Applying the cost of generating force hypothesis to uphill running

Historically, several different approaches have been applied to explain the metabolic cost of uphill human running. Most of these approaches result in unrealistically high values for the efficiency of performing vertical work during running uphill, or are only valid for running up steep inclines. The purpose of this study was to reexamine the metabolic cost of uphill running, based upon our understanding of level running energetics and ground reaction forces during uphill running. In contrast to the vertical efficiency approach, we propose that during incline running at a certain velocity, the forces (and hence metabolic energy) required for braking and propelling the body mass parallel to the running surface are less than during level running. Based on this idea, we propose that the metabolic rate during uphill running can be predicted by a model, which posits that 1) the metabolic cost of perpendicular bouncing remains the same as during level running, 2) the metabolic cost of running parallel to the running surface decreases with incline, 3) the delta efficiency of producing mechanical power to lift the COM vertically is constant, independent of incline and running velocity, and 4) the costs of leg and arm swing do not change with incline. To test this approach, we collected ground reaction force (GRF) data for eight runners who ran thirty 30-second trials (velocity: 2.0-3.0 m/s; incline: 0-9º). We also measured the metabolic rates of eight different runners for 17, 7-minute trials (velocity: 2.0-3.0 m/s; incline: 0-8º). During uphill running, parallel braking GRF approached zero for the 9º incline trials. Thus, we modeled the metabolic cost of parallel running as exponentially decreasing with incline. With that assumption, best-fit parameters for the metabolic rate data indicate that the efficiency of producing mechanical power to lift the center of mass vertically was independent of incline and running velocity, with a value of ~29%. The metabolic cost of uphill running is not simply equal to the sum of the cost of level running and the cost of performing work to lift the body mass against gravity. Rather, it reflects a constant cost of perpendicular bouncing, decreased costs of parallel braking and propulsion and of course the cost of lifting body mass against

gravity.

1   Wouter Hoogkamer[1], Paolo Taboga[2] and Rodger Kram[2]

2   *[1]Faculty of Human Movement Sciences, VU University, Amsterdam, the Netherlands [2]Department*

3   *of Integrative Physiology, University of Colorado Boulder, CO. USA*

4   Corresponding author:

5   Wouter Hoogkamer

6   Department of Kinesiology, KU Leuven

7   Tervuursevest 101 - bus 1501

8   3001 Heverlee, Belgium

9   Phone: 0032 16 329065

10 Email: wouter.hoogkamer@faber.kuleuven.be

Introduction

11

12 The energetic cost of running affects the behavior/performance of animals in nature, humans

13 seeking fitness and athletes in competition. We believe that reasonable biomechanical

14 explanations for the energetic cost of level running have been developed (Alexander & Ker,

15 1990; Arellano & Kram, 2014; Kram & Taylor, 1990; Minetti & Alexander, 1997; Roberts et al.,

16 1998), but the world is not flat. We all know intuitively that running up even a slight incline is

17 dramatically more exhausting, yet we lack a coherent biomechanical model for the energetic cost

18 of uphill running.

19 In this paper, we develop and test a new model for the metabolic cost of uphill human running.

20 Historically, several different approaches have been applied to this topic. Most of these

21 approaches result in unrealistically high values for the efficiency of performing vertical work

22 (Asmussen & Bonde-Petersen, 1974; Lloyd & Zacks, 1972; Pugh, 1971), or are only valid for

23 running up steep inclines (Margaria et al., 1963; Margaria, 1968; Minetti et al., 2002) and not for

24 running up inclines more typical of recreational/fitness running. The purpose of the current study

25 was to reexamine the cost of uphill running, based upon our understanding of level running

26 energetics (Kram & Taylor, 1990; Roberts et al., 1998) and ground reaction forces during uphill

27 running (Gottschall & Kram, 2005).

28 First, we give an overview of how the energetics of uphill running have been approached in the

29 past. Margaria and co-workers (Margaria et al., 1963; Margaria, 1968) calculated net mechanical

30 efficiency of uphill running as:

31 *Net mechanical efficiency = vertical mechanical power / net metabolic rate*   (eq. 1)

32 Here, the vertical mechanical power is the rate of performing work to raise the body mass (m)

33 against gravity (g):

34   *vertical mechanical power = m·g·sin(θ)·v*   (eq. 2)

35   Where θ is the incline in degrees and v is the running velocity parallel to the incline. Margaria

36   obtained the net metabolic rate by subtracting the basal metabolic rate from the metabolic rate

37   during running. In level running, at a constant velocity, upon landing the body absorbs

38   mechanical power (performs negative work) and then generates positive power (performs

39   positive work) but no net external mechanical power is required because the negative and

40   positive work quantities are opposite in sign but equal in magnitude (Cavagna, Saibene &

41   Margaria, 1964). Margaria (1968) proposed that the equal and opposite positive and negative

42   external work can be considered to be wasted, since performing this work has a metabolic cost

43   but does not propel the runner forward.

44   However, in uphill running, net positive external work and power are produced since the center

45   of mass (COM) is raised against gravity. Margaria et al. (1963) hypothesized and demonstrated

46   that on steeper inclines, the wasted external work decreases and the observed net mechanical

47   efficiency approaches the same value as the efficiency of predominantly concentric exercise, such

48   as cycle ergometry (~25%). It is important to note that this approach only results in such

49   physiologically realistic efficiency values when the energetic cost of running is dominated by the

50   work needed to raise the COM (i.e. at steep inclines) (Minetti et al., 2002). For running up

51   inclines more typical of recreational/fitness running the net mechanical efficiencies calculated are

52   much lower than the values for concentric muscle contractions (Smith, Barclay & Loiselle,

53   2005).

54   Another approach is to calculate "vertical efficiency" by dividing the mechanical power needed

55   to lift the COM vertically by the difference in metabolic rates between locomotion on an incline

56   and level locomotion at the same velocity (e.g. Full & Tullis, 1990; Rubenson et al., 2006).

57   Published values for vertical efficiency range from 30% for red kangaroos (Kram & Dawson,

58   1998) to ~46% for humans (Asmussen & Bonde-Petersen, 1974; Lloyd & Zacks, 1972; Pugh,

59   1971), to values near 50% (walking turtles (Zani & Kram 2008)) or even higher (60% for mice

60   and 66% for chimpanzees (Taylor, Caldwell & Rowntree, 1972)). In running, these efficiency

61   values, which are much higher than isolated muscle contraction efficiency, have been attributed

62   to elastic energy storage and reutilization in muscle-tendon complexes (Asmussen & Bonde-

63   Petersen, 1974; Lloyd & Zacks, 1972; Cooke et al., 1991). But, as emphasized by Roberts et al.

64   (1997), the increase in potential energy of the body in uphill locomotion can only be done by

65   active concentric muscle work, since passive elastic mechanisms simply return energy stored

66   previously in a step. Thus, these high efficiency values remain enigmatic.

67   Alternatively, Minetti, Ardigò & Saibene (1994) developed a model which assumed that the

68   metabolic cost can be predicted completely based on measures of mechanical work. In their

69   model, internal work (due to the kinetic energy changes of body segments relative to the body

70   COM), positive external work and negative external work were each assumed to be performed

71   with a separate efficiency value. Minetti, Ardigo & Saibene's model (1994) also estimates the

72   amount elastic energy storage and release, however the costs of muscle force production to

73   generate tension to allow this energy storage and release is not taken into account.

