HOPPING locomotion at different gravity: metabolism and mechanics in humans

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Submitted 1 October 2015; accepted in final form 25 November 2015

Pavei G, Minetti AE. Hopping locomotion at different gravity: metabolism and mechanics in humans. J Appl Physiol 120: 1223–1229, 2016. First published December 3, 2015; doi:10.1152/japplphysiol.00839.2015.—Previous literature on the effects of low gravity on the mechanics and energetics of human locomotion already dealt with walking, running, and skipping. The aim of the present study is to obtain a comprehensive view on that subject by including measurements of human hopping in simulated low gravity, a gait often adopted in many Apollo Missions and documented in NASA footage. Six subjects hopped at different speeds at terrestrial, Martian, and Lunar gravity on a treadmill while oxygen consumption and 3D body kinematic were sampled. Results clearly indicate that hopping is too metabolically expensive to be a sustainable locomotion on Earth but, similarly to skipping (and running), its economy greatly (more than ×10) increases at lower gravity. On the Moon, the metabolic cost of hopping becomes even lower than that of walking, skipping, and running, but the general finding is that gaits with very different economy on Earth share almost the same economy on the Moon. The mechanical reasons for such a decrease in cost are discussed in the paper. The present data, together with previous findings, will allow also to predict the aerobic traverse range/duration of astronauts when getting far from their base station on low gravity planets.

low gravity; cost of transport; mechanical work; efficiency

SPACE EXPLORATION OF THE NEXT centuries will increasingly deal with the adaptation of our extant musculoskeletal system, which could not genetically change in the short term, to environments where bipedal locomotion is challenged by different terrains and gravity levels. From reading NASA technical debriefing of Apollo missions, astronauts’ concerns were not just about gait options, stability, comfort, and safety. Buzz Aldrin (Apollo 11) reported that he worried about the range to which the bipedal traverses could be extended and still ensure a sustainable return to the Lunar Module. In exercise physiology, talking about distance travelled implies gait type, progression speed, subject’s aerobic capacity, and the metabolic cost of transport [C; J/(kg m)]. Additional variables when bipedally moving on other celestial bodies are the spacesuit and the terrain characteristics, which both potentially increase the metabolic burden of locomotion.

In the past, the suitability of the different human gaits to other gravity levels has been widely discussed. The main outcomes were that, as gravity decreases, walking was mechanically impeded (13, 16) and running should have been replaced by hopping (13). Only rarely investigators tried to address the spontaneous gait choice, based on economy on Earth, by analyzing the metabolic cost of locomotion in simulated low gravity (10, 23).

Differently from biomechanical aspects of low gravity gaits, for the study of which the golden standard of heterogravity simulation on Earth, namely parabolic flights with controlled dives, could be used, metabolic features require much longer sessions for them to reach a reliable steady state. Hence the best simulator of low gravity for this purpose is still a body suspension system with long elastic cables (to ensure almost constant force) and a high pulley (to prevent fore–aft force interference).

For this reason we recently revamped a vertical, 17-m high “cavaedium” (vent shaft) where Margaria and Cavagna (13) arranged their pioneering experiments on low gravity about 50 years ago. By using 20-m bungee jumping bands, a pulley, and an electric winch, controlled body suspension allowed subjects to locomote on a treadmill with different gaits and speeds in simulated hypogravity. The very long elastic suspension ensures that the relatively small vertical excursion of the body does not affect the “constant” upward force. Walking (W), running (R), and unilateral skipping (S; as adopted by Apollo missions astronauts) were metabolically and mechanically analyzed, and the final message was that gaits with very different cost on Earth (C_S > C_R > C_W) share almost the same economy when they are performed on the Moon (20).

By inspecting NASA footage and reading debriefing reports, the importance of hopping emerged. Eugene Cernan (Apollo 17) reported that, although skipping was a very preferred gait on level, hopping was often chosen for downhill locomotion on the Moon. Also, that gait was encountered as a transitional phase between other gaits (skipping to walking, for instance) on level.

