Humans trade-off energetic cost with fatigue avoidance while walking

Kirsty A. McDonald[1,2,3,*], Joseph P. Cusumano[4], Andrew Hieronymi[5], Jonas Rubenson[2,3,6]

[1]Department of Exercise Physiology, School of Health Sciences, University of New South Wales, Sydney, New South Wales, Australia, 2052

[2]School of Human Sciences, The University of Western Australia, Crawley, Perth, Western Australia, Australia, 6009

[3]Biomechanics Laboratory, Department of Kinesiology, The Pennsylvania State University, University Park, Pennsylvania, United States of America, 16802

[4]Department of Engineering Science and Mechanics, The Pennsylvania State University, University Park, Pennsylvania, United States of America, 16802

[5]School of Visual Arts, The Pennsylvania State University, University Park, Pennsylvania, United States of America, 16802

[6]Integrative and Biomedical Physiology, The Huck Institutes of the Life Sciences, The Pennsylvania State University, University Park, Pennsylvania, United States of America, 16802

[*]Kirsty A. McDonald

Email: kirsty.mcdonald@unsw.edu.au

18 **Abstract**

19 Metabolic cost minimization is widely regarded as the principal optimality criterion that governs
20 walking. Minimizing muscle activation has, nevertheless, outperformed energy optimization in
21 simulating human gait and predicting certain gait behaviors. The highly coupled nature of metabolic
22 and muscle activation costs makes it difficult to empirically discern the interrelationship between
23 these objectives. We implemented a unique experimental design that pits metabolic cost against
24 muscle activation costs estimated from electromyography of seven lower limb muscles. Healthy
25 adults (*N*=10) selected between walking on a treadmill incline versus walking in a crouched posture
26 (that disproportionately affected activation cost), forcing a choice between minimizing metabolic
27 cost or activation cost. When experiencing these *Competing-Cost-Pairs*, participants systematically
28 protected their activation cost at the expense of high metabolic power ($\overline{C}_{met,P}$; 19% penalty,
29 p<0.05). This held true when activation cost was expressed as the sum of the muscle activations
30 squared ($\overline{C}_{a^2}$; 66% saving, p<0.05) and as the maximal activation across muscles ($\overline{C}_{a,max}$; 44%
31 saving, p<0.05), both of which penalize overburdening any individual muscle and thus indicate
32 fatigue avoidance. Activation cost, expressed as the sum of muscle volume-normalized activation
33 ($\overline{C}_{a,vol}$), more closely models energy use and was also protected by the participants' decision (23%
34 saving, p<0.05) demonstrating that activation was, at best, an inaccurate proxy signal for metabolic
35 energy. Energy minimization was only observed when there was no adverse effect on muscle
36 activation. By decoupling metabolic and activation costs, we provide the first empirical evidence of
37 humans embracing non-energetic optimality in favor of a clearly defined alternate neuromuscular
38 objective.

Introduction

Humans often move in ways that save metabolic energy. For example, preferred walking speed (1–5), step frequency (6–12), step width (13) and arm swing (14,15) are classic examples known to minimize the metabolic cost of locomotion. More recently, it has been demonstrated that humans continue to exhibit energy-favoring behaviors, even after normal gait mechanics are disrupted (8,16,17). Given the consistency of these observations in human locomotion, and the selective advantage that they purportedly bestow, it is argued that whole-body energy minimization is a central factor dictating human gait behavior and its evolution (18,19).

However, whether metabolic cost minimization is itself the principal, overriding, optimality criterion during gait remains a matter of debate. For example, it has been proposed that other factors, such as fatigue avoidance, may be prioritized in the control scheme of locomotion (20–22), with low metabolic cost arising as a byproduct. Similarly, others suggest that economical human gait arises not from minimization of metabolic cost alone, but rather via the control of metabolic energy in conjunction with several additional optimality criteria (23,24).

Of the possible non-energetic optimality criteria, a compelling argument can be made for a muscle activation-based control signal in human locomotion. Several groups have developed successful simulations of human locomotion based on minimizing total muscle activation. This approach has proven particularly powerful in predicting realistic locomotor mechanics and energetics, often outperforming simulations based on minimizing total energy cost alone (21,22,25,26). For example, Miller et al. (21) discovered that more realistic gait biomechanics and whole-body metabolic cost could be predicted by minimizing muscle activation compared to metabolic cost itself, despite the longstanding view that humans consistently prioritize energy optimizing gaits (5,11). Likewise, Falisse et al. (23), and more recently, Veerkamp et al. (24), demonstrated that the inclusion of muscle activation in a multi-objective performance criterion is essential for generating the most physiologically realistic simulations of human gait. There also exists experimental data that point to muscle activation as a control signal in human locomotion. For example, the metabolic cost of walking on inclines of up to 10% can be predicted using muscle activation data (27). Preferred stride frequencies (28,29) and the walk-run transition (30–32)—a fundamental locomotor behavior that is not always tracked by whole-body energy cost (20)—can also be predicted by a muscle activation minimizing criterion. Similarly, self-selected cadence in cycling has been found to coincide with low muscle activity (33), more so than with minimization of metabolic energy expenditure (34,35). Together, these simulation and experimental data indicate that muscle activation may indeed be among the primary optimality criteria governing human gait.

On closer examination of the aforementioned studies, the activation cost functions that have been most successful in predicting gait mechanics and energetics (often better than energy optimization) penalize high activations in any given muscle. These cost functions minimize the sum of individual muscle activations (A) raised to an integer power (e.g., A^2, A^3 *etc.*), where the activation of a muscle is defined as the fraction (between 0 and 1) of the total muscle fibers activated (21,22). Other successful simulations of muscle control have used a similar, but more extreme formulation, whereby the maximum activation of any single muscle is minimized (the min-max model; (36)). As above, the resulting recruitment pattern is one that favors a uniform distribution of activations across muscles as opposed to high activations among a select few muscles—even in cases where the latter results in lower total energy consumption (22,26). This avoidance of high muscle activation that arises from non-uniform muscle recruitment has been regarded as a fatigue-minimizing (endurance maximizing) strategy (22,37,38). Thus, the nervous system may prioritize a 'division of labor' across muscles that minimizes muscle fatigue, as opposed to a strict 'economy of labor'. In this scenario, economical gait may arise not as the principal optimization criterion, but rather secondary to a control paradigm favoring even muscle recruitment (22).

Establishing the mechanism(s) driving locomotor behavior is key to understanding the control of human gait and the resulting energetics. Previous investigations have largely been limited to simulation studies that assign objective functions (optimality criteria) *a priori* and subsequently

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90 assess their efficacy based on their ability to reproduce a high number of human gait features. To
91 the best of our knowledge, no study has empirically addressed whether whole-body energy use or
92 fatigue-like muscle activation costs (e.g., sum of A^2; (22)) are prioritized during locomotion.
93 Therefore, we designed an experiment to pit fatigue-like muscle activation costs against the total
94 metabolic cost during walking by disrupting the distribution of activation across the lower limb
95 muscles. Importantly, in this design, moving with low energy expenditure while simultaneously
96 favoring a low muscle activation cost (i.e., low muscle fatigue) was unfeasible, therefore providing
97 an opportunity to empirically test whether one criterion was favored over the other.

Materials and methods

Participants

100 Ten healthy adults (5F, 5M; age 31.1±7.2 years; mass 69.6±11.1 kg; height 1.70±0.07 m;
101 mean±SD) participated in this study after providing informed consent. The study was approved by
102 the Institutional Review Board at The Pennsylvania State University and received reciprocal
103 approval by the Human Research Ethics Committee at the University of Western Australia.
104 Volunteers were required to be free from medical conditions that could make moderate-intensity
105 exercise unsafe (e.g., heart, respiratory and/or musculoskeletal conditions).

