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RESEARCH ARTICLE

Disentangling the energetic costs of step time asymmetry and step length asymmetry in human walking

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ABSTRACT

The metabolic cost of walking in healthy individuals increases with spatiotemporal gait asymmetries. Pathological gait, such as post-stroke, often has asymmetry in step length and step time which may contribute to an increased energy cost. But paradoxically, enforcing step length symmetry does not reduce metabolic cost of post-stroke walking. The isolated and interacting costs of asymmetry in step time and step length remain unclear, because previous studies did not simultaneously enforce spatial and temporal gait asymmetries. Here, we delineate the isolated costs of asymmetry in step time and step length in healthy human walking. We first show that the cost of step length asymmetry is predicted by the cost of taking two non-preferred step lengths (one short and one long), but that step time asymmetry adds an extra cost beyond the cost of non-preferred step times. The metabolic power of step time asymmetry is about 2.5 times greater than the cost of step length asymmetry. Furthermore, the costs are not additive when walking with asymmetric step time and asymmetric step length: the metabolic power of concurrent asymmetry in step length and step time is driven by the cost of step time asymmetry alone. The metabolic power of asymmetry is explained by positive mechanical power produced during single support phases to compensate for a net loss of center of mass power incurred during double support phases. These data may explain why metabolic cost remains invariant to step length asymmetry in post-stroke walking and suggest how effects of asymmetry on energy cost can be attenuated.

KEY WORDS: Locomotion, Gait asymmetry, Energy cost, Biomechanics, Walking economy

INTRODUCTION

Healthy humans prefer a symmetric gait pattern. Deviations arising from asymmetry in step time (Ellis et al., 2013) or step length (Roemmich et al., 2019; Nguyen et al., 2020) increase metabolic energy cost in healthy individuals. Individuals walking post-stroke or with a prosthesis following lower-limb amputation frequently display spatiotemporal asymmetries (Isakov et al., 2000; Patterson et al., 2008). Asymmetry is often thought to contribute to the increased metabolic energy cost in pathological gait, but previous studies have found that metabolic cost is invariant to changes in step length asymmetry in post-stroke walking (Sánchez and Finley, 2018; Roemmich et al., 2019; Nguyen et al., 2020; Padmanabhan et al., 2020). In all studies to date, step time asymmetry or step length asymmetry has been enforced in isolation so that the non-constrained gait parameter could vary freely. The isolated and interacting effects of asymmetry in step time and step length are therefore unknown, which hinders a deeper understanding of the relationship between energetic cost and spatiotemporal gait asymmetry. Understanding how and why gait asymmetry influences the energy cost of walking has important implications in the fields of rehabilitation (Awad et al., 2015; Finley and Bastian, 2017; Roemmich et al., 2019), assistive robotic devices (Quesada et al., 2016; Awad et al., 2017; Bae et al., 2018; McCain et al., 2019) and motor learning (Finley et al., 2013; Stenum and Choi, 2020).

Recent studies that focused on energy optimization during split-belt treadmill walking have also shed new light on the energetics of gait asymmetry (Finley et al., 2013; Sánchez et al., 2017, 2019; Stenum and Choi, 2020). Characterizations of energetic ‘cost landscapes’ that outline how a given gait parameter influences energy cost have shown that cost depends strongly on step time asymmetry, but that the effect of step length asymmetry is more variable. Furthermore, the control of step time asymmetry, but not step length asymmetry, is associated with energy optimization during split-belt treadmill walking (Stenum and Choi, 2020). It is currently unknown how the costs of gait asymmetry in step length and step time generalize between split-belt treadmill walking and walking on a normal (tied-belt) treadmill or over-ground and so it is unclear how these studies may be interpreted in a broader context to improve rehabilitation efforts.

In order to study the isolated and interacting effects of asymmetry in step time and step length on metabolic and mechanical costs, we instructed healthy participants to walk on a treadmill while we enforced a range of combinations in step time asymmetry and step length asymmetry via real-time visual feedback (see Fig. 1A,B for experimental setup and a schematic diagram of gait parameters). Enforcing asymmetry in step time and step length simultaneously is an important distinction from previous studies where step time asymmetry or step length asymmetry was manipulated in isolation so that the non-constrained gait parameter could vary freely. Here, we specifically examined the costs of either only step time asymmetry or only step length asymmetry, and how the costs interact when walking with concurrent asymmetry in step time and step length.

MATERIALS AND METHODS

Participants

Ten healthy participants (five males and five females; mean±s.d. age 24±3 years; body mass 71.7±13.7 kg) without orthopedic or neurological disorders completed the study. All participants were

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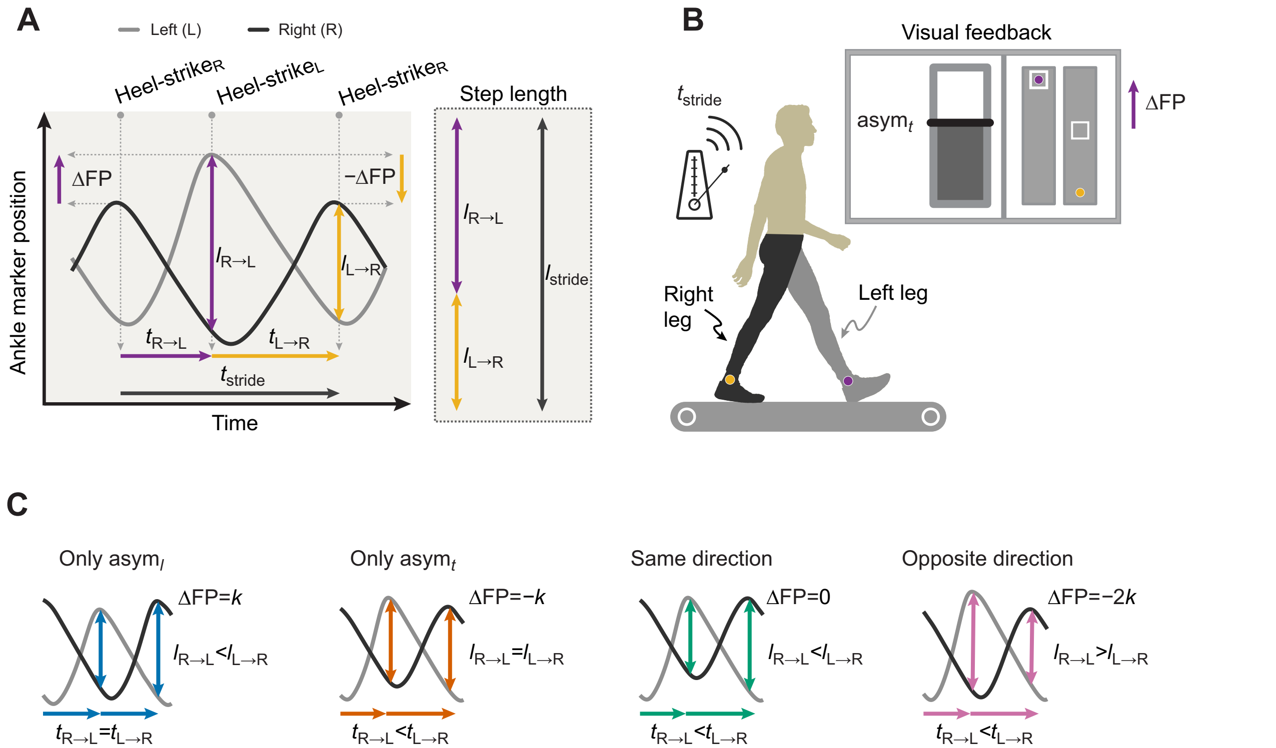

Fig. 1. Experimental setup and overview of gait parameters and asymmetry conditions. (A) Overview of gait parameters. Diagram shows time series of the anterior–posterior position of ankle markers on the left and right legs (gray and black curves, respectively) together with gait parameters (arrows): step time (t), stride time (t_{stride}), step length (l), stride length (l_{stride}) and foot placement difference (ΔFP); the subscripts L→R and R→L denote left-to-right and right-to-left steps. Inset shows step and stride lengths. (B) Experimental setup. Participants walked on a treadmill while stride time was enforced by the beat of a metronome and step time asymmetry ($asym_t$) and foot placement difference were enforced by real-time visual feedback projected onto a screen in front of the treadmill. (C) Asymmetry conditions: asymmetry only in step length (l) or step time (t), and concurrent asymmetry in step time and step length in the same or opposite directions. Values of foot placement difference are designated by the constant k, which depends on the value of asymmetry in step time and step length (see Eqn 3).

right leg dominant. Our inclusion criteria included that leg length difference was 1 cm or less, which is estimated to have a negligible effect on metabolic power of walking (Gurney, 2002). All participants gave informed written consent before the study in accordance with the protocol approved by the local Institutional Review Board at the University of Massachusetts Amherst (protocol 2018-4813).

