

# Skipping vs. running as the bipedal gait of choice in hypogravity

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**Pavei G, Biancardi CM, Minetti AE.** Skipping vs. running as the bipedal gait of choice in hypogravity. *J Appl Physiol* 119: 93–100, 2015. First published April 30, 2015; doi:10.1152/jappphysiol.01021.2014.—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 analog (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  $\approx 2$  J·kg<sup>-1</sup>·m<sup>-1</sup>). Nonmetabolic factors may thus be allowed to dominate the choice of skipping on the Moon. On the basis of center 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.

locomotion; low gravity; cost of transport; work; efficiency

DESPITE 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 musculoskeletal 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 (PE) and kinetic energy (KE) of the body center 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 are 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 (KE + PE) 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).

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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 with a higher vertical ground reaction force (Fz) (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 Supplement S1). 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 (C) 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 with walking at slow speeds and mainly with running at high speeds.

Although quite encouraging, all of 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 O<sub>2</sub> consumption ( $\dot{V}O_2$ ) 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.

## MATERIALS AND METHODS

**Heterogravity laboratory.** The cavaedium (skylight shaft) is a narrow (3 × 3 m) and tall (17 m) space inside the Human Physiology building where a motorized treadmill (PPS 55Ortho, Woodway) 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), with rest length of 4 m and stiffness of 92.7 N/m, linked in-series by an inextensible short cable (Gottifredi & Maffioli, Dyneema SK78, diameter 4 mm, length, 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., 750 W) to unload the body by the desired vertical force checked by means of a balance (Vandoni Salus) and a force transducer (REP Transducers, TS 300 kg) positioned in-series with the suspension cable. Different from most of the hypogravity simulators (e.g., 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 lateral or horizontal force 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 allows the use of just one pulley to accommodate a 20-m ( $10 \times 2$  m when extended) rubber band, with benefits in terms of low friction and displacement independence of the vertical force (for a vertical diameter of 0.2 m, vertical force 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 are affected by Earth gravity (12, 13, 15).

**Subjects.** Thirteen subjects (7 women and 6 men,  $23.3 \pm 3.3$  yr,  $1.70 \pm 0.07$  m height,  $62.4 \pm 10.0$  kg mass; means  $\pm$  SD) took part in 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 familiarization sessions to get used to gaits on low-gravity conditions, where, particularly at high speeds, balance and proprioception were largely involved. After familiarization, subjects came to the laboratory five times to complete the metabolic and kinematic protocol.

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

**Metabolic measurements.** Each experimental session started with 8 min of basal  $\dot{V}O_2$  ( $\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) assessment, after which subjects started locomoting on the treadmill. Data acquisition lasted 4 min to reach a steady state for  $\dot{V}O_2$ . Respiratory gas was analyzed breath by breath with a portable metabograph (K4b<sup>2</sup>, Cosmed), and the 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  $\dot{V}O_2$  (total-basal  $\dot{V}O_2$ ) by the progression speed. Each metabolic level resulted in being submaximal (respiratory quotient < 1), and the respiratory quotient caloric equivalent ( $\text{J/ml O}_2$ ) was multiplied by  $\dot{V}O_2$  for C calculation. Terrestrial running and skipping data in Figs. 1 and 2 and Fig. 6 are from Ardigó et al. (3) and Minetti et al. (21), respectively.

**Kinematics.** Three-dimensional body motion was sampled by a eight-camera system (Vicon MX, Oxford Metrics), measuring at a sampling rate of 100 Hz the spatial coordinates of 18 reflective markers located on the main joint centers. Each acquisition lasted 1 min, 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 three-dimensional trajectory, the time course of PE and KE were computed to obtain the total mechanical energy ( $\text{TE} = \text{PE} + \text{KE}$ ). The summation of all increases in TE time course constitutes the positive external work ( $W_{\text{EXT}}$ ,  $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ ) and represents the positive work necessary to accelerate and lift BCoM (6). The work necessary to rotate and accelerate limbs with respect to BCoM [internal work ( $W_{\text{INT}}$ ),  $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ ] (6, 16) (see Supplement S2) was also calculated and summed to  $W_{\text{EXT}}$  to obtain the total mechanical work ( $W_{\text{TOT}}$ ,  $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ ). The ratio between

$W_{\text{TOT}}$  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). All data have been analyzed with purposely written LabView programs (release 10, National Instruments).