74   Although we believe that the cost of generating force to support body weight is the major

75   determinant of the metabolic cost of level running (for review, see Arellano & Kram, 2014;

76   Kram, 2000), none of the models for uphill running explicitly include this cost. Briefly, the cost

77   of generating force hypothesis posits that in running the muscles primarily act to generate tension

78   that allows the tendons to store and return elastic energy. Muscles consume energy whenever they

79   generate tension, regardless of whether they perform work. The cost of generating force to

80   support body weight has been found to be inversely proportional to the foot-ground contact time,

81   presumably because generating force more rapidly requires faster and less economical muscle

82   fibers (Roberts et al., 1998).

83   In this study, we introduce a model for the metabolic cost of uphill running which combines the

84   cost of generating force and the cost of performing mechanical work approaches. Our overall

85   view is that the net metabolic cost of running is comprised of the costs of generating force to

86   support body weight, braking and propelling body mass in the forward (parallel) direction,

87   swinging the legs and arms and maintaining balance (Arellano & Kram, 2011; Arellano & Kram,

88   2014; Chang & Kram, 1999; Farley & McMahon, 1992; Kram & Taylor, 1990; Modica & Kram,

89   2005; Moed & Kram, 2005; Teunissen, Grabowski & Kram, 2007). For level running, obviously

90   body weight must be dynamically supported in the vertical direction, but for uphill running, we

91   prefer to call this term the cost of "perpendicular bouncing" to emphasize that the metabolic

92   power required to lift the COM vertically is not included in that term (Figure 1). This

93   approximation introduces only a small error because the perpendicular component is only slightly

94   less than the vertical component, for example, the cosine of 9 degrees equals 0.988. Furthermore,

95   Gottschall & Kram (2005) observed that both the perpendicular active force peaks and the

96   contact times during uphill running (up 3, 6 and 9°) were not significantly different from those

97   during level running. Thus, based on the cost of generating force hypothesis, the cost of

98   perpendicular bouncing should not change with incline. So, in uphill running, the net metabolic

99   rate should be equal to the sum of the rates of metabolic energy consumption for perpendicular

100 bouncing, braking and propelling body mass parallel to the surface, swinging the legs and arms

101 and, of course, raising of the COM vertically. In Figure 1 parallel running refers to the task of

102 running parallel to the surface whether that surface is level or inclined. The task of parallel

103   running intrinsically requires bouncing perpendicular to the surface and that bouncing incurs a

104   metabolic cost.

105   **<Figure 1 approximately here>**

106   In contrast to the vertical efficiency approach, we propose that at a certain velocity the metabolic

107   rate required for braking and propelling the body mass parallel to the running surface is less

108   during inclined running (compared to level running), because there is less braking (negative

109   external work) and thus less wasted work (Margaria, 1968; Minetti, Ardigò & Saibene, 1994).

110   Gottschall & Kram (2005) quantified how in uphill running the braking Ground Reaction Forces

111   (GRFs) parallel to the running surface decrease with steeper inclines. The propulsive GRFs

112   parallel to the running surface are greater during uphill running, but the majority of the

113   propulsive GRF impulse parallel to the running surface compensates for the gravitational braking

114   impulse parallel to the surface $m \cdot g \cdot sin(\theta) \cdot t_{step}$, where t_{step} is the time between two consecutive foot

115   strikes. During steeper incline running, most of the propulsive parallel GRF impulse is required

116   to overcome the component of the gravitational braking impulse parallel to the surface. Thus,

117   only a small part of the parallel propulsive GRF impulse is compensating for the braking GRF

118   impulse (Figure 2). Although initially counterintuitive, the metabolic costs of both braking and

119   propelling forces, parallel to the running surface, should decrease during uphill running. By

120   taking that into account, the efficiency of producing mechanical power to lift the COM vertically

121   should be closer to the efficiency of concentric muscle contractions.

122   **<Figure 2 approximately here>**

123   Based on these ideas, we propose that the metabolic rate during uphill running can be predicted

124   by a model, which posits that *1)* the metabolic cost of perpendicular bouncing remains the same

125   as during level running, 2) the metabolic cost of running parallel to the running surface decreases

126 with incline, *3)* the delta efficiency (Gaesser & Brooks, 1975) of producing mechanical power to

127 lift the COM vertically (Eff_{vCOM}) is constant, independent of incline and running velocity, and *4)*

128 the costs of leg and arm swing do not change with incline. We expect Eff_{vCOM} to be similar to the

129 delta efficiency of cycling (~25-30%) (Gaesser & Brooks, 1975; Bijker, De Groot & Hollander,

130 2001). To test these ideas, we measured GRFs for level and a range of uphill running inclines (1-

131 9º) for a range of velocities (2.0-3.0 m/s). Additionally, we measured the metabolic rate during

132 uphill running for a feasible range of grades at the same velocities (0-8º at 2.0 m/s; 0-4 º at 2.5

133 and 3.0 m/s).

134 **Materials & Methods**

135 Ground Reaction Forces

136 For this part of the study, eight participants ran on a force treadmill (Treadmetrix, Park City, UT,

137 USA). Six males and two females participated (31.2±11.0 yr, 177.6±7.1 cm, 69.5±7.9 kg; all

138 mean±SD). The participants gave written informed consent and the testing protocol was approved

139 by the University of Colorado Institutional Review Board (13-0710).

140 Each trial lasted 30 seconds and the first 20 steps after the first 10 seconds were analyzed. Forces

141 were collected at 1000 Hz. Before each trial forces were zeroed by regulating the amplifiers

142 (MSA-6 MiniAmp, AMTI Watertown, MA, USA) and the acquisition software (Vicon Nexus,

143 Vicon Motion Systems Ltd., Oxford, UK). Signals were digitally filtered using a first-order

144 Butterworth filter (pass band frequency of 35Hz and stop band frequency of 50Hz) implemented

145 in a Matlab script (Mathworks Inc., USA). A 10N threshold was used to determine the instants of

146 foot strike and toe-off. Per step, we calculated the average braking and propelling GRF impulses

147 parallel to the running surface by integrating all negative (braking) or positive (propelling) values

148 during each ground contact. We used the time between two consecutive foot strikes t_{step} (for

149 example from left foot strike to right foot strike) to calculate the average gravitational impulses

150 parallel to the surface:

151 $I\_Gravity_{parallel} = m{\cdot}g{\cdot}sin(\theta){\cdot}t_{step}$ (eq. 3)

152 We defined the total propelling impulse per step as the propelling GRF impulse minus the

153 component of the gravitational impulse, all parallel to the running surface:

154 $I\_GRF_{propelling\_total} = I\_GRF_{propelling} - I\_Gravity_{parallel}$ (eq. 4)

155 Summation of the absolute values of the braking impulse and of the total propulsive impulse per

156 step gave the value of the wasted GRF impulse per step:

157 $I\_GRF_{wasted} = I\_GRF_{braking} + I\_GRF_{propelling\_total}$ (eq. 5)

158 For level running, the wasted GRF impulse per step equals the summation of the absolute values

159 of the braking impulse and the propulsive impulse per step, similar to the concept of wasted work

160 per step as introduced by Margaria (1968). We note that not all of the wasted impulse is actively

161 done by muscle length changes; a substantial part is likely provided through passive elastic

162 storage and return. Based on earlier studies with kinetic (Gottschall & Kram, 2005) and

163 kinematic (Minetti, Ardigò & Saibene, 1994) measurements of uphill running and the fact that

164 I_GRF_{wasted} cannot be negative, we hypothesized that I_GRF_{wasted} decreases exponentially to zero

165 for steeper inclines:

166 $I\_GRF_{wasted} = I\_GRF_{wasted\_level}{\cdot}e^{-\gamma{\cdot}sin(\theta)}$ (eq. 6)

167 Parameter $I\_GRF_{wasted\_level}$ represents the value of the wasted GRF impulse per step during level

168 running. The decay constant γ determines how steeply I_GRF_{wasted} decreases with incline

169 (expressed as $sin(\theta)$).

