Reducing gravity takes the bounce out of running

Delyle T. Polet[1,‡], Ryan T. Schroeder[2], John E. A. Bertram[3]

Keywords: bipedal running, reduced gravity, leg swing, energetics, optimization

Summary Statement: As gravity decreases, humans reduce peak vertical speed in running to optimally balance energetic costs of ground-contact collisions and frequent steps, contributing to lower vertical displacement during the non-contact phase.

Abstract

In gravity below Earth normal, a person should be able to take higher leaps in running. We asked ten subjects to run on a treadmill in five levels of simulated reduced gravity and optically tracked center of mass kinematics. Subjects consistently *reduced* ballistic height compared to running in normal gravity. We show that this trend is partially explained by considering maximum vertical speed during the stride (MVS). Energetically optimal gaits should balance energetic costs of ground-contact collisions (favouring lower MVS), and step frequency penalties such as leg swing work (favouring higher MVS, but less so in reduced gravity). Measured MVS scaled with the square root of gravitational acceleration, following energetic optimality predictions and explaining why ballistic height does not increase in lower gravity. While it may seem counterintuitive, using less "bouncy" gaits in reduced gravity is a strategy to reduce energetic costs, to which humans seem extremely sensitive.

Introduction

Under normal circumstances, why do humans and animals select particular steady gaits from the myriad possibilities available? One theory is that the chosen gaits minimize metabolic energy expenditure (Alexander and Jayes, 1983; Ruina et al., 2005). To test this theory, one can subject organisms to abnormal circumstances. If the gait changes to a new energetic optimum, it can be inferred that energetics also govern gait choice under normal conditions (Bertram and Ruina, 2001; Long and Srinivasan, 2013; Selinger et al., 2015).

One "normal" gait is the bipedal run, and one abnormal circumstance is that of reduced gravity. Movie S1 demonstrates the profound effect reducing gravity has on running kinematics. A representative subject runs at 2 m s^{-1} in both Earth-normal and simulated lunar gravity (about one-sixth of Earth-normal). In both cases, the video is slowed by a factor of four. The change in kinematics is apparent; the gait in normal gravity involves pronounced center-of-mass undulations compared to the near-flat trajectory of the low-gravity gait. This gait modification seems paradoxical: in reduced gravity, people are free to run with much higher leaps. Instead, they seem to flatten the gait. Why should this be?

[1]Department of Biological Sciences, University of Calgary, Calgary T2N 1N4, Canada [2]Biomedical Engineering, University of Calgary, Calgary T2N 1N4, Canada [3]Cumming School of Medicine, University of Calgary, Calgary T2N 1N4, Canada [‡]Author for correspondence: dtpolet@ucalgary.ca

He et al. (1991) noticed that subjects in reduced gravity lower vertical center of mass speed at the beginning of the non-contact phase. This observation implies a constant height, relative to height at takeoff, achieved during the ballistic phase, and a flattening of the parabolic arc. He et al. did not point to a specific mechanism for why vertical takeoff speed scales in this way, but proposed the relationship on the basis of dimensional analysis.

A simple explanation posits that the behaviour is energetically beneficial. To explore the energetic consequences of modifying vertical takeoff speed in running, and to understand more thoroughly the dynamics of the running gait, we follow Rashevsky (1948) and Bekker (1962) by modelling a human runner as a point mass body bouncing off rigid vertical limbs (Fig. 1). This simple model does not invoke elastic energy recoil from the leg, so should be a conservative estimate of contact loss in running. During stance, all vertical velocity is lost through an inelastic collision with the ground (Fig. 1b). Horizontal speed, however, is conserved. The total kinetic energy lost per step is therefore $E_{\text{col}} = mV^2/2$, where m is the runner's mass and V is their vertical takeoff speed (Fig. 1). Lost energy must be recovered through muscular work to maintain a periodic gait, and so an energetically-optimal gait will minimize these losses. If center-of-mass kinetic energy loss were the only source of energetic cost, then the optimal solution would always be to minimize vertical takeoff velocity. However, such a scenario would require an infinite stepping frequency, as this frequency (ignoring stance time and air resistance) is $f = g/(2V)$, where g is gravitational acceleration.

