Learning to be economical: the energy cost of walking tracks motor adaptation

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Key points
• Neuroscientists often suggest that we adapt our movements to minimize energy use; however, recent studies have provided conflicting evidence in this regard.
• In the present study, we show that motor learning robustly increases the economy of locomotion during split-belt treadmill adaptation.
• We also demonstrate that reductions in metabolic power scale with the magnitude of adaptation and are also associated with a reduction in muscle activity throughout the lower limbs.
• Our results provide strong evidence that increasing economy may be a key criterion driving the systematic changes in co-ordination during locomotor adaptation.
• These findings may also facilitate the design of novel interventions to improve locomotor learning in stroke survivors.

Abstract Many theories of motor control suggest that we select our movements to reduce energy use. However, it is unclear whether this process underlies short-term motor adaptation to novel environments. Here we asked whether adaptation to walking on a split-belt treadmill leads to a more economical walking pattern. We hypothesized that adaptation would be accompanied by a reduction in metabolic power and muscle activity and that these reductions would be temporally correlated. Eleven individuals performed a split-belt adaptation task where the belt speeds were set at 0.5 and 1.5 m s\(^{-1}\). Adaptation was characterized by step length symmetry, which is the normalized difference in step length between the legs. Metabolic power was calculated based on expired gas analysis, and surface EMG was used to record the activity of four bilateral leg muscles (tibialis anterior, lateral gastrocnemius, vastus lateralis and biceps femoris). All participants initially walked with unequal step lengths when the belts moved at different speeds, but gradually adapted to take steps of equal length. Additionally, net metabolic power was reduced from early to late adaptation (early, 3.78 ± 1.05 W kg\(^{-1}\); and late, 3.05 ± 0.79 W kg\(^{-1}\); \(P < 0.001\)). This reduction in power was also accompanied by a bilateral reduction in EMG throughout the gait cycle. Furthermore, the reductions in metabolic power occurred over the same time scale as the improvements in step length symmetry, and the magnitude of these improvements predicted the size of the reduction in metabolic power. Our results suggest that increasing economy may be a key criterion driving locomotor adaptation.

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Introduction

Human walking is often highly stereotyped. Our legs oscillate in a reciprocal relationship, and we walk with symmetric step lengths (Reisman et al. 2005) and step times. When the regularity associated with walking is disturbed, we often adapt our movements gradually to restore certain kinematic features through an error-based learning process (Reisman et al. 2005; Emken & Reinkensmeyer, 2005; Lam et al. 2006). For example, an asymmetry between right and left step lengths can be introduced on a split-belt treadmill by moving each belt at a different speed. However, individuals gradually adapt their walking pattern to reduce this asymmetry and produce symmetric step lengths (Reisman et al. 2005, 2007; Choi et al. 2009). During normal walking, changes in step length can either increase or reduce the economy of walking (Donelan et al. 2002; Umberger & Martin, 2007), defined as the metabolic power required to walk at a given speed, and therefore one might expect that changes in economy occur during split-belt adaptation.

Why does the nervous system adapt to take symmetric step lengths in an asymmetric environment? Symmetry is by no means obligatory. People are capable of maintaining asymmetric step lengths given appropriate feedback (Malone & Bastian, 2010) or when the cerebellum is damaged (Morton & Bastian, 2006). Additionally, adapting to symmetric step lengths requires that other parameters, such as the time between foot strikes, become increasingly asymmetric (Malone et al. 2012). Many theories of motor control suggest that movements are refined so as to minimize energetic cost (Zarrugh et al. 1974; Hatze & Buys, 1977; Alexander, 1997; Todorov, 2004; Emken et al. 2007). This is an intuitive goal, because economical movements enable us to use more energy to perform other tasks relevant to survival (Alexander, 2002); therefore, it is possible that the adaptation patterns observed during split-belt walking are driven by a process that maximizes economy.

There is evidence that many elements of our locomotor pattern are selected to maximize economy during normal walking. Economy is typically characterized by measuring the rate of energy use, or metabolic power, which is computed from rates of oxygen consumption and carbon dioxide production (Brockway, 1987). For a given speed, we select a step rate (Zarrugh & Radcliffe, 1978; Bertram & Ruina, 2001; Kuo, 2001; Umberger & Martin, 2007) and step width (Donelan et al. 2001) that minimize metabolic power. Thus, the walking pattern developed through years of practice appears to be the most economical for tasks that we commonly experience. However, our walking pattern must also be flexible to adapt to novel environments.

What remains to be seen is whether short-term adaptation to novel locomotor tasks is consistent with a strategy to maximize economy. Motor adaptation occurs through trial-and-error practice when a well-learned motor skill is performed in the presence of a novel, perturbing context or environment (Martin et al. 1996). Therefore, although people gradually increase economy when learning a novel skill over weeks to months (Childs et al. 2002; Lay et al. 2002; Galna & Sparrow, 2005; Sawicki & Ferris, 2008), it is still unknown whether economy is maximized during locomotor adaptation which occurs on a much shorter time scale of minutes.

