Running on the Moon: work-based optimization explains flatter gait in reduced gravity

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Summary Statement: As gravity decreases, humans reduce running takeoff velocities to minimize energy from muscular work.

Abstract

Removing a person from the confines of normal gravity should allow them to achieve long and high trajectories during the non-contact phase in running. Yet, in simulated reduced gravity, runners consistently lower their vertical speed at takeoff from the ground-contact phase, producing a flatter gait than in normal gravity. We show that this phenomenon results from a tradeoff of energetic costs associated with ground contact collisions and frequency-based mechanisms (*e.g.* leg swing work). We asked ten healthy subjects to run on a treadmill in five levels of simulated reduced gravity and measured their center-of-mass vertical speed at takeoff. Vertical takeoff speeds decreased with the square root of gravitational acceleration. These results are consistent with optimization of a work-based model where energy expenditure arises from collisional losses during stance and work done due to swinging the leg. While not exploiting greater takeoff speeds in reduced gravity may be counterintuitive, it is a strategy for minimizing energetic cost to which humans seem extremely sensitive.

Introduction

Why are particular gaits chosen under normal circumstances, of the myriad possibilities available? One way to explore this question is to subject people to abnormal circumstances, and observe how they adapt their gait. If particular principles govern gait choice in the new circumstances, it can be inferred that the same principles are at play in normal circumstances.

One "normal" gait is the bipedal run, and one abnormal circumstance is that of reduced gravity. As gravity decreases, runners reduce their vertical speed at the beginning of the non-contact phase (takeoff) (He et al., 1991). Movie 1 demonstrates the profound effect gravity can have 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 vertical takeoff speed is quite apparent; the gait in normal gravity is relatively bouncy compared to the near-flat trajectory of the

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low-gravity gait. This is an apparent paradox: in reduced gravity conditions, people are free to run with much higher leaps, even with the same takeoff speed. Instead, they *reduce* their takeoff speed and flatten the gait. Why should this be?

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). 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 $E_{\mathrm{col}} = mV^2/2$, 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 $E_{\mathrm{freq}} \propto f^k \propto g^k/V^k$, 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 low takeoff speeds, while frequency-based cost promotes high takeoff speeds.

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

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

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 $\frac{\partial E_{\mathrm{tot}}}{\partial V} = 0$. Solving the latter equation yields

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

as the only 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.

In particular, He et al. (1991) suggested that $V^* \propto \sqrt{g}$, implying $k = 2$. 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. 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 takeoff speed in a larger number of subjects using a reduced gravity harness.

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 the two-minute measurement trial. In each case, the subject was asked to run in any way that felt comfortable. Data were collected between 30 and 90 s, 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 large 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 level of reduced gravity, 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 could be 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 only 3% of the subject's Earth-normal body weight.

Achieving exact target gravity levels was not possible since moment arm adjustment had coarse resolution. 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, whose 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) and finally 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 velocity measurements

A marker was placed at the lumbar region of the subject's back, approximating the position of the center of mass (Slawinski et al., 2004). 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$^{\text{th}}$-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 following stance where the net vertical force on the body is approximately null, in accordance with a definition of takeoff proposed by Cavagna (2006).

Vertical takeoff velocities were averaged across all gait cycles in each trial for each subject. 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. Data were analyzed using custom scripts written in MATLAB (v. 2016b).

Results and Discussion

Pooled data from all trials are shown in Fig. 2. 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 vertical velocity 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.

While we did not directly measure the frequency-based cost in this study, our results suggest that a dominant source of this cost is leg swing. Using a simple model of a biped, Alexander 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 (Alexander, 1992) 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 relationship between step frequency and 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; 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 go down as gravity decreases. According to our model, the observed changes in kinematics with gravity occur only because frequency-based costs are gravity-sensitive. 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 model presented here is admittedly simple and makes unrealistic assumptions, including impulsive stance, 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. Although simple, the model 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-velocity takeoffs between foot contacts. Rather, humans use relatively 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 $E_{\text{freq}} = Af^k$
E_{col}	collisional energetic cost
E_{freq}	energetic cost related to step-frequency
E_{tot}	total energetic cost ($E_{\text{col}} + E_{\text{freq}}$)
f	step frequency
g	gravitational acceleration
G	Earth-normal gravitational acceleration (9.8 m s^{-2})
k	scalar power in proportionality $E_{\text{freq}} \propto f^k$
m	total subject mass
U	average horizontal speed
V	vertical speed at takeoff
V^*	optimal and predicted vertical takeoff speed

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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.