Metabolic measurements

171 We recruited a different eight participants for this part of the study (4 males and 4 females,

172 26.2±4.0 yr, 174.3±12.4 cm, 67.3±11.8 kg; all mean±SD). All participants had extensive

173 treadmill running experience and had recently run a 5km race in less than 20 minutes (18:28±52

174 sec; mean±SD). Based on pilot testing, we were confident that for this caliber of runner, the most

175 demanding test condition would be submaximal. We applied this 20-minute 5km criteria to

176 ensure that the energy supply during our experimental trials was predominately oxidative and to

177 avoid fatigue effects. The participants gave written informed consent that followed the guidelines

178 of the University of Colorado Institutional Review Board (0606.29).

179 Participants completed different sessions on two separate days. They ran a total of 17 different

180 conditions on a classic Quinton 18-60 treadmill with adjustable velocity and incline. Note that we

181 modified this treadmill so that we had calibrated, digital electronic readouts for velocity and

182 incline. On the first day, participants ran at a velocity of 2.0 m/s at seven different inclines

183 ranging from 0 to 8º. The second day consisted of five trials at both 2.5 m/s and 3.0 m/s at

184 inclines ranging from 0 to 4 º (for a complete list of the trials, refer to Table 2 in the Results

185 section). We measured the rates of oxygen consumption and carbon dioxide production during

186 these 7-minute trials. Each experimental day started with determining the body mass of the

187 participant. We then determined metabolic rate during a 7-minute standing trial. This was

188 followed by a 10-minute warm-up of level running at 2.0 m/s or 2.5 m/s, for the first and second

189 day, respectively. During warm-up, participants breathed through the expired-gas analysis system

190 to allow acclimatization. For each running velocity, the different incline conditions were

191 randomized to prevent order effects.

192 We measured the rates of oxygen consumption (VO_2) and carbon dioxide production (VCO_2)

193 using an open-circuit expired-gas analysis system (True One 2400, Parvo Medics, Salt Lake City,

194 UT, USA). We calibrated the gas analyzers before each test using reference gases. The flow-rate

195 transducer was calibrated using a 3 liter syringe (Rudolph Inc., Kansas City, MO, USA). Each

196 trial lasted 7 minutes based on pilot data showing that steady state was reached in less than 5

197 minutes during the different trials. We averaged VO_2, VCO_2 and respiratory exchange ratios

198 (RER) for the last 2 minutes of each trial. Rest periods of at least 4 minutes occurred between the

199 trials. During the rest periods, the treadmill was adjusted to the incline and velocity of the

200 following trial.

201 Calculations

202 To fit a generic curve to the wasted impulse data (eq. 6), we first normalized the impulse data to

203 body mass and divided the values by running velocity, similar to the cost of transport concept

204 (see below). Mechanical vertical COM power (in Watts) was calculated using belt velocity and

205 incline (similar to equation 2):

206 *Mechanical vertical COM power = m·g·sin(θ)·v*   (eq. 7)

207 Where θ is the incline in degrees and v is velocity in m/s. Metabolic rates (in W/kg) were

208 calculated from respiratory measurements using the Brockway equation (Brockway, 1987). Net

209 metabolic power was calculated as running metabolic rate minus the standing metabolic rate. We

210 calculated the traditional values of delta efficiency of producing mechanical power to lift the

211 COM vertically as the ratio of mechanical vertical COM power to the difference in metabolic rate

212 between level running and running on incline at the same velocity (Gaesser & Brooks, 1975).

213 Net metabolic Cost of Transport (CoT) is the net metabolic cost per unit distance traveled parallel

214 to the running surface. It is calculated by dividing the net metabolic rate by the running velocity

215 and is expressed in J/(kg·m). Cost of Transport values allowed us to develop a generalized

216 equation, independent of running velocity. Based on the general concepts underlying our uphill

217 running model, we generated a custom equation and fitted this to the data to calculate the

218 parameters resulting in the best fit (see below). The format of the equation is:

219 $Net\ CoT\ (J/(kg·m)) = A + B·e^{-\lambda·sin(\theta)} + \dfrac{g}{Eff_{vCOM}}·sin(\theta)$ (eq. 8)

220 In this equation, the CoT of parallel running is represented by $A + B·e^{-\lambda·sin(\theta)}$. We postulated that

221 the cost of parallel running decreases exponentially with incline. We expected that at steep

222 inclines, where I_GRF_{wasted} equals zero, the cost of braking and propelling would be reduced to

223 zero and that the cost of parallel running would consist of only the costs of perpendicular

224 bouncing, leg swing and arm swing. In terms of our model, the first term A represents the CoT

225 related to perpendicular bouncing, leg swing and arm swing. Parameter B represents the CoT for

226 braking and propelling during level running. For inclined running, the CoT for braking and

227 propelling parallel to the running surface decreases exponentially with the sine of the incline

228 angle θ: $CoT_{braking/propelling} = B·e^{-\lambda·sin(\theta)}$. The decay constant λ determines how steeply the

229 $CoT_{braking/propelling}$ decreases with $sin(\theta)$. Logically, the $CoT_{braking/propelling}$ decreases proportionally to

230 the wasted GRF impulse per step I_GRF_{wasted}, i.e. that λ in equation 8 is equal to γ in equation 6.

231 The CoT of producing mechanical power to lift the COM vertically is represented by the third

232 term in equation 8. To relate the mechanical vertical COM power (equation 7) to the metabolic

233 CoT, it should be divided by body mass, velocity and the efficiency of producing mechanical

234 power to lift the COM vertically, resulting in $\dfrac{g}{Eff_{vCOM}}·sin(\theta)$.

235   Statistical Analyses

236   We present all results in the text as mean values ± SD. We used a traditional level of significance

237   (α = 0.05) for all statistical tests. To test for significant differences between the three tested

238   running velocities and between different angles, we applied two-way analyses of variance

239   (ANOVAs) on the impulse, step frequency and contact time data. We applied the non-linear least

240   squares method to fit non-linear curves on the data and the linear least squares method to fit lines.