Here we asked whether adaptation to a split-belt treadmill leads to a more economical walking pattern. In this context, economy refers to the metabolic power used to walk at a specific combination of belt speeds. It has been demonstrated that individuals with asymmetric gaits are less economical than able-bodied individuals (Waters & Mulroy, 1999); thus, it is possible that energy minimization drives the restoration of step length symmetry observed during split-belt adaptation. Alternatively, the asymmetry in step timing developed over the course of adaptation may result in a higher metabolic power as adaptation progresses. We hypothesized that both metabolic power and muscle activity would decrease over the course of adaptation, consistent with the idea that the motor adaptation is driven in part by energy minimization.

Methods

Ethical approval

Eleven individuals participated in this study (six men, 22 ± 2 years old). The experimental protocol was approved by the The Pennsylvania State University Institutional Review Board and conformed to the standards set by the Declaration of Helsinki. All participants provided written informed consent before testing.

Protocol

The participants learned to walk on a custom-built split-belt treadmill capable of operating at independent speeds for the left and right legs. This treadmill was similar to previously described devices (Kram et al. 1998; Collins et al. 2009) and included two, 4.5 kW variable speed, alternating current electronic motors. The treadmill belts
were controlled manually and accelerated from rest to the maximal speed used in our experiments in less than 0.5 s for all participants. Throughout the experiment, the participants walked while maintaining light hand contact with rails on each side of the treadmill to provide stability when the belt speeds changed. The overall study protocol is illustrated in Fig. 1. The experiment began with a 10 min warm-up period, with both belts matched at 1.0 m s$^{-1}$. For the transition between each phase of the experiment, the belt speeds were abruptly changed to the new speeds by one of the experimenters. The warm-up was followed by two baseline periods, during which participants walked with the belts matched at 0.5 or 1.5 m s$^{-1}$. The order of these baseline periods was randomized for each participant to minimize possible order effects on the metabolic power measured during the adaptation period. Upon completion of baseline walking, the participants walked for 12 min with the left belt moving at 1.5 m s$^{-1}$ while the right belt moved at 0.5 m s$^{-1}$ (3:1 ratio). These parameters were selected to be consistent with previous studies of split-belt adaptation (Reisman et al. 2005; Malone & Bastian, 2010).

Data collection

Expired gas analysis. As the participants walked on the treadmill, the rate of oxygen consumption and carbon dioxide production was measured using a TrueOne® 2400 metabolic measurement system (Parvomedics, Sandy, UT, USA). Before data collection, the system was allowed to warm up for 30 min to heat the pneumotachometer. After the warm-up period, the gas analyser and pneumotachometer were calibrated to the manufacturer’s specifications. Expired gas was sampled by the sensors on a breath-by-breath basis, and the rates of oxygen consumption and carbon dioxide production were computed. Metabolic data were collected for 5 min during quiet standing and subtracted from the metabolic measurements made during all subsequent walking periods to yield net metabolic rate.

Kinematics. Kinematic data were acquired with a digital camera system (Motion Analysis 3D Eagle, Santa Rosa, CA, USA). Prior to data collection, retroreflective markers were placed on the following anatomical landmarks bilaterally: anterior superior iliac spine; lateral femoral epicondyle; lateral malleolus; posterior calcaneous; and first metatarsal. The motion-analysis system consisted of six digital cameras connected through an Ethernet hub to the data-collection computer. Kinematic data were sampled at 100 Hz. Data were collected with EvaRT (version 3.21; Motion Analysis Corporation, Santa Rosa, CA, USA) for reduction and processing. Before each data-collection session, the motion-analysis system was calibrated to the manufacturer’s recommendations.

Electromyography. Electromyographic signals were measured using a telemetered amplifier system (Bortec, Calgary, CA, USA). Prior to electrode placement, the skin was prepared with fine sandpaper and alcohol. Bipolar, silver–silver chloride, surface electrodes (1-cm-diameter discs, 2 cm interelectrode distance; Vermed, Bellows Falls, VT, USA) were placed over the following four muscles bilaterally: tibialis anterior (TA); lateral gastrocnemius (LG); vastus lateralis (VL); and biceps femoris (BF), according to the recommendations by Cram & Kasman (1998). For the TA, LG and BF muscles, electrodes were placed over the approximate centre of the muscle belly. For VL, the electrodes were placed over the distal third of the muscle lateral to the rectus femoris. The EMG amplifier gain was set to 2000, and the EMG signals were sampled at 1000 Hz. We verified that the cross-talk between muscles was negligible with a series of contractions suggested by Winter et al. (1994) and Cram & Kasman (1998).