Experimental design and protocol

Our goal was to enforce a range of different combinations of asymmetry in step time and step length during treadmill walking. Step time asymmetry ($asym_t$) was defined as:

$$asym_t = \frac{t_{L\rightarrow R} - t_{R\rightarrow L}}{t_{L\rightarrow R} + t_{R\rightarrow L}}, \quad (1)$$

and step length asymmetry ($asym_l$) was defined as:

$$asym_l = \frac{l_{L\rightarrow R} - l_{R\rightarrow L}}{l_{L\rightarrow R} + l_{R\rightarrow L}}, \quad (2)$$

where t is step time, l is step length and the subscript L→R refers to the step from heel-strike on the left leg to heel-strike on the right leg and R→L refers to the step from heel-strike on the right leg to heel-strike on the left leg. An asymmetry value of zero means equal step times or step lengths. Our asymmetry measure is directional: positive asymmetry is step times or step lengths that are greater from left-to-right heel-strikes than from right-to-left heel-strikes, and vice versa for negative asymmetry.

Participants had to control stride time (t_{stride}; sum of two step times), step time asymmetry and foot placement difference (ΔFP), which indirectly enforced a specific value of step length asymmetry (see Fig. 1A for a diagram of gait parameters). Foot placement difference is defined as the anterior–posterior distance between the position of the lateral malleolus on one foot at its heel-strike relative to the position of the lateral malleolus on the other foot at its previous heel-strike. A positive foot placement difference indicates that the right leg steps anteriorly to the left leg, and vice versa for negative foot placement difference. We indirectly enforced a specific value of step length asymmetry by setting foot placement difference according to (see Appendix for derivation):

$$\Delta FP = \frac{1}{2} \cdot t_{stride} \cdot v \cdot (asym_l - asym_t), \quad (3)$$

where v is treadmill belt speed.

We use an experimental setup (Fig. 1B) in which stride time was enforced by the beat of a metronome while step time asymmetry and foot placement difference were enforced by real-time visual feedback projected onto a screen in front of the treadmill (Bertec, Columbus, OH, USA). The setup is described in Stenum and Choi (2020).

On a day prior to the data collection visit, participants visited the laboratory to train to walk on the treadmill while simultaneously controlling their stride time, step time asymmetry and foot placement difference. The visit lasted between 1.5 and 2 h with about 1 h of training broken into shorter bouts.

Before the data collection visit, participants fasted and refrained from coffee or caffeinated drinks for 4 h. At the beginning of the data collection visit, participants sat for 10 min after which they stood for 5 min while we measured their standing metabolism. Next, participants walked on the treadmill for 10 min at 1.25 m s^{-1} to warm up. We presented no feedback during the warm-up period. After minute 7 of the warm-up period, we found each participant's preferred stride time. In all subsequent trials, stride time was enforced to the participant's preferred value. We chose to keep stride time constant as it is well documented that there is a U-shaped relationship between stride time and metabolic power when walking at a fixed speed (Umberger and Martin, 2007); by keeping stride time constant, we avoided the confounding effect of varying stride time on metabolic power.

Following the warm-up period, participants completed 17 experimental trials, each lasting 5 min, in which different combinations of step time asymmetry and step length asymmetry were enforced while participants walked on the treadmill at 1.25 m s^{-1}. The 17 trials comprised: four asymmetry conditions of each four trials with increasing values of asymmetry in step time and step length; and one symmetric condition in which step time and step length were enforced to symmetry ('symmetry'). The four asymmetry conditions were made up of one condition with only step length asymmetry ('only asym$_l$'), one condition with only step time asymmetry ('only asym$_t$'), and two conditions with concurrent asymmetry in both step time and step length that were either in the same direction ('same direction') or in opposite directions ('opposite direction'). See Fig. 1C for graphical representations of asymmetry conditions. For all asymmetry conditions, the target asymmetry values in either step time or step length were 0.05, 0.10, 0.15 and 0.20. In the symmetric condition, the target asymmetry in both step time and step length was 0. Participants rested 2 min, or longer if necessary, between trials. The order of the 17 trials were randomized between participants.

Data collection

Four high-speed cameras (Qualisys Oqus, Gothenburg, Sweden) recorded eight reflective markers at 100 Hz that we placed bilaterally on the fifth metatarsal, lateral malleolus, fibular head and greater trochanter. Force plates imbedded in each treadmill belt recorded ground reaction forces for the left and right legs at 1000 Hz. We recorded breath-by-breath rates of oxygen consumption and carbon dioxide production (Parvo Medics Trueone 2400, Sandy, UT, USA).

Data processing

We low-pass filtered kinematic data at 7 Hz and kinetic data at 10 Hz, and removed offset and drift. We defined heel-strikes and toe-offs as the instants the vertical ground reaction force crossed 10 N. Step time was calculated as the duration between consecutive bilateral heel-strikes. We calculated foot placement differences for left-to-right and right-to-left steps as the anterior–posterior difference between the lateral malleolus at subsequent bilateral heel-strikes. Step lengths were calculated from step-by-step values of foot placement difference and the product of step time and belt speed (see Eqn A2 and A3 in the Appendix). Step time asymmetry, step length asymmetry and foot placement difference were averaged over the last 2 min of each 5 min trial.

In order to express the values of step time asymmetry and step length asymmetry according to a single scalar value, we calculated an aggregate asymmetry variable (asym). Aggregate asymmetry was calculated as the average of the absolute values of step time asymmetry and step length asymmetry. For the 'only asym$_t$' and 'only asym$_l$' conditions, aggregate asymmetry was set to the values of step time asymmetry and step length asymmetry, respectively.

We used two methods to calculate the average mechanical power performed (1) on the center of mass, which was used to assess center of mass mechanics, and (2) by the joints of the lower limb, which was used to assess musculotendon work (Sasaki et al., 2009). We calculated the instantaneous power that each leg produced on the center of mass using the individual limbs method: as the dot product of the center of mass velocity (obtained by integration of net ground reaction forces) and ground reaction forces of each leg (Donelan et al., 2002). We used sagittal plane inverse dynamics to obtain the instantaneous power at the hip, knee and ankle of each limb (Winter, 1990). By integrating the positive and negative portions of the power curves of each leg over intervals of the stride, we calculated the following terms: positive work during the single support phase; positive push-off work performed by the trailing limb during the double support phase; negative collision work performed by the leading limb during the double support phase; and total positive work performed during the entire stride period (note that the mechanical work that the leg performs on the center of mass during the swing period is zero when using the individual limbs method). We calculated the net work during double support as the sum of push-off work and collision work. For both measures of instantaneous mechanical power (on the center of mass or at the joints), we discarded the stance phases in which we detected that the stance leg produced force on the opposite force plate. We summed the mechanical work across the hip, knee and ankle to obtain the total joint work. Mechanical work (on the center of mass and summed across joints) was summed over left and right legs and then divided by stride time in order to get average mechanical power. We calculated gross metabolic power from the rates of oxygen consumption and carbon dioxide production (Brockway, 1987) and subtracted standing metabolism to obtain net metabolic power. Mechanical and metabolic power were calculated from the last 2 min of each 5 min trial. In order to express the effect of asymmetry on mechanical and metabolic power, we subtracted the value obtained during the symmetric condition from the values in the asymmetric conditions – this normalization was completed for data presentation in figures and for further data analysis.

