skipping, running, walking, from the most to the least costly), suggests that those relationships
could change in low gravity. Thus, a detailed study of locomotion mechanics could help to interpret
the associated metabolic changes.

The aim of this study was to calculate biomechanical parameters and metabolic cost of the three
human gaits in simulated low gravity conditions that would ensure steady state measurements.

Material and Methods

Heterogravity Laboratory

The cavaedium (skylight shaft) is a narrow (3 x 3 m) and tall (17 m) space inside the Human
Physiology building where a motorized treadmill (PPS 55Ortho, Woodway, Germany) has been
installed on the floor, and a body suspension device hung up to a mobile pulley on the top of the
ceiling. The suspension device is formed by two bungee jumping rubber bands (Exploring Outdoor
srl, Italy), with rest length 4 m and stiffness 92.7 N/m, linked in-series by an inextensible short
cable (Gottifredi & Maffioli, Italy, Dyneema SK78, ø 4 mm, L 1.2 m), working on the top pulley.
One end of the rubber band was fixed to the wall, while the other end was connected to a harness.
The mobile pulley could be lifted or lowered by means of a suspension cable connected to a
motorized winch (E.C.E., Italy, 750 W), to unload the body by the desired vertical force checked by
means of a balance (Vandoni Salus srl, Italy), and a force transducer (REP Transducers, TS 300 kg, Italy), positioned in-series with the suspension cable. Differently from most of the hypo-gravity simulators (e.g. as He et al. (12)), the pulley is located so far above the subject (16 m) as to reduce to a minimum the horizontal forces that could be generated by the (small) forward-backward and lateral displacement during locomotion on the treadmill (with the Moon gravity, a horizontal move of 0.03 m with respect to pulley resulted in an additional Fx or Fy of 0.92 N, which represents 0.4% and 0.7% of the peak push force during terrestrial stance, respectively (22)). Also, the cavaedium height allow to use just one pulley to accommodate a 20 m (10 m x 2 when extended) rubber band, with benefits in terms of low friction and displacement-independence of the vertical force (for a dz of 0.2 m, Fz varied by 5 N when the system was set for the Moon gravity). Although this apparatus quite accurately reproduces the low-gravity condition by applying to BCoM a constant vertical force, it is important to consider that pendulum-like dynamics of swinging limbs is affected by Earth gravity (12, 13, 15).

Subjects

Thirteen subjects (7 females and 6 males, 23.3 ± 3.3 yr, 1.70 ± 0.07 m height, 62.4 ± 10.0 kg mass; mean ± SD) took part to the study. The study was approved by the Ethics Committee of the University of Milan, and participants, after becoming aware of the potential risks involved in the experimental sessions, gave their informed consent. Subjects undertook two familiarisation sessions to get used with gaits on low gravity conditions where, particularly at high speeds, balance and proprioception were largely involved. After familiarisation subjects came to the laboratory 5 times in order to complete the metabolic and kinematic protocol.

Experimental protocol

Walking, skipping and running were tested on Earth (1g) and two simulated gravity level, Mars (0.36g) and Moon (0.16g) at different speeds from 0.83 to 3.61 m/s.
Metabolic measurements

Each experimental session started with 8 minutes of basal $\dot{V}_{O_2}$ (mlO$_2$/kg min) assessment after which subjects started locomoting on the treadmill. Data acquisition lasted 4 minutes in order to reach a steady state for $\dot{V}_{O_2}$. Respiratory gas were analysed breath by breath with a portable metabolograph (K4b$^2$, Cosmed, Italy), and the cost of transport (C), i.e. the metabolic energy to move 1 kg of body mass for a distance of 1 m was estimated from the data collected during the last minute by dividing the measured net O$_2$ consumption (total-basal $\dot{V}_{O_2}$) by the progression speed. Each metabolic level resulted to be submaximal (RQ <1) and RQ caloric equivalent (J/mlO$_2$) was multiplied to O$_2$ consumption for C calculation. Terrestrial running and skipping data in figure 1, 2 and 6 are from Ardigó et al. (3) and from Minetti et al. (21), respectively.