Humans moving by hopping lose their bipedalism, as kangaroos do, and tend to behave as a spring mass model monopod [similar to Raibert’s one legged hopping machine (21)]. As far as the mechanical paradigm is concerned, the combined lower limbs move as an individual limb of a running biped or of a trotting quadraped (15).

By realizing that hopping locomotion in humans has been seldom investigated at Earth gravity and never before in simulated low gravity, we decided to use the facility in Milan
to assess the metabolic cost and the most crucial biomechanical characteristics of human hopping at different speeds and gravity, with the aim to provide a comprehensive picture of the physiological burdens of all the feasible gaits when moving on low gravity planets.

MATERIALS AND METHODS

Heterogravity laboratory. The cavaedium (vent shaft) is a narrow (3 × 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 cavity. 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, Dynaemra SK78, ø 4 mm, l 1.2 m) working on the top pulley. One end of the rubber band was fixed to the wall, whereas 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 [see (20) for further details].

Subjects. Six subjects (27.2 ± 2.3 yr, 1.71 ± 0.05 m height, 66.0 ± 9.1 kg mass; mean ± 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 written informed consent. Subjects undertook two familiarization sessions to get used with hopping in simulated low gravity conditions where, particularly at high speeds, balance and proprioception were largely involved. After familiarization, subjects came to the laboratory four times to complete the metabolic and kinematic protocol.

Experimental protocol. Hopping was tested on Earth (1 g) and two simulated gravity levels, Mars (0.38 g) and Moon (0.17 g) at different speeds from 0.56 to 2.50 m/s, as already tested for other gaits previously (20); fastest speeds were excluded because of high level of motor control required during flight (further evidence that the apparatus does not apply forces that constrain the trajectory and could help balance). The three gravity levels were tested on different, not consecutive, days.

Metabolic measurements. Each experimental session was preceded by an 8-min standing resting V\textsubscript{O2} (ml O\textsubscript{2}·kg\textsuperscript{-1}·min\textsuperscript{-1}) assessment after which subjects started locomoting on the treadmill. Data acquisition lasted 4 min to reach a steady-state V\textsubscript{O2}. Respiratory gas were analyzed breath by breath with a portable metabograph (K4b 2, Cosmed, Italy), and the cost of transport [C; J/(kg·m)] is 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\textsubscript{2} consumption (total – resting V\textsubscript{O2}) by the progression speed. Each metabolic level in hypogravity resulted to be submaximal (RQ < 1), and the average RQ during the last minute of data collection was adopted as the caloric equivalent (J/mO\textsubscript{2}) of O\textsubscript{2} for C calculation. Blood lactate was sampled (Lactate Plus, Nova Biomedical) 5 min after each test to check the aerobic regime of hopping experiments. When exceeding basal values, lactate accumulation was used to correct C values [energy equivalent of 3.3 ml/ (kg·m\textsubscript{2}·s)](9).

Kinematics. Three-dimensional body motion was sampled by an eight 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 centers. Each acquisition lasted 1 min and the time course of the 3D body center of mass (BCoM) position was computed from a 11-segment model (17) based on Dempster inertial parameters of body segments (24). From BCoM 3D trajectory, the time course of potential (PE) and kinetic (KE) energies were computed to obtain the total mechanical energy (TE = PE + KE). The summation of all increases in TE time course constitutes the positive external work \([W_{\text{EXT}}, J/(kg\cdot m)]\) and reflects acceleration and lift of BCoM (5, 6). The work necessary to rotate and accelerate limbs with respect to BCoM \([W_{\text{INT}}, J/(kg\cdot m)]\) (15, 14) was also calculated and summed to \(W_{\text{EXT}}\) to obtain the total mechanical work \([W_{\text{TOT}}, J/(kg\cdot m)]\). The ratio between \(W_{\text{TOT}}\) and C was used to estimate net locomotion efficiency. All data have been analyzed with purposely written Labview programs (release 10, National Instruments). A total of 3,900 strides have been analyzed.