Statistics

To test whether the metabolic power of step length asymmetry ('only asym$_l$' condition) or step time asymmetry ('only asym$_t$' condition) was predicted by the metabolic power of walking with non-preferred steps, we used previously published datasets that contained metabolic power values for a range of different preferred and non-preferred step lengths and step times when walking on a treadmill at a fixed speed (Umberger and Martin, 2007; Ellis et al., 2013; Stenum and Choi, 2017). We made a quadratic fit to the values in order to obtain prediction lines for the metabolic power of non-preferred step lengths and step times (see Fig. S1). Note that the metabolic power predictions of non-preferred step lengths and step times are identical because these datasets are based on fixed speed treadmill walking (which is similar to the experimental setup of the current study). We tested how well the predicted metabolic power of non-preferred steps explained the measured metabolic power of step length asymmetry ('only asym$_l$' condition) and step time asymmetry ('only asym$_t$' condition) by comparing predicted and measured metabolic power for all data points using paired *t*-tests.

Next, we tested whether the metabolic power of walking with concurrent asymmetry ('same direction' and 'opposite direction' conditions), was determined by (1) the cost of step length

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asymmetry ('only asym$_l$' condition), (2) the cost of step time asymmetry ('only asym$_t$' condition) or (3) the additive costs of step length asymmetry and step time asymmetry (sum of 'only asym$_l$' and 'only asym$_t$' conditions). We first created three alternative cost models based on the metabolic power of step length asymmetry, step time asymmetry and the added costs, and second tested which cost model best explained the measured metabolic power of concurrent asymmetry. For each individual participant, we used linear fits to the metabolic power values of the 'only asym$_l$' and 'only asym$_t$' conditions. From the two fits of each participant, we used the slope and intercept of 'only asym$_l$' data as the cost of step length asymmetry, the slope and intercept of 'only asym$_t$' data for the cost of step time asymmetry and the sum of the slopes and the averaged intercept for the additive cost of step length asymmetry and step time asymmetry (see Fig. S2 for cost models of individual participants). From each participant's measured metabolic power of concurrent asymmetry, we calculated residuals between the actual cost and each cost model as the difference at each data point's value of asymmetry. We used one-sample *t*-tests of the residuals of each model to test whether the models tended to under- or over-estimate the cost of concurrent asymmetry. We used two-sample *t*-tests of the residuals obtained from the 'same direction' and 'opposite direction' conditions to test whether the models predicted the metabolic power of concurrent asymmetry differently when the directionality varied between step length asymmetry and step time asymmetry.

We performed linear regressions to evaluate trends and associations between asymmetry, mechanical and metabolic data. All linear regressions were made using all individual data points, not clustered data points which are only plotted for visualization purposes. We set the level of significance at 0.05. All statistical tests were performed in MATLAB (Mathworks, Natick, MA, USA).

RESULTS

Participants walked on the treadmill at 1.25 m s^{-1} with a range of values of step time asymmetry and step length asymmetry according to the four asymmetry conditions (Fig. 2A). The desired value of step length asymmetry was indirectly enforced by foot placements such that foot placement difference (i.e. the distance between the position of the lateral malleolus on one foot at its heel-strike relative to the position of the lateral malleolus on the other foot at its previous heel-strike) changed systematically between asymmetry conditions (Fig. 2B). In all trials, stride time was enforced to the participant's preferred value (ensemble mean±s.d. 1.08±0.05 s) and was kept constant throughout the experiment (coefficient of variation was 0.4%). As a result of constant stride time and treadmill belt speed, stride length (ensemble mean±s.d. 1.35±0.07 m) was also kept constant throughout the experiment.

Cost of non-preferred steps explains the metabolic power of step length asymmetry, whereas step time asymmetry incurs an added energetic penalty

We first asked whether the isolated costs of walking with only step time asymmetry or only step length asymmetry are explained by taking step times or step lengths that are non-preferred, e.g. walking with asymmetric step lengths can be accomplished by taking two non-preferred step lengths (one short and one long) that are expected to increase metabolic power because of the U-shaped relationship between metabolic power and variations in step length. If the metabolic power of walking with step length asymmetry is explained by the cost of non-preferred steps, that suggests that there is no extra cost of asymmetry.

We used previously published data of the metabolic power of walking with non-preferred step times and step lengths at constant-speed treadmill walking (Umberger and Martin, 2007; Ellis et al., 2013; Stenum and Choi, 2017) to calculate the predicted cost of non-preferred step times and step lengths (see Fig. S1). We compared the predictions with our measured metabolic power of isolated step length asymmetry ('only asym$_l$' condition) and isolated step time asymmetry ('only asym$_t$' condition). The metabolic power of step length asymmetry was well predicted by the cost of non-preferred step lengths (Fig. 3A; P=0.083; on average, the metabolic power of step length asymmetry was 0.07±0.25 W kg^{-1} greater than the predicted cost of non-preferred step lengths). In contrast, the metabolic power of step time asymmetry was greater than the predicted cost of non-preferred step times, which is consistent with previous findings by Ellis et al. (2013) (Fig. 3B; P<0.001; on average, the cost of step time asymmetry was 0.58±0.41 W kg^{-1} greater than the predicted cost of non-preferred step times). The metabolic power of step time asymmetry (y=9.42x−0.18, r^2=0.73, P<0.001) was about 2.5 times greater than the metabolic power of step length asymmetry (y=3.70x−0.04, r^2=0.40, P<0.001).

Metabolic power of step time asymmetry determines the cost of walking with concurrent asymmetry in step time and step length

Second, we asked whether the metabolic power of walking with concurrent step time asymmetry and step length asymmetry is explained by the cost of walking with (1) only step length asymmetry, (2) only step time asymmetry or (3) additive cost components of step time asymmetry and step length asymmetry. Based on previous studies showing metabolic energy cost determined by additive components that are associated with gait parameters such as step length and step time (Kuo, 2001; Donelan et al., 2002; Doke et al., 2005), we hypothesized that the metabolic power of concurrent asymmetry in step time and step length is best explained by the additive cost.

The metabolic power of walking with concurrent asymmetry was similar regardless of whether asymmetry in step time and step length were combined so that they were in the same or opposite directions (Fig. 4A; 'same direction' condition: y=9.96x−0.03, r^2=0.60, P<0.001: 'opposite direction' condition: y=10.68x−0.17, r^2=0.73, P<0.001). We created three alternative cost models in order to explain the metabolic power of concurrent asymmetry in step time and step length: (1) the cost of step length asymmetry derived from the metabolic cost observed in the 'only asym$_l$' condition; (2) the cost of step time asymmetry derived from the metabolic cost observed in the 'only asym$_t$' condition; and (3) the additive cost of step length asymmetry and step time asymmetry derived from the sum of the metabolic power observed in the 'only asym$_l$' and 'only asym$_t$' conditions (see Fig. S2 for cost models of individual participants). The model of the cost of step time asymmetry best explained the metabolic power of concurrent asymmetry (Fig. 4C; sum of absolute value of residuals=21.9). The cost of step time asymmetry slightly underestimated the metabolic power of concurrent asymmetry (mean±s.d. −0.17±0.33 W kg^{-1}, P<0.001) but the underestimation was not affected by the magnitude of asymmetry (Fig. 4C; y=−1.4x+0.0, r^2=0.04, P=0.062). The models of the cost of step length asymmetry and the additive costs of asymmetric step time and step length were poorer fits to the measured metabolic power of concurrent asymmetry (Fig. 4B,D: sum of absolute value of residuals was 54.1 and 29.3, respectively). We conclude that the isolated metabolic power components of walking with step time asymmetry and step length asymmetry are