Let us suppose there is an energetic penalty that scales with step frequency, as $E_{\text{freq}} \propto f^k \propto g^k/V^k$, where $k > 0$. Such a penalty may arise from work-based costs associated with swinging the leg, which are frequency-dependent (Alexander, 1992; Doke et al., 2005), or from short muscle burst durations recruiting less efficient, fast-twitch muscle fibres (Kram and Taylor, 1990; Kuo, 2001). This penalty has minimal cost when V is maximal and, notably, increases with gravity (this fact comes about since runners fall faster in higher gravity, reducing the non-contact duration). Therefore, the two sources of cost act in opposite directions: collisional loss promotes lower takeoff speeds, while frequency-based cost promotes higher takeoff speeds.

If these two effects are additive, then it follows that the total cost per step is

$$\begin{aligned} E_{\text{tot}} &= E_{\text{col}} + E_{\text{freq}} \\ &= mV^2/2 + Ag^k/V^k \end{aligned} \tag{1}$$

where A is an unknown proportionality constant relating frequency to energetic cost. As the function is continuous and smooth for $V > 0$, a minimum can only occur either at the boundaries of the domain, or when $\frac{\partial E_{\text{tot}}}{\partial V} = 0$. Solving the latter equation yields

$$V^* \propto g^{k/(k+2)} \tag{2}$$

as the unique critical value. Here the asterisk denotes a predicted (optimal) value. Since E_{tot} approaches infinity as V approaches 0 and infinity (equation 1), the critical value must be the global minimum in the domain $V > 0$. As $k > 0$, it follows from equation 2 that the energetically-optimal solution is to reduce the vertical takeoff speed as gravity decreases.

The observation of He et al. (1991) that $V^* \propto \sqrt{g}$ implies $k = 2$. However, their empirical assessment of the relationship used a small sample size, with only four subjects. We tested the prediction of the relationship between V^* and g by measuring the maximum vertical speed over each running stride, as a proxy for takeoff speed, in ten subjects using a harness that simulates reduced gravity. We also measured the maximum vertical displacement in the ballistic phase to verify whether the counter-intuitive observation of lowered ballistic COM height in hypogravity, as exemplified in Movie S1, is a consistent feature of reduced gravity running.

Methods

We asked ten healthy subjects to run on a treadmill for two minutes at 2 m s^{-1} in five different gravity levels (0.15, 0.25, 0.35, 0.50 and 1.00 G, where G is 9.8 m s^{-2}). A belt speed of 2 m s^{-1} was chosen as a comfortable, intermediate jogging pace that could be accomplished at all gravity levels. Reduced gravities were simulated using a harness-pulley system similar to that used by Donelan and Kram (2000). The University of Calgary Research Ethics Board approved the study protocol and informed consent was obtained from all subjects.

Due to the unusual experience of running in reduced gravity, subjects were allowed to acclimate at their leisure before indicating they were ready to begin each two-minute measurement trial. In each case, the subject was asked to run in any way that felt comfortable. Data from 30 to 90 s from trial start were analyzed, providing a buffer between acclimating to experimental conditions at trial start and possible fatigue at trial end.

Implementation and measurement of reduced gravity

Gravity levels were chosen to span a broad range. Of particular interest were low gravities, at which the model predicts unusual body trajectories. Thus, low levels of gravity were sampled more thoroughly than others. The order in which gravity levels were tested were randomized for each subject, so as to minimize sequence conditioning effects.

For each gravity condition, the simulated gravity system was adjusted in order to modulate the force pulling upward on the subject. In this particular harness, variations in spring force caused by support spring stretch during cyclic loading over the stride were virtually eliminated using an intervening lever. The lever moment arm was adjusted in order to set the upward force applied to the harness, and was calibrated with a known set of weights prior to all data collection. A linear interpolation of the calibration was used to determine the moment arm necessary to achieve the desired upward force, given subject weight and targeted effective gravity. Using this system, the standard deviation of the upward force during a trial (averaged across all trials) was 3% of the subject's Earth-normal body weight.

Achieving exact target gravity levels was not possible since the lever's moment arm is limited by discrete force increments (approximately 15 N). Thus, each subject received a slight variation of the targeted gravity conditions, depending on their weight. A real-time data acquisition system allowed us to measured tension forces at the gravity harness and calculate the effective gravity level at the beginning of each new condition. The force-sensing system consisted of an analog strain gauge (Micro-Measurements CEA-06-125UW-350), mounted to a C-shaped steel hook connecting the tensioned cable and harness. The strain gauge signal was passed to a strain conditioning amplifier (National Instruments SCXI-1000 amp with SCXI-1520 8-channel universal strain gauge module connected with SCXI-1314 terminal block), digitized (NI-USB-6251 mass termination) and acquired in a custom virtual instrument in LabView. The tension transducer was calibrated with a known set of weights once before and once after each data collection trial to correct for modest drift error in the signal. The calibration used was the mean of the pre- and post-experiment calibrations.