Experimental design overview

107 The primary objective of our experimental design was to create two competing conditions
108 (Competing-Cost-Pairs) that required the participants to select between either a low whole-body
109 metabolic cost or a low activation cost (see below for cost functions). Importantly, in selecting
110 between the Competing-Cost-Pairs, the metabolic cost and activation cost could not be
111 simultaneously reduced. Through pilot testing, two locomotor conditions were established to meet
112 this experimental design goal. The first condition, crouch walking on a level treadmill, was
113 determined to elicit a moderate metabolic cost and a high activation cost due to the uneven
114 distribution of muscle recruitment across lower limb muscles. The second condition, incline walking,
115 included five levels of treadmill incline that ranged from 0-24% and that predominantly taxed
116 metabolic cost. As the incline level was increased, a Competing-Cost-Pair was determined by
117 identifying the incline level that elicited a metabolic cost exceeding that of crouch walking, while at
118 the same time having a lower muscle activation cost (see Fig. 1).

119 To establish the Competing-Cost-Pairs, five independent comparison trials were performed in a
120 random order between flat (i.e., level treadmill) crouch walking and upright walking on one of the
121 five incline levels (0%, 6%, 12%, 18% or 24%; Fig. 1). For each comparison, participants were
122 asked to explore both crouch walking and upright walking on the assigned incline for three minutes.
123 After this time, they selected their preferred state (crouch or upright incline walking), in which they
124 then walked for an additional five minutes. The steepest incline level that was selected over crouch
125 walking was referred to as the pre-transition incline. The first incline level for which the crouch
126 walking was preferred was referred to as the post-transition incline (data were collected at the end
127 of the five comparison trials for all incline levels that were rejected in favor of crouch walking).

Crouch walking

129 Crouch walking was achieved by having participants walk on a level treadmill (0% incline) while
130 avoiding contact between their body and a virtual ceiling, with the specific instruction to maintain
131 their trunk and head in a normal, upright walking posture (i.e., crouched, but not hunched or with
132 lowered head). A motion sensing device (Xbox Kinect, Microsoft, WA, USA), situated behind the
133 participant, was programmed to detect the participant's body shape and produce a two-dimensional
134 body silhouette. This silhouette was displayed on a large screen in front of the treadmill together
135 with the virtual ceiling projection (Fig. 2). The ceiling height was programed to equal 93% of the
136 participant's standing height. This height was established in pilot testing to result in a crouch posture
137 that elicited the desired increases in our metric of activation cost (see below). During periods of
138 silhouette-ceiling collision, the outline of the silhouette was filled blue to alert the participant of
139 contact. The number and duration of collisions was recorded for each trial. The real-time motion-

140 tracking and visual feedback was implemented in a custom program developed with the
141 openFrameworks open-source C++ toolkit.

142 At the beginning of each experiment, participants were provided a crouch walking familiarization
143 trial. Participants walked at a set speed of 1.0 m s^{-1}, crouching below the virtual ceiling. After three
144 minutes of crouch walking with unlimited silhouette-ceiling collisions, the participant was informed
145 that, to end the familiarization session, they must perform one minute of walking with no recorded
146 collisions.

147 All participants achieved the one-minute benchmark and progressed to the next phase of data
148 collection, in which their crouch preferred walking speed (PWS$_{C/W}$; m s^{-1}) was assessed in
149 accordance with the method outlined by Dingwell and Marin (39). All crouch and incline walking
150 trials described below were administered at the PWS$_{C/W}$ so as not to disadvantage metabolic
151 energy use in the crouch condition: i.e., it was assumed that preferred walking speed selection
152 would minimize metabolic cost of transport for the crouch condition (2,40).

153 **Comparison trials**
154 Following PWS$_{C/W}$ determination, a five-minute trial of crouch walking was recorded (initial crouch).
155 In a randomized order, five levels of upright incline walking (on treadmill inclines of 0%, 6%, 12%,
156 18% and 24%) were then pitted against crouch walking, one by one. Each comparison trial (crouch
157 versus a single incline level) commenced with 30 seconds of crouch walking and 30 seconds of
158 incline walking (the order of which was reversed for consecutive comparison trials), followed by a
159 further two minutes where the participant was free to explore both the crouch and incline. During
160 the two-minute exploratory period, transition between the crouch and incline walking was verbally
161 requested by the participant and manually initiated by the investigator, taking less than 10 seconds
162 to implement.

163 At the conclusion of the exploratory period, the participant verbally expressed the condition (crouch
164 or incline) in which they would prefer to walk for the following five minutes. Their preference was
165 then imposed for a five-minute period, during which metabolic, surface electromyography (EMG),
166 and ground reaction force (GRF) data were collected (details below). On discussions with
167 participants at the conclusion of the experiment, it was confirmed that, together, the one minute
168 (total) of imposed walking in the two conditions and the two minutes of free exploration was
169 adequate for all participants to conclusively decide on a preferred condition.

170 Once crouch walking had been compared to the five incline levels, an additional five-minute crouch
171 walking trial was recollected to account for fatigue/familiarization effects (final crouch). Any
172 outstanding incline levels for which data was not collected as part of the comparison trials (because
173 crouch walking was preferred) were then completed at PWS$_{C/W}$, each for five minutes (randomized
174 order), to provide insight into the participant's motivation for transitioning (rejecting these inclines).
175 To minimize any persistent muscle fatigue effects, participants commenced each consecutive trial
176 when they had returned to a baseline (resting) level of exertion. When describing the protocol,
177 participants were made aware that they may be asked to complete at most 12 walking trials.
178 However, the nature of the trials following the comparison trials were not revealed to the participants
179 to ensure it did not influence their prior decisions.

180 **Whole-body energetics and electromyography measurements**
181 Breath-by-breath oxygen uptake and carbon dioxide production were sampled using a portable
182 metabolic system (Cosmed K4b^2, Rome, Italy). A portable metabolic device was necessary to
183 facilitate adherence to the required crouching posture and free regulation of body position on the
184 treadmill. The final minute of data was used to compute a steady-state mass-specific metabolic
185 power ($C_{met,P}$; W kg^{-1}) for each trial (details below). Surface EMG recordings were made
186 synchronously from gluteus maximus (Gmax), biceps femoris (BF), rectus femoris (RF), vastus
187 medialis (VM), medial gastrocnemius (MG), soleus (SOL) and tibialis anterior (TA) of the right leg,
188 using silver-tipped surface electrodes placed according to SENIAM guidelines (41). Signals were
189 recorded using a Bortec Octopus AMT-8 system (Calgary, Canada). Twenty strides of EMG data
190 were collected at 2000 Hz. Ground reaction forces from the custom-built instrumented treadmill

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191 were also obtained (again sampled at 2000 Hz) to determine foot contacts and were later used to
192 crop the EMG data into strides during data processing. Metabolic, EMG and GRF data were
193 collected during the initial and final crouch trials, all comparison trials where the incline was
194 selected, and any outstanding incline trials (thus, there were seven total recording trials).

195 **Data processing**
196 Data processing was performed in MATLAB 2018a (MathWorks, Natick, USA) using in-built
197 functions and custom scripts.

198 *Metabolic power* $\left(C_{met,P}\right)$
199 The rate of oxygen uptake ($\dot{V}O_2$; L s^{-1}) and carbon dioxide production ($\dot{V}CO_2$; L s^{-1}) were averaged
200 from the final minute of each trial and the following stoichiometric equation was applied to determine
201 metabolic power (42,43):

202
$$C_{met,P} = \frac{\left(16.89(\dot{V}O_2) + 4.82(\dot{V}CO_2)\right)1000}{M}$$

203 Where M represents participant body mass. Because speed was constant across trial, we did not
204 convert to a cost per distance traveled.

205 *Muscle activation*
206 Two participants' activation data were eliminated from further analyses due to notable and
207 persistent signal artefact in one of their processed electromyograms. For the remaining participants
208 (N=8), the raw EMG data were DC offset, band-pass filtered (20-350 Hz) to remove any movement
209 artefact and high frequency noise, and full-wave rectified. A linear envelope was applied to the
210 rectified data using a low-pass filter with 6 Hz cut-off frequency (EMG_{env}). All data filtering utilized
211 fourth-order Butterworth underdamped filters (44). For each of the seven trials for which data was
212 collected, five strides ($j = 1, 2, \ldots 5$) of EMG_{env} data per muscle ($i = 1, 2, \ldots 7$) were individually
213 integrated to produce scalar muscle activation values for each muscle, for each stride $\left(a_{ij}\right)$, as
214 below:

215
$$a_{ij} \triangleq \int_0^{tf} (EMG_{env})_{ij} \, dt$$

216 where $(EMG_{env})_{ij}$ represents the processed linear envelop of the ith muscle for the jth stride, 0 is
217 the time at the initial contact of the right foot and tf is the time at the consecutive contact of the
218 same (ipsilateral) foot determined from force plate thresholds (2% of peak signal).

