Why do we transition from walking to running? - Energy cost and lower leg muscle activity before and after gait transition under body weight support

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Background. Minimization of the energetic cost of transport (CoT) has been suggested for the walk-run transition in human locomotion. More recent literature argues that lower leg muscle activities are the potential triggers of the walk-run transition. We examined both metabolic and muscular aspects for explaining walk-run transition under body weight support (BWS; supported 30% of body weight) and normal walking (NW), because the BWS can reduce both leg muscle activity and metabolic rate.

Methods. Thirteen healthy young males participated in this study. The energetically optimal transition speed (EOTS) was determined as the intersection between linear CoT and speed relationship in running and quadratic CoT-speed relationship in walking under BWS and NW conditions. Preferred transition speed (PTS) was determined during constant acceleration protocol (velocity ramp protocol at 0.00463 m·sec^{-2} (1 km·h^{-1} per minute) starting from 1.11 m·s^{-1}. Muscle activities and mean power frequency (MPF) were measured using electromyography of the primary ankle dorsiflexor (*tibialis anterior*; TA) and synergetic plantar flexors (calf muscles including *soleus*) before and after the walk-run transition.

Results. The EOTS was significantly faster than the PTS under both conditions, and both were faster under BWS than in NW. In both conditions, MPF decreased after the walk-run transition in the dorsiflexor and the combined plantar flexor activities, especially the *soleus*.

Discussion. The walk-run transition is not triggered solely by the minimization of whole-body energy expenditure. Walk-run transition is associated with reduced TA and *soleus* activities with evidence of greater slow twitch fiber recruitment, perhaps to avoid early onset of localized muscle fatigue.

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Abstract

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Results. The EOTS was significantly faster than the PTS under both conditions, and both were faster under BWS than in NW. In both conditions, MPF decreased after the walk-run transition in the dorsiflexor and the combined plantar flexor activities, especially the *soleus*.

34   **Discussion.** The walk-run transition is not triggered solely by the minimization of whole-body

35   energy expenditure. Walk-run transition is associated with reduced TA and *soleus* activities with

36   evidence of greater slow twitch fiber recruitment, perhaps to avoid early onset of localized

37   muscle fatigue.

Introduction

39   Human terrestrial locomotion involves two major gait patterns: walking and running. A

40   biological benefit of these two patterns is in facilitation of economical energy expenditure

41   (*Margaria, 1938*). When humans gradually increase their walking speed, they reach a speed at

42   which they naturally change their gait pattern from walking to running, and it has been suggested

43   that such a walk-run gait transition minimizes their metabolic rate (*Cavagna & Kaneko, 1977;*

44   *Minetti AE, Ardigò LP, Saibene, 1994*). In walking, there is a U-shaped relationship between the

45   energetic cost of transport per unit distance (CoT) and speed (*s*); for running, the relationship is

46   approximately constant (*Abe, Fukuoka & Horiuchi, 2015*). Consequently, there is an intersection

47   between the CoT-*s* relationship for walking and running; this is known as the energetically

48   optimal transition speed (EOTS). However, the EOTS calculated in this way has been shown to

49   be approximately 5-6 % faster than the 'preferred' transition speed (PTS) at which humans make

50   the walk-run transition (*Hreljac, 1993; Rotstein et al., 2005; Tseh et al., 2002*), so factors other

51   than a minimization of the metabolic rate are needed to explain the trigger for the walk-run

52   transition in human locomotion.

53   An abrupt increase in muscle activity of the dorsiflexor (*tibialis anterior*; TA) has been

54   observed when participants walked at a speed close to the PTS (*Hreljac, 1995; Hreljac et al.,*

55   *2008; Prilutsky & Gregor, 2001; Bartlett & Kram, 2008; Malcolm et al., 2009; Shih et al.,*

56   *2016*), and our recent studies showed muscle activity of the TA decreased when participants

57   switched from walking to running at the EOTS (*Abe, Fukuoka & Horiuchi, 2017; Abe et al.,*

58   *2018*). In association with a decrease in TA activity when switching the gait pattern, mean power

59   frequency (MPF; Hz) of the TA became lower, suggesting that more Type 1 muscle fibers were

60   recruited in the TA during running than walking at the EOTS. These findings suggest that muscle

61   activity of the TA could be a trigger of the walk-run transition. Conversely, other reports have

62   proposed that the medial head of *gastrocnemius* muscle (MG) of the plantar flexors, an

63   antagonist of the TA, plays a key role in the walk-run transition (*Farris & Sawicki, 2012;*

64   *Neptune & Sasaki, 2005*), because ankle force production by the MG was observed to decrease

65   in proportion to the increase in walking speed. Thus, the trigger for the walk-run transition

66   remains under debate.

67   One approach to resolve this matter is to perform experiments using simulated reduced

68   gravity and/or body weight support (BWS) conditions. This reduces not only leg muscular

69   activity but also the required energy expenditure (EE) during walking (*Grabowski, 2010;*

70   *McGowan, Kram & Neptune, 2008; 2009; Pavei, Biancardi & Minetti, 2015*) and running

71   (*Raffalt, Hovgaard-Hansen & Jensen, 2013; Teunissen, Grabowski & Kram, 2007*). Because EE

72   is potentially reduced by the decreased plantar flexor activity (*Hamner, Seth & Delp 2010;*

73   *Neptune, Zajac & Kautz, 2004*), it would be expected that the muscular activity of the plantar

74   flexors would be lower in BWS than in normal walking (NW) conditions. In that case, the PTS

75   and/or EOTS would be faster in BWS than in NW conditions. Summarizing the results of the

76   above previous studies, we hypothesized that the PTS and/or EOTS would be faster in BWS

77   compared to NW. We also hypothesized that TA activities would decrease after the walk-run

78   transition under both conditions and that muscular activity of the plantar flexors would decrease

79   in BWS than in NW, while it remained constant regardless of walk-run transition. The purpose

80   of this study was to investigate the muscular activity and the motor unit recruitment patterns of

81   the dorsiflexor and plantar flexors before and after the walk-run transition under BWS and NW

82   conditions.