Kinematics

3D body motion was sampled by a 8 cameras system (Vicon MX, Oxford Metrics, UK) measuring at a sampling rate of 100 Hz the spatial coordinates of 18 reflective markers located on the main joint centres. Each acquisition lasted 1 minute and the time course of BCoM position was computed from a 11-segment model (19) based on Dempster inertial parameters of body segments (26). From BCoM 3D trajectory the time course of potential (PE) and kinetic (KE) energies were computed in order to obtain the Total Mechanical Energy (TE=PE+KE). The summation of all increases in TE time course constitutes the positive external work (W$_{EXT}$, J/(kg m)), and represents the positive work necessary to accelerate and lift BCoM (6). The work necessary to rotate and accelerate limbs with respect to BCoM (W$_{INT}$, J/(kg m)) (6, 16) was also calculated and summed to W$_{EXT}$ in order to obtain the total mechanical work (W$_{TOT}$, J/(kg m)). The ratio between W$_{TOT}$ and C was used to estimate locomotion efficiency. Energy Recovery, the ability of the moving system to save energy by behaving like a pendulum-like system, was calculated according to Cavagna and Kaneko (6).
Data have been analysed with purposely written Labview programs (release 10, National Instruments, US).

Statistics

Data were compared between speeds and gravity level using one way ANOVA with significance set at p < 0.05 and Bonferroni post hoc test. Statistical analyses were performed with SPSS v20 (IBM, USA).

Results

Cost of Transport

The results show an 18% reduction in metabolic cost of walking when low gravity is simulated (Fig. 1a), although the difference was not significant. The U shape of walking cost was similar between Earth and Mars/Moon, with minimum not different among planets.

The cost of transport of bouncing gaits, (Fig. 1b) decreased at low gravity much more in skipping than in running, and on the Moon the two gaits involve almost the same economy. C was statistically lower in each gravity condition in both gaits (p<0.001 Earth vs. low gravity pooled; p<0.01 Mars vs. Moon), and running cost retained its speed independency. The same aerobic power (say, 30 mlO₂/(kg min)) allowing to skip on Earth only at very low speeds (21) (e.g., 1.4 m/s or 5.0 km/h) is enough to steadily run and skip on the Moon at 4.2 m/s (or 15.1 km/h), with a gain in performance (3x for skipping, 2x for running) that could be considered almost speed- and, within some limits, additional load mass-independent.

Biomechanical Parameters
The mechanical external, internal and total work in the three gaits and gravity conditions are plotted against speed in figure 2.

$W_{\text{EXT}}$ for walking significantly increased with speed at all gravities, but mean values significantly decreased when gravity was low (p<0.001 Earth vs. low gravity), mainly due to the PE reduction. When Skipping in hypo-gravity $W_{\text{EXT}}$ seemed speed independent, with a significant reduction compared to Earth: 3-fold lower on Mars and 4-fold on Moon (p<0.001 Earth vs. low gravity pooled; p<0.01 Mars vs. Moon). In running the external work significantly increased with speed at lunar gravity, while in the other cases it was speed independent. As in skipping the reduction among gravity was significant (p<0.001 Earth vs. low gravity pooled; p<0.001 Mars vs. Moon). Walking values were always smaller than bouncing gaits, whereas skipping values became slightly lower than running in low gravity conditions.

$W_{\text{INT}}$ in walking increased with speed at all gravities but decreased as average when gravity was low (p<0.01) without significant difference between low gravity levels. As for skipping $W_{\text{INT}}$ increased significantly with speed on Earth and Mars and decreased significantly with low gravity (p<0.001 Earth vs. low gravity pooled; p<0.01 Mars vs. Moon). The same trend was found in running (p<0.001 Earth vs. low gravity pooled; p<0.05 Mars vs. Moon). Skipping $W_{\text{INT}}$ was higher than running on Earth, but became lower than it when gravity was decreased.

Average $W_{\text{TOT}}$ as the sum of $W_{\text{EXT}}$ and $W_{\text{INT}}$ decreased with low gravity in walking (p<0.001 Earth vs. low gravity pooled; p<0.05 Mars vs. Moon at fastest speed) and in bouncing gaits (p<0.001 Earth vs. low gravity pooled; p<0.01 Mars vs. Moon) with a tendency of skipping towards speed independence.

Energy Recovery (Fig. 3) in walking showed a maximum on Earth at intermediate speed. At Mars gravity the maximum value was lower and the decay at faster speed higher than on Earth. On Moon, the maximum recovery was reached at slower speed and its value was even smaller, with a steeper
decay over speed. When speed was normalised for dynamic similarity, the maximal Energy Recovery value was reached at similar Froude number (Fr = v^2/gL). The mean values of mechanical and bioenergetics parameters including Fr can be found in Supplementary material). In skipping Energy Recovery was almost constant on Earth (around 25%), and its maximal value increased slightly, but not significantly, when gravity decreased, reaching on Moon walking values.

Stride Frequency (SF, Fig. 4) in walking significantly increased with speed but was gravity independent. Skipping SF was speed independent in hypo-gravity and differences among gravities were statistically significant at all speeds (p<0.001 Earth vs. low gravity pooled; p<0.01 Mars vs. Moon). Running values were speed dependent, and decreased with low gravity (p<0.01 Earth-low gravity) however SF was not different between Mars and Moon.