219 To take into consideration fluctuations in the activation integral $\left(a_{ij}\right)$ that can occur due to changes
220 in stride time $\left(T_j\right)$, each stride's muscle activation values were expressed as a rate $\left(\frac{a_{ij}}{T_j}\right)$. A
221 normalized (unitless) activation $\left(A_{ij}\right)$ was computed for each muscle, for each stride by normalizing
222 by the average value obtained from the five strides of the 0% incline trial:

223
$$A_{ij} \triangleq \frac{a_{ij}}{T_j} \bigg/ \left(\frac{1}{5}\sum_{j=1}^{5} \frac{a^0_{ij}}{T^0_j}\right)$$

224 where a^0 and T^0 are the activation integral and stride time of the 0% incline trial, respectively.

225 *Activation cost functions*
226 We used what have previously been classified as 'fatigue-like' activation cost functions that
227 penalized large, fatigue-inducing, muscle activations irrespective of the size of the muscle (21,22).
228 Our cost functions are based on those previously adopted, minimizing a) the sum of individual

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229   muscle activations raised to an integer power $(p > 1)$ (22) or b) the individual maximal muscle
230   activation across all muscles $(p \rightarrow \infty)$ (Rasmussen et al., 2001).

231   **a) Sum of activations squared $(\overline{C}_{a^2})$;** For each trial, a total muscle activation cost was computed
232   as the sum of the seven muscles' normalized activations (A_{ij}) squared. This value was then
233   averaged across five strides:

234
$$\overline{C}_{a^2} \triangleq \frac{1}{5} \sum_{j=1}^{5} \sum_{i=1}^{7} \left(A_{ij}{}^2\right)$$

235   **b) Maximal muscle activation $(\overline{C}_{a,max})$;** At the extreme end of fatigue-like activation cost
236   functions, i.e., the integer power limit $(p \rightarrow \infty)$, the cost function depends only on the maximally
237   activated muscle (22). Thus, for each trial, the maximum activation cost was computed as the
238   maximum value (max_i) from the seven muscles' normalized activation (A_{ij}). This value was then
239   averaged across five strides:

240
$$\overline{C}_{a,max} \triangleq \frac{1}{5} \sum_{j=1}^{5} \left[max_i\left(A_{ij}\right)\right]$$

241   By adopting these two cost functions we capture a range of fatigue-like activation cost formulations,
242   with the latter most strongly penalizing high activation in individual muscles. Both activation costs
243   represent fatigue through a combined effect of the amount of fibers active within the muscles (a_{ij}),
244   as well as the rate at which they are used during continuous walking $\left(\frac{1}{T_j}\right)$, similar to the fatigue
245   activation cost function in Miller et al. (21).

246   **c) Sum of the volume-weighted activations $(\overline{C}_{a,vol})$;** In addition to the two aforementioned
247   fatigue-like activation costs, we also included an 'effort-like' activation cost (22). This cost function
248   does not penalize an uneven distribution of muscle activation. Rather, it takes into consideration
249   active muscle volume, a key determinant of muscle energy expenditure (45,46), by weighting the
250   activations by muscle size. Therefore, unlike the fatigue-like functions, this cost is more sensitive
251   to activation of large muscles (22). This cost was included to assess the possibility that muscle
252   activation serves as a proxy for metabolic energy expenditure (47).

253   The normalized activation rate (A_{ij}) for each muscle was weighted (w_i) according to the muscle
254   volumes documented in the supplementary material of Handsfield et al. (48). These weightings
255   were 0.33, 0.08, 0.10, 0.17, 0.10, 0.17 and 0.05 for Gmax, BF, RF, VM, MG, SOL, and TA,
256   respectively, and represent each muscle's volume as a proportion of the sum of all seven muscles.
257   The seven volume-weighted normalized activation rates were then summed, and this value was
258   averaged across five strides:

259
$$\overline{C}_{a,vol} \triangleq \frac{1}{5} \sum_{j=1}^{5} \sum_{i=1}^{7} w_i \left(A_{ij}\right)$$

260   **Data analysis**
261   For each metric described above, five values were initially analyzed; mean crouch (the mean value
262   of the initial crouch and final crouch trials), initial crouch, final crouch, pre-transition incline (the
263   steepest incline level which was selected over crouch walking) and post-transition incline (the
264   lowest incline level that was rejected in favor of crouch walking). Whether the mean, initial or final
265   crouch data were compared to the pre- and post- transition inclines had no bearing on the
266   interpretation of the results discussed herein. Thus, the mean crouch data is represented by all
267   future references to the crouch walking data.

268 *Competing-Cost-Pairs*
269 Each participant's mean crouch walking data was compared to the pre-transition incline to
270 determine whether Competing-Cost-Pairs had been established (i.e., the two trials were designed
271 to provide mutually exclusive $C_{met,P}$ and $\overline{C}_{a^2}$ advantages). We accepted a Competing-Cost-Pair
272 when $C_{met,P}$ decreased between the pre-transition incline and crouch walking trials, and $\overline{C}_{a^2}$
273 increased. The $C_{met,P}$ and $\overline{C}_{a^2}$ advantages were assessed because our aim was to compare
274 metabolic and fatigue-like muscle activation costs, and $\overline{C}_{a^2}$ represents the less extreme (least
275 biased) of our fatigue-like cost functions. A secondary analysis was then performed to determine
276 whether Competing-Cost-Pairs were also present between $C_{met,P}$ and $\overline{C}_{a,max}$, and $C_{met,P}$ and $\overline{C}_{a,vol}$.

Statistical analyses
277
278 Summary statistics (group mean±SD) were computed for crouch walking performance variables
279 (number and duration of silhouette-ceiling collisions), and for key cost metrics ($C_{met,P}$, $\overline{C}_{a^2}$, $\overline{C}_{a,max}$
280 and $\overline{C}_{a,vol}$) during the crouch and incline walking trials. Normality was assessed using the Shapiro-
281 Wilk test. One-way repeated measures analysis of variance (ANOVA) tests were used to confirm
282 main effects of the normally distributed incline data (0, 6, 12, 18, 24% inclines) for $C_{met,P}$, $\overline{C}_{a^2}$, $\overline{C}_{a,max}$
283 and $\overline{C}_{a,vol}$.

284 For the crouch, pre-transition incline and post-transition incline comparisons, key cost metrics were
285 each analyzed via a one-way repeated measures ANOVA (normally distributed) or Friedman test
286 (non-normally distributed). *Post hoc* testing was then administered as paired-samples t-tests
287 (normally distributed) or Wilcoxon tests (non-normally distributed). Results were compared against
288 an adjusted alpha level (p=0.017; Bonferroni correction). All other analyses employed a standard
289 0.05 alpha level. In group-level analyses, all available data (*N*=10 for $C_{met,P}$ and *N*=8 for $\overline{C}_{a^2}$, $\overline{C}_{a,max}$,
290 $\overline{C}_{a,vol}$) was used. Paired samples t-tests/Wilcoxon tests analyzed $C_{met,P}$, $\overline{C}_{a^2}$, $\overline{C}_{a,max}$ and $\overline{C}_{a,vol}$ in
291 the sub-sample of participants for whom a Competing-Cost-Pair was successfully established
292 (*N*=7).

293 To discern whether the use of the initial, final or mean crouch data to represent crouch walking
294 $C_{met,P}$, $\overline{C}_{a^2}$, $\overline{C}_{a,max}$ and $\overline{C}_{a,vol}$ would make a difference to our interpretation of results, all relevant
295 statistical tests (above) were performed three times: i) using the initial crouch data, ii) using the final
296 crouch data, and iii) using the mean of the initial and final crouch data. No difference in
297 interpretation was present and so mean crouch data is presented in the Results section below.
298 Initial and final crouch data comparisons can be found in the Supplementary Material.