Materials & Methods

Participants

Thirteen young healthy males participated in the present study. Their physical characteristics are summarized in Table 1. In accordance with the Declaration of Helsinki, all participants were provided all information about the purposes, benefits, possible risks, and experimental protocols. A written informed consent was obtained from all participants. An ethical committee established in Kyushu Sangyo University approved all procedures of this study (H28-0001-1).

Body weight support (BWS)

BWS was established with a custom-made body suspension apparatus that lifted the participant's torso via an elastic rehabilitation harness (Fig. 1). This was installed around a motor-driven treadmill (Well Load 200E, Takei Scientific Instruments Co., Ltd., Niigata, Japan). For the BWS condition, we chose a 30% decrement in the participant's body weight (BW), equivalent to that used in some previous studies (*Grabowski, 2010; McGowan, Kram & Neptune, 2008; 2009; Raffalt, Hovgaard-Hansen & Jensen, 2013; Teunissen, Grabowski & Kram, 2007*). A force transducer (TSA-110, Takei Scientific Instruments Co., Ltd., Niigata, Japan) was located between a control box and spring (with 30 cm free length and a spring constant of $5.7\ \mathrm{kg \cdot cm^{-1}}$) to slide a rigid main frame (see supplemental video). Before the participant walked or ran, he stood stationary on the treadmill while wearing the harness, and 30% of his BW was lifted by the spring system. The set-up allowed normal leg swing.

Protocols and determination of EOTS

All participants continuously walked on a motor-driven treadmill at four walking speeds (1.33, 1.56, 1.78, and $2.00\ \mathrm{m \cdot s^{-1}}$) on a level ($\pm 0\%$) gradient. After measuring the metabolic cost of walking, the participants took a sitting rest for 7-8 minutes. They started at three running speeds (2.00, 2.22, and $2.44\ \mathrm{m \cdot s^{-1}}$) with 1 min standing rests between the running stages. Each walking and/or running speed was kept constant for 4 min. At all stages, the participants chose their preferred step frequencies. They wore underwear, shirts, socks, and the same model of shoes in the appropriate sizes (Wave Wing, Mizuno, Japan).

Oxygen uptake (VO_2; $\mathrm{mL \cdot kg^{-1} \cdot s^{-1}}$) and carbon dioxide output (VCO_2; $\mathrm{mL \cdot kg^{-1} \cdot s^{-1}}$) were continuously measured with a computerized breath-by-breath system (AE-310S, Minato Ltd, Japan). Calibrated gas concentrations (O_2 15.22%, CO_2 5.17%, and N_2 79.61%) and room air

115 were used for the calibration of the gas analyzer. An average VO_2 and VCO_2 for the final 2-min

116 at each speed was used to calculate the CoT values using a following equation (*Brouwer, 1957*).

117 $$\text{CoT (J·kg}^{-1}\text{·m}^{-1}\text{)} = \frac{4.186 \times (3.869 \times VO2 + 1.195 \times VCO2)}{s} \quad (eq.1).$$

118 Where the *s* is the walking or running speed. The CoT values were compared at each gait speed

119 between both conditions. The relationship between the CoT values and walking speeds was

120 approximated with a quadratic equation (*Abe, Fukuoka & Horiuchi, 2015*):

121 $$\text{CoT }(s) = as^2 + bs + c \quad (eq.2).$$

122 Where the coefficients a, b, and c are determined by the least squares regression with data

123 obtained from four walking speeds. The relationship between CoT values and running speeds

124 was approximated using a linear equation (*Abe, Fukuoka & Horiuchi, 2015*). The running CoT

125 values was described as follows:

126 $$\text{CoT }(s) = ps + q \quad (eq.3).$$

127 Where the coefficients p and q are determined by the least squares regression with the CoT

128 values from three running speeds. An extrapolation of the quadratic equation (*eq.2*) meets a

129 linear regression line (*eq.3*), and then an intersection (EOTS) of these equations was obtained.

130 This extrapolation has been normally used for determining the EOTS in other previous studies

131 (*Abe, Fukuoka & Horiuchi, 2015; Hreljac, 1993; Minetti, Ardigò & Saibene, 1994; Rotstein et*

132 *al., 2005; Tseh et al., 2002*). Thus, the EOTS is an extrapolated value when the *eqs*.2 and 3 are

133 equal. Rearranging *eqs*.2 and 3:

134 $$as^2 + (b\text{-}p)s + (c\text{-}q) = 0 \quad (eq.4).$$

135 A following formula gives two solutions of *eq*.4, thus, only the faster one is regarded as the

136 EOTS (*Abe, Fukuoka & Horiuchi, 2015*).

137 $$\text{EOTS }(m \cdot s^{-1}) = \frac{-(b-p) \pm \sqrt{(b-p)^2 - 4a(c-q)}}{2a} \quad (eq.5).$$

138

139 **EMG measurements at the PTS**

140 The participant sat down on a chair to allow placement of the pre-amplified active surface EMG

141 electrodes (BA-U410m, Nihon Santeku Co., LTD, Osaka) on *tibialis anterior* (TA), medial and

142 lateral heads of *gastrocnemius* muscle (MG and LG), and *soleus* (SOL). Before electrode

143 placement, the skin was shaved and wiped with alcohol for an exfoliation. The electrodes were

144 secured using surgical tape to avoid disturbing the locomotor tasks. A foot sensor (PS-20KASF4,

145 Kyowa Electronic Instruments Co., LTD., Tokyo) was inserted into a right shoe to count number

146 of steps, and its signal was amplified with a signal conditioner (CDV-700A, Kyowa Electronic

147 Instruments Co., LTD, Tokyo). This foot sensor also allowed us to visually detect what the

148 participant transitioned from walking to running, because the vertical force suddenly increased

149 when the participant started running. The vertical force itself should be ignored, because the foot

150 sensor is cushioned by the shoe sole and plantaris muscle. The participant was asked to start

151 walking at 1.11 m·s^{-1} for 1 min at a freely chosen step frequency. After this steady-state

152 walking, the treadmill speed was gradually increased at an acceleration of 0.00463 m·sec^{-2} (1

153 km·h^{-1} per minute) in a modified incremental ramp manner. The speed at which the walk-run

154 transition occurred was considered to be the PTS. The participant was asked to keep running for

155 1 min after the walk-run transition. EMG was recorded throughout the whole ramp protocol. The

156 BWS condition was tested before the NW condition because it took several minutes to put on the

157 harness without disturbing the wired EMG electrodes and bio-amplifier attached to the

158 participant's waist. Data for one participant was excluded from the analysis because of an artifact

159 in the EMG. The analyzed time duration was set as 12 s before and after the walk-run transition;

160 in practice, it was 11.972 ± 1.562 s, equivalent to 13.1 ± 1.9 steps when walking or 15.2 ± 2.3

161 steps when running.