**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 version 20 (IBM).

## 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, by displaying a minimum at similar speed regardless of the gravity level.

The C 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,  $30 \text{ ml O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) allowing skipping 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 (3 $\times$  for skipping, 2 $\times$  for running) that could be considered almost speed, and, within some limits, additional load mass-independent.

**Biomechanical parameters.** The mechanical  $W_{\text{EXT}}$ ,  $W_{\text{INT}}$ , and  $W_{\text{TOT}}$  in the three gaits and gravity conditions are plotted against speed in Fig. 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 hypogravity,  $W_{\text{EXT}}$  seemed speed independent, with a significant reduction compared with Earth: threefold lower on Mars and fourfold on Moon ( $P < 0.001$ , Earth vs. low gravity pooled;  $P < 0.01$ , Mars vs. Moon). In running, the  $W_{\text{EXT}}$  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;  $P <$

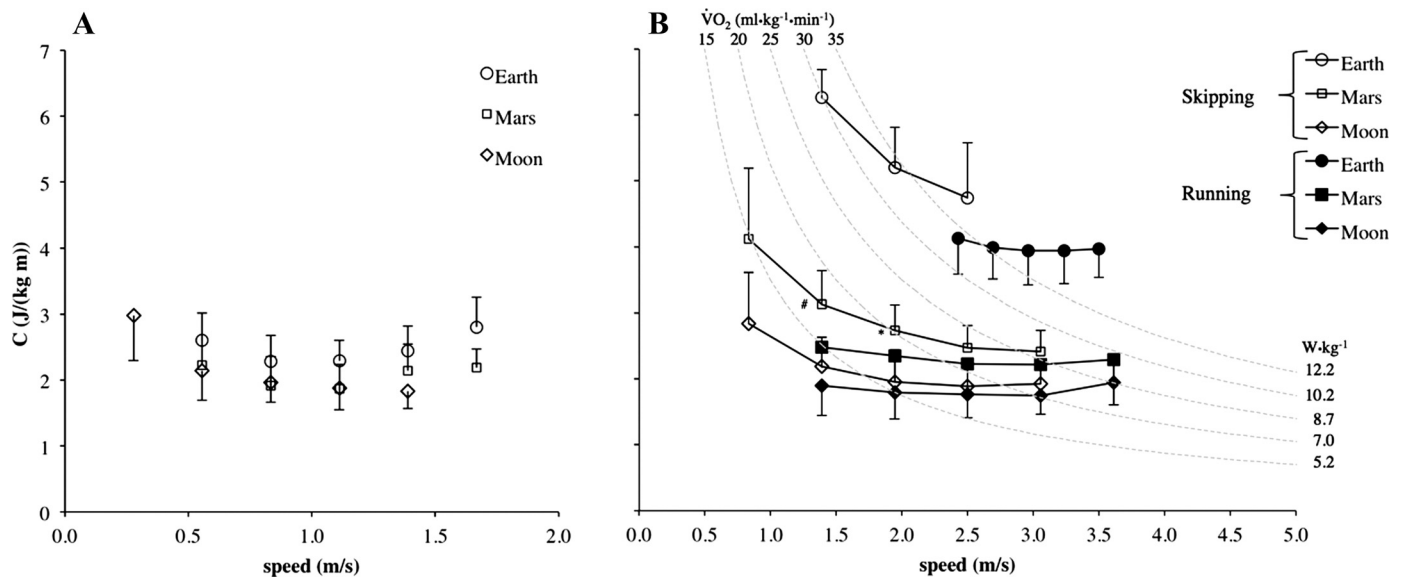


Fig. 1. Cost of transport ( $C$ ) as a function of speed and gravity has been grouped, for sake of clarity, according to bouncing and nonbouncing gait. *A*: walking on Earth (circles), Mars (squares), and Moon (diamond). *B*: running (solid symbols) and skipping (open symbols) on Earth, Mars, and Moon. Values are means  $\pm$  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 ml O<sub>2</sub>·kg<sup>-1</sup>·min<sup>-1</sup> or W/kg of body mass).  $\dot{V}O_2$ , O<sub>2</sub> consumption.