241   We utilized r^2 to evaluate goodness of fit.

242   **Results**

243   Ground Reaction Forces

244   For running at a velocity of 2.0 m/s, the braking GRF impulse per step, parallel to the running

245   surface, normalized to body mass and divided by the running velocity, decreased significantly

246   from -0.128 for level running to -0.003 for running up a 9º incline. For 2.5 m/s and 3.0 m/s

247   similar decreases were observed (Table 1). For two participants, we could not analyze the kinetic

248   data at 2 m/s since they "ran" without a clear aerial phase at this velocity. As such, their stance

249   phases partially overlapped, invalidating the assessment of the braking and propelling impulses

250   during each stance phase. In addition, for the same reason, we excluded 4 separate trials for other

251   participants. Similar to the braking impulse, the total propelling impulse per step, parallel to the

252   running surface, and the wasted GRF impulse per step (I_GRF_{wasted}), also decreased with incline

253   (Table 1; Figure 3; individual trial data is contained in the supplemental material). Recall that

254   total propelling impulses were calculated as the propelling GRF impulse parallel to the surface

255   minus the component of the gravitational impulse parallel to the running surface. Summation of

256   the absolute values of the braking impulse and of the total propelling impulse per step gave

257   I_GRF_{wasted}. In line with our hypothesis, I_GRF_{wasted} values decreased exponentially with incline.

258   Curve fitting of equation 6 to the GRF data resulted in best-fit parameter values of $I\_GRF_{wasted\_level}$

259   = 0.1208 and γ = 18.24, with r^2 = 0.89 (Figure 3). Fitting a linear equation to the data resulted in a

260   lower correlation between the data and the fit (r^2 = 0.79) and implied negative I_GRF_{wasted} values

261   for inclines steeper than about 8 degrees.

262   **<Figure 3 approximately here>**

263   The step frequency increased significantly with incline and with running velocities (Table 1). In

264   contrast, contact times were similar between inclines (p = 0.7) and decreased significantly with

265   velocity (Table 1).

266   **<Table 1 approximately here>**

267   Metabolic measurements

268   In Table 2 we present the mean rates of oxygen consumption (VO_2) and metabolic energy

269   consumption (individual trial data is contained in the supplemental material). For all participants,

270   RER (0.86±0.05; range 0.74 - 0.96) was less than 1.0 for all trials, indicating that the metabolic

271   energy was derived primarily from oxidative sources. The mean metabolic rate for standing was

272   1.53±0.08 W/kg.

273   **<Table 2 approximately here>**

274   Decreasing cost of parallel running

275   Net metabolic Cost of Transport (CoT) data for all participants are shown in Figure 4A for

276   different inclines and velocities. The net CoT data are plotted versus the sine of the incline angle

277   θ on the primary horizontal axis (at the bottom) because the vertical power is proportional to the

278   sine of the incline angle. The net CoT is the net metabolic cost expressed per unit distance

279   traveled parallel to the running surface.

280   We set λ in our model (eq. 8) to be equal to γ (from eq. 6) and calculated the best fit to the

281   metabolic data. The parameter of the best fit with $\lambda = \gamma = 18.24$ were $A = 2.70$, $B = 0.674$ and

282    $Eff_{vCOM} = 29.4\%$ with $r^2 = 0.97$. The best-fit curve is shown in Figure 4A. In Figure 4B this best-

283   fit curve is labeled Net CoT$_{total}$ as it includes all terms of equation 8, i.e. the CoT of parallel

284   running and the CoT of producing mechanical power to lift the COM vertically. The net CoT data

285   are shown as mean values for each running velocity in this figure (Figure 4B). The metabolic

286   CoT of producing mechanical power to lift the COM vertically is also shown (labeled CoT$_{vertical}$).

287   This CoT was calculated based on $Eff_{vCOM} = 29.4\%$. In our model, the CoT of parallel running is

288   represented by $A + B \cdot e^{-\lambda \cdot sin(\theta)}$, and this cost is shown in Figure 4C for $A = 2.70$, $B = 0.674$ and $\lambda =$

289   18.24. Metabolic data points were calculated by subtracting the calculated metabolic CoT of

290   producing mechanical power to lift the COM vertically from the net CoT. This resulted in the

291   following equation:

292    $Net\ CoT\ (J/(kg \cdot m)) = 2.70 + 0.674 \cdot e^{-18.24 \cdot sin(\theta)} + \dfrac{g}{0.294} \cdot sin(\theta)$ (eq. 9)

293   **<Figure 4 approximately here>**

294   Note that the best-fit regression for the net CoT versus the sine of the incline angle θ, using

295   equation 8, is fairly insensitive to changes in the parameters. For instance, curve fitting of

296   equation 8 with λ as a free parameter resulted in $A = 1.16$, $B = 2.20$, $\lambda = 7.60$ and $Eff_{vCOM} = 24.9\%$

297   and produced a similar goodness of fit: $r^2 = 0.97$.

298   **Discussion**

299   In this study, we quantified the ground reaction forces and metabolic cost of uphill human

300   running and introduced a new model to interpret our results. This is the first model for uphill

301   running that incorporates the cost of generating force concept. We have found that the metabolic

302   rate during uphill running can be predicted by a model which posits that *1)* the metabolic cost of

303   perpendicular bouncing remains the same as during level running, 2) the metabolic cost of

304   running parallel to the running surface decreases with incline, *3)* the delta efficiency of producing

305   mechanical power to lift the COM vertically (Eff_{vCOM}) is constant, independent of incline and

306   running velocity, and *4)* the costs of leg and arm swing do not change with incline.

307   Ground Reaction Forces

308   The GRF data confirmed that the wasted braking and propulsive impulses per step decrease

309   exponentially with incline supporting our contention that the metabolic cost of parallel running

310   decreases with incline. Based on this, we generated a general model for the metabolic cost of

311   uphill running.

312   Metabolic cost of uphill running

313 In line with earlier observations of net mechanical efficiency values approaching the efficiency of

314 concentric contracting muscles on steeper inclines (Margaria, 1968; Margaria et al., 1963), our

315 model assumes that the efficiency of producing mechanical power to lift the COM vertically

316 (Eff_{vCOM}) is constant, independent of incline and running velocity, and physiologically realistic.

317 Our method offers an alternative to the model by Minetti and co-workers (Minetti, Ardigò &

318 Saibene, 1994; Minetti et al., 2002) which assumed that the metabolic cost can be predicted

319 completely based on measures of mechanical work. In contrast, our model combines the cost of

320 generating force to support the runner's body weight and the cost of performing mechanical work

321 to lift the COM. In our approach, the different terms in the model each represent different

322 elements of the CoT of uphill running. Unfortunately, the CoT of each of these elements cannot

323 be measured independently. Therefore, we constructed a biomechanical realistic model and

324 applied a fitting procedure to calculate the parameters needed.

325 Metabolic cost of parallel running

326 According to equation 9, for level running ($\theta = 0$; $\sin(\theta) = 0$), about 80% of the net metabolic

327 CoT would be attributed to weight support (perpendicular bouncing), leg swing and arm swing,

328 while 20% would be attributed to braking and propelling the COM. These number relate well

329 with earlier studies on the cost of supporting body weight (at most 74% of the net cost of

330 running; Teunissen, Grabowski & Kram, 2007) and of leg swing (only ~10% of the net cost of

331 running; Moed & Kram, 2005), which sum up to ~84% of the net metabolic cost attributable to

332 weight support and leg swing.