Center of mass kinematic measurements

A marker was placed at the lumbar region of the subject's back, approximating the position of the center of mass. Each trial was filmed at 120 Hz using a Casio EX-ZR700 digital camera. The marker position was digitized in DLTdv5 (Hedrick, 2008). Position data were differentiated using a central differencing scheme to generate velocity profiles, which were further processed with a 4^{th}-order low-pass Butterworth filter at 7 Hz cutoff. The vertical takeoff speed was defined as the maximum vertical speed during each gait cycle (V in Fig. 1). This definition corresponds to the moment at the end of stance where the net vertical force on the body is null, in accordance with a definition of takeoff proposed by Cavagna (2006).

Vertical takeoff velocities were identified as local maxima in the vertical velocity profile. Filtering and differentiation errors occasionally resulted in some erroneous maxima being identified. To rectify this, first any maxima within ten time steps of data boundaries were rejected. Second, the stride period was measured as time between adjacent maxima. If any stride period was 25% lower than the median stride period or less, the maxima corresponding to that stride period were compared and the largest maximum kept, with the other being rejected. This process was repeated until no outliers remained.

Position data used to determine ballistic height were processed with a 4^{th}-order low-pass Butterworth filter at 9 Hz cutoff. Ballistic height was defined as the vertical displacement from takeoff to the maximum height within each stride. No outlier rejection was used to eliminate vertical position data peaks, since the filtering was not aggressive and no differentiation was required. If a takeoff could not be identified prior to the point of maximum height within half the median stride time, the associated measurement of ballistic height was rejected; this strategy prevented peaks from being associated with takeoff from a different stride.

Statistical methods

Takeoff velocities and ballistic heights were averaged across all gait cycles in each trial for each subject. To test whether ballistic height varied with gravity, a linear model between ballistic height and gravitational acceleration was fitted to the data using least squares regression, and the validity of the fit was assessed using an F-test. Since the proportionality coefficient between V^* and $\sqrt{g}$ is unknown *a priori*, we derived its value from a least squares best fit of measured vertical takeoff speed against the square root of gravitational acceleration, setting the intercept to zero. Given a minimal correlation coefficient of 0.5 and sample size of 50, a *post-hoc* power analysis yields statistical power of 0.96, with type I error margin of 0.05. Data were analyzed using custom scripts written in MATLAB (v. 2016b).

Results and Discussion

Pooled data from all trials are shown in Fig. 2. Fig. 2A shows that ballistic height increases with gravity (linear vs constant model, $p = 4 \times 10^{-3}$), validating that the counter-intuitive result exemplified in Movie S1 is a consistent feature of running in hypogravity. Despite being statistically distinguishable from a constant model, the linear fit is a poor predictor of ballistic height, with $R^2 = 0.24$.

Takeoff velocity also increases with gravitational acceleration (Fig. 2B), and a least-squares fit using $k = 2$ is a good predictor of the empirical measurements. The fit exhibits an R^2 value of 0.73, indicating that this simple energetic model can explain over two thirds of the variation in maximum vertical speed resulting from changes in gravity. The remaining variation may come about due to individual differences (*e.g.* leg morphology) that would affect the work needed to accelerate the limbs, or from simplifications of the model that ignore effects such as finite stance time. The agreement of the model with the data supports the relationship found by He et al. (1991), and indicates that a frequency-based cost proportional to f^2 can make accurate predictions of gait adjustments to non-normal functional circumstances.

Though we did not directly measure the frequency-based cost in this study, our results suggest that leg swing is a dominant source. Using a simple model of a biped, Alexander (1992) suggested that swing cost results primarily from adding and removing rotational energy to and from the leg during swing, and should scale with frequency squared, as our model assumes. Though leg swing costs are difficult to measure in humans, they compose up to 24% of total limb work in guinea fowl (Marsh et al., 2004). Humans likely have a similar or higher cost to leg swing: Willems et al. (1995) estimate that at least 25% of total muscular work does not accelerate the center of mass during human running.