Low gravity running involves a smaller descent of the body centre of mass during the contact phase, relative to the resting height, than on Earth (Fig. 5). On the other hand, hypogravity skipping maintains a remarkable descent of BCoM and shows a higher gain in vertical displacement (x2 on the Moon) during the flight phase than in running.

Efficiency

Locomotion efficiency, i.e. the ratio between total work performed (WTOT) and energy consumed (C) increases with speed at all gravities in every gait (Fig. 6), however average efficiency decreases up to 49% (p<0.01), 32% (p<0.001) and 43% (p<0.001) of the values on Earth in walking, running and skipping, respectively, as gravity gets small. The efficiency of skipping in hypogravity is closer to terrestrial walking levels, and running efficiency in hypogravity reaches values of about 40%, approaching muscular efficiency and much lower than the highest efficiency reported on Earth.

Discussion
From a metabolic perspective our results show that bouncing gaits benefit in low gravity more than walking, and that skipping reports the highest gain in cost reduction reaching values for terrestrial walking. This could partly explain astronauts’ choice during Apollo 14 and 17 missions of skipping gait while moving on the Moon (see the movie in Supplementary material).

Differently from previous studies (10, 28) we found no statistical differences in walking cost when gravity is low. An overall reduction of 18% was found between Earth and hypogravity values without differences between Mars and Moon. The simulation apparatus could be the cause of such a discrepancy. Teunissen et al. (25) found a higher running cost in hypogravity than Farley and McMahon (10) and they attributed the discrepancy to adopting a longer cord length over subject head. A short length could in fact help the subject maintaining balance and the elasticity of the rope could store and release more elastic energy during the fore-aft movements acting like a spring. These combined interactions potentially result in a reduced cost.

In our experimental set up the pivot point was at least 12 m over subject’s head and, as mentioned, the maximum induced fore-aft or medio-lateral force would have been 0.92 N, hence we could conclude that our subjects experienced a very small bias from the apparatus, and that the measured C is one of the most reliable metabolic estimate from a (sufficiently long lasting) low gravity simulation. It has to be considered also that, unless astronauts will operate inside a pressurized dome, our metabolic results should be corrected for the additional mass of the space suit (around 117 kg), with a predictable decrease in speed, for the same available metabolic power.

The mechanical external work was reduced by low gravity mostly due to the potential energy in the three gaits. However walking was negatively affected by this reduction, since the pendulum like saving mechanism needs the exchange between potential and kinetic energies in order to minimize muscular work. As showed in figure 3, Energy Recovery decreased at low gravity, and its peak value occurred at slower speeds pointing also out a likely higher muscular work, which ultimately affects metabolic cost. These mechanical data are consistent with Cavagna et al. experiments (8, 9)
collected during parabolic flights and the predictions from the dynamic similarity theory (18). The internal work decreased only between Earth and low gravity planets, whereas stride frequency was not different among gravities in walking witnessing the adoption of similar stride lengths. Although aware of the bias induced by Earth gravity on swinging limbs dynamics, which could affect whole body motion pattern, we found stride frequency values very similar to those collected during parabolic flights (9), which are the gold standard, albeit short lasting, in hetero-gravity simulation. While waiting for analogous data on bouncing gaits that are not available yet, the cavedium can be considered the simulation environment of choice for steady state locomotion.

We will focus the rest of the discussion on the bouncing gaits since they were never been analysed in such detail before, they are quite affected by gravity and because of their relevance in fast locomotion.