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Supplemental Movie S1 Description

A representative subject displays the pronounced difference in center-of-mass running kinematics resulting from a change in gravity. In the first half of the video, the runner experiences normal gravity (9.8 m s^{-2}), and exhibits pronounced center-of-mass undulations. In the second half of the video, the runner experiences simulated lunar gravity (approximately one-sixth of Earth-normal), and the center-of-mass undulations are comparatively shallow. In both cases, the treadmill speed is 2 m s^{-1}. The video is slowed by a factor of four. Consent to publish this video was obtained from the subject depicted.

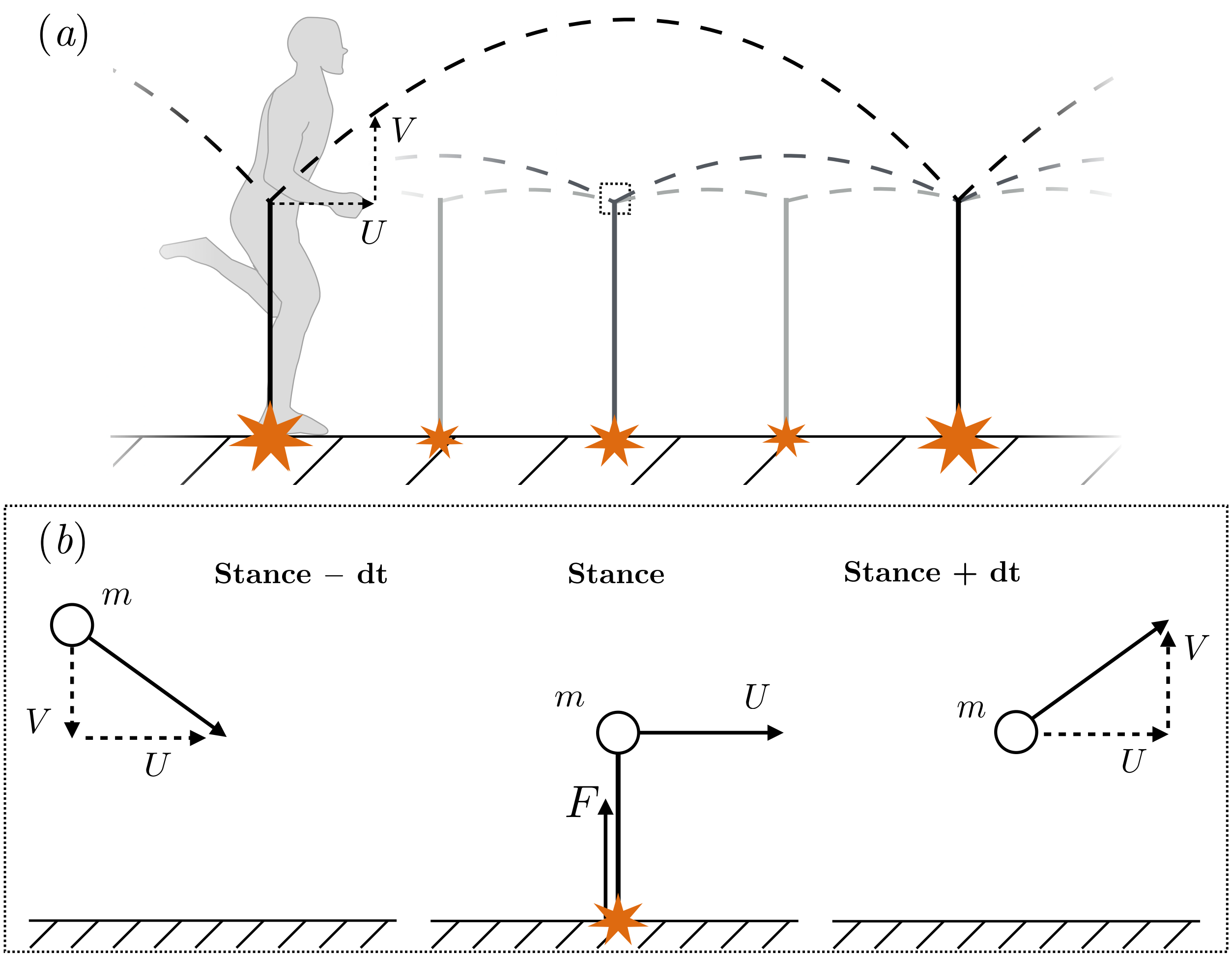