Regardless of the exact mechanism relating step frequency to energetic cost, the present results indicate that the cost of step frequency is a key factor in locomotion. Although the exact value of the optimal takeoff speed depends on both frequency-based penalties and collisional costs, the former penalties change with gravity while the latter do not (Fig. 3). Collisional costs are independent of gravity because the final vertical landing velocity is alone responsible for the lost energy. Regardless of gravitational acceleration, vertical landing speed must equal vertical takeoff speed in the model; so a particular takeoff speed will have a particular, unchanging collisional cost.

However, taking off at a particular vertical velocity results in less frequent steps at lower levels of gravity– thus, the frequency-based costs are reduced as gravity decreases (Fig. 3). According to our model, the observed changes in kinematics with gravity occur only because frequency-based costs are, surprisingly, gravity-sensitive (due to the influence of gravity on non-contact flight time). Frequency-based costs appear to be an important determinant of the effective movement strategies available to the motor control system. Their apparent influence warrants further investigation into the extent of their contribution to metabolic expenditure.

The simple impulsive model underpredicts the changes observed in ballistic height. The dotted line in Fig. 2A is the predicted height achieved given the best-fit of the takeoff velocity in Fig. 2B, assuming ballistic trajectories after takeoff, and is consistently lower than mean values for $g > 0.3\,\mathrm{G}$. We defined "takeoff" as occurring when the net force on the body was null and velocity was maximal; however, this does not equate to the moment when the stance foot leaves the ground. After the point of maximal velocity, upward ground reaction forces decay to zero. During this time, the net deceleration on the body is less than gravitational deceleration. Thus, the body travels higher than would be expected if maximal velocity corresponded exactly to the point where the body entered a true ballistic phase, as in the model.

He et al. (1991) observed that stance times increase with gravity. Since we expect shorter stance times to reduce the time between maximal velocity and foot liftoff, the measured takeoff velocity should better predict the observed ballistic height in lower gravity. This is what we observe (Fig. 2A). The model presented here, therefore, can explain why ballistic height does not *decrease* with increased gravity, but it cannot explain why stance times are longer in higher levels of gravity. Thus, the model does not by itself offer an explanation for why ballistic height increases with gravity.

The model presented here is admittedly simple and makes unrealistic assumptions beyond impulsive stance, including no horizontal muscular work, non-distributed mass, and a simple relationship between step frequency and energetic cost. Future investigations could evaluate work-based costs using more advanced optimal control models (Srinivasan and Ruina, 2006; Hasaneini et al., 2013), eliminating some of these assumptions. Despite its simplicity, the model is able to correctly predict the observed trends in maximal speed with gravity, and demonstrates that understanding the energetic cost of both swing and stance is critical to evaluating why the central nervous system selects specific running motions in different circumstances.

Although many running conditions are quite familiar, running in reduced gravity is outside our general experience. Surprisingly, releasing an individual from the downward force of gravity does not result in higher leaps between foot contacts. Rather, humans use less bouncy gaits with slow takeoff speeds in reduced gravity, taking advantage of a reduced collisional cost while balancing a stride-frequency penalty.

List of Symbols

A	proportionality constant in the relationship $E_{\mathrm{freq}} = Af^k$ (J s^{-k})
E_{col}	collisional energetic cost (J)
E_{freq}	energetic cost related to step-frequency (J)
E_{tot}	total energetic cost ($E_{\mathrm{col}} + E_{\mathrm{freq}}$, in J)
f	step frequency (s^{-1})
g	gravitational acceleration (m s^{-2})
G	Earth-normal gravitational acceleration (9.8 m s^{-2})
k	scalar power in proportionality $E_{\mathrm{freq}} \propto f^k$
m	total subject mass (kg)
MVS	maximum vertical speed (m s^{-1})
U	average horizontal speed (m s^{-1})
V	vertical speed at takeoff (m s^{-1})
V^*	optimal and predicted vertical takeoff speed (m s^{-1})

Data Availability

The dataset supporting this article have been uploaded as part of the supplementary material (Table S1).

Acknowledgements

The authors would like to thank Art Kuo, Jim Usherwood, David Lee and Allison Smith for comments on earlier drafts.

Competing Interests

The authors declare no competing financial interests.

Author Contributions

All authors assisted in designing the experiment, collecting data and writing the manuscript; D.T.P. conceived the energetics-based model and performed data analysis. All authors gave final approval for submission.

