

SHORT COMMUNICATION

Neuromuscular effort predicts walk–run transition speed in normal and adapted human gaits

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ABSTRACT

Often, humans and other animals move in a manner that minimizes energy costs. It is more economical to walk at slow speeds, and to run at fast speeds. Here, we asked whether humans select a gait that minimizes neuromuscular effort under novel and unfamiliar conditions, by imposing interlimb asymmetry during split-belt treadmill locomotion. The walk–run transition speed changed markedly across different gait conditions: forward, backward, hybrid (one leg forward, one leg backward) and forward with speed differences (one leg faster than the other). Most importantly, we showed that the human walk–run transition speed across conditions was predicted by changes in neuromuscular effort (i.e. summed leg muscle activations). Our results for forward gait and forward gait with speed differences suggest that human locomotor patterns are optimized under both familiar and novel gait conditions by minimizing the motor command for leg muscle activation.

KEY WORDS: Human locomotion, Gait transition, Split-belt treadmill, Electromyography

INTRODUCTION

Human walking and running are two forms of locomotion that have distinct muscle activation patterns (Cappellini et al., 2006). People generally prefer an inverted-pendulum walk at slow speeds and switch to a bouncing run at fast speeds (Margaria et al., 1963; Alexander, 1989; Minetti et al., 1994; Srinivasan and Ruina, 2006). Walking and running at non-preferred speeds require excessive muscle activation (Prilutsky and Gregor, 2001), suggesting that the locomotor system switches between forms to minimize neuromuscular effort.

The locomotor system can assume a different motor pattern on each leg. For example, humans can walk with one leg forward and one leg backward (i.e. hybrid gait) on a split-belt treadmill (Choi and Bastian, 2007). Moreover, autonomous central pattern generators enable the two legs to take asymmetric steps (e.g. 2:1, 3:1 coupling) on a split-belt treadmill (Yang et al., 2005). However, the human locomotor system favors symmetric, out-of-phase coordination patterns during steady-state split-belt treadmill walking (Dietz et al., 1994; Reisman et al., 2005) and running (Ogawa et al., 2015).

Here, we examined the effect of interlimb speed and direction differences on the walk–run transition speed. In addition, we measured the neuromuscular effort (i.e. summed leg muscle activations) of walking and running at different speeds across gait conditions. The gait conditions included the familiar forward gait,

the seldom-used backward gait and the unfamiliar hybrid and speed-difference gait conditions. To our knowledge, this is the first study to examine how the walk–run transition speed changes for one leg depending on the speed and direction of the opposite leg. By making the legs move at different speeds or in different directions, we could determine whether humans select a gait to minimize neuromuscular effort even under novel conditions. If neuromuscular effort does indeed play a role in the gait-selection process, we would expect the following to be true: walking decreases neuromuscular effort at preferred walking speeds; running decreases neuromuscular effort at preferred running speeds; neuromuscular effort for walking and running converge around the walk–run transition speed.

MATERIALS AND METHODS**Subjects**

Ten healthy young subjects (9 male, 1 female; age 27.0 ± 3.3 years, mean \pm s.d.) participated in the study. Informed written consent was obtained from all subjects before the study began. The study was approved by the local institutional review board (protocol no. 2014-1940).

Experimental setup

We determined the walk–run transition speed for six gait conditions on a split-belt treadmill (Bertec, Columbus, OH, USA): forward, forward with speed differences of 0.5, 1.0 and 1.5 m s^{-1} between the belts (right belt was faster), backward and hybrid (left belt moving backward, right belt forward). At the beginning of each condition, subjects adapted for 5 min to reach steady-state phasing between legs (Choi and Bastian, 2007). After the adaptation period, a parameter estimation by sequential testing (PEST) algorithm (Taylor and Creelman, 1967) provided quick estimates of the walk–run transition speed with a speed resolution of 0.025 m s^{-1} . Using this algorithm, the walk–run transition speed was defined as the speed at which walking and running were equally likely gait modes. Here, the walk–run transition speed was not directional (i.e. transition from walk to run or vice versa).