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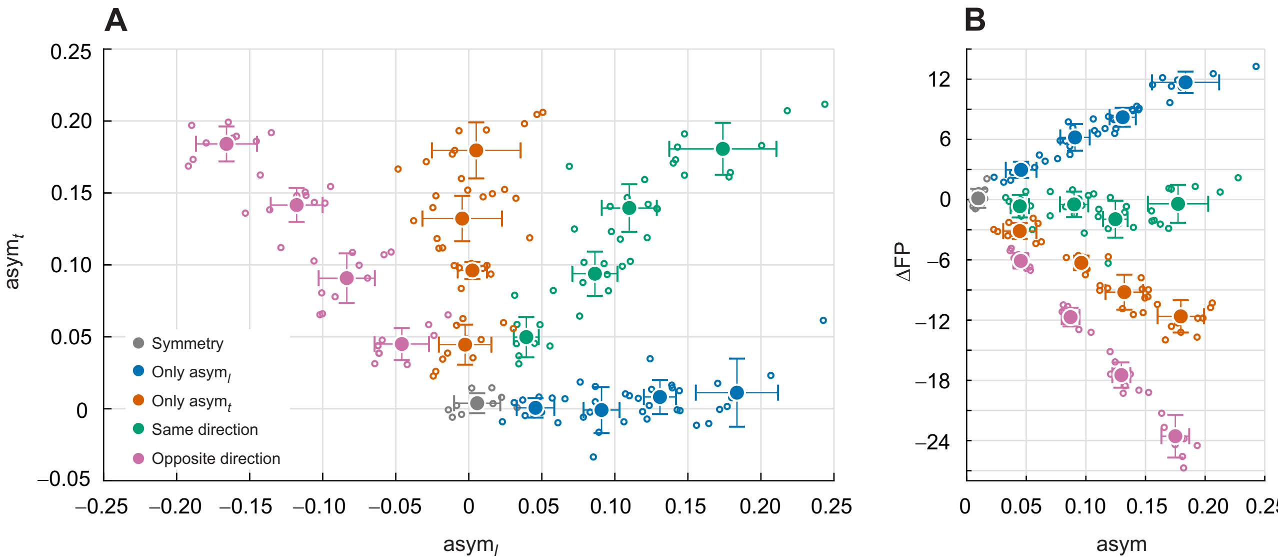

Fig. 2. Experimentally enforced gait parameters. (A) Values of step length asymmetry (asym$_l$) and step time asymmetry (asym$_t$). (B) Foot placement difference (ΔFP) was varied to indirectly enforce step length asymmetry according to Eqn 3. Aggregate asymmetry (asym) is the average of the absolute value of step length asymmetry and step time asymmetry. Large circles with error bars are ensemble means±s.d. (N=10). Small open circles are data points for individual participants.

not additive when walking with concurrent asymmetry in step time and step length. Rather, the metabolic power of walking with concurrent asymmetry in step time and step length is determined by the metabolic power of step time asymmetry alone regardless of the directional combination of step time asymmetry and step length asymmetry within a step.

Net loss of center of mass power in double support phases is compensated by positive power in single support phases

Based on the different trends on metabolic power, we grouped the subsequent analyses of the effects of gait asymmetry on center of mass mechanics (see Fig. 5) into the 'only asym$_l$' condition and the three conditions with step time asymmetry ('only asym$_t$', 'same direction' and 'opposite direction'). Asymmetry was associated with a net loss of center of mass power during double support phases in the conditions with step time asymmetry (y=−1.69x−0.04, r^2=0.31, P<0.001; Fig. 6A) and in the condition with only step length asymmetry (y=−0.75x+0.00, r^2=0.15, P=0.014; Fig. 6B). Asymmetry was also associated with increased positive power performed during single support phases in the conditions with step time asymmetry (y=1.35x+0.00, r^2=0.30, P<0.001; Fig. 6C) and in the condition with only step length asymmetry (y=0.60x+0.00, r^2=0.15, P=0.015; Fig. 6D). We found an association between the net loss of center of mass power during double support phases and positive power during single support phases (y=−1.19x−0.05, r^2=0.87, P<0.001; Fig. 6E) that suggests the positive power is

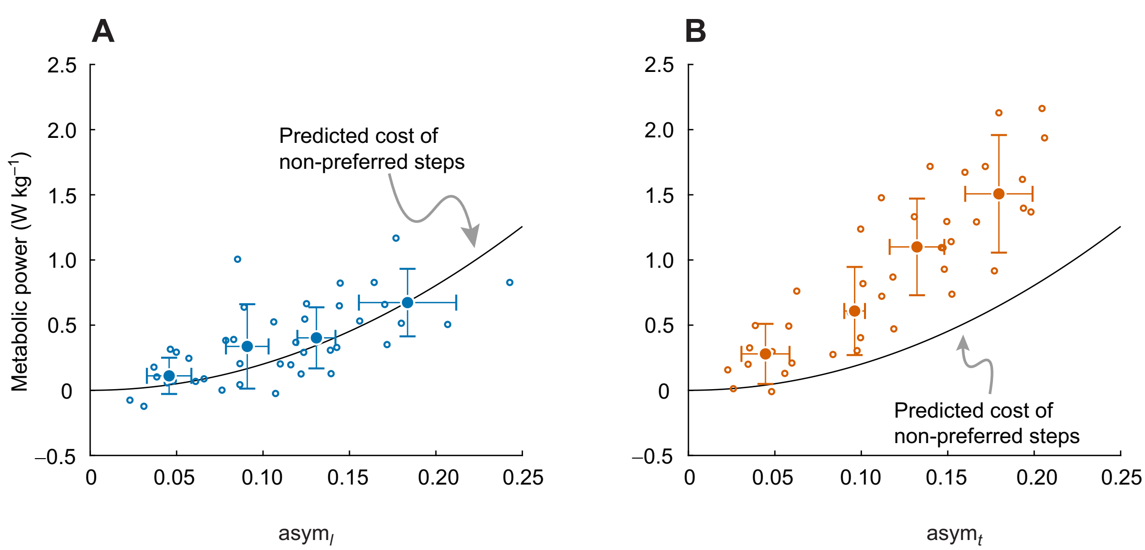

Fig. 3. Metabolic power of isolated step length asymmetry and step time asymmetry. The metabolic power (change relative to symmetry) of the 'only asym$_l$' condition (asym$_l$) (A) and 'only asym$_t$' condition (asym$_t$) (B) with predicted costs based on previously published data of non-preferred step lengths or step times, respectively (Umberger and Martin, 2007; Ellis et al., 2013; Stenum and Choi, 2017; see Fig. S1). Large circles with error bars are ensemble means±s.d. (N=10). Small open circles are data points for individual participants.

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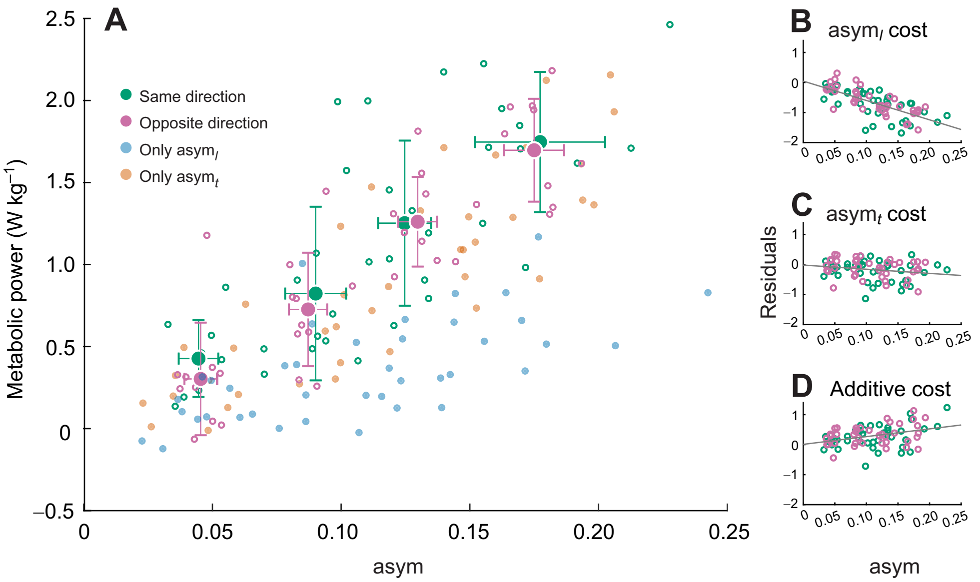

Fig. 4. Metabolic power of concurrent asymmetry in step time and step length with three alternative cost models. (A) Measured metabolic power (change relative to symmetry) of concurrent asymmetry, with data from the 'only asym$_l$' and 'only asym$_t$' conditions plotted for reference. (B–D) Three models based on the cost of step length asymmetry (B), the cost of step time asymmetry (C) and the additive cost of step length asymmetry and step time asymmetry (D). Residuals of cost models are measured metabolic power subtracted from predicted power at each data point's value of asymmetry. Large circles with error bars are ensemble means±s.d. (*N*=10). Small open circles are data points for individual participants. See Fig. S2 for cost models of individual participants.

produced during single support phases to compensate for the net loss in center of mass power incurred during double support phases. Fig. 7 shows an example of how asymmetry affects single support positive work, push-off work and collision work.