Figure 2 shows that kinematic $W_{\text{INT}}$, diminishes in low gravity (stride frequency effect) and that running and skipping are quite similar on Earth, with a tendency in skipping to be smaller at lower gravities, due to a further reduction of stride frequency. The internal work can also be predicted by a model equation (16) that has as input variables the progression speed, stride frequency, duty factor and a (compound) estimate of the inertial characteristics of upper and lower limbs. The predictive equation can also be used to evaluate the determinants of measured internal work changes in terms of the involved variables. In the present investigation, for example, the -67.5% change of running $W_{\text{INT}}$ when on the Moon can be partly explained by the 24.7% decrease in stride frequency and the 38.8% lowering of the duty factor (which sums up to a -41.1% expected change in the model equation). In addition, the angular excursion of lower limb segments was found to be 40% lower than on Earth. In addition to the 'kinematic' $W_{\text{INT}}$ reduction, we can expect a much smaller 'frictional' $W_{\text{INT}}$ due to the minimal overlap between swinging thighs (with or without space suit) on the sagittal plane, which is a peculiar aspect of unilateral skipping.
Although not directly reflecting the exploitation of tendons in storing and releasing the elastic energy particularly needed in bouncing gaits, it is intuitive that a very small BCoM descent (Fig. 5), with respect to the straight limb posture, could not be associated to a substantial mechanical energy saving based on that strategy. Less 'compressed' limbs (running) need to rely more on muscle contraction to achieve a high take-off speed, which will be penalized anyway by the lack of the power-amplification effect operated by tendon stretch/recoil. This is one of the reasons for the decrease of 'apparent' efficiency of the two bouncing gaits in low gravity (Fig. 6). Locomotion efficiency is often called 'apparent' when it exceeds muscle efficiency (0.25-0.30 (27)). An efficiency greater than the 'engine' value often reflects a numerator inflated by some positive work that should not be considered, being the consequence of a previously 'absorbed' negative work. This is mainly caused by elastic structures as muscle tendons and the arch of the foot (14), which are stretched during the first half of the contact time and recoil thereafter. Thus, the excess of 'apparent' efficiency with respect to 0.25-0.30, particularly high in galloping horses, can be regarded as an index of elastic contribution to locomotion (20). Along this line of thought, running and skipping show a decrease of elastic contribution in low gravity, and on the Moon their efficiency does not need to be called 'apparent' any more, albeit at very high speeds. Our muscle-tendon units, with the muscle acting almost isometrically during bounces on Earth, similarly to other running bipeds (23), cannot cope efficiently with the reduced load as the stiffness of the inert component remains the same in all gravitational environments. This implies a smaller elastic stretch (and recoil) in hypogravity, as indirectly shown for running in figure 5. By combining the lower impairment of the pogo-stick (elastic) paradigm and the invariance or slight improvement of the pendulum-like mechanics (see Energy Recovery in Fig. 3), skipping seems to relay on the two energy saving strategy better than the other gaits.

Other mechanical differences between the two bouncing gaits deal with the specialization of lower limbs. In running, the contact phase of each limb incorporates a braking action followed by a propulsive push before the flight (17, 22). In skipping that sequence is reversed, and propulsion and
Braking are separately provided by trailing and leading limbs (11, 17), respectively, whose consecutive action on the ground prepares the flight phase along a more extended base of support (Fig. 7). The foot contact pattern suggests that skipping could be the preferred gait in terms of movement control. Besides space suits, also lunar dust (regoliths) and its low friction coefficient are likely to hinder locomotion. When compared to running, the duty factor (2) (df, i.e. the fraction of the stride duration at which each foot is on the ground) is significantly shorter, at the same progression speed. Since the average vertical ground reaction force (Fz) during the entire stride has to equal body weight, the shorter the contact phase, the higher the average force each limb must exert during that phase (mean Fz = mg/(2 df) ) (17). Our kinematic measurements of simulated locomotion on the Moon show that mean Fz is significantly greater (+26.0 ± 7.4 %) in skipping than in running, at the same progression speed. That is quite beneficial in hypogravity as the risk of skidding on regoliths is reduced by a higher vertical force, not followed by a corresponding increase in horizontal force (take-off angle, with respect to the horizontal line in the sagittal plane, was found to be 77.1 ± 4.9° and 73.1 ± 3.1° for running and 82.4 ± 4.7° and 77.8 ± 5.7° for skipping, at 9 and 11 km/h, respectively). Also, yaw control is supposed to be assisted by the peculiar footfall of skipping. The temporally contiguous placement of trailing and leading foot on the ground greatly prolongs the distance travelled by the Centre of Pressure (CoP, i.e. the ideal point on the ground where all the forces are 'summarized' at each instant of the contact phase). Although quite fast moving from the trailing and the leading foot (Fig. 7), CoP persistence on the ground allows, particularly in slippery conditions, to re-adjust the overall BCoM direction of motion before the flight. In running such a correction has to be made (twice) within shorter (single) contact times during which BCoM travels a shorter distance. In addition, fewer muscles would be involved in the correction.

Early biomechanists (7) assimilated legged locomotion to a rimless wheel, where limbs are the wheel spokes. In bouncing gaits, we need to imagine a bouncing rimless wheel. Differently from
running, skipping uses 2 adjacent spokes during the bounce, making the contact paradigm more similar to a normal rolling wheel.