333 In our model, the CoT related to perpendicular bouncing, leg swing and arm swing is independent

334 of incline. However, step frequency increased slightly with incline, which could result in higher

335 values for "internal work" (Minetti, 1998) or joint mechanical power (Swanson & Caldwell,

336 2000). We estimated mechanical internal work values (in J/(kg·m)) based on step frequency, duty

337 factor and velocity as per the Minetti equation (1998), using different values for factor q for level

338 and uphill running (Nardello, Ardigò & Minetti, 2011). These estimates of mechanical internal

339 work increased both with incline and running velocity. Although the Minetti equation (1998)

340 suggests that internal power would increase by 37% between 2.0 and 3.0 m/s, we did not observe

341 any change in the overall metabolic CoT. Similar increases in the internal mechanical power were

342 estimated between level and uphill running (32 - 33%, for our range of velocities). It is unclear

343 how these mechanical internal work estimates relate to the metabolic CoT, because of

344 overestimations of internal work related to the ballistic pendulum-like part of the swing phase of

345 the limbs (Alexander, 1989). Furthermore, Nardello, Ardigò & Minetti (2011) reevaluated the

346 1998 Minetti equation for humans of both sexes, for different age groups, running at different

347 velocities and inclines and they observed no increase in measured internal work as function of

348 incline for velocities below 2.78 m/s. Additionally, evidence from our laboratory suggests that the

349 metabolic cost of leg swing in human running is relatively small, ~10-20% of net metabolic cost

350 of running (Modica & Kram, 2005; Moed & Kram, 2005). Finally, guinea fowl blood flow data

351 suggest that the majority of the increased energy expenditure in uphill running is used by stance

352 phase muscles (Rubenson et al., 2006). Thus, for simplicity in our model, we assumed that the

353 cost of leg swing is independent of incline.

354 It is difficult to estimate the metabolic cost of arm swing. Experiments that restrict arm swing

355 increase the cost of running by at least 3% (Arellano & Kram, 2014) suggesting that arm swing

356 produces a net energy savings rather than a net cost. In any case, it seems unlikely that the

357 metabolic cost or savings due to arm swing at a certain running speed would change greatly

358 during uphill running. Thus, we subsume the cost of arm swing into the cost of perpendicular

359 bouncing and assume that it does not change.

360 Metabolic cost of producing mechanical power to lift the COM vertically

361 The CoT of producing mechanical power to lift the COM vertically increases linearly with $\sin(\theta)$,

362 proportional to the mechanical vertical COM power. This is a direct consequence of our

363 assumption that the efficiency of producing mechanical power to lift the COM vertically (Eff_{vCOM})

364 is constant, independent of incline and running velocity. The efficiency of producing mechanical

365 power to lift the COM vertically (Eff_{vCOM}), according the best fit of our model was 29.4%. This

366 value is in the same range as earlier reported values of similar measures of whole body efficiency

367 in cycling. Gaesser & Brooks (1975) defined work efficiency as work accomplished divided by

368 the energy expended above that in cycling without a load. They found values ranging from 25.4

369 to 30.3% for increasing cadence and power output. Bijker, De Groot & Hollander (2001) reported

370 a mean delta efficiency (delta work accomplished over delta energy expended) of 25.8% in

371 ergometer cycling. In contrast, Margaria's net mechanical efficiency (vertical mechanical power /

372 net metabolic rate) values were rather low (~9-16%; Minetti et al., 2002) for running up inclines

373 typical of recreational running. Alternatively, the traditional vertical efficiency (vertical

374 mechanical power / difference in metabolic rate between locomotion on an incline and level

375 locomotion at the same velocity) and similarly calculated measures result in high values (~36-

376 46%; Asmussen & Bonde-Petersen, 1974; Bijker, De Groot & Hollander, 2001; Cooke et al.,

377 1991; Lloyd & Zacks, 1972; Pugh, 1971).

Limitations and future directions

Our study has several limitations worthy of mention. As discussed earlier, we performed the two

parts of the study (GRF and metabolic data collection) with two different groups of participants.

We acknowledge this as a limitation of the study, however, because our model parameters were

calculated using regression equations for group data we consider this not to be a serious concern.

Further, we are not attempting to make subject specific conclusions, rather we are seeking general

principles. Overall, we were limited by the aerobic capacity of the participants. We tried to

include a broad range of velocities and inclines, but we were restricted by our aim to consider

only conditions that could be run at truly submaximal intensities by all our participants.

Although, we did not quantify the elastic energy storage and reutilization, we accounted for this

by introducing the cost of perpendicular bouncing, which we assumed to be independent of

incline and proportional to velocity.

The, overall, promising agreement between the experimental data and the equations based on the

assumptions underlying our approach, call for further validation of this approach in future

studies. Addressing any effects on cost of potential changes in internal work (CoT of leg swing),

mechanical joint work and joint posture could refine the accuracy of and increase the confidence

in our approach. It would be interesting to study the energetics of uphill walking with the same

approach as we have done here for running. More insights into the energetics of downhill running

may be gained with our approach. Of course, our concept of decreased parallel braking impulses

would need to be reversed.

Conclusions

399 Overall, we postulate that the metabolic rate during uphill running is not simply equal to the sum

400 of the cost of level running and the cost of performing work to lift the body mass against gravity.

401 Rather, our new approach suggests that the metabolic cost of running at a certain velocity, parallel

402 to the running surface, decreases with incline, and that the efficiency of producing mechanical

403 power to lift the COM vertically is constant, independent of incline and running velocity. With

404 this approach, we have been able to model the observed metabolic rates during uphill running at

405 different velocities and inclines.

409 **References**

410 Abbott BC, Bigland B, Richie JM. 1952. The physiological cost of negative work. *Journal of*

411 *Physiology* 117:380-390

412 Alexander RM. 1989. Optimization and gaits in the locomotion of vertebrates. *Physiological*

413 *Reviews* 69:1199-1227

414 Alexander RM. 1992. A model of bipedal locomotion on compliant legs. *Philosophical*

415 *Transactions of the Royal Society B: Biological Sciences* 338:189-198

416 Alexander RM, Ker RF. 1990. Locomotion. Running is priced by the step. *Nature* 346:220-221

417 American College of Sports Medicine. 2009. *ACSM's Guidelines for Exercise Testing and*

418 *Prescription*, 8th ed. Philadelphia: Lippincott Williams & Wilkins. 158

419 Arellano CJ, Kram R. 2014. On the metabolic cost of human running: is swinging the arms worth

420 it? *Journal of Experimental Biology* In press

421 Arellano CJ, Kram R. 2014. Partitioning the Metabolic Cost of Human Running: A Task-by-Task

422 Approach. *Integrative and Comparative Biology* [Epub ahead of print] doi:10.1093/icb/icu033

423 Asmussen E, Bonde-Petersen F. 1974. Apparent efficiency and storage of elastic energy in human

424 muscles during exercise. *Acta Physiologica Scandinavica* 92:537-545

425 Bijker KE. 2003. *Metabolic cost of running and walking*. Dissertation, VU University of

426 Amsterdam

427 Bijker KE, De Groot G, Hollander AP. 2001. Delta efficiencies of running and cycling. *Medicine*

428 *and Science in Sports and Exercise* 33:1546-1551

429 Brockway JM. 1987. Derivation of formulae used to calculate energy expenditure in man.

430 *Human Nutrition - Clinical Nutrition* 41:463-471

431 Brooks GA, Fahey TD, Baldwin KM. 2005. *Exercise Physiology: Human Bioenergetics and its*

432 *Applications*, 4th ed. New York: McGraw-Hill. 698-700

433 Cavagna GA, Saibene FP, Margaria R. 1964. Mechanical work in running. *Journal of Applied*

434 *Physiology* 19:249-256

435 Chang Y-H, Kram R. 1999. Metabolic cost of generating horizontal forces in running. *Journal of*

436 *Applied Physiology* 86:1657-1662

437 Cooke CB, McDonagh MJN, Nevill AM, Davies CTM. 1991. Effects on load on oxygen intake in

438 trained boys and men during treadmill running. *Journal of Applied Physiology* 71:1237-1244