Statistics. Hopping data were compared using two-factor ANOVA with both speeds and gravity level as within-subjects effect. When significant effects were found, a one-way ANOVA with repeated measures was applied to the factor with significance set at \(r = 0.05\) (with Bonferroni post hoc test). “Frog” and “kangaroo” hopping values were compared with a Student’s t-test for paired data. Hopping data (present study) were compared with walking, running, and skipping data [different subjects from (20)] at the different gravity levels using a two-way ANOVA with speed and gait as between-subjects factors. When significant effects were found, a one-way ANOVA was applied to the factor with significance set at \(r = 0.05\) (with Bonferroni post hoc test). Statistical analyses were performed with SPSS V20 (IBM). Regression models for C as a function of gravity and speed are described in RESULTS.

RESULTS

Cost of transport. On Earth, subjects employed two different hopping techniques, one resembling the “frog hopping” (F-type) with a long stance phase and the presence of a great knee flexion; this allowed to move only at 0.56 m/s. The second, similar to a “kangaroo hopping” (K-type), used a slight knee flexion and a massive ankle plantar and dorsiflexion, which enabled subjects to hop also at 0.83 m/s (subjects were asked to hop also in the “not preferred technique”). In both cases, the cost of transport of hopping (CH) on Earth was very high (and not significantly different at 0.56 m/s; Fig. 1) and lactate concentration was taken into account for CH calculation, because its value was 6 ± 2 mM.

![Fig. 1. Cost of transport as a function of speed and gravity.](http://jap.physiology.org/)
When moving in simulated hypogravity, only the K-type was chosen, \( C_\text{H} \) decreased, and hopping became aerobically sustainable in the whole range of investigated speeds. On Mars, \( C_\text{H} \) was speed independent at speeds greater than 1.39 m/s and was still significantly higher than skipping and running \( (C_\text{R}, P < 0.05) \) and running \( (C_\text{R}, P < 0.001) \) at paired speed. On the Moon, \( C_\text{H} \) decreased compared with Mars \( (P < 0.01) \) and hopping was slightly, but not significantly, more economical than both skipping and running; at low speed, hopping displayed the same cost of walking \( [C_\text{W}; \text{all the data about terrestrial and low gravity values of } C_\text{W}, C_\text{R}, \text{and } C_\text{S} \text{ in Fig. 1 are from (20)}] \). By visual inspection of metabolic cost data on a 3D graph with axes \( C \), speed \( (v, \text{m/s}) \), and gravity \( (g, \text{fraction of Earth gravity}) \), it seemed that a regression model with a parabolic profile in the \( C \) vs. \( v \) plane and a linear relationship in the \( C \) vs. \( g \) plane would have accurately interpolated the experimental data. Thus the nonlinear multiple regression univariate model \( C = a + b\cdot v + c\cdot v^2 + d\cdot g \) was set in a web-based statistical package (http://statpages.org/nonlin.html) and the results were \( C_\text{W} = 3.531 - 3.374 \cdot v + 1.535 \cdot v^2 + 0.557\ g \ [r^2 = 0.904]; p(g) = 0.0001]; C_\text{R} = 2.004 - 0.525 \cdot v + 0.093 \cdot v^2 + 2.701\ g \ [r^2 = 0.995]; p(g) = 0.0000]; C_\text{S} = 3.993 - 2.266 \cdot v + 0.420 \cdot v^2 + 4.126\ g \ [r^2 = 0.974]; p(g) = 0.0000]; C_\text{H} = 3.829 - 3.363 \cdot v + 0.769 \cdot v^2 + 3.630\ g + 13.267\ g^2 \ [r^2 = 0.999]; p(g1) = 0.1497 \text{ and } p(\text{g2}) = 0.0018] \text{ data about hopping on Earth referred to two speeds only; thus, to obtain a 3D contour profiling, and running values (from 20) are superposed for comparison.}