Figure 1: **These schematics explain the logic in deriving the energetic model** (a) In the impulsive model of running, a point mass bounces off vertical, massless legs during an infinitesimal stance phase. As the horizontal velocity U is conserved, the vertical takeoff velocity V dictates the step frequency 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 subfigure (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 supplied through impulsive force F.

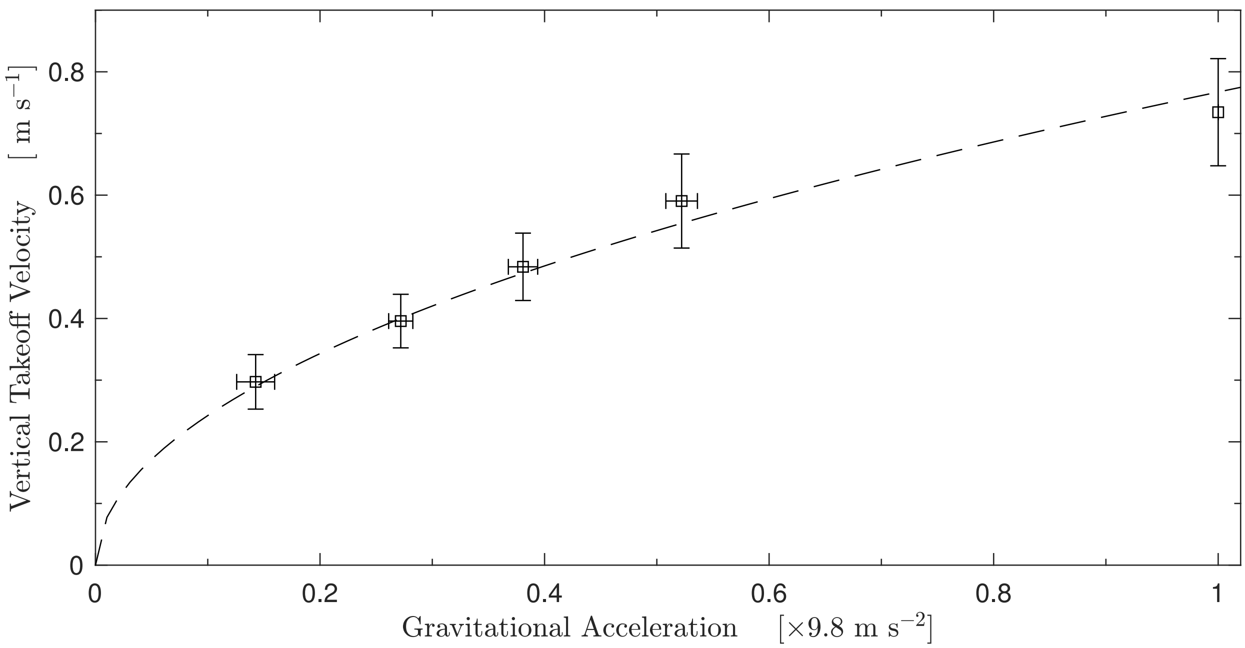

Figure 2: **Measured vertical takeoff velocities (V_m) increase with gravity according to the prediction $V_m = V^* \propto \sqrt{g}$, where V^* is the energetically-optimal value.** The least squares fit is shown as a dashed line. The fit has an R^2 value of 0.73 (N = 50). Data points are the average gravity and vertical takeoff speed 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 (G = 9.8 m s^{-2}); 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 this graphic are given in Table S1