299 Any non-normally distributed data is denoted by a caret (^), in the Results section below. SPSS
300 26.0 (IBM, Chicago, USA) was used to perform all statistical analyses.

301 **Results**

302 **Gait selections**
303 The current experiment used the selection of one locomotor mode over another—in this case,
304 walking in a crouch posture versus walking upright at one of five incline levels (0, 6, 12, 18 and
305 24%)—to reveal underlying prioritization objectives. Thus, in total, five decisions were made by our
306 participants, i.e., one for each incline level. At low levels of incline (0-12%), all participants (*N*=10)
307 chose the incline over the crouch. At 18% incline, the decision divided our sample; seven
308 participants continued to select the incline, while three preferred the crouch (Fig. 3A). Those three
309 participants also chose crouch over the 24% incline. The remaining seven participants all chose
310 crouch walking over walking on the 24% incline.

311 The task performance of crouch walking was assessed by the total number and duration of
312 silhouette-ceiling collisions during a single five-minute trial. To determine potential learning effects,
313 these metrics were recorded at the beginning (initial crouch trial) and end (final crouch trial) of the
314 data collection session. Total number (start: 1.2±1.5; end: 2.3±2.4) and duration (start: 0.11±0.15

315 seconds; end: 0.22±0.25 seconds) of collisions did not change significantly (p=0.131^ and
316 p=0.075^, respectively).

Incline and crouch effects on activation and energy costs

318 All key cost metrics ($C_{met,P}$, $\overline{C}_{a^2}$, $\overline{C}_{a,max}$ and $\overline{C}_{a,vol}$) increased with increasing incline level (Fig. 3A-
319 D). This was confirmed by one-way repeated measures ANOVAs, which demonstrated a main
320 effect of incline for $C_{met,P}$ (p<0.001), $\overline{C}_{a^2}$ (p=0.001), $\overline{C}_{a,max}$ (p<0.001), and $\overline{C}_{a,vol}$ (p<0.001).

321 Crouch walking disrupted the distribution of muscle activation compared to upright walking, such
322 that select muscles had proportionately higher activation values. In particular, Figure 4 highlights
323 the increased activation requirements of knee extensor musculature (vastus medialis and rectus
324 femoris) to facilitate the crouch gait, while the steepest incline gaits are achieved with a more even
325 distribution of activation.

326 When statistical comparisons were made between the crouch, pre-transition incline and post-
327 transition incline, the one-way repeated measures ANOVAs/Friedman tests demonstrated a main
328 effect for $C_{met,P}$ (p<0.001, *N*=10), $\overline{C}_{a^2}$ (p=0.008^; *N*=8), $\overline{C}_{a,max}$ (p=0.001, *N*=8) and $\overline{C}_{a,vol}$ (p=0.003;
329 *N*=8; Fig. 3E-H).

Competing-Cost-Pairs

331 Competing-Cost-Pairs (i.e., two trials providing mutually exclusive $C_{met,P}$ and $\overline{C}_{a^2}$ advantages) were
332 effectively established for seven of the eight participants for whom we acquired a complete set of
333 EMG data (Table 1; Fig. 5). Competing-Cost-Pairs could also be established for these participants
334 between $C_{met,P}$ and $\overline{C}_{a,max}$, and $C_{met,P}$ and $\overline{C}_{a,vol}$ (Table 1).

335 All seven participants (1-4 and 8-10) chose incline walking over crouch walking and thus selected
336 low muscle activation at the expense of a high $C_{met,P}$. The average $\overline{C}_{a^2}$ advantage in the Competing-
337 Cost-Pairs was 66% (*N*=7; p=0.018^; range: 31 to 95%) and for $\overline{C}_{a,max}$ was 44% (*N*=7; p=0.003;
338 range: 15 to 89%; Table 1). The average $C_{met,P}$ penalty was 19% (*N*=7; p=0.002; range: 4% to
339 31%; Table 1). Participant #6 had a $C_{met,P}$ that was nearly identical in the crouch and incline
340 condition (1% difference) and therefore did not present a clear energetic advantage/disadvantage
341 for gait selection (Table 1). However, Participant #6 achieved the group's largest activation
342 advantage by selecting the incline condition (210% reduction in $\overline{C}_{a^2}$; 103% reduction in $\overline{C}_{a,max}$). We
343 also found an advantage in the effort-like activation cost ($\overline{C}_{a,vol}$) when the participants selected
344 incline walking over crouch walking (Table 1). The average $\overline{C}_{a,vol}$ advantage in the Competing-
345 Cost-Pairs was 23% (*N*=7; p=0.007; range: 8 to 38%).

346 In addition to the Competing-Cost-Pairs, prioritization objectives can be further assessed from
347 comparing the group mean $C_{met,P}$ (*N*=10) and activation costs (*N*=8) of the crouch walking and pre-
348 and post-transition incline conditions (Fig. 3E-H). Crouch walking incurred a $C_{met,P}$ of 7.84±1.38 W
349 kg^{-1}, which was significantly lower than both the pre- (9.46±0.91 W kg^{-1}; p=0.007) and post-
350 (11.92±1.31 W kg^{-1}; p=0.005) transition incline levels, with the pre- and post-transition inclines
351 being significantly different from one another (p=0.005; Fig. 3E). In contrast, the $\overline{C}_{a^2}$ and $\overline{C}_{a,max}$ for
352 the crouch walking were significantly greater (84%; p=0.012^ and 52% p=0.006, respectively) than
353 the pre-transition incline (Fig. 3F-G). These data show, at a group level, a selection (pre-transition
354 incline) for lower fatigue-like activation costs at the expense of higher $C_{met,P}$. We also found that
355 the $\overline{C}_{a^2}$ and $\overline{C}_{a,max}$ in crouch walking were statistically equivalent to the post-transition incline
356 (p=0.263^ and p=0.214, respectively), indicating that the disadvantage in the fatigue-like activation
357 costs was no longer present when crouch walking was finally selected (crouch walking versus post-
358 transition incline walking). The effort-like activation metric ($\overline{C}_{a,vol}$ followed a similar pattern (Fig.
359 3H). $\overline{C}_{a,vol}$ for crouch walking was significantly greater (27%) than for the pre-transition incline
360 (p=0.003) but not for the post-transition incline (p=0.779).

Discussion

Metabolic energy expenditure is widely regarded as a principal determinant of animal locomotor behavior (5,8,11,49). However, simulation studies of human locomotion suggest muscle activation may also be a key control parameter (21,22). It is difficult to discern how these criteria are weighted in the control scheme of locomotion due to their highly coupled nature. The current study utilized an experimental design that systematically pitted whole-body metabolic cost against muscle activation costs. In these competing conditions, global energy expenditure was clearly not prioritized, and our empirical data provide promising support for muscle activity prioritization.

Energy expenditure is not always the principal objective in human locomotion
There are a handful of previous studies in which humans have been observed to expend more energy than minimally required for both upper and lower limb movement tasks (40,50–56). These studies suggest that energy minimization may be task-dependent. Perhaps the most well documented example of non-energetically optimal movement is self-selected cycling cadence (for a review see Vercruyssen and Brisswalter, 2010). In the context of gait, Yandell and Zelik (56) show inconsistent prioritization of metabolic cost when participants used their preferred step frequency during barefoot walking. The authors propose this may be related to the discomfort/pain associated with an unshod gait (56). Some evidence also suggests humans do not prioritize metabolic cost minimization when moving in less stable environments, e.g., walking downhill (50) (but this remains inconclusive (57)) or walking with experimentally imposed asymmetrical leg lengths (40). Humans have also been observed to perform walking tasks in more effortful ways to eliminate a cognitive burden (51). Furthermore, there exist several studies of human movement in which immediate, independent detection and/or acute prioritization of the energetic minima is not evident (8,40,58,59). The costs driving gait selection in the aforementioned studies remain speculative. The current study is, in contrast, among the first to explicitly and experimentally demonstrate an alternative criterion, namely muscle activation, that is prioritized over metabolic cost in the control scheme of locomotion (at least under the conditions studied here).