Increased positive mechanical power during single support explains the increased metabolic power of asymmetric step time and step length

In order to estimate the musculoskeletal work of lower-limb muscles and their effect on metabolic power, we calculated mechanical power from hip, knee and ankle joint power (see Fig. S3) using inverse dynamics. Total positive mechanical power across the stride cycle poorly explained the metabolic power of asymmetric step time and step length (y=0.04x+0.00, r^2=0.05, P=0.003; Fig. 8A). In contrast, the increase in metabolic power of walking with asymmetric step time and step length was well explained by the increase in positive power performed during single support phases (y=0.10x+0.03, r^2=0.63, P<0.001; Fig. 8B). This suggest that it is the mechanical work performed during single support phases that drives the metabolic power of asymmetry in step time and step length.

DISCUSSION

We have shown that the metabolic power of isolated step time asymmetry is greater than the metabolic power of isolated step length asymmetry. The separate costs of step time asymmetry and step length asymmetry are not additive when walking with concurrent asymmetry. Rather, the metabolic power of walking with concurrent asymmetry in step time and step length is determined by the metabolic power of step time asymmetry alone. We found that asymmetry is associated with a net loss of center of mass energy during double support phases that is compensated for by greater positive power during single support phases. The increased metabolic power in all combinations of asymmetry in step time and step length is explained by increased positive mechanical power performed during single support phases.

We showed that the metabolic power of step time asymmetry is beyond the metabolic power predicted by taking two non-preferred step times. The cost of non-preferred steps can be regarded as the summed cost of two unequal steps that are independent and therefore are linearly additive. Because step time asymmetry incurs an extra cost relative to two non-preferred steps, we regard the cost of step time asymmetry as a 'true' cost of the asymmetry in the gait pattern. In contrast, the metabolic power of step length asymmetry was well predicted by the metabolic power of two non-preferred step lengths. This suggests that the cost of step length asymmetry is a by-product of taking two steps of unequal length and that the cost is well captured by linearly additive and independent cost components of each step (Srinivasan, 2011). The distinction between (1) the cost of step time asymmetry as a 'true' cost of asymmetry and (2) the cost of step length asymmetry as a by-product of taking two non-preferred steps offers a framework for the determination of the cost of asymmetry that is useful for understanding the cost of our concurrent asymmetry conditions.

We found that the metabolic power of step time asymmetry explains the metabolic power of concurrent asymmetry in step time and step length. That means that there is no interaction between the costs of step time asymmetry and step length asymmetry when walking with concurrent asymmetry – rather, step time asymmetry is the dominant cost. This finding supports the abovementioned idea that the dominant cost of asymmetry is derived from the 'true' asymmetry cost of step time asymmetry. Biomechanically, we suggest that the dominance of step time asymmetry is driven by the energetic consequences of greater losses of center of mass power during double support phases compared with the condition with only step length asymmetry. The loss of center of mass power during double support with step time asymmetry does not appear to be influenced by concurrent step length asymmetry and therefore step time asymmetry remains the dominant factor that dictates the metabolic power of concurrent asymmetry in step time and step length.

Our results for the metabolic power of concurrent asymmetry in healthy participants may resolve previous paradoxical findings showing that metabolic cost in post-stroke walking is invariant to changes in step length asymmetry (Sánchez and Finley, 2018; Roemmich et al., 2019; Nguyen et al., 2020; Padmanabhan et al., 2020). We have shown that, when walking with concurrent asymmetry in step time, metabolic power is invariant to changes in step length asymmetry. Post-stroke gait is characterized by concurrent asymmetries in step length and step time (Roerdink and Beek, 2011). As predicted from our results, the metabolic cost of pathological gait that demonstrate concurrent step time asymmetry is therefore

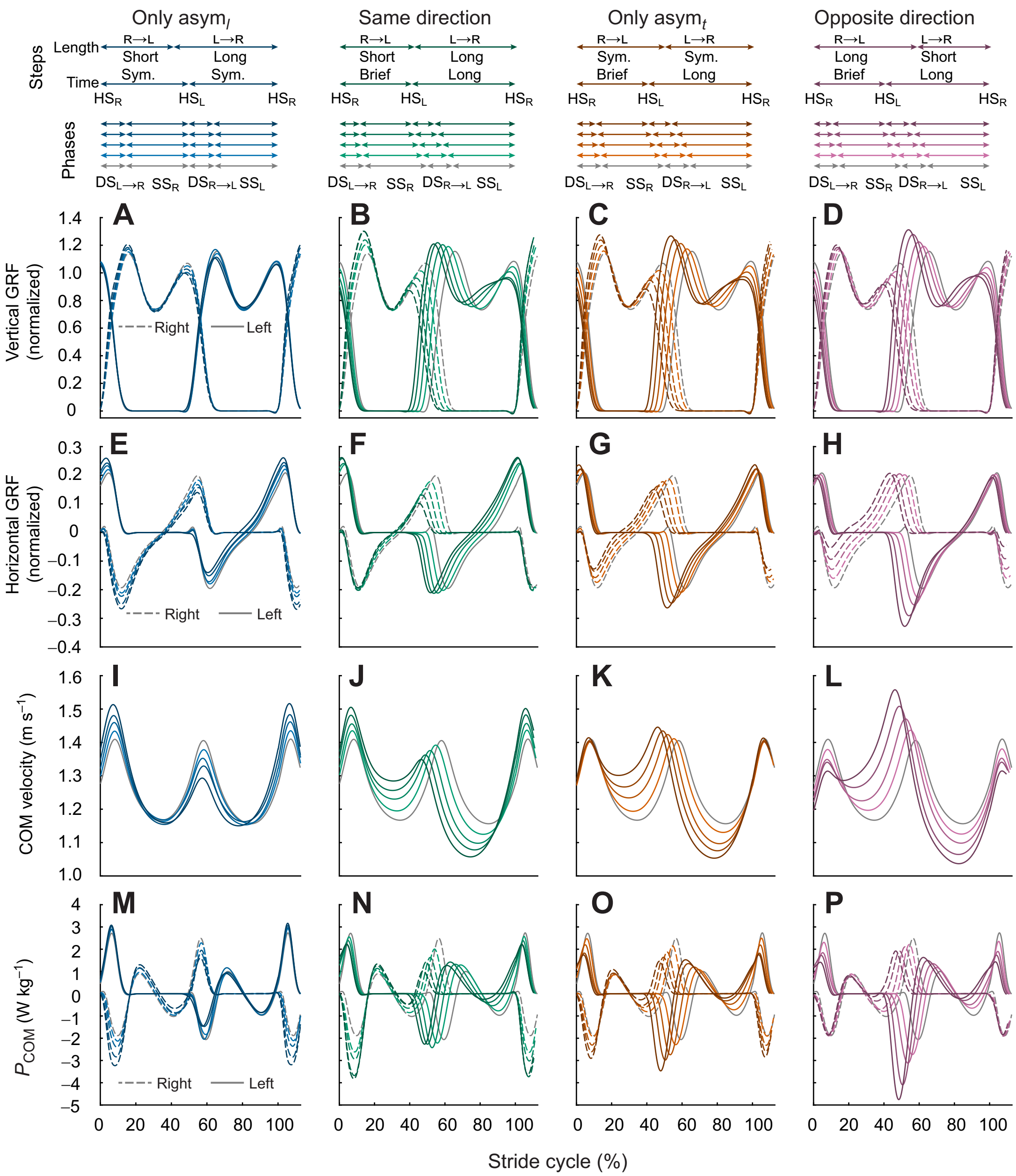

Fig. 5. Center of mass mechanics. (A–D) Vertical ground reaction force (GRF) for individual limbs. (E–H) Anterior–posterior (horizontal) ground reaction force for individual limbs. (I–L) Anterior–posterior center of mass (COM) velocity. (M–P) Instantaneous power performed on the center of mass (P_{COM}) by individual limbs. Increased asymmetry is shown by progressively darker line coloring. Gray lines show the symmetric condition. Arrows above the graphs show relative durations within the stride cycle. Steps from right-to-left (R→L) and left-to-right (L→R) heel-strike (HS) are indicated. Double support (DS) and single support (SS) phases are indicated with subscripts denoting double support phase when transitioning from left-to-right stance ($DS_{L→R}$) and right-to-left stance ($DS_{R→L}$), and for right (SS_R) and left (SS_L) single support phase. Ground reaction forces in A–H were normalized by body weight. All lines are ensemble means (N=10) for a specific level of enforced asymmetry.

expected to remain invariant to changes in step length asymmetry. As a result, we therefore propose that step length asymmetry should not be the only targeted outcome variable in interventions seeking to improve the walking economy of pathological gait.