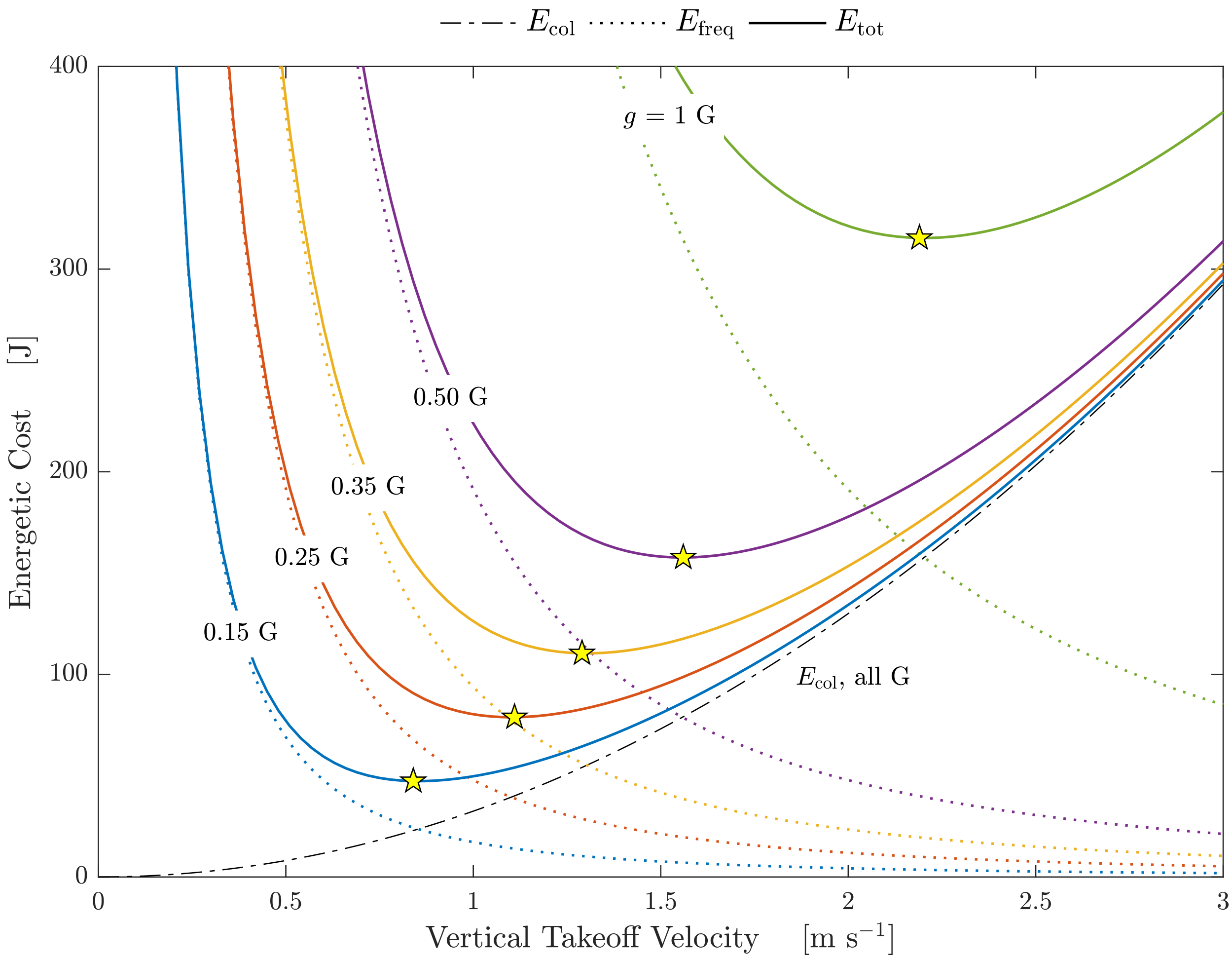

Figure 3: **The energetic costs according to the model are plotted as a function of vertical takeoff speed for the five levels of gravity tested.** The hypothetical subject has a mass of 65 kg and a frequency-based proportionality constant (A in $E_{\mathrm{freq}} = Af^2$) derived from the best fit in Fig. 2. The collisional cost (E_{col}) 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 balances collisional and frequency-based costs. Gravity levels (g) are placed on the colours they represent.