While it is clear that a $C_{met,P}$ penalty occurs with the selection of incline walking in the Competing-Cost-Pairs (and in the pre-transition incline selection more generally; Fig. 3E), we do not suggest that energy minimization is unimportant to the control of walking, even in less common situations such as the crouch walking investigated in this study. Indeed, in the final incline condition (post transition incline), when the $C_{met,P}$ was the highest and the activation penalty of crouch walking was reduced or eliminated, participants opted to save energy by selecting crouch walking. Rather, our study supports the idea that locomotion tasks are regulated in a multi-objective manner that includes metabolic cost as one important, but not the sole, factor. Taken together, our data across all conditions suggest that a priority for energy minimization is not an inevitability, but also that as $C_{met,P}$ increases so might the relative weighting of $C_{met,P}$ in the control scheme of walking.

Does a 'division of muscle labor' dictate gait control?
The non-volume-weighted exponential activation cost function, $\overline{C}_{a^2}$, penalizes high (fatiguing) activations in any single muscle and thus favors an even muscle recruitment strategy (22). The hypothesis that gait is under a control scheme that minimizes muscle fatigue is not new, but has been mostly limited to simulation studies (21,22). To the best of our knowledge, the current study is the first to observe this phenomenon empirically. Our finding that subjects protected their $\overline{C}_{a^2}$ at the direct expense of $C_{met,P}$ was observed both in the individual participants' Competing-Cost-Pair trials (Table 1), and also at a group (average) level (Fig. 3E-F).

The clear preference for protecting $\overline{C}_{a^2}$ over energy cost suggests a strong control objective for maintaining an even muscle recruitment and thus avoiding high, fatiguing, activations that can cause local muscle exhaustion (22). This is also evident from the more extreme cost function, $\overline{C}_{a,max}$, which showed that all participants' gait selection in the Competing-Cost-Pairs protected their would-be maximally activated muscle, in line with a *min/max* cost function (36). This further suggests that the decision to avoid crouch walking may, in fact, have been specifically predicated

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411 on not exhausting the primary contributing muscle. Even if highly activated individual muscles
412 represent a small fraction of the total muscle mass, they can have an important limit on performance
413 because maximally fatigued muscles set the bottle neck for the endurance of the whole muscle
414 system (22,60).

415 Further support for activation-driven gait selection comes from our observations of the post-
416 transition incline gait (i.e., when crouch walking was finally chosen). When crouch walking is
417 compared to the post-transition incline, we observe a diminished activation advantage. This can be
418 seen in the group average data, where similar and not statistically different $\overline{C}_{a^2}$, $\overline{C}_{a,max}$ and $\overline{C}_{a,vol}$
419 values were observed between conditions (Fig. 3F-H). This suggests that not only avoiding, but
420 also selecting crouch walking, involved information from muscle activation. It may be that only when
421 there is minimal/no activation disadvantage, do participants accept a $C_{met,P}$ advantage (whether
422 this was selecting incline over crouch walking, or vice versa, selecting crouch walking over very
423 steep incline walking). It is also worth pointing out that the high $\overline{C}_{a^2}$ cost associated with crouch
424 walking and the steepest incline walking resulted from different muscle recruitment patterns (Fig.
425 4); high activations in crouch walking are primarily in the vastus medialis (for 6/8 participants), while
426 in the post-transition incline the muscles that exhibit the high activations are more variable between
427 subjects.

428 Why should muscle activation be prioritized over energy cost? One answer may be that minimizing
429 high activations that fatigue a given muscle will likely permit longer movement duration, a
430 performance criterion that is regarded to be fundamental to the evolution of human bipedalism and
431 with known ecological relevance (61–63). For instance, to effectively travel long distances in
432 persistence hunting (regarded as a key feature of human evolution; 62) there is a clear selective
433 advantage to resist fatigue. Muscle activation is a compelling control signal for sensing a division
434 of labor among muscles and for avoiding overburdening individual muscles. It is thought that muscle
435 effort can be readily sensed using central (e.g., via an efference copy) and peripheral (e.g., Group
436 III and IV muscle afferents) mechanisms (64,65).

437 **Does muscle activation represent a proxy for metabolic energy use?**
438 Notwithstanding the clear acceptance of a $C_{met,P}$ penalty, could it be possible that the nervous
439 system was attempting to prioritize total metabolic energy expenditure using a proxy sensor, but
440 failed? In their recent work, Wong and colleagues (66) concluded that blood-gas receptors are an
441 unlikely sensor for whole-body locomotor energy expenditure and raised the possibility of a muscle-
442 level sensor for metabolic cost. Muscle activation is a promising candidate for sensing energy cost
443 because it is related to the fraction of the muscle that is metabolically active and because activation
444 itself exacts a substantial metabolic cost in the form of calcium pumping (67–69). If activation serves
445 as a proxy sensor for energy expenditure, the high volume-weighted activation signal associated
446 with crouch walking may have 'tricked' the nervous system into registering a higher metabolic cost
447 than that which was actually present. This could occur, in part, due to the inflated activation
448 contribution of the large (high volume) knee-extensor muscles (Fig. 4). It is worth noting that in
449 tasks where energy minimization is ubiquitously demonstrated (e.g., steady level walking), muscle
450 activation and whole-body metabolic costs respond similarly to changing task parameters [e.g.,
451 step frequency; (11,28)], thus indicating that the muscle activations can, indeed, serve as a proxy
452 for the energy consumption. This was, however, not the case in the present study. Both $\overline{C}_{a^2}$, $\overline{C}_{a,max}$,
453 and $\overline{C}_{a,vol}$ were disassociated from $C_{met,P}$, with $\overline{C}_{a,vol}$ considered a proxy for energy use because it
454 takes into account active muscle volume (22)—a key determinant of locomotor energy use
455 (46,69,70).

456 Thus, if activation was used as a proxy for energy, it resulted is a misrepresentation of the relative
457 energy cost of the crouch versus incline walking conditions. This scenario affects our interpretation
458 of the energy optimization hypothesis in important ways. First, it would indicate that locomotor
459 energy sensing is imperfect and may be cruder than previously thought. This implies that high-
460 precision, rapid, energy sensing and subsequent gait control may be confined to common and
461 predictable steady-state movements (e.g., steady level ground walking), and, in-turn, that energy

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462 optimization may not be particularly robust outside of a narrow range of conditions. Other
463 experiments that have altered the mechanics of walking in novel ways have found that subjects
464 often need guidance to discover energy minimizing movements (8,16). This suggests that while
465 energy minimization may be achieved *eventually*, after sufficient motor learning has taken place, it
466 may not be prioritized *acutely*. Whether trial-and-error learning can bring about versatile energy
467 sensing across a myriad of natural conditions for human locomotion remains unclear. This question
468 will prove key, both for practical reasons (e.g., development of assistive devices), as well as
469 informing theories into the evolution of human locomotor energetics.

470 Among the most interesting questions that remains is *how* the central nervous system uses muscle-
471 level signaling to determine the physiological state of the body. For example, does the central
472 nervous system achieve this by summing the activity of all muscles involved in a given task,
473 weighted according to their size and tracked over a given distance or time period, and finally
474 referencing this against a threshold representing global (whole-body) effort or energy use (i.e.,
475 $\overline{C}_{a,vol}$)? Or, at the other end of the spectrum, is the control signal based on assessing individual
476 muscle activation levels against local thresholds unique to each actuator (i.e., $\overline{C}_{a,max}$)? Luu et al.
477 (71) provide support for the latter strategy. The authors observed that when elbow flexors and knee
478 extensors were isometrically contracted in unison (at 25, 50 and 100% of their individual maximal
479 voluntary contraction values), participants' ventilation did not increase to a level that reflected the
480 cumulative effect of contracting the individual muscle groups. In fact, the ventilatory response did
481 not change significantly between the single and combined muscle group contractions at any
482 contraction intensity level (71).