162   The EMG signals were amplified with a gain of ×1000 (BA 1104B, Digitex Lab Co., LTD,

163 Tokyo). Sampling frequency was set at 2 kHz, and a band-pass filter (8-500 Hz) was applied for

164 the EMG signals. All signals from each sensor were simultaneously recorded with software

165 (MaP 1038 ver.7.4, Nihon Santeku Co., LTD, Osaka). Subsequently, a fast Fourier transform

166 was applied to the stored EMG signals to obtain mean power frequency (MPF; Hz). MPF reflects

167 motor unit recruitment pattern in the exercising muscles (*De Luca, 1997; Wakeling, 2004*). An

168 alteration of the MPF values between walking and running allows us to evaluate muscle fiber

169 recruitment pattern in each gait. The sum of the rectified EMG (μV·sec) was normalized by

170 measured time (sec) and number of steps to cancel the effects of step frequency (*Abe, Fukuoka &*

171 *Horiuchi, 2017; Abe et al., 2018*). The EMG values obtained were further normalized to those

172 obtained at 1.11 m·s^{-1} under each condition.

173

174 **Statistical analysis**

175 Data were presented as mean ± SD. The CoT values were compared with two-way repeated

176 measures analysis of variance (ANOVA) within participants (BW × speed) using online software

177   (ANOVA 4 Copyright (c) 2002 Kiriki Kenshi; https://www.hju.ac.jp/~kiriki/anova4/). Two-way

178   repeated measures of ANOVA was also applied for comparisons among the EOTS and PTS

179   obtained under both gravities. Each muscle activity and MPF were also compared in the same

180   way. The present study was exploratory in design, and the minimum detectable F value was

181   4.747 when using G*Power 3.1 (*Faul et al., 2007*) with an actual number of 13 participants. A

182   partial eta-squared value (η^2) was also presented (*Cohen, 1988*). If a significant F value was

183   obtained on the dependent variables, *Ryan*'s post hoc test was applied to the appropriate data sets

184   to detect significant mean differences. Its statistical power has been reported to be equivalent to

185   *Tukey*'s post hoc test (*Ryan, 1960*), and it can be used regardless of the data distribution (*Ryan,*

186   *1960*). Statistical significance was accepted at $p < 0.05$.

Results

Figure 2A shows the CoT-s relationships obtained under the two conditions. In walking, significantly lower CoT values were observed with BWS than with NW at speeds faster than 1.56 m·s^{-1} ($F = 16.019$, $p = 0.002$, $\eta^2 = 0.178$; Fig. 2A). In running, the CoT values were significantly lower with BWS than with NW at all speeds ($p < 0.001$). The mean EOTS was significantly faster with BWS than with NW (2.304 ± 0.141 vs. 2.031 ± 0.086 m·s^{-1}; $F = 32.326$, $p < 0.001$, $\eta^2 = 0.327$; Fig. 2B). The same was the case with the PTS (2.068 ± 0.153 vs. 1.932 ± 0.075 m·s^{-1}; $F = 43.209$, $p < 0.001$, $\eta^2 = 0.331$; Fig. 2B). A post hoc test revealed that the PTS was significantly slower than the EOTS under both conditions ($F = 7.865$, $p = 0.010$; Fig. 2B).

Comparisons of activities of the dorsiflexor (TA) and the combined plantar flexor activities (the average for MG, LG, and SOL) are shown in the upper panels of Figure 3. TA activity significantly decreased after the walk-run transition under both conditions ($F = 12.896$, $p = 0.004$, $\eta^2 = 0.183$; Fig. 3A). Muscle activities of the combined plantar flexors also decreased after the walk-run transition with both BWS ($F = 57.091$, $p < 0.001$, $\eta^2 = 0.111$; Fig. 3B) and NW ($F = 5.177$, $p = 0.026$, $\eta^2 = 0.019$; Fig. 3B). The lower panels of Figure 3 show each muscle activity of the synergic plantar flexors; only SOL activity became significantly lower after the walk-run transition under both conditions ($F = 33.539$, $p < 0.001$, $\eta^2 = 0.203$; Fig. 3E). Figure 4 shows comparisons of the MPF values for each muscle. The MPF of the TA was significantly lower after the walk-run transition under both conditions ($F = 7.484$, $p = 0.019$, $\eta^2 = 0.028$; Fig. 4A), whereas the MPF of the MG was significantly higher after the walk-run transition only with the BWS ($F = 10.516$, $p = 0.004$, $\eta^2 = 0.067$; Fig. 4B). No significant differences were observed for the LG ($F = 0.125$, $p = 0.730$, Fig. 4C). The SOL showed significantly lower MPF values after the walk-run transition under both conditions ($F = 22.355$, $p < 0.001$, $\eta^2 = 0.057$; Fig. 4D).

Discussion

211

212   One of the major findings of this study was that the walking CoT values were significantly lower

213   with BWS than with NW at speeds faster than 1.56 m·s⁻¹ (Fig. 2A). The running CoT values

214   were also lower with BWS than with NW at all speed measured (Fig. 2A); this was consistent

215   with the results of previous studies (*Raffalt, Hovgaard-Hansen & Jensen, 2013; Teunissen,*

216   *Grabowski & Kram, 2007; Pavei, Biancardi & Minetti, 2015; Pavei & Minetti, 2016;*

217   *Grabowski, Farley & Kram, 2005; Grabowski & Kram, 2008*). These results also demonstrated

218   that the EOTS was faster in BWS than in NW (Fig. 2B). Although it has been proposed that the

219   walk-run transition minimizes whole-body EE (*Cavagna & Kaneko, 1977; Minetti, Ardigò &*

220   *Saibene, 1994*), other previous studies have found that the PTS was 5-6% slower than the EOTS

221   in humans (*Hreljac, 1993; Rotstein et al., 2005; Tseh et al., 2002*), suggesting that the other

222   factors may be related to the walk-run transition. The results of the present study were consistent

223   with those of the latter studies (*Hreljac, 1993; Rotstein et al., 2005; Tseh et al., 2002*), with the

224   PTS being significantly slower than the EOTS by 5.2% under the NW condition and 11.4%

225   under the BWS condition (Fig. 2B). These results indicate that the walk-run transition is not

226   triggered exclusively to minimize whole-body EE.