0.01, Mars vs. Moon) with a tendency of skipping toward 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 normalized for dynamic similarity, the maximal energy recovery value was reached at similar Froude number ( $Fr = v^2/gL$ ), where  $v$  is the progression speed,  $g$  is the acceleration due to gravity, and  $L$  is the leg length. The mean values of mechanical and bioenergetics parameters including  $Fr$  can be found in Supplement S3. In skipping, energy recovery was almost constant on Earth ( $\sim 25\%$ ), and its maximal value increased slightly, but not significantly, when gravity decreased, reaching Moon walking values.

Stride frequency (SF, Fig. 4) in walking significantly increased with speed, but was gravity independent. Skipping SF was speed independent in hypogravity, 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 vs. low gravity); however, SF was not different between Mars and Moon.

Low-gravity running involves a smaller descent of the BCoM 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 ( $\times 2$  on the Moon) during the flight phase than in running.

**Efficiency.** Locomotion efficiency, i.e., the ratio between  $W_{TOT}$  performed 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  $\sim 40\%$ , 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 Supplement S1).

Different 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 the subject's head. A short length could in fact help the subject maintain 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 setup, the pivot point was at least 12 m over the subject's head, and, as mentioned, the maximum induced fore-aft or mediolateral 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 operate inside a pressurized dome, our metabolic results should be corrected for the additional