How does step time asymmetry affect metabolic power? The relationship between gait asymmetry and energy cost can be demonstrated by an energetic cost landscape that outlines how a given gait parameter affects energy cost. Based on our data and those of a previous study (Ellis et al., 2013), the cost landscape of step time asymmetry in healthy human walking shows that metabolic power is lowest at zero step time asymmetry (equal step times) and that increases in step time asymmetry increase metabolic power. However, symmetry is not necessarily optimal during walking with different constraints. The idea that people self-select their step time asymmetry to lower energy cost is supported by a recent study that showed that preferred step times in split-belt treadmill walking of healthy humans were asymmetric and that the preferred values reduced metabolic power (Stenum and Choi, 2020). Furthermore, recent work suggests that asymmetric step times (or stance times) are energetically optimal with unilateral lower limb amputation (Handford and Srinivasan, 2018; Wedge, 2019).

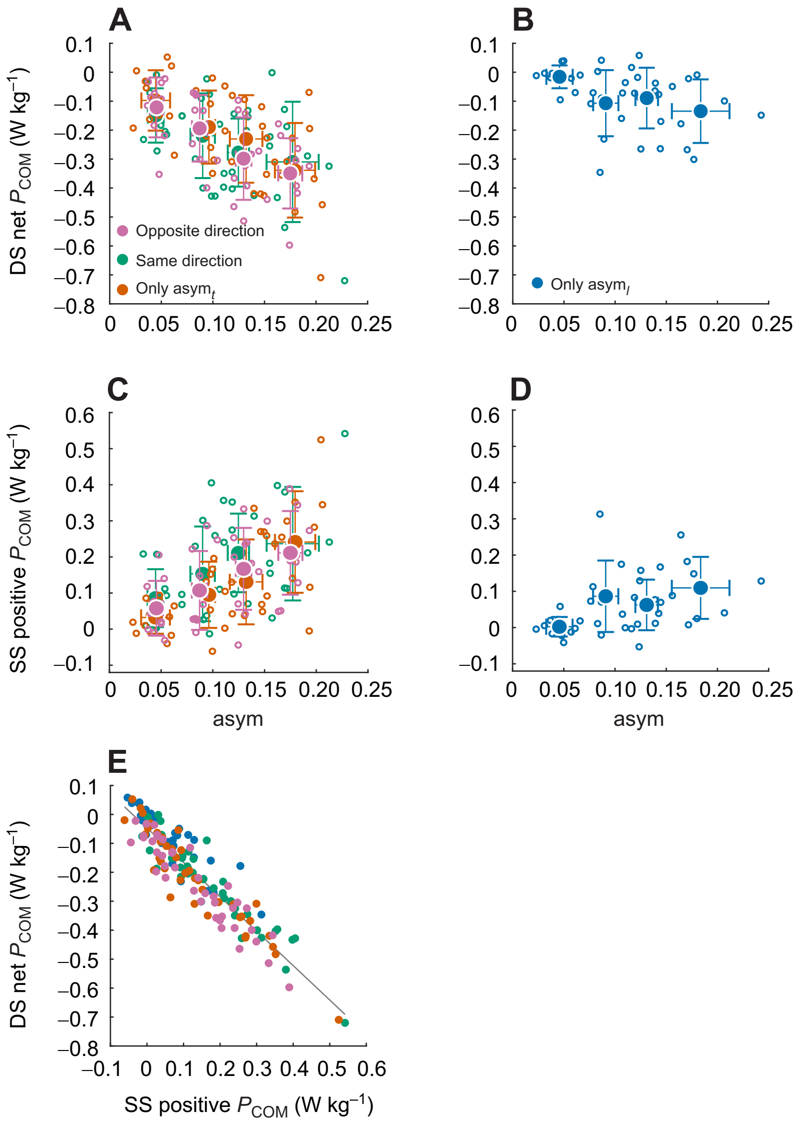

Fig. 6. Compensation of net loss of center of mass power during double support phases. (A–D) Relationships between asymmetry and net power performed on the center of mass during double support phases (A,B) and positive power performed during single support phases (C,D). A and C show relationships for conditions with step time asymmetry ('only asym$_t$', 'same direction' and 'opposite direction'). B and D show relationships for the 'only asym$_l$' condition. (E) Relationship between positive power performed during single support and net power performed during double support phases. In A–E, power is given as the change relative to symmetry. Large circles with error bars are ensemble means±s.d. (*N*=10). Small open (A–D) and filled (E) circles are data points for individual participants.

We found that the metabolic power of asymmetry in step time and step length were explained by positive power performed during single support phases. This mechanical cost is similar to findings in studies of post-stroke gait that show that the increased metabolic cost is related to increased positive power generated during single support (Chen et al., 2005; Stoquart et al., 2012). Rehabilitation through training, therapy or robotics has focused much attention on restoring push-off in clinical populations. However, the dominant cost of producing positive power during single support also suggests that rehabilitation strategies that aim to reduce single support work may be an effective approach to lower metabolic cost in clinical populations.

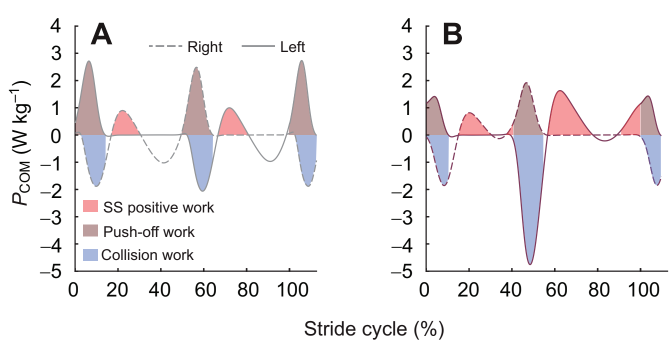

Fig. 7. Example of changes to work performed on the center of mass with asymmetry. Plots are for the 'symmetry' condition (A) and the 'opposite direction' condition with asymmetry set to 0.20 (B).

The increase in positive power during single support explained the metabolic power in all combinations of asymmetry in step time and step length. Positive power performed during single support has been proposed to be an important determinant of the metabolic cost of walking (Neptune et al., 2004). This cost therefore reflects a general cost of walking that may be an important determinant with and without gait asymmetry. The cost of mechanical work during single support (Neptune et al., 2004) contrasts with the cost of step-to-step transition work (Donelan et al., 2002). Step-to-step transition work has been proposed to be a major determinant of the cost of walking (Donelan et al., 2002), but the positive push-off work is primarily performed by ankle plantar flexors at relatively low metabolic cost with significant contributions from elastic storage and return (Sawicki and Ferris, 2009; Umberger, 2010). While the metabolic cost derived during step-to-step transitions may not be high, a primary effect on cost may be the coordination between push-off work performed by the trailing leg and concomitant