Funding

This work was funded by the Natural Sciences and Engineering Research Council of Canada [CGSD3-459978-2014 to D.T.P., 312117-2012 to J.E.A.B.]

References

Alexander, R. and Jayes, A. (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *Journal of Zoology* **201**, 135–152.

Alexander, R. M. (1992). A Model of Bipedal Locomotion on Compliant Legs. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **338**, 189.

Bekker, M. G. (1962). II. Locomotion in nature. In *Theory of Land Locomotion*, pp. 4–26. University of Michigan Press, 2 edition.

Bertram, J. E. and Ruina, A. (2001). Multiple walking speed–frequency relations are predicted by constrained optimization. *Journal of Theoretical Biology* **209**, 445–453.

Cavagna, G. A. (2006). The landing-take-off asymmetry in human running. *J. Exp. Biol.* **209**, 4051–4060.

Doke, J., Donelan, J. M. and Kuo, A. D. (2005). Mechanics and energetics of swinging the human leg. *J. Exp. Biol.* **208**, 439–445.

Donelan, J. M. and Kram, R. (2000). Exploring dynamic similarity in human running using simulated reduced gravity. *J. Exp. Biol.* **203**, 2405–2415.

Hasaneini, S. J., Macnab, C., Bertram, J. E. and Leung, H. (2013). The dynamic optimization approach to locomotion dynamics: Human-like gaits from a minimally-constrained biped model. *Adv. Robot.* **27**, 845–859.

He, J. P., Kram, R. and McMahon, T. A. (1991). Mechanics of running under simulated low gravity. *J. Appl. Physiol.* **71**, 863–870.

Hedrick, T. L. (2008). Software techniques for two-and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 034001.

Kram, R. and Taylor, C. R. (1990). Energetics of running: A new perspective. *Nature* **346**, 265–7.

Kuo, A. D. (2001). A simple model of Bipedal Walking Predicts the Preferred Speed–Step Length Relationship. *J. Biomech. Eng.* **123**, 264.

Long, L. L. and Srinivasan, M. (2013). Walking, running, and resting under time, distance, and average speed constraints: Optimality of walk–run–rest mixtures. *Journal of The Royal Society Interface* **10**, 20120980.

Marsh, R. L., Ellerby, D. J., Carr, J. A., Henry, H. T. and Buchanan, C. I. (2004). Partitioning the Energetics of Walking and Running: Swinging the Limbs Is Expensive. *Science* **303**, 80–83.

Rashevsky, N. (1948). On the locomotion of mammals. *Bull. Math. Biophys.* **10**, 11–23.

Ruina, A., Bertram, J. E. and Srinivasan, M. (2005). A collisional model of the energetic cost of support work qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. *Journal of Theoretical Biology* **237**, 170–192.

Selinger, J. C., O'Connor, S. M., Wong, J. D. and Donelan, J. M. (2015). Humans Can Continuously Optimize Energetic Cost during Walking. *Current Biology* **25**, 2452–2456.

Srinivasan, M. and Ruina, A. (2006). Computer optimization of a minimal biped model discovers walking and running. *Nature* **439**, 72–75.

Willems, P. A., Cavagna, G. A. and Heglund, N. C. (1995). External, internal and total work in human locomotion. *J. Exp. Biol.* **198**, 379–393.