The PEST algorithm consisted of two input arguments, five rules for changing the treadmill speed and one output. The inputs were initial treadmill speed and initial speed change (set at 0.1 m s^{-1}). At each treadmill speed, the subject was given 3 s to choose a gait mode (walk or run) that was most comfortable or natural at the given speed. We defined walking as a vaulting gait and running as a bouncing gait. If the experimenter was not certain of the response, the subject was asked to state the gait mode. The speed was increased if the response was walk and decreased if the response was run. The rules for changing the treadmill speed were: (1) the speed change was halved at direction reversal (i.e. walk followed by run, or vice versa); (2) the second speed change in the same direction (i.e. consecutive walking or consecutive running responses) was equal to the previous speed change; (3) following a reversal, the third speed change in the same direction was equal to the previous one; if the

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third speed change did not follow a reversal (i.e. it is the third speed change since the beginning of the sequence, so no reversals have occurred yet), then it was double the previous; (4) the fourth and subsequent speed changes in the same direction were each double the previous (only implemented when the experimenter considered large speed changes safe); (5) the sequence was terminated when the speed change was 0.025 m s^{-1} . The output of the algorithm was the treadmill speed of the right belt at termination. The preferred walk–run transition speed was determined as the average output of two trials: one with a slow initial treadmill speed that elicited a walking response and another with a fast initial treadmill speed that elicited a running response.

Subjects then walked and ran at 70%, 80%, 90%, 100%, 110%, 120% and 130% of their preferred walk–run transition speed. Each trial lasted 10 s. Only a subset of subjects were able to successfully walk and run at all seven speeds in each condition: forward ($N=9$), backward ($N=9$), hybrid ($N=7$) and speed differences of 0.5 m s^{-1} ($N=8$), 1.0 m s^{-1} ($N=8$) and 1.5 m s^{-1} ($N=7$). The order of gait conditions was randomized within subjects and the treadmill speed was presented incrementally in each condition.

Data collection

Electromyographic (EMG) data were collected using bipolar surface electrodes on the following muscles: tibialis anterior, medial gastrocnemius, soleus, vastus medialis, rectus femoris, biceps femoris long head, gluteus medius and gluteus maximus. Two systems were used to collect 16 EMG signals (8 on each leg): a wired amplifier (Motion Lab System, Baton Rouge, LA, USA) connected to two electrodes (Ambu, Copenhagen, Denmark) spaced 2 cm apart on each muscle belly, and a telemetric system (Delsys, Natick, MA, USA). EMG and vertical ground reaction forces from each belt were collected at 2000 Hz.

Data analysis

EMG data were high-pass filtered at 30 Hz, demeaned, rectified and low-pass filtered at 40 Hz. EMG data from each trial were averaged across strides, aligned on heel-strike determined using the vertical ground reaction forces. EMG data were normalized to the peak value of forward walking at 100% of the walk–run transition speed. Neuromuscular effort was calculated as the mean value of the averaged muscle activation, summed across the eight leg muscle pairs.

Statistical analysis

A one-way repeated measures analysis of variance (rmANOVA) determined the effect of gait conditions on transition speeds. *Post hoc* tests compared the transition speed of forward gait to the transition speeds of the remaining gait conditions. A two-way rmANOVA determined the interaction effect of treadmill speed and gait mode (walking and running) on neuromuscular effort during each gait condition. *Post hoc* tests compared neuromuscular effort between walking and running at each speed. A Pearson correlation analysis of right belt speed and the difference between neuromuscular effort of walking and running was performed for each gait condition. For each condition, data were only included in the statistical analysis if the subject completed walking and running at all speeds. A *P*-value less than 0.05 was considered statistically significant.

RESULTS AND DISCUSSION

Interlimb speed and direction differences change the walk–run transition speed

During forward gait with no speed differences, subjects transitioned between walk and run at 2.10 m s^{-1} (Fig. 1). This transition speed

was consistent with previous reports in the literature (Minetti et al., 1994; Prilutsky and Gregor, 2001). With speed differences between the belts, all subjects transitioned between walk and run on both legs simultaneously, i.e. we did not observe walking on one leg and running on the other leg. This suggests that the human locomotor system has a preference for generating the same locomotor form on both legs. Subjects transitioned between walk and run at increasing right belt speeds for greater speed differences; for speed differences of 0.5, 1.0 and 1.5 m s^{-1} , subjects transitioned at right belt speeds of 2.29, 2.62 and 2.91 m s^{-1} , respectively ($F_{5,35}=129.7$, $P\leq 0.001$; *post hoc* tests $P<0.05$). Note that the average belt speeds at the walk–run transition across the speed difference conditions (2.04, 2.12 and 2.16 m s^{-1} at speed differences of 0.5, 1.0 and 1.5 m s^{-1} , respectively) approximated the walk–run transition speed in normal forward gait (2.10 m s^{-1}). A possible explanation for this invariance is that the center of mass mechanics of these speed difference gaits may be similar to normal gait mechanics, which have been shown to be important for determining walk–run transitions (Kram et al., 1997). During backward gait, subjects transitioned from walk to run at 1.43 m s^{-1} ($P<0.001$), which is consistent with previous findings (Hreljac et al., 2005). In the hybrid condition, where belts moved in opposite directions, all subjects transitioned between walk and run on both legs simultaneously. The transition speed for the hybrid condition was 1.18 m s^{-1} ($P<0.001$).