227   In support of our first hypothesis, TA activity and the associated MPF decreased when the

228   gait pattern was switched from walking to running under both conditions (Figs. 3A and 4A).

229   These results were equivalent to those of our recent studies that measured TA activity during

230   walking and running at the EOTS (*Abe, Fukuoka & Horiuchi, 2017; Abe et al., 2018*), which

231   suggested that the motor unit recruitment pattern of the TA shifted more toward Type I (slow

232   twitch) fibers rather than Type II (fast twitch) fibers after the walk-run transition. Several studies

233   have also reported that an abrupt increase in TA activity associated with the walk-run transition

234   (*Hreljac, 1995; Hreljac et al., 2008; Bartlett & Kram, 2008; Malcolm et al., 2009; Shih et al.,*

235   *2016*). However, a careful consideration is necessary, because the TA does not contribute to

236   producing mechanical power for forward acceleration. It is the ankle plantar flexors (MG, LG,

237   and SOL), that play an essential role in forward acceleration during walking (*Francis et al.,*

238   *2013; Franz & Thelen, 2016; Gottschall & Kram, 2003*) and running (*Hamner, Seth & Delp,*

239   *2010*). Indeed, the MG might be a potential trigger for the walk-run transition, because its power

240   production has been shown to decrease when walking faster (*Farris & Sawicki, 2012; Neptune &*

241   *Sasaki, 2005*). However, these previous results were based on simulated calculations; functional

242   differences in other synergic ankle plantar flexors remain to be elucidated during human

243   locomotion. We found that the combined activities of the plantar flexors (the average of MG,

244   LG, and SOL activities) were significantly lower during running than walking under both

245   conditions (Figs. 3A and 3B). These results clearly suggest that the plantar flexors also

246   contribute to triggering the walk-run transition.

247   Considering muscle activity between before and after the walk-run transition, LG activity

248   decreased significantly after the walk-run transition only under the BWS condition (Fig. 3C), and

249   the MPF of both MG and LG was not significantly different between before and after the walk-

250   run transition, except for the MPF of the MG under the BWS (Figs. 4B and 4C). These results

251   were partly consistent with the results of our recent studies (*Abe, Fukuoka & Horiuchi, 2017;*

252   *Abe et al., 2018*). The inconsistency in MG and LG activities can be explained by SOL activity.

253   The functional role of the SOL has not been as well investigated as that of the MG and LG

254   complex. In fact, the gastrocnemius muscles and SOL are anatomically independent. The

255   anatomical volume of the SOL is much larger than that of the MG and LG complex, but the SOL

256   exerts more mechanical power in the upward direction (*Franz & Thelen, 2016*). Thus, the SOL

257   should contribute to supporting the body during walking. Another study reported that a

258   difference of the functional role between the gastrocnemius muscles and SOL mainly appeared

259   in the late stance phase (*Zajac, Neptune & Kautz, 2003*). The SOL in association with the MG

260   and LG complex support the body in the early and middle stance phases (*Neptune, Zajac &*

261   *Kautz, 2001*), but the push-off is mainly executed by the SOL only in the late stance phase

262   (*Zajac, Neptune & Kautz, 2003*). These previous studies suggest that the SOL executes multi-

263   tasks in one gait cycle: forward acceleration of the trunk in the late stance phase and body

264   support in the early and middle stance phases.

265   One of the major limitations of our experimental approach was that we could not quantify *in*

266   *vivo* Achilles tendon behavior. The ankle torque produced by the plantar flexors increases as

267   walking speed increases. However, the change in length of the SOL and its tendon complex has

268   been observed to decrease drastically during walking around the PTS (*Lai et al., 2015*),

269   suggesting an extreme increase in the shortening length of the SOL itself in a gait cycle. This

270   potentially increases the force production by the SOL to compensate for the decreased length

271   change of the SOL and tendon complex in a gait cycle. After the walk-run transition, length

272   change of the SOL abruptly increased (*Lai et al., 2015*), indicating that the SOL force production

273   and related activations can be reduced. This finding was supported by our result for changes in

274   SOL activity under both conditions (Fig. 3E). In addition, the MPF of the SOL decreased at the

275 walk-run transition (Fig. 4D), indicating that the SOL plays a role not only in supporting the

276 body but also in triggering the walk-run transition. Given these complex observations, the ankle

277 plantar flexors may all contribute to the required forces, in association with changes to each

278 motor unit recruitment pattern, to avoid the early onset of localized muscle fatigue.

279 Methodological considerations are necessary, because we found a faster PTS in BWS than that in

280 NW, which contradicted numerous previous results (e.g. *Kram, Domingo & Ferris, 1999*). This

281 conflicting result could be attributed to a difference of the used apparatus. The BWS apparatus

282 used in some previous studies retained much larger stretch in the elastic component compared to

283 our apparatus (*Kram, Domingo & Ferris, 1999; Pavei, Biancardi & Minetti, 2015; Pavei &*

284 *Minetti, 2016)*, and small vertical movements of the participants using our apparatus could result

285 in fluctuations of the vertical force. Figure 5 shows a representative example of fluctuations of

286 the vertical force (weight) during both gaits in the BWS condition. The baseline represents 70%

287 of this participant's BW (30% reduction of his BW from 63.2 kg to 43.8 kg), so the suspended

288 weight is 18.8 kg. As the fluctuation of the vertical force was about ±4 kg during running, it was

289 fluctuated between 24%BW and 36%BW during running. During walking, the fluctuation of the

290 vertical force was within ±2 kg, indicating that it was fluctuated between 27%BW and 33%BW

291 during walking. These fluctuations of the vertical force are not negligible, so we used the term

292 body weight support (BWS) rather than simulated reduced gravity. In the previous studies, the

293 PTS became slower as a function of reduced body weight level (*Kram, Domingo & Ferris, 1999;*

294 *Pavei, Biancardi & Minetti, 2015; Pavei & Minetti, 2016)*, which can be predicted from the

295 Froude number (*Alexander, 1989*). The spring of our apparatus is much shorter (only 30cm) than

296 that of previously used apparatus due to a limitation of the room height. Thus, our spring-like

297 apparatus yielded relatively large fluctuations of the vertical force. This intrinsic characteristic of

298 our apparatus could reduce the mechanical power output for the vertical direction, which should

299 be related to the decreased whole-body EE during running and walking at faster speeds (Fig.