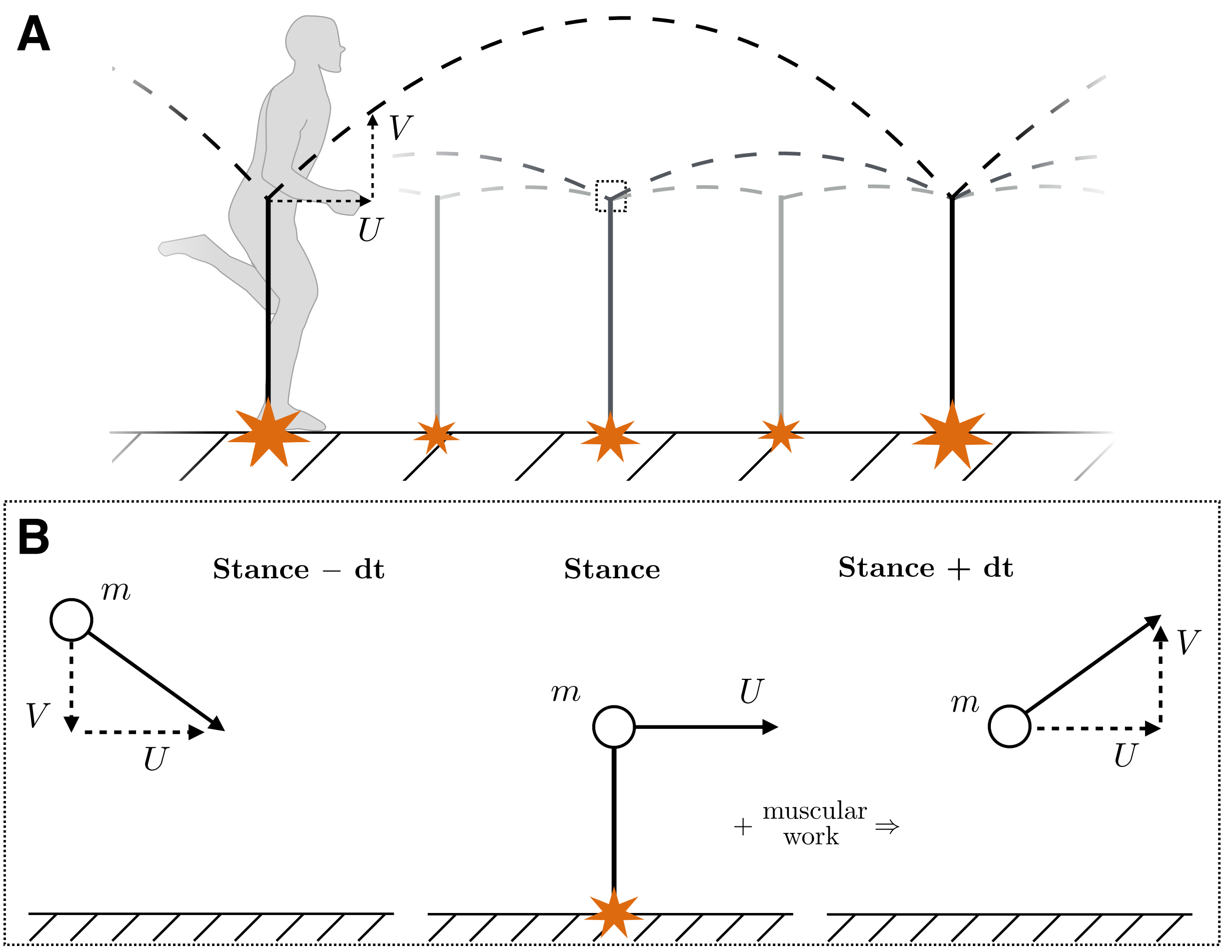

Figure 1: **Schematics explaining the energetic model** (A) In the impulsive model of running, a point mass bounces off vertical, massless legs during an infinitesimal stance phase. As the horizontal velocity U is conserved, the vertical takeoff velocity V dictates the step frequency and stride length. Smaller takeoff speeds result in more frequent steps that incur an energetic penalty. The small box represents a short time around stance that is expanded in panel B. (B) We assume that the center-of-mass speed at landing is equal to the takeoff speed. The vertical velocity V and its associated kinetic energy are lost during an impulsive foot-ground collision. The lost energy must be resupplied through muscular work.