483 We posit a strategy assessing individual muscle activation levels against local thresholds is also a
484 simpler control strategy for the following reasons. First, $\overline{C}_{a,max}$ (and also, to a lesser extent, $\overline{C}_{a^2}$)
485 has a computational advantage, limiting the synthesis of information required by the central nervous
486 system. Individual muscle activation thus presents a promising sensory modality when considering
487 the credit-assignment problem (66,72), which refers to the direct or indirect nature of the signal(s)
488 used by the central nervous system to steer gait selection behavior. The internal monitoring of
489 individual muscle activations to minimize muscle fatigue is an example of a highly direct signal-to-
490 optimality criterion coupling. Conversely, weighting and summing the individual activations requires
491 the additional collation of information and is therefore a less direct signaling method for ascribing
492 locomotor 'cost'. The latter would therefore likely require greater computational effort and time.
493 Whilst we are not aware of any literature explicitly detailing preferences for computationally
494 inexpensive control strategies in locomotion, a reduction in cognitive load at the expense of physical
495 effort was previously observed by Rosenbaum and colleagues (51).

496 We also do not, at present, have an effective way to rank the likelihood that one activation
497 parameter is a more likely target of control than the other, although we do note that the pre-
498 transition incline selection saw participants avoid greater $\overline{C}_{a^2}$ and $\overline{C}_{a,max}$ penalties than that
499 associated with $\overline{C}_{a,vol}$ (84% and 52% versus 27%, respectively; *N*=8). Simulation studies that have
500 established both mass- or volume-weighted activation and distribution cost functions also support
501 this perspective, with more realistic gait patterns predicted by a non-volume-weighted or low
502 volume-weighted muscle activation criterion (21,22). Irrespective of what optimality criterion
503 activation minimization serves (e.g., a proxy for metabolic cost minimization, improved distribution
504 of muscle effort, fatigue minimization, etc.), activation itself seems like a reasonable control target
505 that can utilize relatively simple computational cost strategies.

506 **Alternate explanations for the observed gait selection**
507 Despite the systematic prioritization of a gait with low muscle activation in the Competing-Cost-
508 Pairs, we cannot rule out alternate hypotheses for the observed gait selection. For example,
509 discomfort, pain, or other psychological motivators of gait selection behaviors (56,73) could, in
510 theory, be at the source of the selection of incline walking over crouch walking in the Competing-
511 Cost-Pairs. Clearly delineating the role of discomfort versus activation *per se* in our observed gait
512 selections is challenging because the two are related. In crouch walking, muscles with

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513   disproportionately high activations are prone to fatigue, which is known to cause discomfort (74).
514   High muscle activations may also result in high local mechanical stresses that could trigger a pain
515   response. It is conceivable, therefore, that high muscle activations are the proxy signals used in a
516   neural computation of a 'comfort' cost. In this regard, the minimization of muscle activation in the
517   Competing-Cost-Pairs could underlie a higher-level comfort objective.

518   **Limitations**
519   The current study captured the activity of seven lower limb muscles that play a key role in human
520   locomotion. Expanding upon previous empirical studies (47), we also include a weighting factor
521   when determining the total activation cost. However, incorporating a greater selection of muscles
522   when computing $\overline{C}_{a^2}$ and $\overline{C}_{a,vol}$ would likely provide further insight into prioritization behaviors.

523   While $C_{met,P}$ is susceptible to changes in both walking speed and step frequency (5,11), the latter
524   was not imposed for any condition, and the former may have provided a metabolic advantage to
525   crouch walking because all trials occurred at the preferred speed established for crouch walking.
526   Yet, irrespective of this, participants still accepted a metabolic penalty through their pre-transition
527   incline selection. It must be noted that whether one variable was closer to its physiological
528   maximum than the other (e.g., V̇O₂max versus maximal activation) was not measured in the current
529   study. How close a variable is to its maximum may impact the priority for minimizing that variable.
530   In this sense it is possible that selectively impairing other (more) important optimality criteria through
531   energetic minimization will only occur in situations where a very high metabolic cost needs to be
532   avoided. We acknowledge that the relative importance of activation and $C_{met,P}$ may also be different
533   in steady-state level gait, and that it is likely task- and condition-dependent.

534   It is of course possible that other physiological signals exist whose distribution across muscles may
535   parallel that of activation, for example afferent signals from muscle metabolism receptors (class III
536   and IV afferents), or proprioceptive signals from muscle spindles and/or Golgi tendon organs.
537   These may also be involved in the control scheme of walking and deserve further exploration
538   together with muscle activation.

539   **Conclusion**

540   Here, we provide among the first empirical evidence of locomoting humans accepting a metabolic
541   cost penalty in favor of a predefined, alternative neuromuscular criterion. When choosing between
542   crouch walking and walking on a series of increasing inclines, our healthy participants protected
543   both fatigue-like and effort-like activation cost metrics. This observation is concomitant with
544   activation cost prioritization in the control of steady-state walking (22) and running (21). Further
545   research is required to determine whether muscle activation is used to estimate global energy or
546   effort, or if local muscle costs are of greater importance in the control scheme of gait, independent
547   of their relationship to energy costs *per se*.