300 2B), resulting in a faster PTS in BWS than in NW.

301   There had been a debate whether the spectral properties of the surface EMG provide

302 information about motor unit recruitment strategies and muscle fiber type (*von Tscharner &*

303 *Nigg, 2008; Farina, 2008*). In recent years, many articles provided the motor unit activity using

304 power spectral properties (MPF) of the surface EMG during dynamic exercise *in vivo* (*De Luca*

305 *et al., 2015; Kallio et al., 2013; von Tscharner et al., 2018*) along with the Henneman's size

306 principle (*Henneman, Somjen & Carpenter, 1965*). To the best of our knowledge, Henneman's

307 size principle cannot be applied during instantaneous heavy power output (*Moritani, Oddsson &*
308 *Thorstensson, 1990*) and/or instantaneous eccentric contraction (*Smith et al., 1980; Nardone &*
309 *Schieppati, 1988; Kallio et al., 2013*). Our experimental condition partially met such specific
310 conditions, suggesting that alterations of the MPF values before and after the walk-run transition
311 reflected a shift toward more Type 1 motor unit recruitment. That is, the walk-run transition is
312 associated with greater slow twitch fiber recruitment of the TA and SOL, perhaps to avoid early
313 onset of localized muscle fatigue.
314

315 **Conclusions**
316 The PTS was significantly slower than the EOTS under both conditions, indicating that the walk-
317 run gait transition is not only triggered by the minimization of whole-body EE. In the BWS
318 condition, both PTS and EOTS were faster due to the potential reduction of muscular activity in
319 both the dorsiflexor (TA) and the plantar flexors, particularly in the SOL. Reductions in the
320 activity of these muscles in association with changes to the motor unit recruitment patterns make
321 a considerable contribution to the walk-run transition in human locomotion.

Acknowledgements

We specially thank to Mr. Akinobu Sakamoto, Mr. Tomokazu Iwatani, Mr. Hiromichi Ikegami, Mr. Takeshi Saito, Mr. Masaru Hashimura, and Mr. Shizuo Takatoh (Takei Scientific Instruments Co., Ltd.) for customizing both body suspension apparatus and treadmill. We also thank to Hideki Kaneko and Shouichi Matsuyama (Nihon Santeku Co., Ltd.) for their continuous technical assistance of the EMG recording and analysis.

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462   **Table and Figure Legends**

463

464   **Table 1. Physical characteristics of each participant.**

465   BW; body weight, BF; percent of body fat, and BMI; body mass index, respectively.

466

467   **Fig. 1. Body weight support apparatus.**

468   A schematic illustration of the participants walking with a custom-made body weight support

469   (BWS) apparatus. This setting ensured that the BWS apparatus applied purely vertical force

470   without disturbing leg swing motion.

471

472   **Fig. 2. Comparisons of CoT values under normal walking (NW) and body weight support**

473   **(BWS) conditions.**

474   (A) Cost of transport (CoT) as a function of gait speed under NW (black solid and open squares)

475   and BWS (blue solid and open circles). Solid lines are the approximations using actually

476   observed CoT values. Dotted lines are the extrapolations. (B) Comparisons of energetically

477   optimal transition speed (EOTS) and preferred transition speed (PTS) under NW (black-white

478   bars) and BWS (blue-green bars). Values are mean ± SD. [*] $p < 0.05$, [#] $p < 0.01$, and [†] $p < 0.001$.

479

480   **Fig. 3. Comparisons of muscle activities.**

481   Comparisons of dorsiflexor (A; *tibialis anterior*, TA) and average of a complex of the entire

482   plantar flexors (B). Lower panels presented each muscle activity of the *gastrocnemius medialis*

483   (C; MG), *gastrocnemius lateralis* (D; LG), and *soleus* (E; SOL) before and after the walk-run

484   transition under the NW and BWS. Values are mean ± SD. [*] $p < 0.05$ and [#] $p < 0.01$.

485

486   **Fig. 4. Comparisons of mean power frequency (MPF).**

487   Comparisons of MPF in the lower leg extremities before and after walk-run transition under NW

488   and BWS. (A) TA: *tibialis anterior*; (B) MG: *gastrocnemius medialis*; (C) LG: *gastrocnemius*

489   *lateralis*; and (D) SOL: *soleus*, respectively. Values are mean ± SD. [*] $p < 0.05$ and [#] $p < 0.01$.

490

491   **Fig. 5. Time-vertical force relationship using body weight support (BWS) apparatus.**

492   A representative example of fluctuations of the vertical force during walking (upper panels) and

493   running (lower panels) at each speed in the BWS condition. BW means body weight.

Table 1. Physical characteristics of each participant.

BW; body weight, BF; percent of body fat, and BMI; body mass index, respectively.

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Participant	Age (yrs)	Stature (m)	BW (kg)	BF (%)	BMI (kg·m⁻²)
A	19.6	1.696	72.0	19.8	25.0
B	21.1	1.700	66.4	19.8	23.0
C	21.7	1.638	56.5	16.2	21.1
D	19.8	1.703	54.2	10.6	18.7
E	19.8	1.635	62.6	20.2	23.4
F	20.0	1.650	70.0	25.1	25.7
G	21.2	1.665	66.5	16.5	24.0
H	19.5	1.684	56.9	13.0	20.1
I	19.9	1.740	81.0	24.3	26.8
J	19.3	1.634	56.7	17.6	21.2
K	20.6	1.736	49.2	10.4	16.3
L	19.9	1.746	55.8	13.6	18.3
M	21.3	1.620	56.4	17.6	21.5
Average	20.3	1.681	61.9	17.3	21.9
SD	0.8	0.044	8.9	4.6	3.1

BW; body weight, BF; percent of body fat, and BMI; body mass index, respectively.