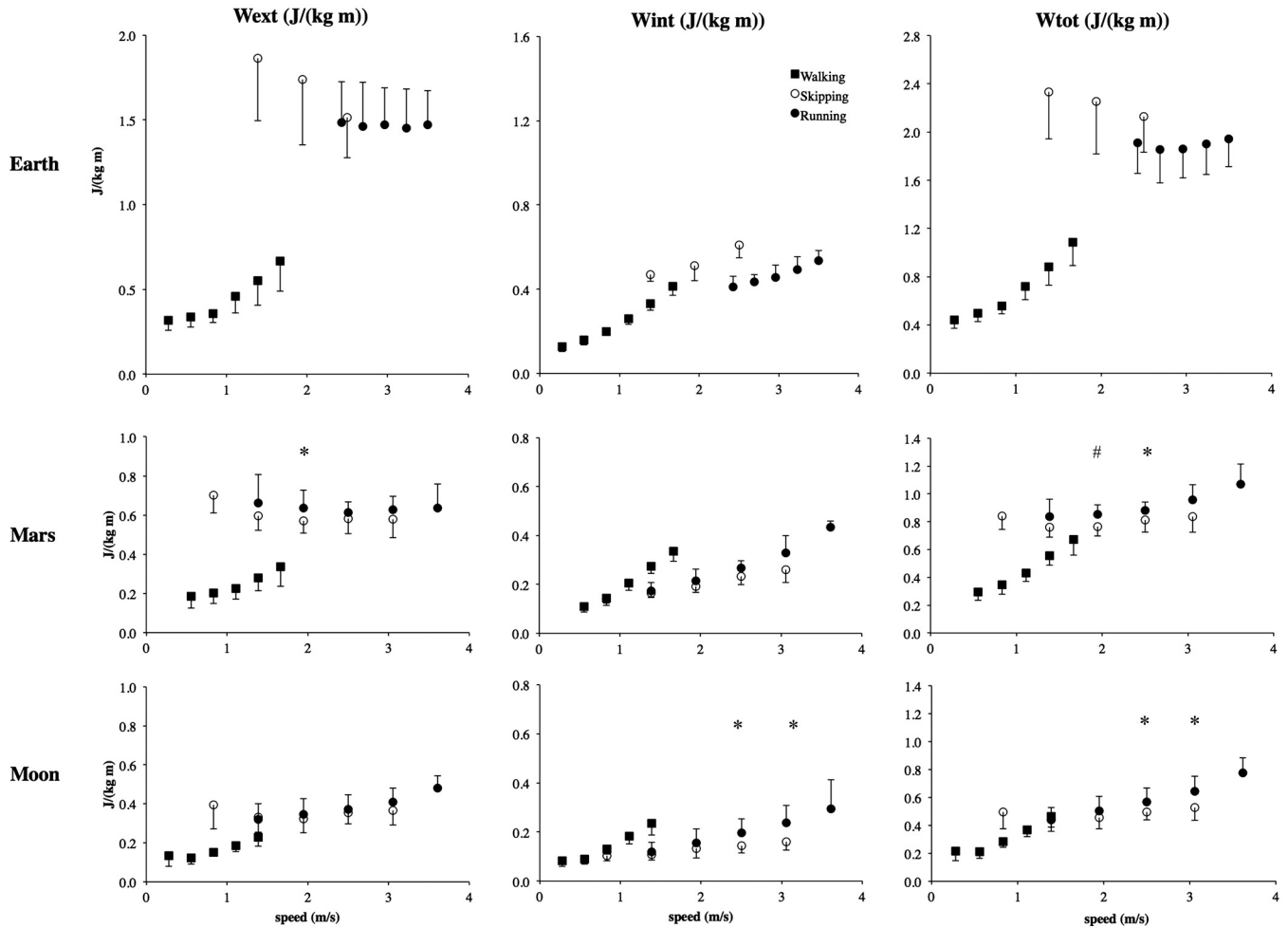


Fig. 2. Mechanical work. External work ( $W_{EXT}$ ;  $J \cdot kg^{-1} \cdot m^{-1}$ ), “kinematic” internal work ( $W_{INT}$ ;  $J \cdot kg^{-1} \cdot m^{-1}$ ), and total work ( $W_{TOT}$ ;  $J \cdot kg^{-1} \cdot m^{-1}$ ) of walking (■), running (●), and skipping (○) as a function of speed on Earth and on simulated Mars and Moon is shown. Values are means  $\pm$  SD. \* $P < 0.05$ . # $P < 0.01$ .

mass of the space suit (~117 kg), with a predictable decrease in speed, for the same available metabolic power.

The mechanical  $W_{EXT}$  was reduced by low gravity, mostly due to the PE in the three gaits. However, walking was negatively affected by this reduction, since the pendulum-like

saving mechanism needs the exchange between PE and KE to minimize muscular work. As showed in Fig. 3, energy recovery decreased at low gravity, and its peak value occurred at slower speeds, pointing out also a likely higher muscular work, which ultimately affects metabolic cost. These mechanical data