\( W_\text{EXT} \) for hopping decreased with speed in hypogravity, and mean values significantly decreased when gravity was low \( (\text{Earth vs. low gravity pooled } P < 0.001) \). On Mars, hopping \( W_\text{EXT} \) values were higher compared with skipping and running \( (P < 0.001) \), whereas on the Moon at higher speed the values were comparable. Compared with walking at paired speed, hopping \( W_\text{EXT} \) was always higher \( (P < 0.001) \). The value on Earth was over two times higher than skipping. The K-type showed higher values than F-type \( (P < 0.01) \) due to the higher stride frequency, which involves more BCoM rises for the same unit distance.

\( W_\text{INT} \) was almost speed independent both on Mars and on the Moon, decreased as average when gravity was low \( (\text{Earth vs. low gravity pooled } P < 0.001; \text{Mars vs. Moon } P < 0.05 \text{ at } 1.39 \text{ and } 1.94\text{ m/s}) \). Compared with the other bouncing gaits, hopping showed similar values on Mars, but lower values on Moon both with respect to running \( (P < 0.01) \) and skipping \( (P < 0.05) \). As for \( W_\text{EXT} \), Earth values were about two times higher than the highest known value, and the two hopping strategies lead to different, although not statistically significant, values, with F-type showing higher values.

Average hopping \( W_\text{TOT} \), as the sum of \( W_\text{EXT} \) and \( W_\text{INT} \), decreased when comparing pooled low gravity data with terrestrial values \( (P < 0.001) \); Moon \( W_\text{TOT} \) was lower than Mars (at 0.83 m/s, \( P < 0.05 \), in the range 1.39-2.5 m/s, \( P < 0.001 \)). \( W_\text{TOT} \) decreased also at increasing speed within each low gravity level. Compared with the bouncing gaits, on Mars hopping \( W_\text{TOT} \) was statistically higher at all speeds \( (P < 0.0001) \), whereas on the Moon it was higher than skipping only at 0.83 m/s \( (P < 0.001) \) and lower than running at 2.5 m/s \( (P < 0.05) \). The K-type displayed higher total work than F-type at the same speed \( (P < 0.05) \) on Earth.

Stride frequency \( (\text{SF}, \text{Hz}; \text{Fig. 3}) \) on Earth was significantly different between K-type and F-type \( (P < 0.001) \). In low gravity, SF significantly decreased \( (\text{average Mars vs. Moon } P < 0.01) \) and appeared to be speed independent. Compared with the bouncing gaits, hopping SF was lower \( (P < 0.01) \) above 0.83 m/s in both gravity conditions. Figure 4 shows that the decrease in hopping SF at low gravity is mainly caused by a higher flight duration, while contact time is almost invariant at all speeds and gravity levels.

**Efficiency.** Locomotion efficiency, i.e., the ratio between total work performed \( (W_\text{TOT}) \) and energy consumed \( (C) \) was, on average, the same in the two low gravity conditions \( (about 36\%; \text{Fig. 5}) \). The efficiency of hopping in all gravity conditions \( (\text{K-type on Earth}) \) was higher than muscle efficiency \( (about 25–30\% (25)) \), indicating some elastic energy storage and release. Compared with the other bouncing gaits, on Mars hopping efficiency was similar to running. However, when moving on the Moon, running efficiency drop and the values are similar only for the highest speed.

**DISCUSSION**

Hopping, in all its forms, is revealed to be a very expensive gait on Earth, close to the maximum aerobic capacity of sedentary healthy subjects. There is no surprise, therefore, that it is never used as a sustainable terrestrial gait. The reasons for this debacle in economy can be found in the mechanical measures \( (\text{Fig. 2, first row of graphs}) \). The external work, being the main component of total mechanical work, is four times higher than for the other bouncing gaits. Even by considering that its value incorporates the unknown effect of springs, it is likely that most of the measured increase in \( W_\text{EXT} \) can be ascribed to an increased cumulative vertical excursion of BCoM per meter travelled. Together with the smaller increase in \( W_\text{INT} \), \( W_\text{TOT} \) results to be 3.5 times higher than the other bouncing gaits, almost the same gain we observed in metabolic cost.