439 Farley CT, McMahon TA. 1992. Energetics of walking and running - insights from simulated

440 reduced-gravity experiments. *Journal of Applied Physiology* 73:2709-2712

441 Full RJ, Tullis A. 1990. Energetics of ascent: insects on inclines. *Journal of Experimental*

442 *Biology* 149:307-317

443 Gaesser GA, Brooks GA. 1975. Muscular efficiency during steady-rate exercise: effects of speed

444 and work rate. *Journal of Applied Physiology* 38:1132-1139

445 Gottschall JS, Kram R. 2005. Ground reaction forces during downhill and uphill running.

446   *Journal of Biomechanics* 38:445-452

447   Kram R. 2000. Muscular force or work: what determines the metabolic energy cost of running?

448   *Exercise and Sport Sciences Reviews* 28:138-143

449   Kram R, Dawson TJ. 1998. Energetics and biomechanics of locomotion by red kangaroos

450   (Macropus rufus). *Comparative Biochemistry and Physiology* 120B:41-49

451   Kram R, Taylor CR. 1990. Energetics of running: a new perspective. *Nature* 346:265-267

452   Lloyd BB, Zacks RM. 1972. The mechanical efficiency of treadmill running against a horizontal

453   impeding force. *Journal of Physiology* 223:355-363

454   Margaria R. 1968. Positive and negative work performances and their efficiencies in human

455   locomotion. *Internationale Zeitschrift für Angewandte Physiologie* 25:339-351

456   Margaria R, Ceretelli P, Aghemo P, Sassi G. 1963. Energy cost of running. *Journal of Applied*

457   *Physiology* 18:367-370

458   Minetti AE. 1998. A model equation for the prediction of mechanical internal work of terrestrial

459   locomotion. *Journal of Biomechanics* 31:463-468

460   Minetti AE, Alexander RM. 1997. A theory of metabolic costs for bipedal gaits. *Journal of*

461   *Theoretical Biology* 186:467-476

462   Minetti AE, Ardigò LP, Saibene F. 1994. Mechanical determinants of the minimum energy cost of

463   gradient running in humans. *Journal of Experimental Biology* 195:211-225

464   Minetti AE, Moia C, Roi GS, Susta D, Ferretti G. 2002. Energy cost of walking and running at

465   extreme uphill and downhill slopes. *Journal of Applied Physiology* 93:1039-1046

466   Modica JR, Kram R. 2005. Metabolic energy and muscular activity required for leg swing in

467   running. *Journal of Applied Physiology* 98:2126-2131

468   Moed B, Kram R. 2005. *Metabolic costs of forward propulsion and leg swing at different*

469   *running speeds*. In: Proceedings from the XXth Congress of the International Society of

470   Biomechanics. Cleveland State University, Cleveland.

471 Nardello F, Ardigò LP, Minetti AE. 2011. Measured and predicted mechanical internal work in

472 human locomotion. *Human Movement Science* 30:90-104

473 Pugh GC. 1971. The influence of wind resistance in running and walking and the mechanical

474 efficiency of work against horizontal or vertical forces. *Journal of Physiology* 213:255-276

475 Robbins CT, Cohen Y, Davitt BB. 1979. Energy expenditure by elk calves. *Journal of Wildlife*

476 *Management* 43:445-453

477 Roberts TJ, Kram R, Weyand PG, Taylor CR. 1998. Energetics of bipedal running. I. Metabolic

478 cost of generating force. *Journal of Experimental Biology* 201:2745-2751

479 Roberts TJ, Marsh RL, Weyand PG, Taylor CR. 1997. Muscular force in running turkeys: the

480 economy of minimizing work. *Science* 275:1113-1115

481 Rubenson J, Henry HT, Dimoulas PM, Marsh RL. 2006. The cost of running uphill: linking

482 organismal and muscle energy use in guinea fowl (Numida meleagris). *Journal of Experimental*

483 *Biology* 209:2395-2408

484 Smith NP, Barclay CJ, Loiselle DS. 2005. The efficiency of muscle contraction. *Progress in*

485 *Biophysics and Molecular Biology* 88:1-58

486 Swanson SC, Caldwell GE. 2000. An integrated biomechanical analysis of high speed incline and

487 level treadmill running. *Medicine and Science in Sports and Exercise* 32:1146-1155

488 Taylor CR, Caldwell SL, Rowntree VJ. 1972. Running up and down hills: some consequences of
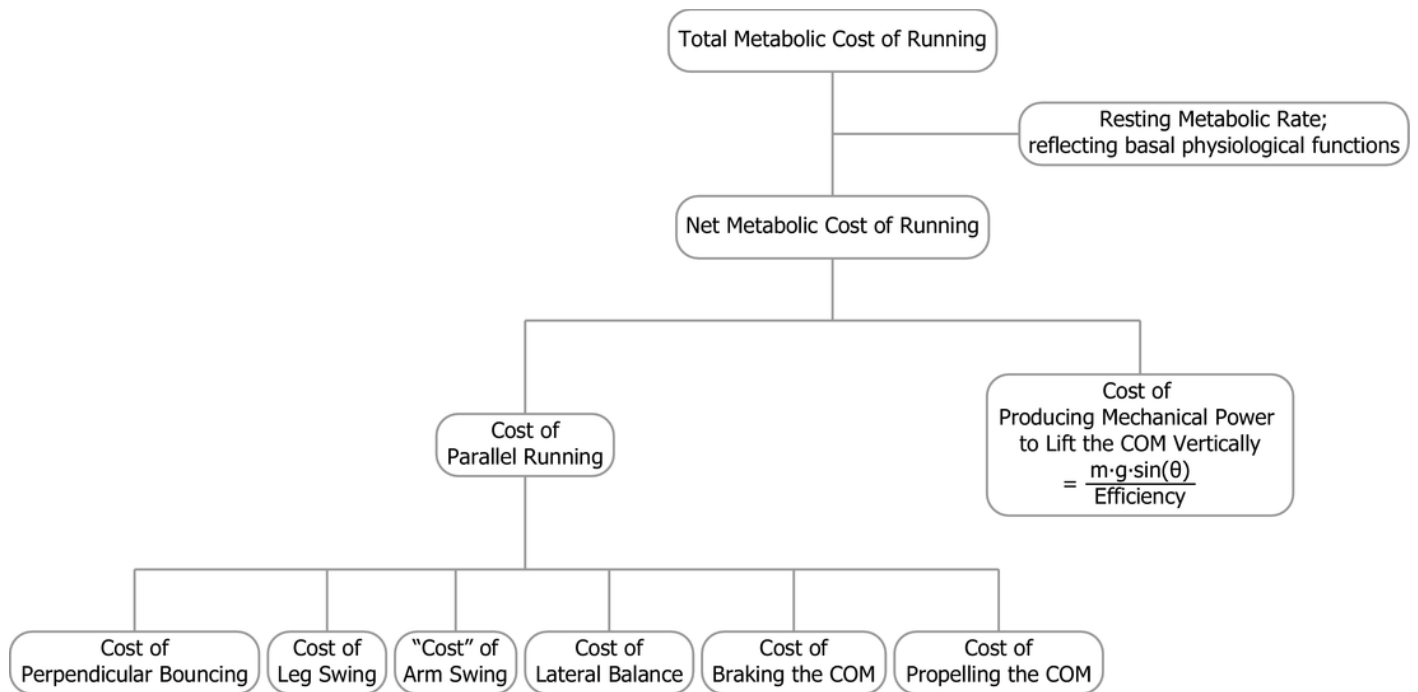
489 size. *Science* 178:1096-1097