Figure 1

Figure 1. Body weight support apparatus.

A schematic illustration of the participants walking with a custom-made body weight support (BWS) apparatus. This setting ensured that the BWS apparatus applied purely vertical force without disturbing leg swing motion.

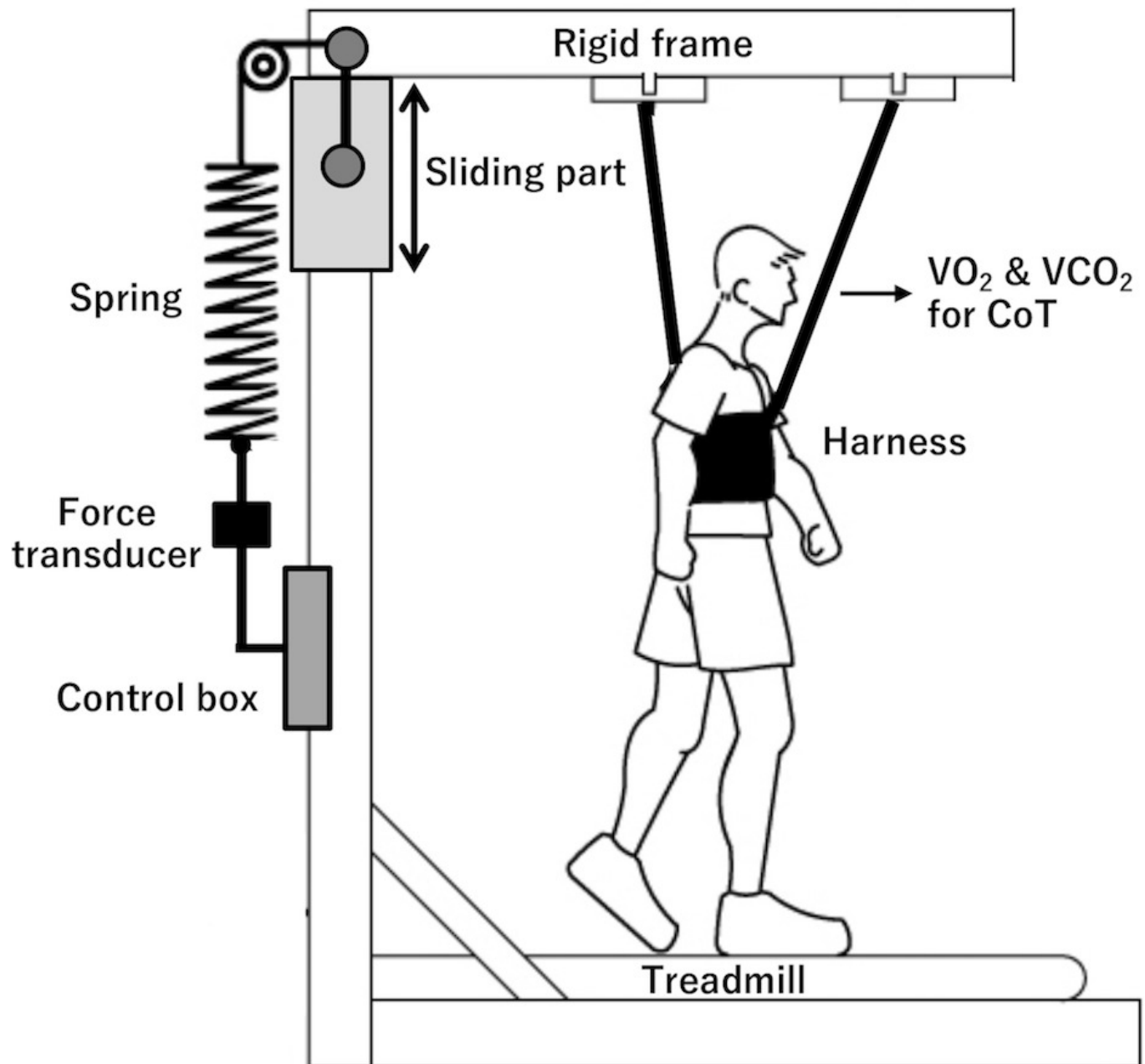
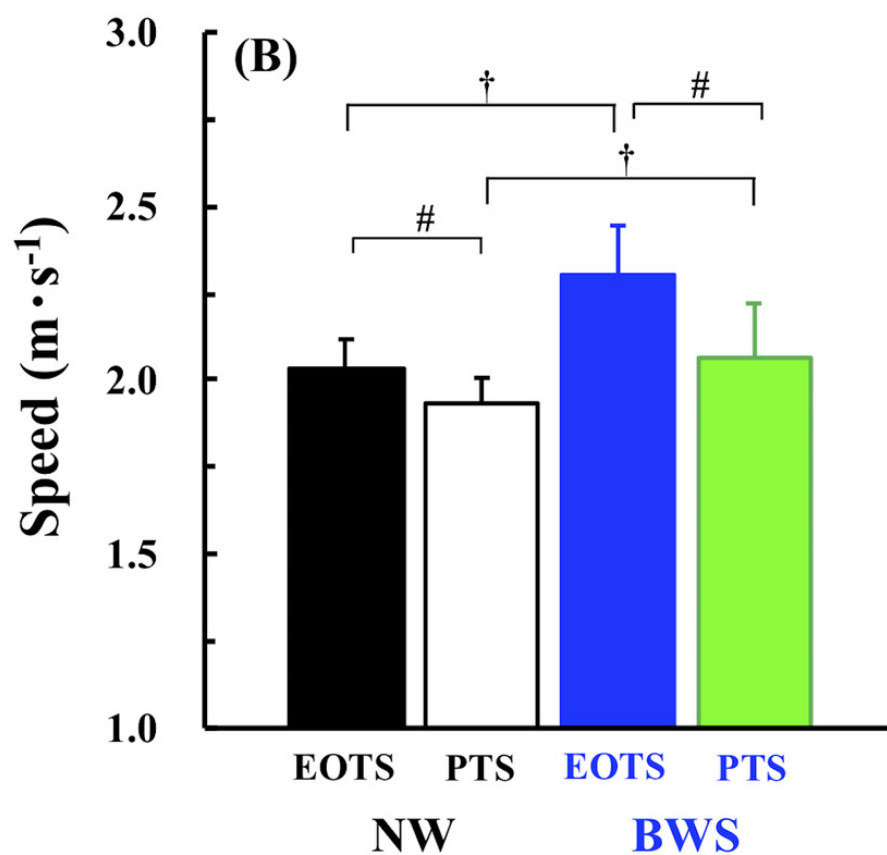
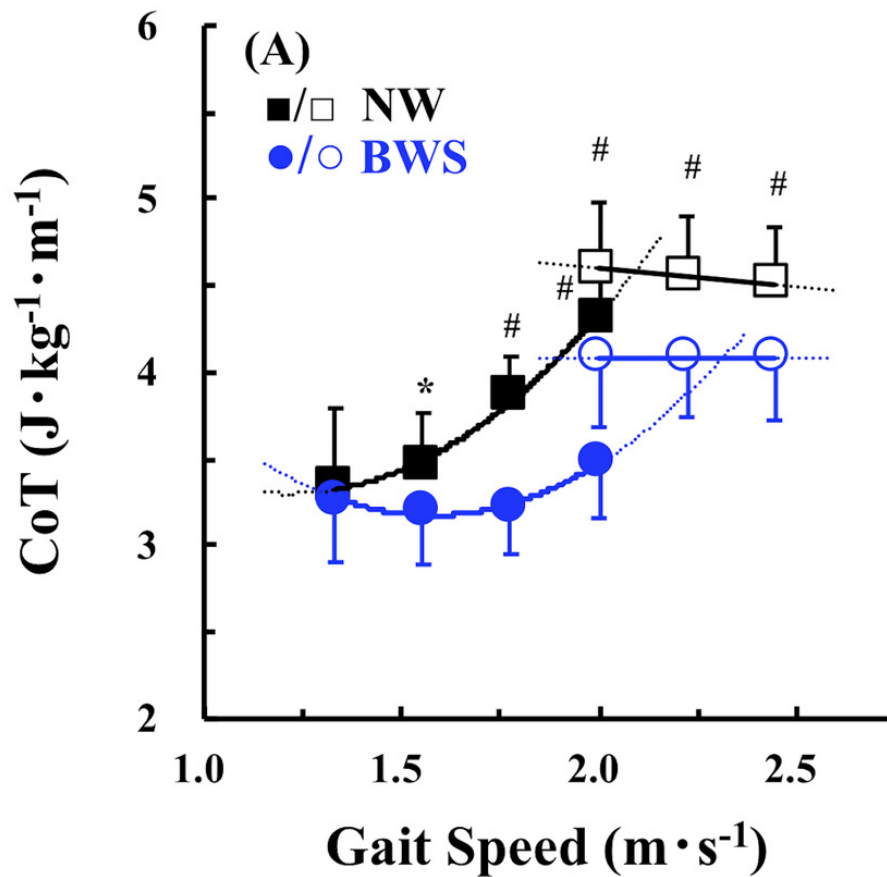