Preferred walk–run transition speed tracks the optimal neuromuscular effort

Walking and running at preferred speeds minimized neuromuscular effort during forward locomotion with moderate to extreme interlimb speed differences. There was a significant change in neuromuscular effort for walking and running across speeds [effect of speed \times gait mode: $F_{6,48}=77.3$ (forward), $F_{6,42}=92.5$ (forward, speed difference 0.5 m s^{-1}), $F_{6,42}=65.7$ (forward, speed difference 1.0 m s^{-1}), $F_{6,36}=37.7$ (forward, speed difference 1.5 m s^{-1}), $P<0.001$] (Fig. 2A,D–F). Walking decreased neuromuscular effort at all preferred walking speeds (*post hoc* tests at 70% $P<0.001$, 80%

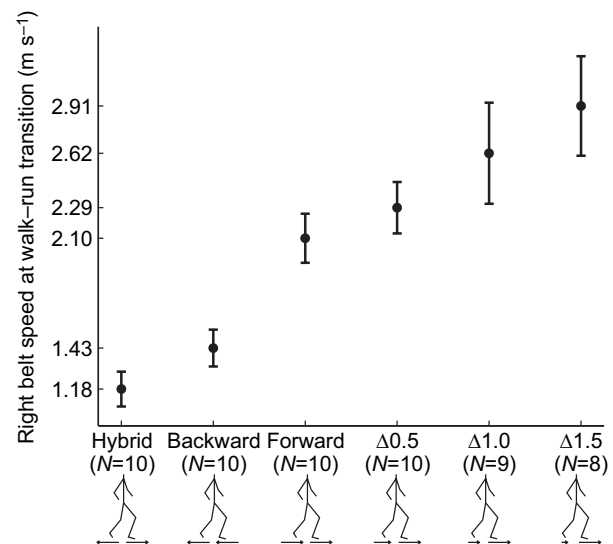


Fig. 1. Preferred walk–run transition speeds of six gait conditions. Gait conditions were as follows: forward, forward with speed differences (Δ) of 0.5, 1.0 and 1.5 m s^{-1} , backward and hybrid (treadmill belts move in opposite directions). Black dots are average speeds of the right belt at the transition and error bars are ± 1 s.d. The transition speed for forward gait is significantly different from the transition speeds of all other gait conditions ($P<0.05$).

$P \leq 0.002$, 90% $P \leq 0.040$), while running decreased neuromuscular effort at preferred running speeds during forward and speed difference gait conditions (*post hoc* tests at 120% $P \leq 0.012$, 130% $P \leq 0.014$).

The difference in neuromuscular effort between walking and running was strongly correlated with treadmill speed [$r^2 = 0.88$ for forward and speed difference of 0.5 and 1.0 m s^{-1} , $r^2 = 0.72$ for speed difference of 1.5 m s^{-1} ($P < 0.001$)] (Fig. 3). For each condition, the convergence speed is the intercept between the linear regression and the horizontal line at 0 (i.e. equivalent neuromuscular effort for walking and running). The convergence speed tracked the changes in transition speed across forward gait conditions with and without speed differences (Fig. 3; open circles lie within horizontal error bars for forward and speed difference gaits).

During backward and hybrid conditions, there was a significant change in neuromuscular effort across speeds [effect of speed \times gait mode: $F_{6,48} = 33.8$ (backward), $F_{6,48} = 15.9$ (hybrid), $P < 0.001$] (Fig. 2B,C). Walking decreased neuromuscular effort at preferred walking speeds (*post hoc* tests at 70% $P \leq 0.005$, 80% $P \leq 0.013$). Neuromuscular effort for running and walking was not significantly different at preferred running speeds. Correlations between treadmill speed and difference in neuromuscular effort between walking and running found moderately predictive relationships for backward and hybrid gait conditions [$r^2 = 0.41$ for backward and $r^2 = 0.68$ for hybrid ($P < 0.001$)] (Fig. 3). The convergence speed of neuromuscular effort for walking and running was within 1 s.d. of the walk–run transition speed for hybrid gait, but not for backward gait (Fig. 3). The convergence speed for backward gait approximated previously reported energetically optimal walk–run transition speeds (Terblanche et al., 2003; Hreljac et al., 2005).