Hopping economy remarkably shows at decreased gravity an almost linear increase, similarly to the other bouncing gaits previously studied \( (\text{Fig. 1}) \), meaning that Mars values lay very close to the surface linearly connecting Earth and Moon values. Another important similarity with all the other gaits is that when at Moon gravity the decrease of \( C_\text{H} \) is so pronounced \( (9.5) \) to reach the other gaits values. We will return on this below when discussing the gait choice based on metabolic energy minimization in low gravity.

When comparing Moon to Earth mechanical results for hopping, we observed a similar reduction scope: about /10 for \( W_\text{EXT} \), about /11 \( W_\text{INT} \), and, obviously, about /11 for \( W_\text{TOT} \). The speed dependence of those values was found to be very similar in the data series of simulated Mars and simulated Moon \( (\text{Fig. 2}) \).

By combining similar reduction scopes of mechanical and metabolic costs, a similar efficiency is expected. Figure 5 shows that this is the case for the three gravity levels. Differ-
ently from the other bouncing gaits, where “apparent” efficiency values tend to reach “muscular” levels as gravity decreases, indicating an impairment in using elastic structures to save mechanical energy (20), the high and almost gravity-independent efficiency of hopping reflects the persistence of a spring mass model paradigm at low gravity. It is a challenge to understand why hopping retains the “spring” attitude, whereas skipping and running progressively lose that feature. A tentative reason is that during hopping (particularly the K-type) the lower limbs are almost fully extended, allowing only a subset of elastic structures (say Achille’s tendon) to be involved in the bounce. It is possible that “tuning” only one anatomical spring for the different gravity levels would be easier than dealing with a system of springs. When performing F-type, subjects were not able to conclude the 0.83 m/s bout. The great knee range of motion, with subsequently BCoM displacement, probably involved a stronger quadriceps concentric contraction, and the longer stance phase required also isometric contractions to stabilize the whole body, which would cause a greater muscular demand and fatigue compared with K-type hopping. Moreover, the different foot/leg approach to the ground and the longer stance phase in F-type could strongly reduce the store and reuse of elastic energy, so that all the work measured is effectively done by muscles.

As far as the metabolic power is concerned, it can be calculated that the same (quite high) terrestrial effort, main-
tained on the Moon, would allow a 10× increase of hopping speed [it was 2× for running and 3× for skipping (20)], allowing to reach an extrapolated speed of about 6 m/s (21.6 km/h).

By linking the metabolic data of low gravity walking, running, skipping (20) and the present results about hopping opens the question about which could be the preferred gait, at a given (low) gravity and speed, based on the economy criterion. On Earth this criterion dominates gait choices in bipeds and quadrupeds (3) and it seems a useful exercise to predict what could happen at lower gravity.

Figure 6 uses regression equations, reported in RESULTS for each gait, to show the most economical [lowest C, J/(kg·m)] gait for each (gravity, speed) condition. Dotted curves represent iso-cost conditions, and the solid black curves delimitates (gravity, speed) pairs where the same gait is the most economical. The graph can be illustrated from right (Earth) to left (Moon). At g = 1 walking is the preferred gait up to a speed of about 2 m/s, with a minimum cost [2.2 J/(kg·m)] of at about 1.2 m/s (optimum speed), at faster speeds running is the most economical choice (with respect to all the other gaits) with a speed-independent cost of about 4 J/(kg·m). When moving to lower gravity planets, the range of feasible walking reduces and the one for running expands, but it has to be noticed that C is reducing more in running than in walking. Still, these two gaits are the best, according to economy, at Mars gravity. At even lower gravity, approaching Moon level, other gaits compete for the best economy: skipping and hopping, in which similarly low values in overlapped speed ranges, beat running, whereas walking still reduces its operative speed range. From this graph we can conclude that, to consume the least amount of metabolic energy per unit distance on the Moon, humans should adopt walking up to a speed of 1.2 m/s, hopping up to 2.5 m/s, skipping up to 3 m/s, and (perhaps) running at higher speeds. However, because walking gait is impaired because of the lost “pendulum like” motion and the occasional appearance of a short flight phase at the highest investigated speed (7, 8, 16), hopping could be mechanically preferred also in the 0.83–1.2 m/s speed range. It is interesting to note that the decrease of speed limit between walking and running at low gravity follows the trend indicated by both the dynamic similarity model [Froude 0.5, white curve in Fig. 6 (16)] and the preferred walk-run transition speed trend as investigated in other simulated gravity studies (11).