490 Teunissen LPJ, Grabowski A, Kram R. 2007. Effects of independently altering body weight and

491 body mass on the metabolic cost of running. *Journal of Experimental Biology* 210:4418-4427

492 Zani PA, Kram R. 2008. Low metabolic cost of locomotion in ornate box turtles, Terrapene

493 ornata. *Journal of Experimental Biology* 211:3671-3676

Figure 1

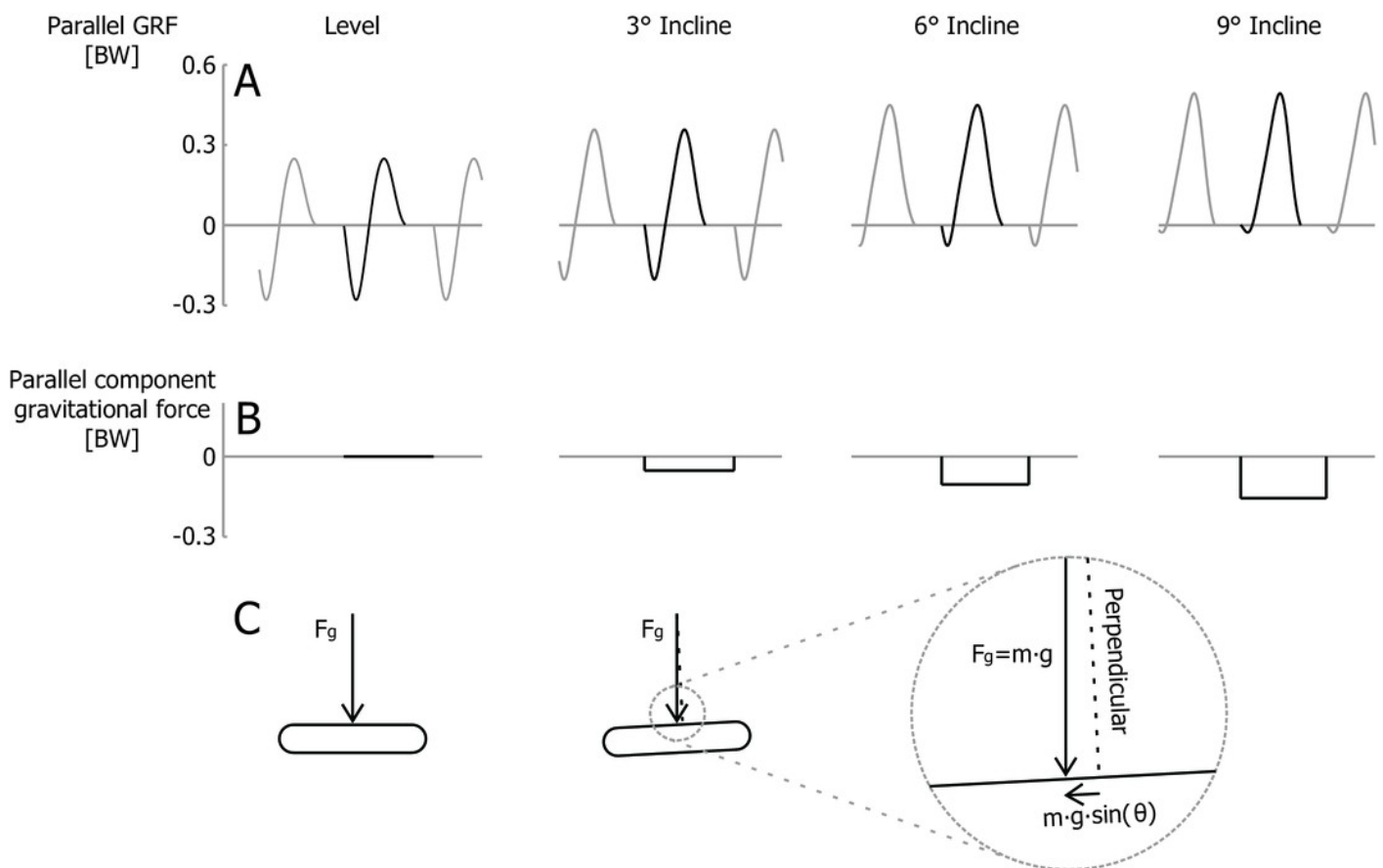The total metabolic cost of running is comprised of several components