Together, these results show that walking decreased neuromuscular effort (i.e. summed leg muscle activations) at preferred walking speeds. Neuromuscular effort at preferred walking speeds was minimized not only for forward gait with no speed difference

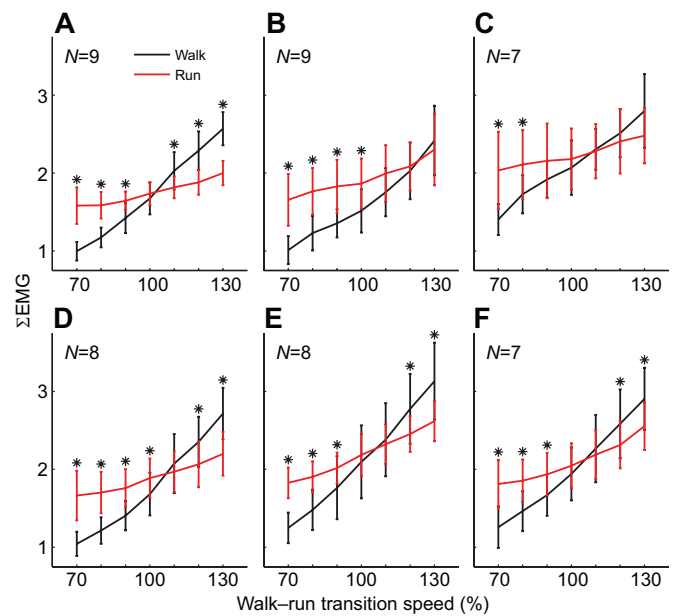


Fig. 2. Neuromuscular effort (ΣEMG) of walking and running at different relative treadmill speeds across gait conditions. Neuromuscular effort, given as the sum of electromyographic data, is plotted against treadmill speed, given as the percentage walk–run transition speed. (A) Forward, (B) backward, (C) hybrid and (D–F) forward with speed differences (Δ) of 0.5 (D), 1.0 (E) and 1.5 m s^{-1} (F). Error bars are ± 1 s.d. *Significant difference ($P < 0.05$). Single muscle activations are presented in Fig. S1.

(Prilutsky and Gregor, 2001) but also for the seldom-used backward gait, and the unfamiliar hybrid and forward with speed difference gaits. Our results support the hypothesis that humans select a gait mode (walking or running) to minimize neuromuscular effort, and do so even for novel locomotor environments on a split-belt treadmill.