It is likely that skipping will be used also for steering and moving in circles on the Lunar surface, as it is an asymmetrical gait quadrupeds deterministically use to turn (in the direction of the leading limb of the front pair first, then followed by the hind limbs), as observable in show jumping competition. Most of the locomotion repertoire in legged species is based on right-left symmetrical limb movements. Gallop and skipping are exceptions, and some evidences point out that asymmetry can be an advantage. When modellistically searching for energetic optimality, limb movement symmetry is often found (24): symmetric inverted pendulum walking gait always requires less work than an inverted pendulum gait with asymmetric steps. Rather, the same study indicated that in springy bipeds with compliant tendons, both symmetric (running) and asymmetric gaits (such as skipping) were optimal.

Our subjects did not experience low gravity locomotion in fully fitted and pressurized space exploration suits. Nevertheless, we can foresee some possible effects that space suit may have on the present results. On Earth added mass causes a proportional increase in metabolic cost. On other planets garments involve extra mass (up to 117 kg on the Moon) and a sort of hexoskeleton, with internal pressure as in octopods. While extra mass is expected to be associated to some metabolic extra cost, the space suit could even assist posture (self supporting suit (5)) and contribute to a more economical propulsion through additional storage and release of pneumatic/elastic energy during the support phase. On the other hand, space suit locomotion increases the mechanical internal work due to the friction between rubber pads around knees during midstance.

In synthesis, even by losing most of their elastic components, fast bipedal gaits from our ancestral repertoire are metabolically sustainable in low gravity. Our measurements show that unilateral skipping, an expensive gallop-derived bipedal gait on Earth used by lemurs and (perhaps vestigially) by humans, has a central role in low gravity locomotion. Other than involving an
economy very close to running, skipping could even result to be the gait of choice due to its peculiar biomechanics, which minimise mechanical work and enhance grip control on a slippery ground. These hypotheses will need to be confirmed by studies on the effects of space suits and regoliths (Lunar dust) on locomotion. The timing of biological evolution cannot cope with space exploration, but specific training programs will potentiate astronauts' muscles to better assist a locomotion pattern that is already embedded in the Central Pattern Generator. Differently from quadrupedal pets (and lemurs), probably already at ease with hypogravitational locomotion, humans will be confident by only restoring an almost dismissed gait.

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References


**Figure captions**

**Figure 1:** Cost of transport as a function of speed and gravity has been grouped, for sake of clarity, according to bouncing and non bouncing gait. a) Walking on Earth (circles), Mars (squares) and Moon (diamond). b) Running and skipping (solid and open symbols, respectively) on Earth (circles), Mars (squares) and Moon (diamond). Vertical lines represent SD, *p*<0.05, # *p*<0.01. Iso-power hyperbolas (dashed curves) represent different sustainable aerobic levels (displayed values include basal metabolism, expressed both as mlO₂/(kg min) or W/kg of body mass).

**Figure 2:** Mechanical work. External work (Wₚₑₓₜ J/(kg m)), ‘Kinematic’ internal work (Wᵢₙₜ J/(kg m)) and Total work (Wₜₒₜ J/(kg m)) of walking (solid square), running (solid circles) and skipping (open circles) as a function of speed on Earth and on simulated Mars and Moon. Vertical lines represent SD, *p*<0.05, # *p*<0.01.

**Figure 3:** Energy Recovery (%) as a function of speed and gravity. a) Walking on Earth (circles), Mars (squares) and Moon (diamond). Data are fit with a quadratic function and its maximum normalised as Froude Number (Fr). b) Running and skipping (solid and open symbols, respectively) on Earth (circles), Mars (squares) and Moon (diamond). Vertical lines represent SD.

**Figure 4:** Stride frequency (Hz) as a function of speed and gravity in the three gaits: walking (solid square), running (solid circles) and skipping (open circles). Vertical lines represent SD.
Figure 5: Vertical BCoM range. Descent (during contact) and ascent (during flight) of the body centre of mass on Earth and on simulated Mars and Moon, as a percentage of the standing value, of running and skipping.

Figure 6: Efficiency of walking (solid square), running (solid circles) and skipping (open circles) as a function of speed on Earth and on simulated Mars and Moon. Grey band indicates the muscular efficiency (0.25-0.30). Vertical lines represent SD * p<0.05, # p<0.01.

Figure 7: Lunar boot prints. a) Foot casts of running (lower trace) and unilateral left skipping (upper trace). Skipping Centre of Pressure is shown as a dotted curve (in running its path is confined within a single cast).

b) skipping boot prints of Alan Shepard during Apollo 14 Mission (www.hq.nasa.org). Body is moving towards bottom-left, showing asymmetry of the trailing and leading (the deeper) cast. The trail starts (from the right) with a right skip (left-right-flight) then, after 3-4 strides, switches to left skip (right-left-flight), as racehorses periodically do with right and left gallop on the straight corridors of the track (4).