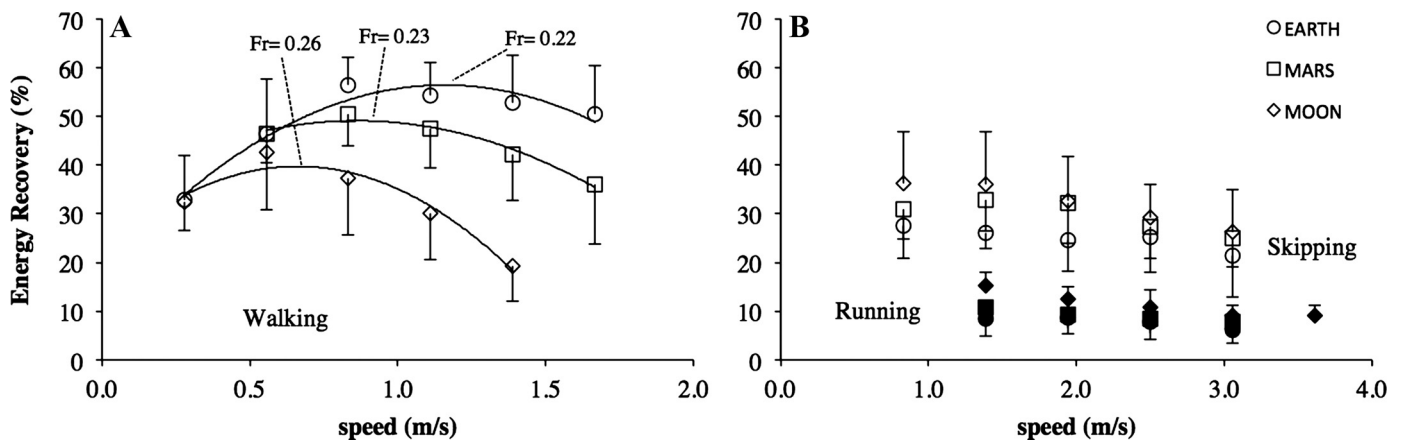


Fig. 3. Energy recovery (%) as a function of speed and gravity. A: walking on Earth (circles), Mars (squares), and Moon (diamond). Data are fit with a quadratic function, and its maximum normalized as Froude number (Fr). B: running (solid symbols) and skipping (open symbols) on Earth, Mars, and Moon. Values are means  $\pm$  SD.

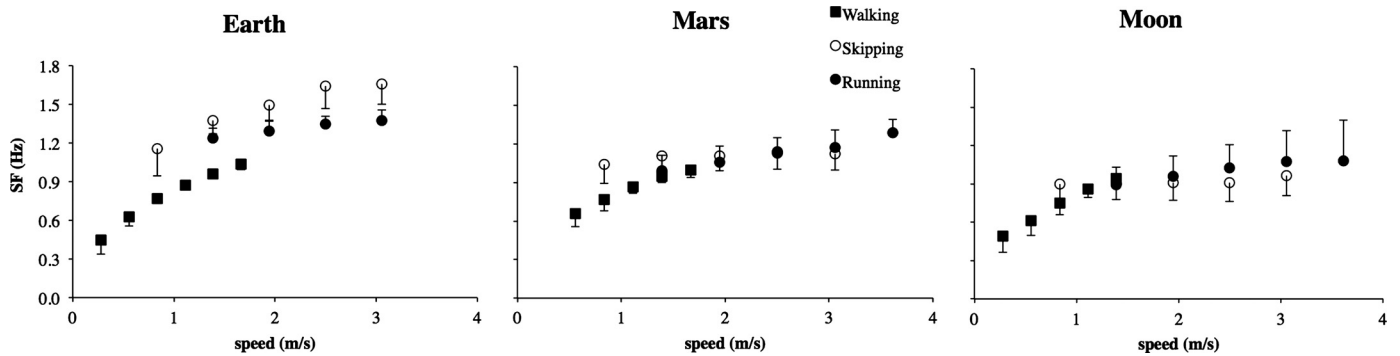


Fig. 4. Stride frequency (SF; Hz) as a function of speed and gravity in the three gaits: walking (■), running (●), and skipping (○). Values are means  $\pm$  SD.

are consistent with experiments by Cavagna et al. (8, 9) collected during parabolic flights and the predictions from the dynamic similarity theory (18). The  $W_{INT}$  decreased only between Earth and low-gravity planets, whereas SF 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 limb dynamics, which could affect whole body motion pattern, we found SF values very similar to those collected during parabolic flights (9), which are the gold standard, albeit short lasting, in heterogravity 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 have never been analyzed in such detail before, they are quite affected by gravity, and because of their relevance in fast locomotion.

Figure 2 shows that kinematic  $W_{INT}$  diminishes in low gravity (SF 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 SF. The  $W_{INT}$  can also be predicted by a model equation (16), which has as input variables the progression speed, SF, duty factor (df), 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  $W_{INT}$  changes in terms of the involved variables. In the present investigation, for example, the  $-67.5\%$  change of running  $W_{INT}$  when on the Moon can be partly explained by the  $24.7\%$  decrease in SF and the  $38.8\%$  lowering of the df (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”  $W_{INT}$  reduction, we can expect a much smaller “frictional”  $W_{INT}$  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 with 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, such 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 Fig. 5. By combining the lower impairment of the pogo stick (elastic) paradigm and the invariance or