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722 **Figures and tables**
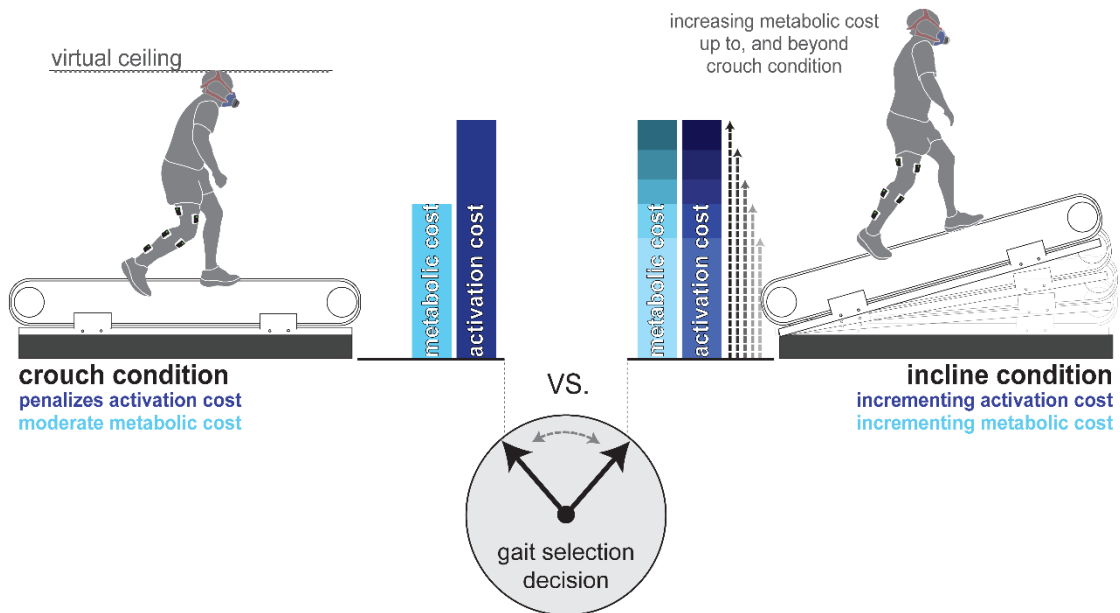
724 **Figure 1.** Experimental design. Participants were asked to select between crouch walking, which
725 moderately affects metabolic cost and penalizes activation cost, and a series of incline levels that
726 incrementally increase both metabolic and activation costs. Competing-Cost-Pairs were
727 established when participants walked on an incline level that incurred a higher metabolic cost but
728 provided an activation cost advantage relative to the crouch condition. A virtual ceiling and the
729 participant's silhouette, displayed on a screen anterior to the treadmill, provided feedback regarding
730 crouch walking task performance.
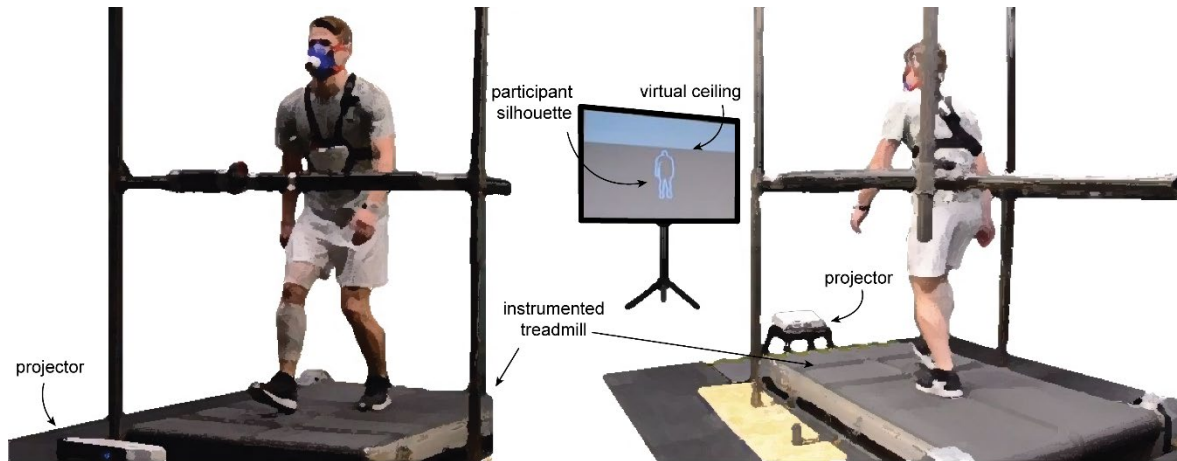
731
Figure 2. Experimental setup for crouch walking. Participants walked on a split-belt treadmill with their silhouette projected onto an anteriorly placed screen. Their objective was to avoid collisions between their silhouette and a virtual ceiling, which was set to 93% of their standing height. Real-time motion-tracking and visual feedback was implemented in a custom program developed with the openFrameworks open-source C++ toolkit, using data from a motion sensing device (Xbox Kinect, Microsoft, WA, USA), situated behind the participant.
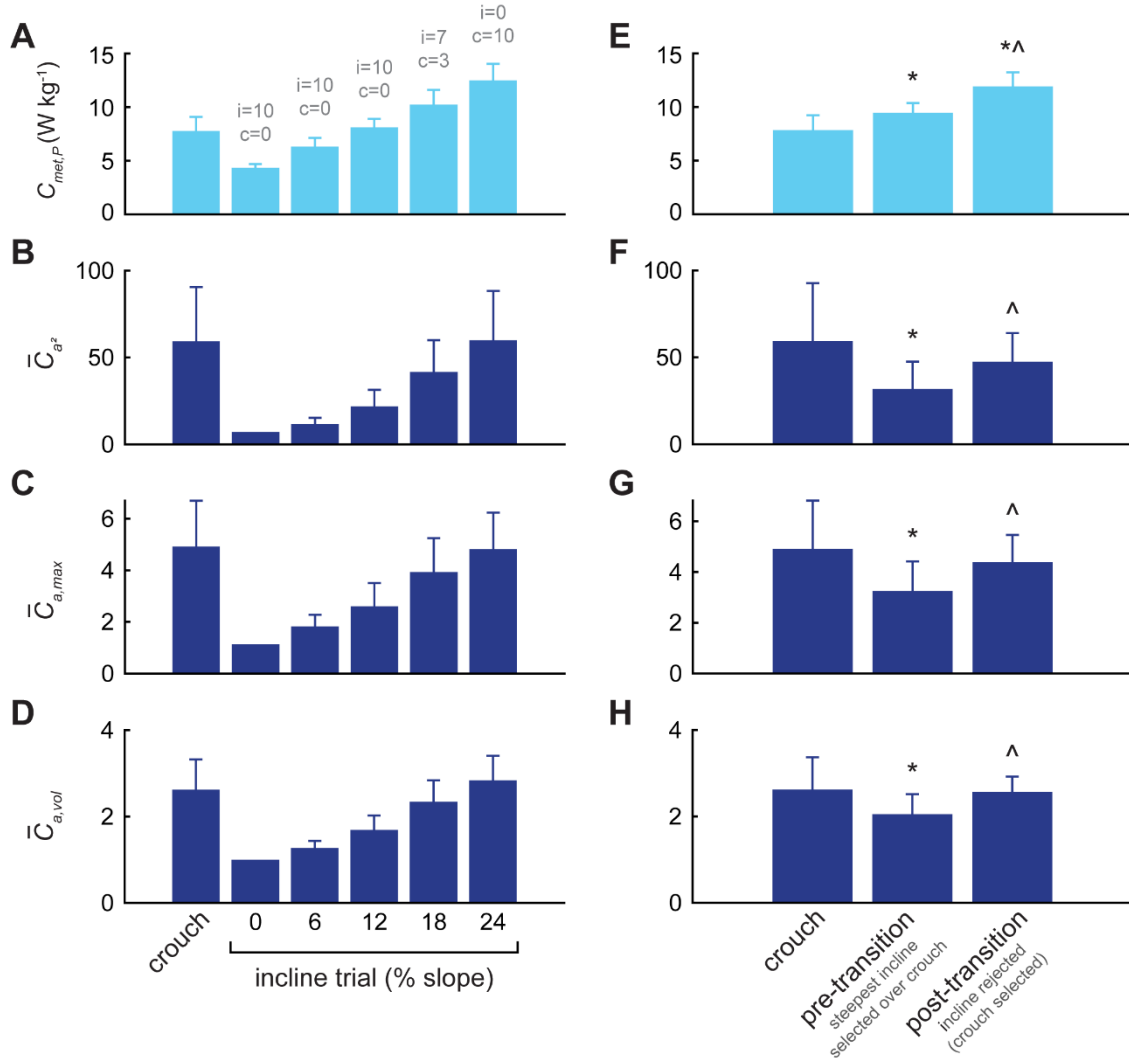
Figure 3. Walking data for the (A-D) mean (±SD) crouch trial versus five levels of incline (from 0-24%) and (E-H) mean (±SD) crouch trial versus pre- and post-transition inclines. (A, E) Metabolic power ($C_{met,P}$; W kg^{-1}; N=10), (B, F) sum of seven lower limb muscles' normalized activations squared ($\bar{C}_{a^2}$; unitless; N=8), (C, G) maximum activation value from seven lower limb muscles' normalized activation ($\bar{C}_{a,max}$; unitless; N=8), and (D, H) sum of the seven lower limb muscles' volume-weighted activations ($\bar{C}_{a,vol}$; unitless; N=8). The number of participants that selected incline (i) or crouch (c) in each condition are indicated in (A) (grey text).