Parallel running refers to the task of running parallel to the surface whether that surface is level or inclined. The task of parallel running intrinsically requires bouncing perpendicular to the surface and that bouncing incurs a metabolic cost.
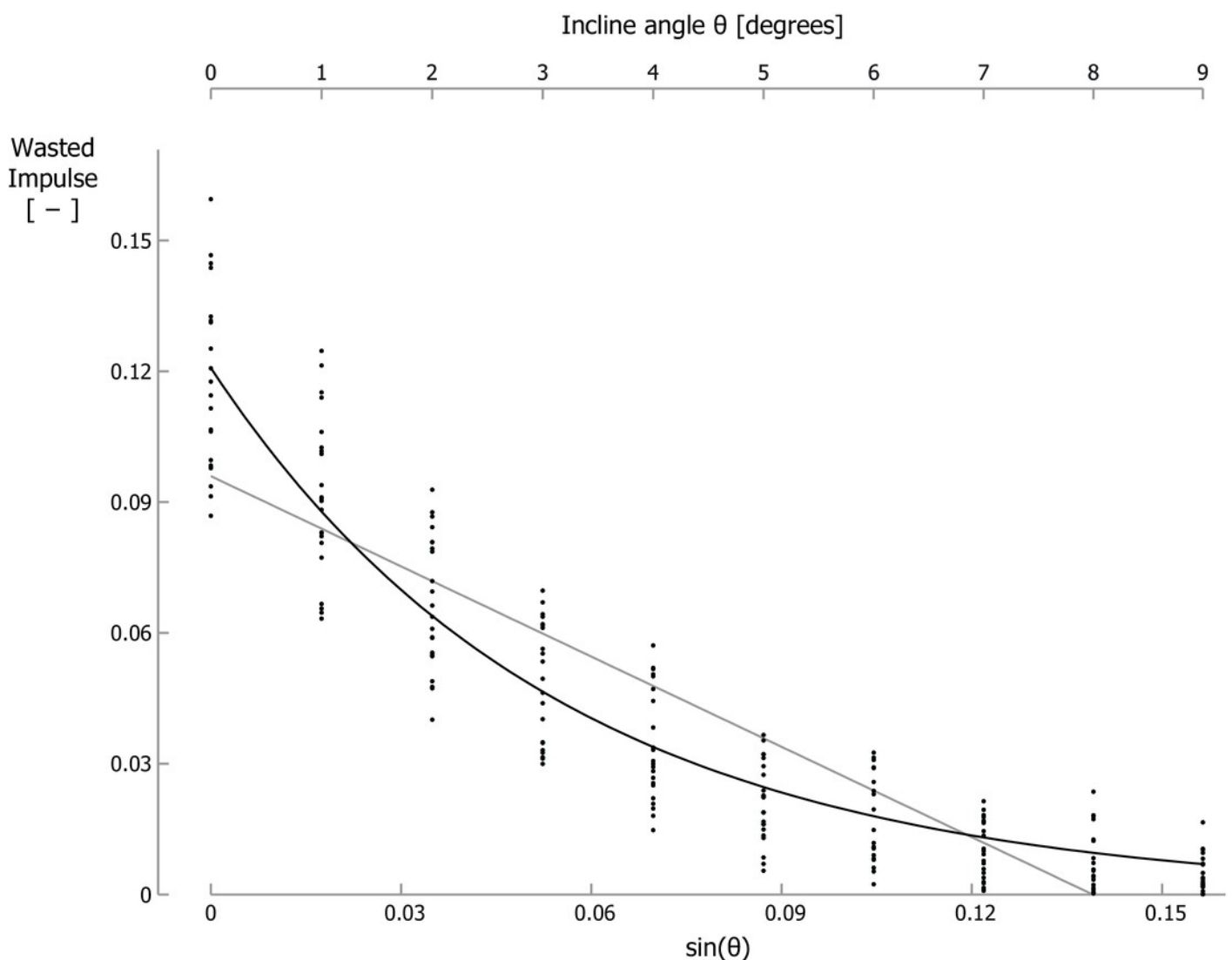
Figure 2

Ground reaction forces for different inclines

A: Idealized parallel ground reaction force versus time traces for running at 3 m/s. *B*: parallel component of gravitational impulse for a single step, and *C*: schematic representation of the gravity force vector and its component parallel to the running surface. Forces are normalized to body weight.

Figure 3

The wasted GRF impulse per step decreases for increasing inclines

Wasted GRF impulse for different inclines and velocities. Each small dot represents a single participant's wasted GRF impulse for a specific trial. The black line is the best-fit curve to the data according equation 6; the grey line is the best-fit linear equation. Note that the secondary horizontal axis at the top is the incline angle θ, which is not linear, so the tick marks are not evenly spaced.

Table 1 (on next page)

Braking, total propelling and wasted impulses, step frequencies and contact times (mean ± SD) for the different test conditions.

		Level	9°
Braking Impulse (10^{-3})	2.0 m/s	-63.9 ± 11.9	-1.7 ± 1.7
	2.5 m/s	-58.3 ± 10.8	-3.4 ± 2.6
	3.0 m/s	-55.1 ± 8.8	-3.5 ± 2.2
Total Propelling Impulse (10^{-3})	2.0 m/s	64.3 ± 12.2	0.9 ± 1.3
	2.5 m/s	58.5 ± 10.7	2.0 ± 2.5
	3.0 m/s	55.3 ± 8.7	2.3 ± 2.1
I_GRF_{wasted} (10^{-3})	2.0 m/s	128.2 ± 24.0	2.6 ± 2.9
	2.5 m/s	116.8 ± 21.5	5.4 ± 5.0
	3.0 m/s	110.3 ± 17.4	5.7 ± 4.2
Step freqency (steps/minute)	2.0 m/s	2.68 ± 0.15	2.72 ± 0.18
	2.5 m/s	2.78 ± 0.20	2.84 ± 0.16
	3.0 m/s	2.84 ± 0.19	2.94 ± 0.16
Contact times (s)	2.0 m/s	0.31 ± 0.03	0.32 ± 0.03
	2.5 m/s	0.28 ± 0.03	0.28 ± 0.03
	3.0 m/s	0.25 ± 0.02	0.25 ± 0.02

Table 2(on next page)

Measured rates of oxygen consumption (VO2) and metabolic rates (mean ± SD) for the different test conditions.

Day	Velocity (m/s)	Angle (degrees)	Grade (%)	VO$_2$ (ml/(kg·min))	Metabolic rate (W/kg)
	Standing	-	-	4.3 ± 0.5	1.5 ± 0.1
		0	0	24.5 ± 1.5	8.3 ± 0.4
		1	1.7	26.1 ± 1.2	8.9 ± 0.4
1		2	3.5	29.1 ± 1.3	9.9 ± 0.4
	2.0	3	5.2	31.6 ± 1.8	10.8 ± 0.5
		4	7.0	34.3 ± 1.1	11.7 ± 0.4
		6	10.5	40.5 ± 1.8	13.9 ± 0.6
		8	14.1	47.1 ± 2.1	16.3 ± 0.7
	Standing	-	-	4.7 ± 0.4	1.6 ± 0.1
		0	0	29.0 ± 1.3	9.8 ± 0.4
		1	1.7	31.6 ± 1.4	10.7 ± 0.4
	2.5	2	3.5	35.4 ± 1.4	12.0 ± 0.4
		3	5.2	38.3 ± 1.2	13.1 ± 0.4
2		4	7.0	42.2 ± 1.0	14.4 ± 0.3
		0	0	35.3 ± 1.6	11.9 ± 0.5
		1	1.7	38.9 ± 2.0	13.2 ± 0.6
	3.0	2	3.5	43.1 ± 1.8	14.7 ± 0.6
		3	5.2	47.1 ± 1.7	16.1 ± 0.5
		4	7.0	51.6 ± 2.2	17.8 ± 0.7

Figure 4

Net metabolic Cost of Transport

A: Net metabolic Cost of Transport (CoT) for different inclines and velocities. CoT is the net metabolic energy consumed per meter traveled parallel to the running surface. Each small dot represents a single participant's CoT for a specific trial. The black line is the best-fit curve of the net CoT according equation 8. Note that the secondary horizontal axis at the top is the incline angle θ, which is not linear, so the tick marks are not evenly spaced. *B*: Net metabolic CoT$_{total}$ and metabolic CoT$_{vertical}$. *C*: Metabolic CoT of parallel running. The grey line represents the constant CoT components of parallel running (perpendicular bouncing, leg and arm swing and lateral balance); the remainder, the CoT of braking and propelling, approaches zero at steeper inclines. Symbols represent mean values: $\bigcirc$ = 2.0 m/s, Δ = 2.5 m/s, $\square$ = 3.0 m/s.