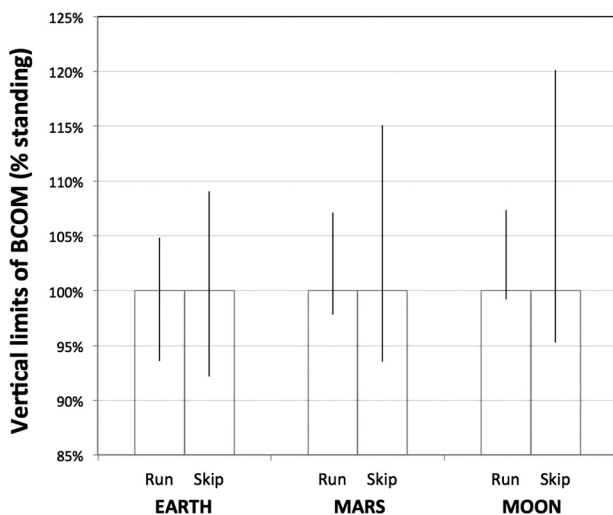


Fig. 5. Vertical body center of mass (BCoM) range. Descent (during contact) and ascent (during flight) of the BCoM is shown on Earth and on simulated Mars and Moon, as a percentage of the standing value, of running and skipping. Values are means  $\pm$  SD.

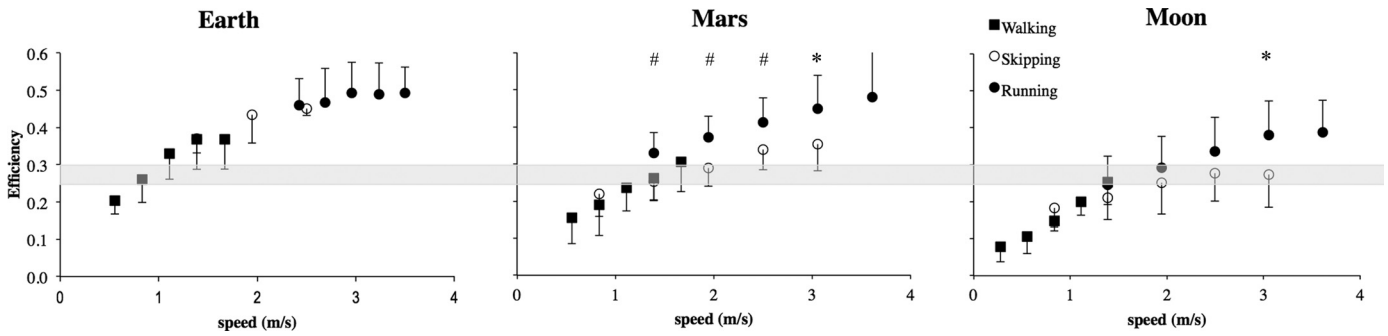


Fig. 6. Efficiency of walking (■), running (●), and skipping (○) as a function of speed on Earth and on simulated Mars and Moon. Shaded band indicates the muscular efficiency (0.25–0.30). Values are means ± SD. \**P* < 0.05. #*P* < 0.01.

slight improvement of the pendulum-like mechanics (see energy recovery in Fig. 3), skipping seems to rely on the two energy-saving strategies more 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. Compared with running, the *df* (2) (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 *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  $Fz = m \cdot g / (2 \cdot df)$ ] (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