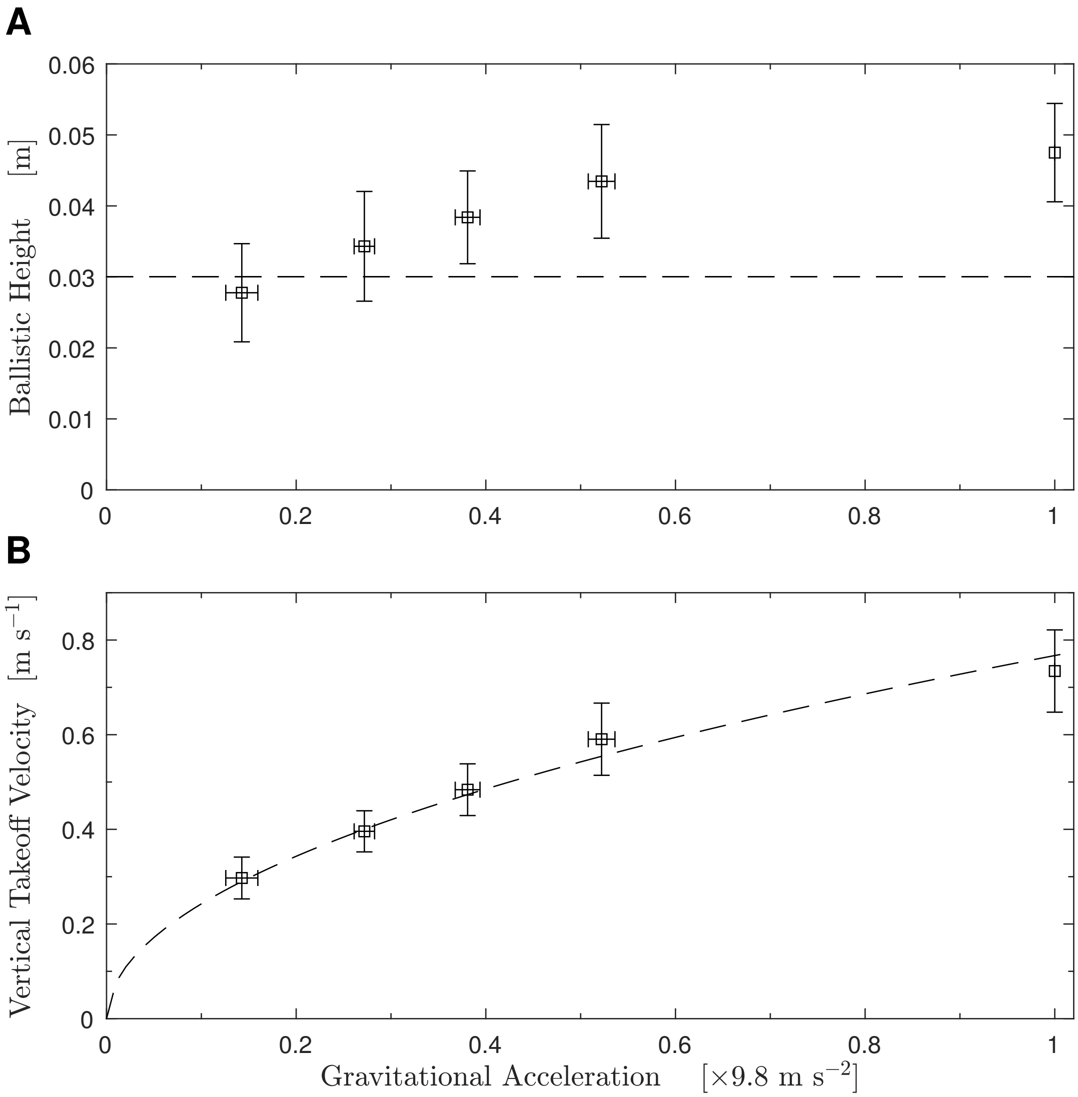

Figure 2: **Human subjects lower both ballistic height and takeoff velocity in reduced gravity.** (A) Mean ballistic height (data points) increases with gravity (p of linear vs constant model under two-tailed F-test: 4×10^{-4}, $N = 50$). The predicted ballistic height is shown with a dotted line, derived from the best fit of takeoff velocities in panel B. At gravity levels greater than 0.3 G (G = 9.8 m s^{-2}), mean ballistic height is greater than predictions beyond error. As takeoff velocity is defined here at the point when net force on the body is null, this discrepancy is due to a prolonged stance phase beyond the takeoff point, reducing the vertical deceleration experienced by the center of mass. (B) Measured vertical takeoff velocities increase proportionally with the square root of gravitational acceleration, following energetic optimality. The least squares fit is shown as a dashed line. The fit has an R^2 value of 0.73 ($N = 50$). For both panels, data points represent the mean gravity (abscissa) and vertical takeoff speed or ballistic height (ordinate) across ten subjects, grouped by target gravity level. An exception is in one subject, where the lowest and second-lowest levels of gravity were both closer to 0.25 G than 0.15 G; therefore, both trials were grouped with the second-lowest gravity regime. From left to right, the sample sizes for means are therefore 9, 11, 10, 10, and 10. Error bars are twice the standard error of the mean. Data used for creating these graphics are given in Table S1