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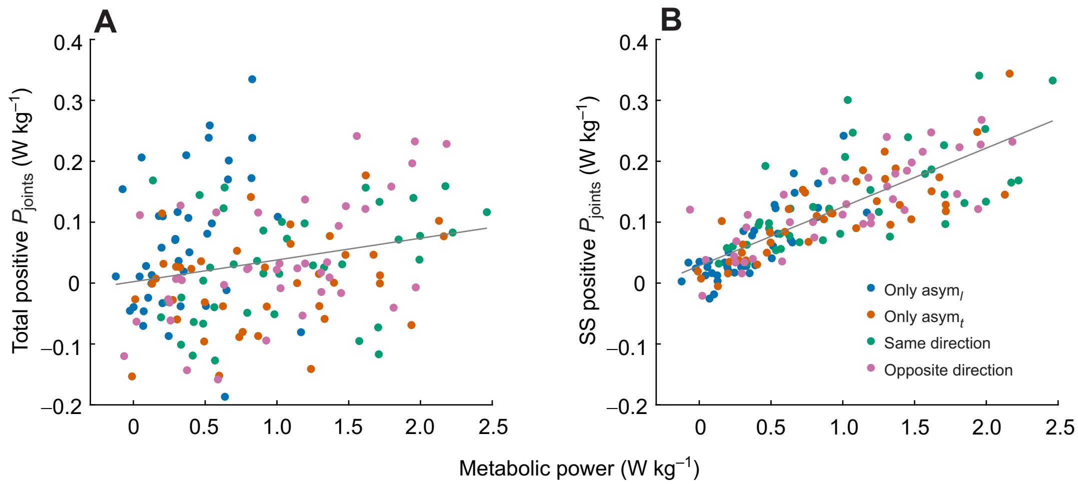

Fig. 8. Relationship between metabolic power and positive power summed across hip, knee and ankle joints. Total summed joint power (change relative to symmetry) performed across the entire stride cycle (A) and positive power performed during single support phases (B) against metabolic power (change relative to symmetry). Circles are data for individual participants. See Fig. S3 for instantaneous hip, knee and ankle joint power values.

negative work performed on the center of mass – so-called collisional losses of center of mass energy – as the leading leg absorbs mechanical energy during double support phases (Soo and Donelan, 2012). In this study, net losses of center of mass power during double support phases were driven by timing shifts in positive power and greater collision work (see Fig. 7). Negative collision work likely does not exact a high metabolic cost because of the relatively low cost of producing negative muscle work and because a portion of the work may be dissipated through soft tissue (Zelik and Kuo, 2010). Rather, the positive work during single support phases is performed to make up for the net loss of center of mass power occurring during double support phases and it is this positive work that exacts a dominant metabolic cost that accounts for the cost of asymmetry.

Additional factors may have influenced metabolic power in the current study. For example, the cost of producing muscle force may not be reflected in our calculations of muscle work. The cost of muscle force may have influenced the conditions with step time asymmetry wherein one leg must be swung quickly and the other more slowly during swing phases, possibly exacting a net gain in cost as the increased cost of rapid force production to swing one leg vigorously may exceed the reduced cost to swing the other leg slowly (Doke et al., 2005; Doke and Kuo, 2007). In order to reduce the effect on cost associated with familiarizing to a novel experimental setup, participants came in for an initial training visit on a day prior to data collection. We expect that the prior training minimized the cost of motor learning that may have been driven by factors such as muscle co-contraction. Foot placement difference varied systematically between the four asymmetry conditions that we used in this study, which could also explain changes in energy cost. While we did not analyze foot placement difference as a primary aim, our results show that the effect of foot placement difference on metabolic power is equivalent to the effect of step length asymmetry: metabolic power increased with greater foot placement differences in the 'only asym$_l$' condition, but metabolic power was invariant to changes in foot placement difference across the three conditions with step time asymmetry ('only asym$_t$', 'same direction' and 'opposite direction'). Therefore, we conclude that there is no effect of foot placement difference on metabolic power when there is concurrent step time asymmetry in the gait pattern (Roemmich et al., 2019).

APPENDIX

Derivation of the relationship between asymmetry and foot placement difference

During steady-state walking in which gait parameters remain equal across strides, foot placement differences (ΔFP) of the two steps are equal and opposite (note that foot placement difference in the main text refers to the value for the left-to-right step):

$$\Delta FP_{L\rightarrow R} = -\Delta FP_{R\rightarrow L}. \tag{A1}$$

Step length (l) can be expressed using combinations of foot placement differences, belt speed (v) and step time (t). Left-to-right step length is:

$$l_{L\rightarrow R} = t_{L\rightarrow R} \cdot v + \Delta FP_{L\rightarrow R}, \tag{A2}$$

whereas right-to-left step length is:

$$l_{R\rightarrow L} = t_{R\rightarrow L} \cdot v + \Delta FP_{R\rightarrow L}. \tag{A3}$$

We first find the step length difference using Eqns A1–A3:

$$l_{L\rightarrow R} - l_{R\rightarrow L} = (t_{L\rightarrow R} - t_{R\rightarrow L}) \cdot v + 2\Delta FP_{L\rightarrow R}. \tag{A4}$$

Next, we express step length difference as the product of step length asymmetry and stride length (sum of step lengths), then express stride length as the product of stride time and belt speed, and finally express step time difference as the product of step time asymmetry and stride time:

$$\mathrm{asym}_l \cdot t_{\mathrm{stride}} \cdot v = \mathrm{asym}_t \cdot t_{\mathrm{stride}} \cdot v + 2\Delta FP_{L\rightarrow R}. \tag{A5}$$

From Eqn A5, we isolate foot placement difference and obtain Eqn 3 in the main text.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: J.S., J.C.; Formal analysis: J.S.; Investigation: J.S.; Writing - original draft: J.S.; Writing - review & editing: J.S., J.C.; Visualization: J.S.; Supervision: J.C.

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Data availability
The dataset is available from the Dryad digital repository (Stenum and Choi, 2021): dryad.00000003g.

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Supplementary Figure 1

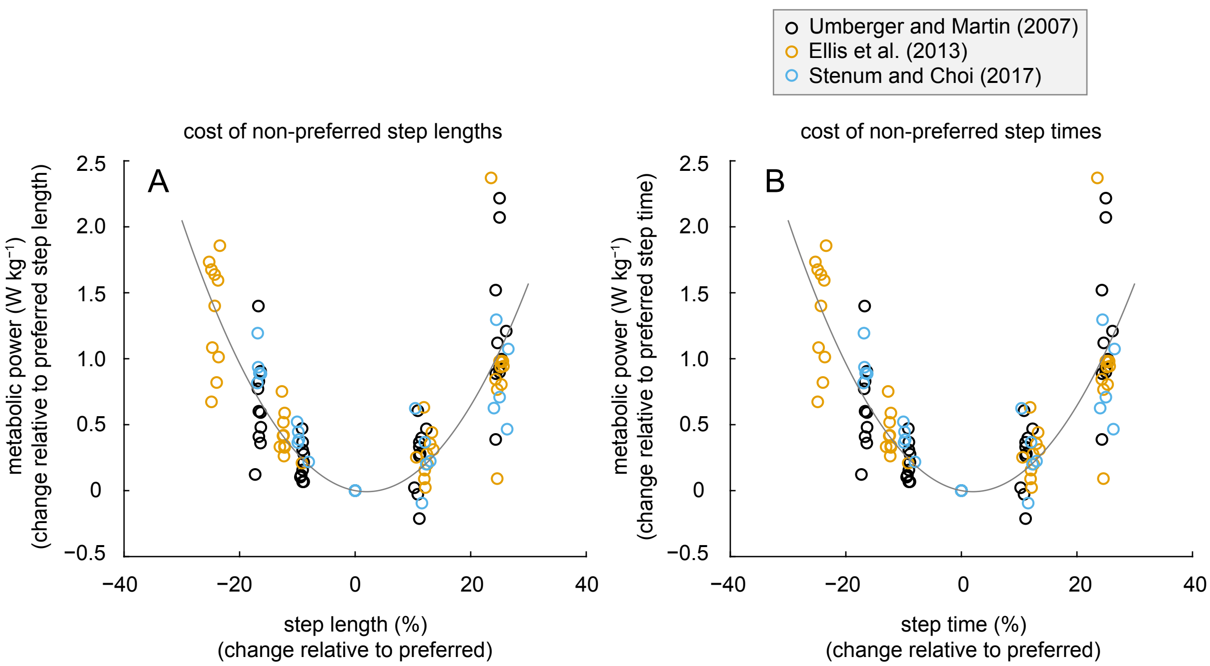

Figure S1. Metabolic power of non-preferred step lengths and step times. Quadratic fits to metabolic power of non-preferred step lengths (A) and step times (B) during constant speed treadmill walking were used to build predicted asym-metry costs based on non-preferred steps that were compared with the measured cost of step length asymmetry and step time asymmetry (see Fig. 3). Metabolic power is expressed as the change in net metabolic power relative to its value during walking at the preferred values of step length (A) or step time (B).