As already mentioned previously (20), economy is not the only criterion. Ackerman and Van den Bogert (1) searched for a model for the minimum locomotion effort and fatigue at Mars and Moon gravity levels. Gaits considered were walking, running and skipping. They found that on Mars walking is still the best gait at low speed (1.1 m/s) and that skipping (fatigue)
and running (effort) are the solution at high speed (2 m/s). On
the Moon, their best prediction was skipping for both criterion
and speeds. Unfortunately hopping was not part of their mod-
elling, thus it is difficult to say how it would have competed
with the other gaits, particularly at Moon gravity. When
considering this omission, the model predictions are consistent
with Fig. 1, where our experimental metabolic minimization is
equivalent to Ackerman and Van den Bogert’s “minimum
effort cost function” (1).

It is worth considering that all the present and past results
about hypogravity locomotion (7, 8, 10, 11, 20) refer to
subjects wearing no spacesuit. Garment could, on one side,
impede normal body movement and increase friction among
limbs but, on the other side, facilitate bouncing gaits by
storing in the pressurized exoskeleton energy during landing
and later releasing it for the successive take off (4). For
these reasons we believe that our results will approximately
reflect the relationship between analogous conditions (dif-
f erent gravity same speed or same gravity different speed),
both for metabolic and mechanical parameters, of astronauts
wearing spacesuits.

In conclusion, human hopping is a metabolically expensive
gait on Earth that at low gravity reduces its cost to values even
smaller that all the other feasible types of bipedal locomotion
(walking, running, and skipping). Because the four gaits were
used in Apollo missions, the present mechanical and metabolic
study about hopping allows us to shed light onto the role of
metabolism and mechanics in setting the spontaneous gait
choice at different speeds and gravity.

All of this deals with level locomotion, but we know that
space exploration includes gradient and different terrain types.
On Earth, an almost linear increase of walking, running, and
skipping cost has been reported when moving uphill, whereas
a minimum cost of walking and running at a downhill gradient
of about −10% has been documented (12, 17–19). However,
there are no data at other gravity. Both Moon and Mars surface
are characterized by craters, reefs, and valleys, with slopes
reaching values up to 13% on the Moon (22) and as steep as
40% on Mars (2). From the Apollo missions, we know that
astronauts used both hopping and skipping when moving on
gradient, but we still do not know if this choice was driven only
by a matter of balance or also by mechanical and metabolic
factors. Other studies are therefore needed to extend to gradient
the mechanical and metabolic characteristics of low gravity
locomotion.

ACKNOWLEDGMENTS

The authors thank J. Storniolo for assistance in data collection.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: G.P. performed experiments; G.P. and A.E.M. ana-
yzed data; G.P. and A.E.M. interpreted results of experiments; G.P. and
A.E.M. prepared figures; G.P. and A.E.M. drafted manuscript; G.P. and

Fig. 5. Efficiency of hopping (circles: Hopping F: F-type; Hopping K: K-type) as a function of speed on Earth and on simulated Mars and Moon. Vertical lines
represent SD. Walking (dotted line), skipping (continuous line), and running (dashed lines) values are presented for comparison [adapted with permission from
(20)]. Gray band indicates the muscular efficiency [0.25–0.30 (25)].
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