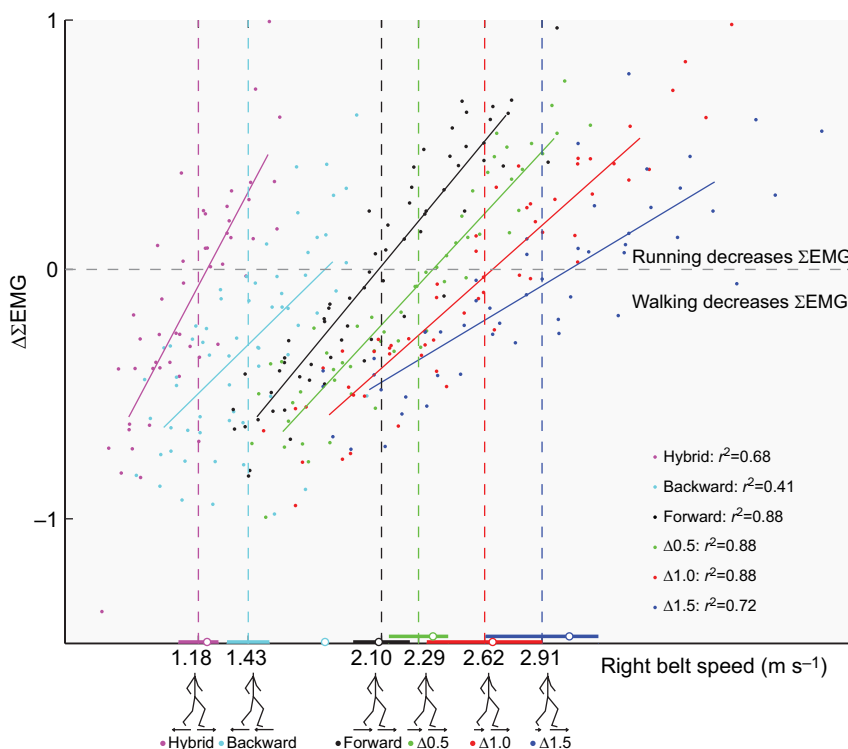


Fig. 3. Difference in neuromuscular effort between walking and running ($\Delta\Sigma\text{EMG}$) at absolute treadmill speeds. Solid lines are the least squares linear regressions. Vertical dashed lines are preferred walk–run transition speeds. Horizontal error bars on the x-axis are ± 1 s.d. of the walk–run transition speeds. Open circles are the speed at the intercept between regression lines and the horizontal line of equal neuromuscular effort of walking and running (at 0). All linear regressions were significantly different ($P < 0.001$).

Our results also show that running decreased neuromuscular effort at preferred running speeds during forward and speed difference gait conditions. The difference was not significant for the backward and hybrid gait conditions. It is possible that additional muscles (e.g. iliopsoas) influence the overall neuromuscular effort for hybrid and backward gaits. Alternatively, other mechanisms may underlie the decision to switch between walking and running when one or both legs are moving backwards. For example, the demand for active stabilization seen in forward walking (Donelan et al., 2004) could be greater in backward locomotion. Specifically, we recorded from leg muscles that are primarily important for progression in the sagittal plane. We do not know how muscle activations for trunk and medio-lateral stabilization change with speed during walking and running.

Across gait conditions, there was a robust relationship between measured walk–run transition speeds and the gait speed at which neuromuscular effort is equivalent for walking and running. The finding that the preferred walk–run transition speed coincides with the speed at which neuromuscular effort is equivalent for walking and running suggests that the nervous system selects a particular gait mode (walking or running) in a manner that reflects the least neuromuscular effort for each gait mode; and, furthermore, walk and run are equally likely when the overall neuromuscular effort is similar between the two gait modes.

Here, we summed muscle activations of eight bilateral lower limb muscles to quantify the overall neuromuscular effort of locomotion. Alternatively, it is possible that individual muscle activations could be a determining factor of the walk–run transition speed and specific muscles (or groups) drive the overall neuromuscular effort. For example, simulation has shown that walking at faster speeds compromises force generation of ankle plantarflexors (Neptune and Sasaki, 2005; Arnold et al., 2013), which creates the need for greater activation. Ultrasound imaging of the gastrocnemius (Farris and Sawicki, 2012) has shown that the walk–run transition produces favorable length and velocity changes that optimize force production at a given activation level. However, manipulating the demand of specific muscle groups only had limited effects on the walk–run transition speed (Segers et al., 2007; Bartlett and Kram, 2008; Malcolm et al., 2009).

Recent studies suggest that humans optimize the energetic costs of movement on short time scales (Snyder et al., 2012; Finley et al., 2013; Selinger et al., 2015). As muscle activation is proportional to metabolic energy expenditure by the active muscle (Umberger et al., 2003; Barclay, 2012), the motor command to a single muscle could provide a quick estimate of the muscle's metabolic energy expenditure. Thus, adopting a gait pattern that minimizes leg muscle activation should then lead to more economical movements (Russell and Apatoczky, 2016). It is important to note that a fully activated small muscle (e.g. tibialis anterior) would consume less metabolic energy than a fully activated large muscle (e.g. soleus). As such, our measure of neuromuscular effort as an unweighted sum of leg muscle activation may not be directly proportional to the metabolic cost. Our results showed that neuromuscular effort strongly predicted the walk–run transition speed in both familiar and novel gait conditions. While the preferred walk–run transition speed changed markedly across gait conditions, the overall neuromuscular effort for walking and running converged at the transition speed. Thus, leg muscle activations are minimized in a manner that is consistent with observations that hallmarks of normal locomotion (e.g. preferred walking speed, step frequency and step width) are observed at

energetic optima (Ralston, 1958; Zarrugh et al., 1974; Donelan et al., 2001).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

J.S. and J.T.C. designed the study and collected data; J.S. performed data analysis; and J.S. and J.T.C. wrote the manuscript.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.140723.supplemental>

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