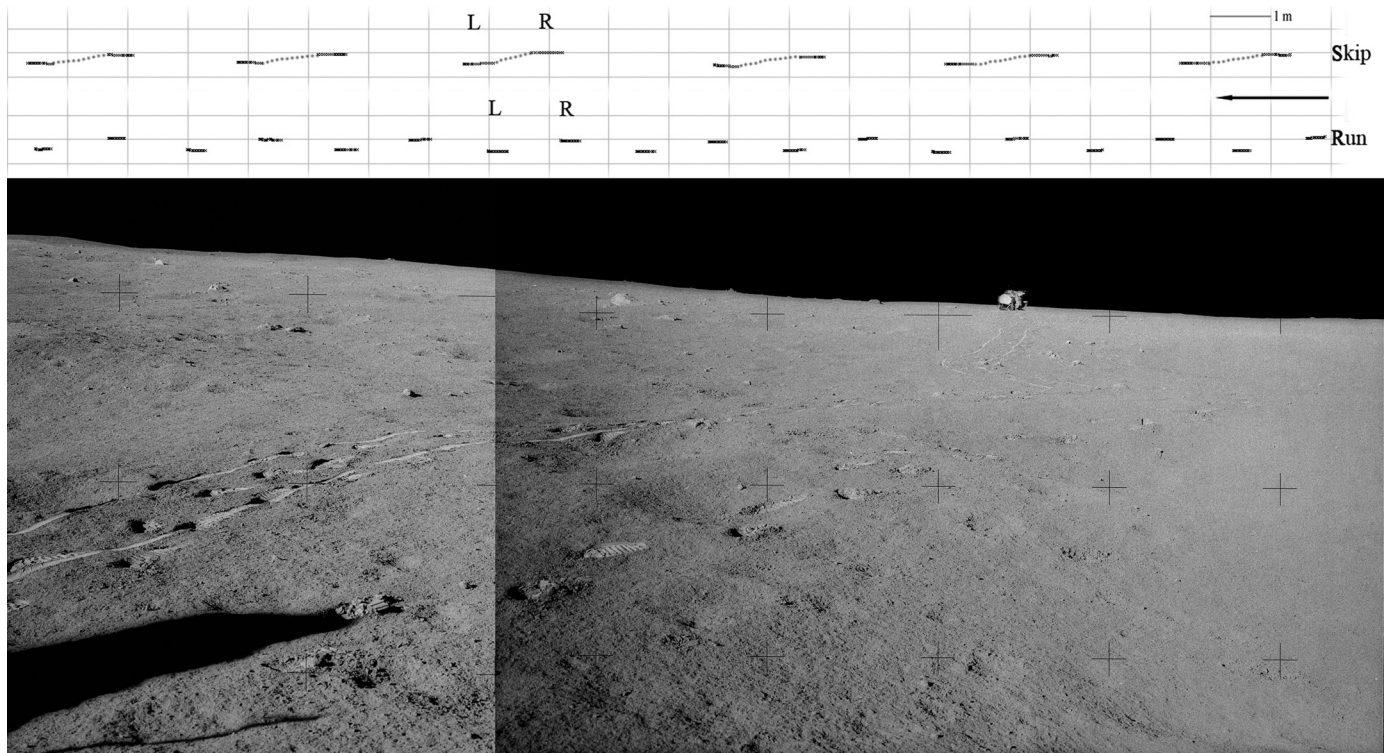


Fig. 7. Lunar boot prints. *Top*: foot casts of running (*bottom* trace) and unilateral left skipping (*top* trace). Skipping center of pressure is shown as a dotted curve (in running its path is confined within a single cast). *Bottom*: skipping boot prints of Alan Shepard during Apollo 14 Mission (<http://www.hq.nasa.gov/office/pao/History/alsj/a14/a14mini9407-8.jpg>). Body is moving toward *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). [Photos courtesy of NASA/JPL-Caltech].

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 traveled by the center of pressure (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), center of pressure persistence on the ground allows, particularly in slippery conditions, readjustment of 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. Different from running, skipping uses two 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 that quadrupeds deterministically use to turn (in the direction of the leading limb of the front pair first, then followed by the hindlimbs), 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 evidence points to asymmetry being an advantage. When modelistically 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 wearing a 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 with 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  $W_{INT}$  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 in being the gait of choice due to its peculiar biomechanics, which minimize 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. Different from quadrupedal pets (and lemurs) and probably already at ease with hypogravitational locomotion, humans will be confident by only restoring an almost dismissed gait.

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#### DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

#### AUTHOR CONTRIBUTIONS

Author contributions: G.P. and A.E.M. conception and design of research; G.P. and C.M.B. performed experiments; G.P. and C.M.B. analyzed data; G.P., C.M.B., and A.E.M. interpreted results of experiments; G.P. prepared figures; G.P. and A.E.M. drafted manuscript; G.P., C.M.B., and A.E.M. edited and revised manuscript; G.P., C.M.B., and A.E.M. approved final version of manuscript.

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