*Significantly different (p<0.017) from crouch (E-H only); ^Significantly different (p<0.017) from pre-transition (E-H only).
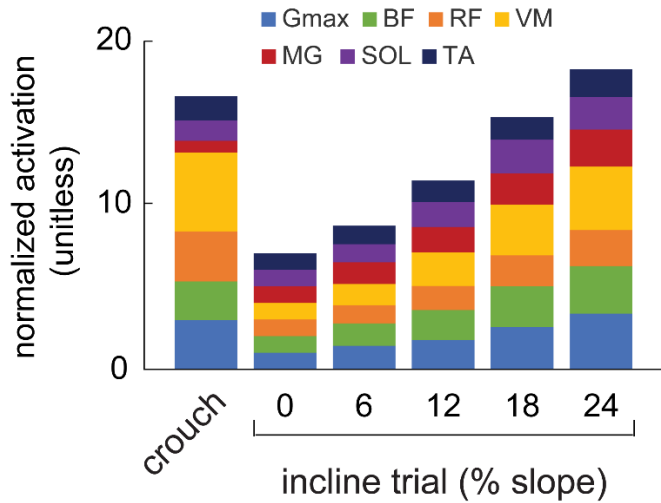
Figure 4 Average (*N*=8) normalized activation costs (A_{ij}) during crouch walking (level treadmill) and incline walking on treadmill slopes of 0-24%. Seven lower limb muscles were analyzed; gluteus maximus (Gmax), biceps femoris (BF), rectus femoris (RF), vastus medialis (VM), medial gastrocneuimus (MG), soleus (SOL) and tibialis anterior (TA). The unitless quantity A_{ij} was established by integrating the linear envelope (activation integral (a_{ij})), expressing this as a rate $\left(\frac{a_{ij}}{T_j}\right)$ and normalizing data for each muscle to the average value obtained from the 0% incline trial.
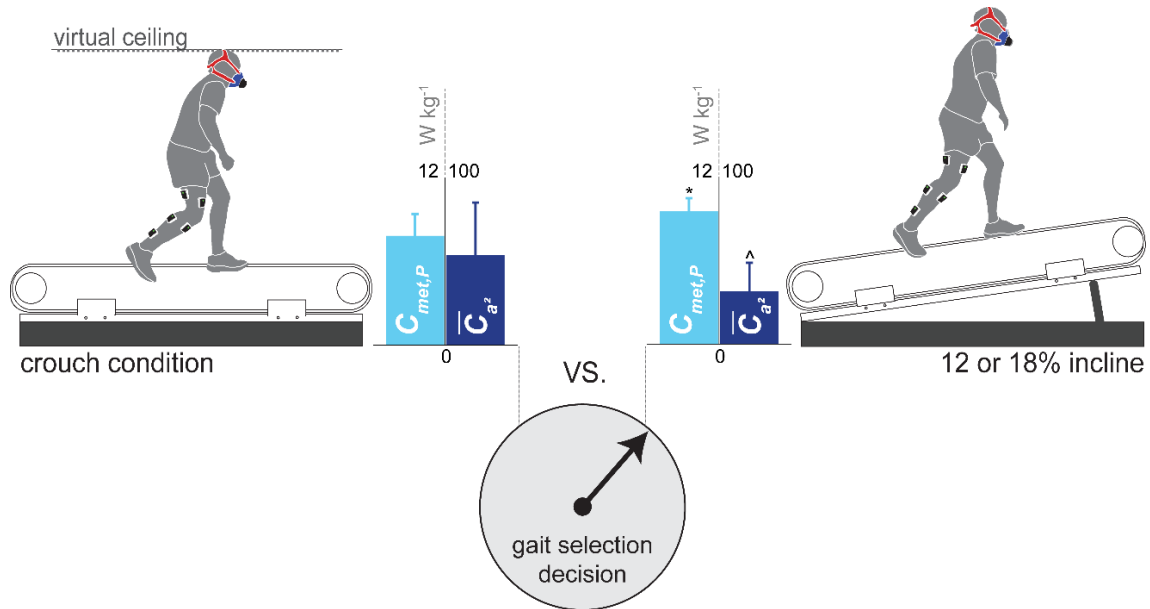
Figure 5. Competing-Cost-Pairs were established for seven of the eight participants for which this was feasible. All seven participants selected the incline condition that favored the sum of activations squared $(\bar{C}_{a^2})$ and penalized metabolic power $(C_{met,P})$. In doing this, they rejected the crouch walking condition that favored metabolic power and penalized the sum of the activations squared. Data is presented as the mean±SD.

*Significantly different (p<0.05) from crouch $C_{met,P}$; ^Significantly different (p<0.05) from crouch $\bar{C}_{a^2}$.

763 **Table 1.** Competing-Cost-Pairs (CCP) were established for seven of the eight participants for which this was feasible. The presence of a Competing-
764 Cost-Pair was determined by comparing the mean crouch and pre-transition incline's percentage change from upright (normal) walking on a 0%
765 incline for: i) metabolic power ($C_{met,P}$) and the sum of activations squared ($\bar{C}_{a^2}$), ii) $C_{met,P}$ and the maximal muscle activation ($\bar{C}_{a,max}$), and iii) $C_{met,P}$
766 and the sum of the volume-weighted activations ($\bar{C}_{a,vol}$). The pre-transition incline is defined as the steepest incline that was selected over crouch.

Participant ID	$C_{met,P}$* % Crouch	Pre-transition incline	$\bar{C}_{a^2}$* % Crouch	Pre-transition incline	CCP established?	$\bar{C}_{a,max}$* % Crouch	Pre-transition incline	CCP established?	$\bar{C}_{a,vol}$* % Crouch	Pre-transition incline	CCP established?
1	172.5	189.5	566.0	290.8	Y	292.2	196.8	Y	167.1	125.7	Y
2	226.4	236.3	1382.3	794.3	Y	575.9	399.7	Y	308.1	236.9	Y
3	229.9	266.9	1410.1	799.4	Y	533.8	463.1	Y	222.5	161.4	Y
4	137.6	182.5	605.2	373.1	Y	429.4	227.2	Y	169.5	155.9	Y
5	170.9	200.6	NA	NA	-	NA	NA	-	NA	NA	-
6	204.9	202.5	1409.4	454.2	N	747.6	368.4	N	239.7	154.4	N
7	174.6	245.6	NA	NA	-	NA	NA	-	NA	NA	-
8	137.6	199.3	284.4	211.4	Y	219.5	165.6	Y	166.9	143.4	Y
9	169.6	215.9	584.3	308.0	Y	380.7	249.3	Y	198.8	156.8	Y
10	160.1	217.0	469.2	359.1	Y	297.3	233.9	Y	167.2	154.2	Y

767 *Significant difference ($p<0.05$) between the crouch and pre-transition incline trials for participants with a CCP ($N=7$).

Supplementary material

769 **Table S1.** Competing-Cost-Pairs (CCP; *N*=7) and whole-group ($C_{met,P}$: *N*=10; $\bar{C}_{a^2}$: *N*=8; $\bar{C}_{a,max}$: *N*=8; $\bar{C}_{a,vol}$: *N*=8) statistical analyses using the
770 mean crouch, initial crouch, and final crouch data. The pre-transition incline is defined as the steepest incline that was selected over crouch, whereas
771 the post-transition incline is the first rejected incline in favor of crouch.
772

			$C_{met,P}$		$\bar{C}_{a^2}$		$\bar{C}_{a,max}$		$\bar{C}_{a,vol}$	
			CCP	Group	CCP	Group	CCP	Group	CCP	Group
Mean crouch	*Distribution*		*Normal*	*Normal*	*Non-normal*	*Non-normal*	*Normal*	*Normal*	*Normal*	*Normal*
	Main effect	*p-value*	-	<0.001*	-	0.008*	-	0.001*	-	0.003*
	Crouch vs. pre-transition incline		0.002*	0.007*	0.018*	0.012*	0.003*	0.006*	0.007*	0.003*
	Crouch vs. post-transition incline		-	0.005*	-	0.263	-	0.214	-	0.779
	Pre-transition incline vs. post-transition incline		-	0.005*	-	0.017*	-	0.003*	-	0.002*
Initial crouch	*Distribution*		*Normal*	*Normal*	*Non-normal*	*Non-normal*	*Normal*	*Normal*	*Normal*	*Normal*
	Main effect	*p-value*	-	<0.001*	-	0.003*	-	0.002*	-	0.002*
	Crouch vs. pre-transition		0.002*	0.007*	0.018*	0.008*	0.003*	0.008*	0.008*	0.003*
	Crouch vs. post-transition		-	0.005*	-	0.071	-	0.117	-	0.329
	Pre-transition incline vs. post-transition incline		-	0.005*	-	0.011*	-	0.003*	-	0.002*
Final crouch	*Distribution*		*Normal*	*Normal*	*Non-normal*	*Non-normal*	*Normal*	*Normal*	*Normal*	*Normal*
	Main effect	*p-value*	-	<0.001*	-	0.013*	-	0.001*	-	0.002*
	Crouch vs. pre-transition		0.002*	0.005*	0.018*	0.013*	0.004*	0.005*	0.009*	0.005*
	Crouch vs. post-transition		-	0.005*	-	0.698	-	0.513	-	0.453
	Pre-transition incline vs. post-transition incline		-	0.005*	-	0.011*	-	0.003*	-	0.002*

773 *Significant difference (p<0.05 for CCP; p<0.05 for whole-group main effect; p<0.017 for whole-group *post hoc* test comparisons).