Figure 2

Comparisons of CoT values under normal walking (NW) and body weight support (BWS) conditions.

(A) Cost of transport (CoT) as a function of gait speed under NW (black solid and open squares) and BWS (blue solid and open circles). Solid lines are the approximations using actually observed CoT values. Dotted lines are the extrapolations. (B) Comparisons of energetically optimal transition speed (EOTS) and preferred transition speed (PTS) under NW (black-white bars) and BWS (blue-green bars). Values are mean ± SD. $^*p < 0.05$, $^\#p < 0.01$, and $^\dagger p < 0.001$.

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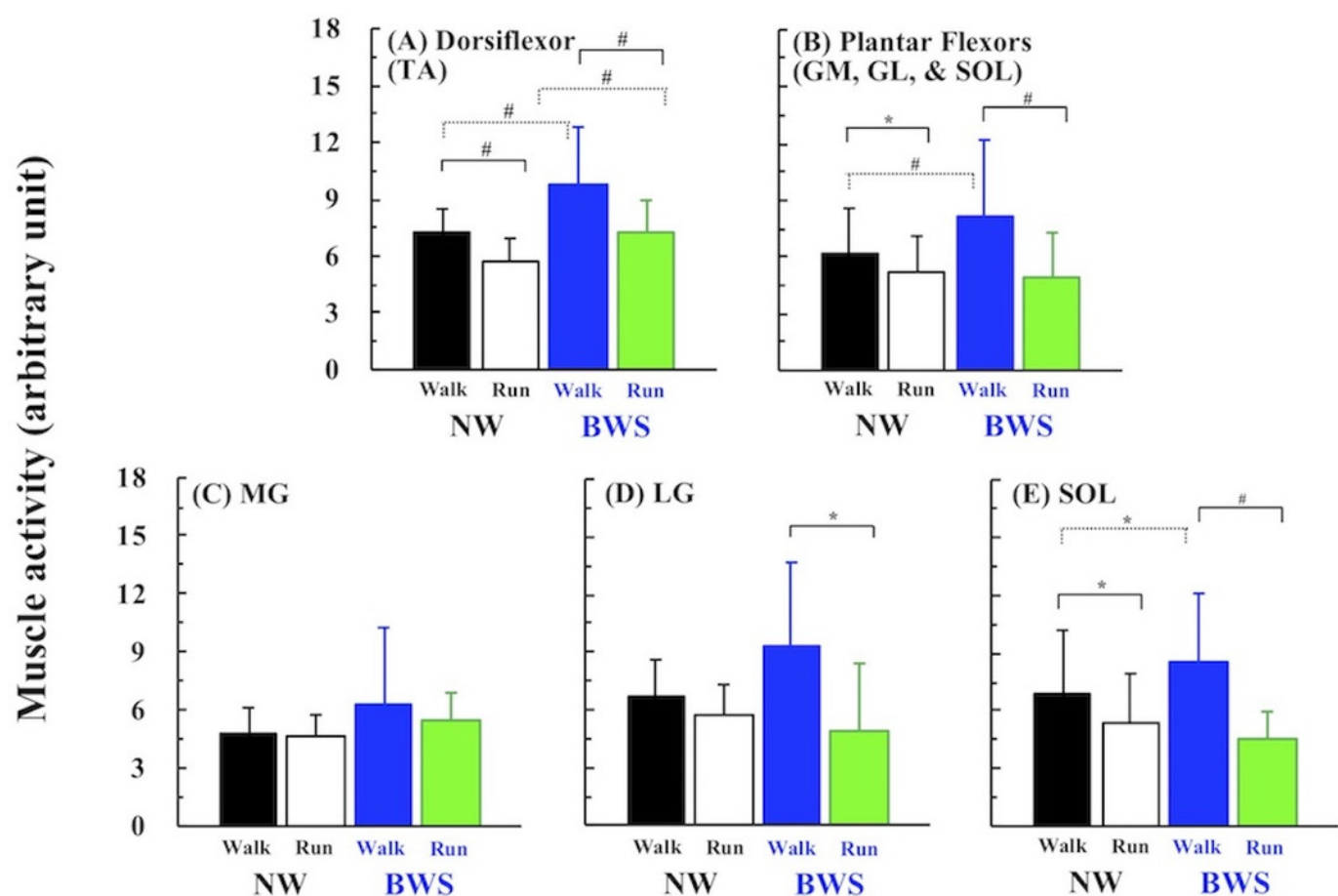
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Comparisons of MPF in the lower leg extremities before and after gait transition under NW and BWS. (A) TA: *tibialis anterior*; (B) GM: *gastrocnemius medialis*; (C) GL: *gastrocnemius lateralis*; and (D) SOL: *soleus*, respectively. Values are mean ± SD. [*]$p< 0.05$ and [#]$p< 0.01$.
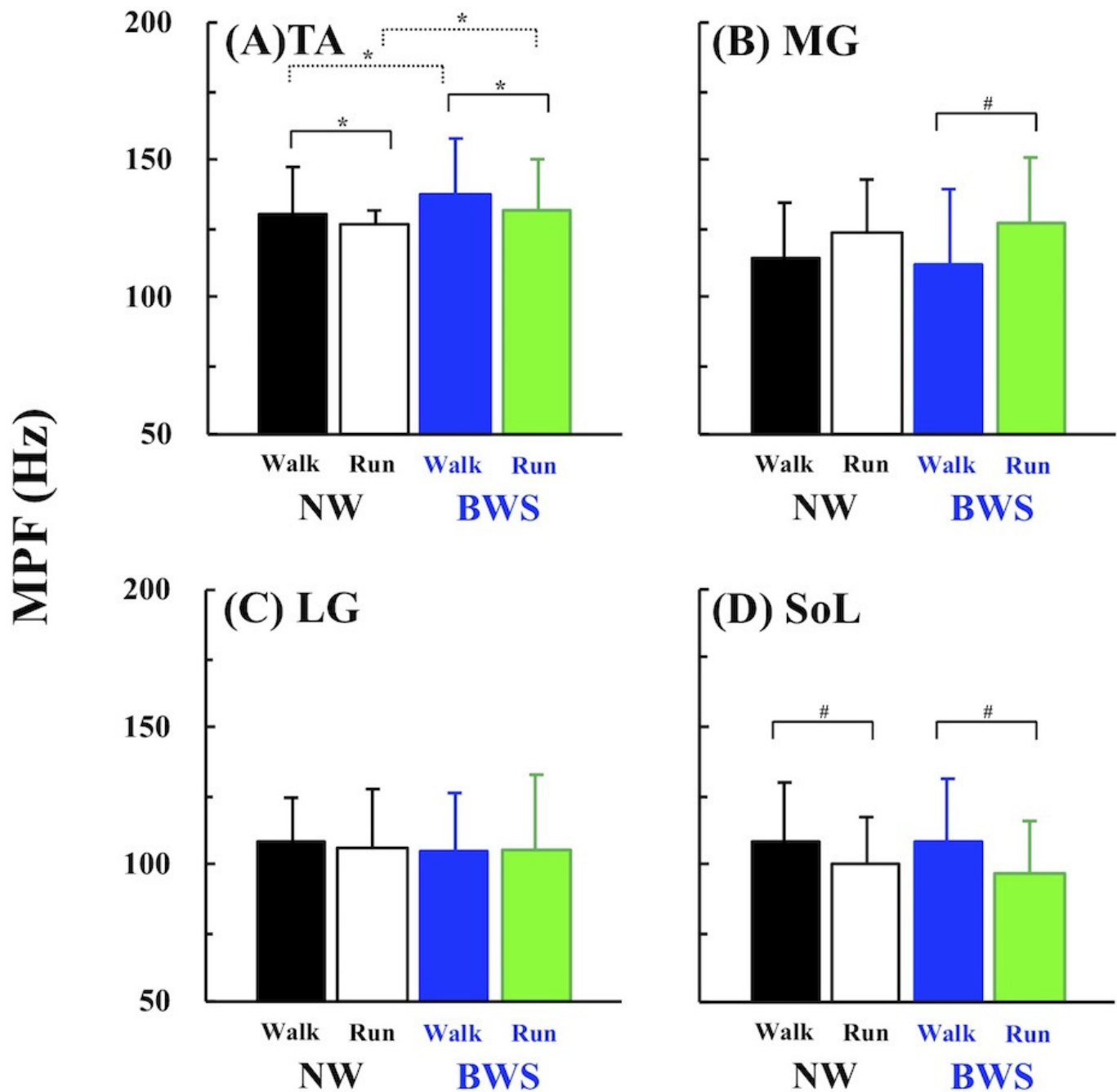
Figure 5

Figure 5. Time-vertical force relationship using body weight support (BWS) apparatus.

A representative example of fluctuations of the vertical force during walking (upper panels) and running (lower panels) at each speed in the BWS condition. BW means body weight.