Supplementary Figure 2

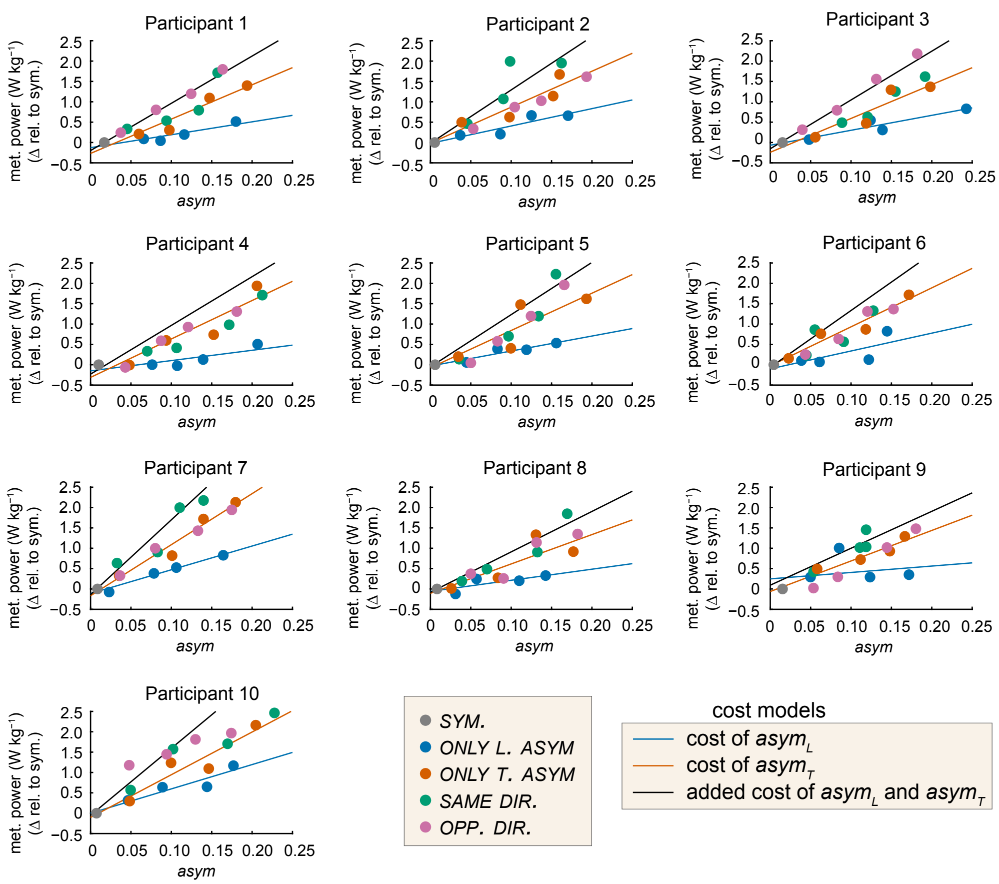

Figure S2. Individual participants' metabolic power. Cost models are based on linear fits of data in ONLY L. ASYM and ONLY T. ASYM conditions and are used to predict the measured metabolic power of SAME DIR. and OPP. DIR. conditions (see Fig. 4).

Supplementary Figure 3

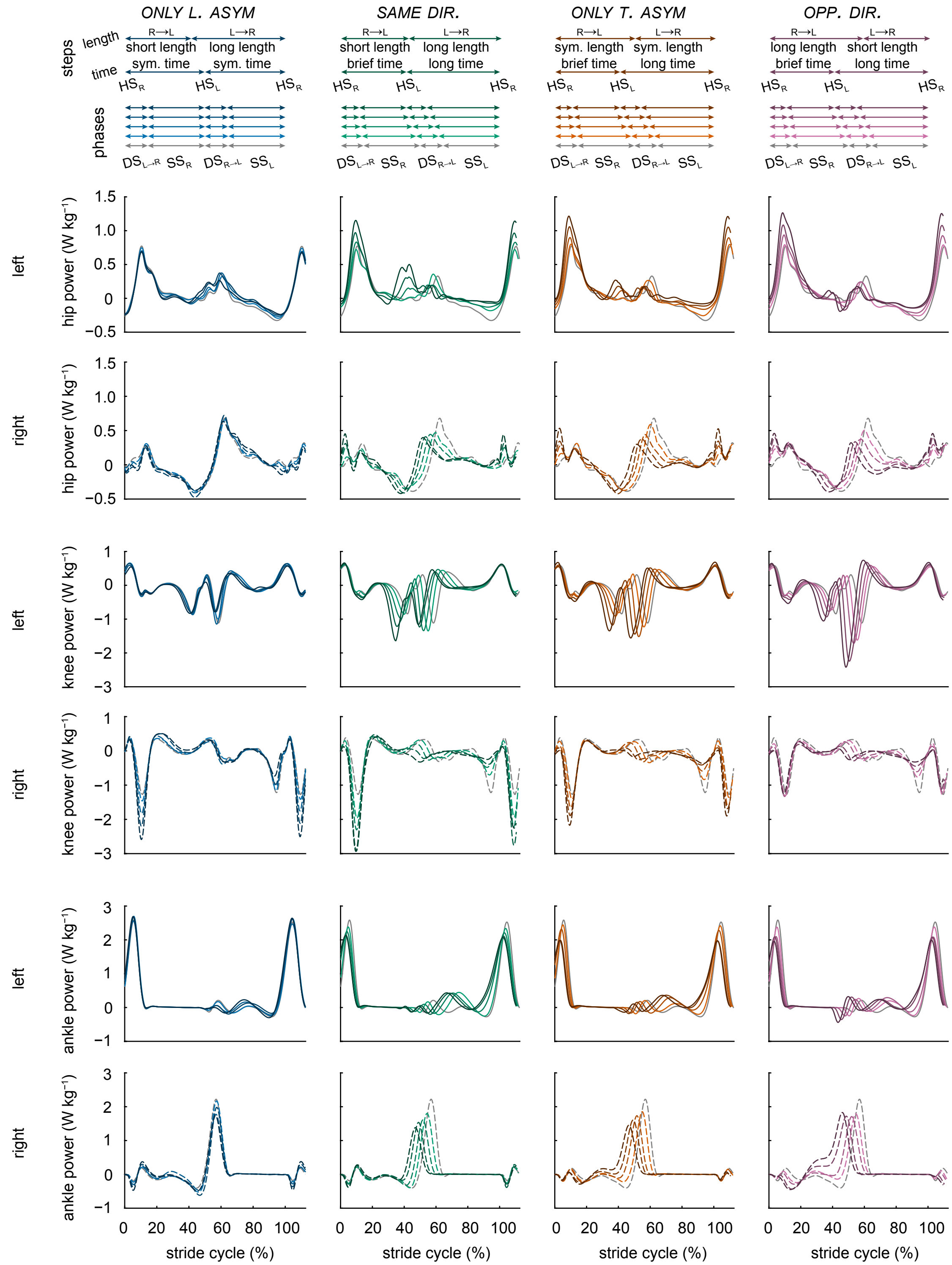

Figure S3. Hip, knee and ankle joint powers. Increased asymmetry is shown by progressively darker line coloring. Grey lines show symmetric condition. Arrows at top of figure show relative durations within in the stride cycle. Steps are denoted R→L and L→R and represent durations from right-to-left heel-strike (HS) and left-to-right heel-strike, respectively. Durations of double support (DS) and single support (SS) phases have subscripts denoting double support phase when transitioning from left-to-right stance (L→R), right single support phase (R), double support when transitioning from right-to-left stance (R→L) and left single support phase (L). All lines are ensemble mean (*N* = 10) for a specific level of enforced asymmetry.