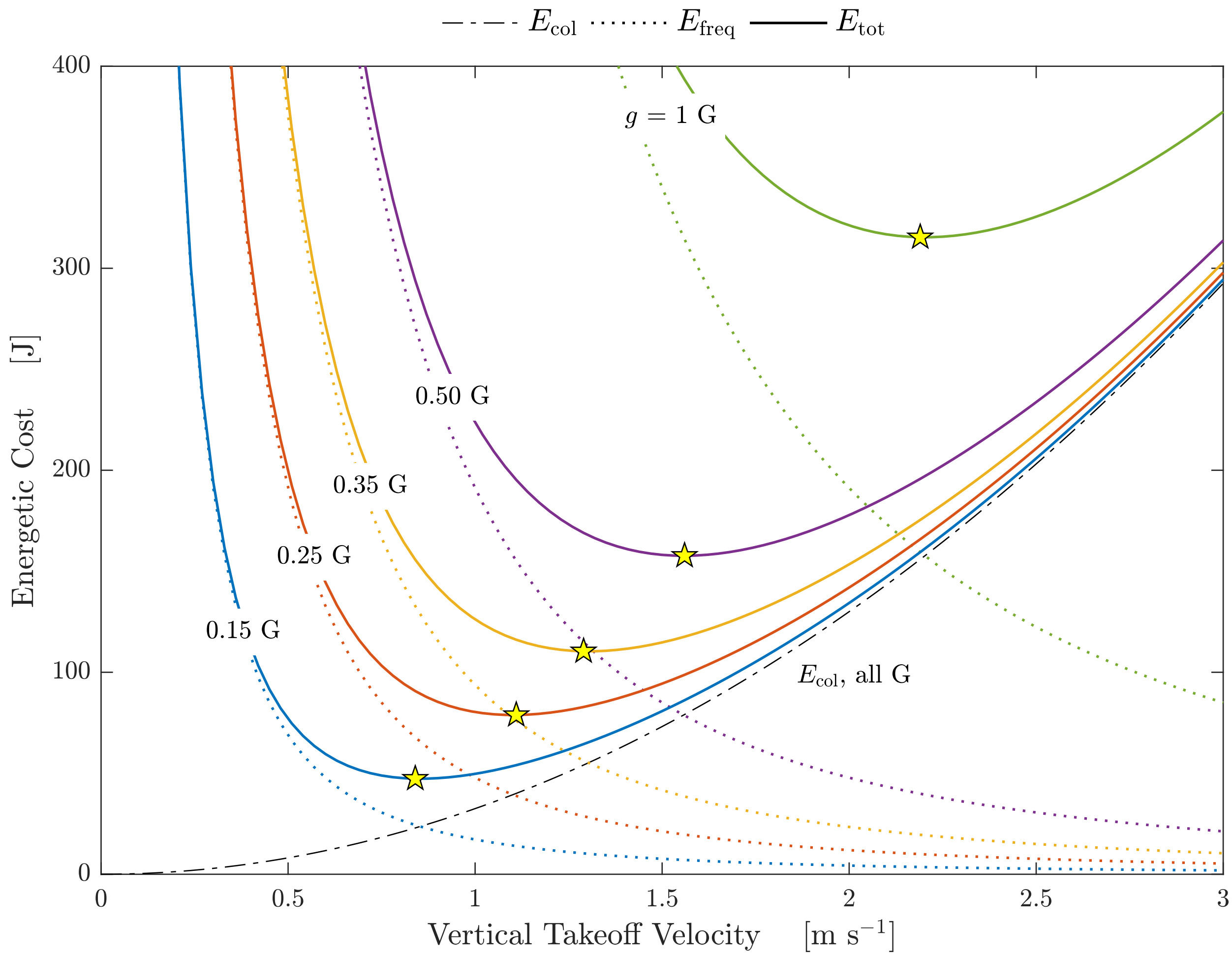

Figure 3: **The energetic costs according to the model are plotted as a function of vertical takeoff speed (V) for the five levels of gravity tested.** The hypothetical subject has a mass of 65 kg and a frequency-based proportionality constant (A in $E_{\text{freq}} = Af^2$) derived from the best fit in Fig. 2B. The collisional cost ($E_{\text{col}} = mV^2/2$) does not change with gravity (black dot-dash line), while the frequency-based energetic cost (E_{freq}, dotted lines) is sensitive to gravity, leading to an effect on total energy (E_{tot}, solid lines). The optimal takeoff speed (yellow stars) changes with gravity only because frequency-based cost is gravity-sensitive; however, the unique value of the optimum at any given gravity level always balances collisional and frequency-based costs. Labels of gravity levels (g) are placed over the colours they represent.