Data analysis

Adaptation parameters. We calculated kinematic parameters associated with locomotor adaptation using three-dimensional marker positions. We evaluated changes in step length and step time because each has been determined to make significant contributions to the economy of walking (Kuo, 2001; Donelan et al. 2002; Doke et al. 2005). The onset of stance and swing were estimated by computing the peak anterior and posterior limb angle

![Figure 1. Experimental protocol](image-url)
excursions for each step, respectively. For this study, step length symmetry was used as the primary measure of adaptation, because prior studies have demonstrated that healthy individuals adapt this parameter robustly across multiple speed ratios (Reisman et al. 2005, 2007; Malone & Bastian, 2010). Step length symmetry (SS) is defined as the normalized difference between the step lengths of each limb, as follows [eqn (1)]:

\[ SS = \frac{SL_{fast} - SL_{slow}}{SL_{fast} + SL_{slow}} \] (1)

Step length (SL) was defined as the anterior–posterior distance between the markers on the lateral malleolus of each leg at heel strike. Fast step length was measured at heel strike of the limb on the fast belt and slow step length was measured in a similar manner at heel strike of the slow limb. Positive values for step length symmetry indicate that the fast step is larger than the slow step, and the converse holds for negative values. A step length symmetry value of zero indicates that the fast and slow steps are of equal length and thus represents symmetry. A representative example of these parameters for a single participant illustrates how step length and step length symmetry vary during the adaptation and postadaptation periods (Fig. 2A and B).

Temporal changes in the walking pattern were assessed using measures of step timing. Step time was defined as the time between consecutive heel strikes, where the slow step time \( (t_s) \) refers to the time between a heel strike on the slow belt and the following heel strike on the fast belt. Fast step time \( (t_f) \) was likewise defined as the time between a heel strike on the fast belt and the subsequent heel strike on the slow belt. This measure is equivalent to the reciprocal of cadence computed on a step-by-step basis. Step time symmetry (STS) was defined as the normalized difference in step times across limbs as described in eqn (2):

\[ STS = \frac{t_f - t_s}{T_{stride}} = \frac{t_f - t_s}{t_f + t_s} \] (2)

Here, \( T_{stride} \) is the time between two consecutive heel strikes on one limb, also known as the stride time. A step time symmetry of zero indicates that the fast and slow step times are equal. A representative example from a single participant demonstrates how individual step times and step time symmetry vary throughout the course of adaptation and postadaptation (Fig. 2C and D).

In all figures showing time series data, each of our kinematic parameters was averaged within consecutive 10 s bins. This facilitated comparison between the temporal changes in kinematics and the temporal changes in metabolic power. For the group analysis, average kinematic parameters were computed for the following periods: warm-up; slow baseline; fast baseline; early adaptation; late adaptation; early postadaptation; and late postadaptation. For the warm-up and baseline periods, the average step length and step time parameters for each participant were computed by averaging over all strides recorded during each period. For the early and late phases of adaptation and postadaptation, these parameters were averaged over the first five strides and last five strides, respectively.

Changes in economy associated with split-belt adaptation. During all phases of the experiment, economy was quantified by estimating the metabolic power of each participant. Metabolic power was computed based on the rate of oxygen consumption and carbon dioxide production using a standard equation (Brockway, 1987). Net metabolic power was computed by subtracting the average metabolic power during the 5 min standing period from the power measured during walking and then normalizing to body mass. The breath-by-breath measurements of net metabolic power were averaged in consecutive 10 s bins to maintain consistency between our kinematic and metabolic measurements.

Our experiment involved abrupt changes in effort as participants switched between each phase of the experiment and, as a result, there was a transient change in net metabolic power during the early portion of each phase (Fig. 3). We computed the duration of this transient period for each of the baseline blocks by finding the time between the start of each block and the point when metabolic power reached the average power computed during the last 3 min of the block. This duration was 57 ± 10 s across all subjects and therefore we omitted the initial 60 s of the net metabolic power for each time period (i.e. warm-up, slow baseline, fast baseline, etc) in our group analysis. Part of this transient period stemmed from the transport lag between changes in expired gas concentration and the time when these gases were detected by the sensors. Our recording apparatus included a 1.83 m tube extending from the mouthpiece with a volume of approximately 1.6 litres and a passive mixing chamber with a volume of 4.9 litres. At a ventilation rate of 25 l min\(^{-1}\), near what was observed during adaptation, approximately 16 s would elapse between the time when a breath was expired and when it reached the sensor.

After omitting the first minute of expired gas data from each phase, we computed the average metabolic power for specific phases of the experiment as follows. The metabolic power for warm-up and each baseline phase was computed by averaging the power for the last 2 min of each block. The metabolic power for early adaptation and early postadaptation was averaged over the second and third minutes of each period because the initial minute of data from these periods was omitted. Finally, the metabolic power for late adaptation and late postadaptation was averaged over the last 2 min of each period.
Analysis of EMG. Changes in muscle activity during adaptation were assessed by quantifying the average integrated EMG amplitude for each stride. We first computed the maximal rectified EMG for each muscle during baseline walking at 1.5 m s\(^{-1}\). The EMG time series for each subsequent block were then rectified and expressed as a percentage of the maximal baseline activity (MBA). To quantify changes in muscle activity during adaptation, we computed the integrated stance and swing phase EMG for each stride and expressed these values as a percentage of the maximal integrated stance and swing phase EMG during baseline walking at 1.5 m s\(^{-1}\) (MIBA). Overall changes in muscle activity during adaptation were computed by comparing the stance and swing phase EMG during the first five strides (early) and last five strides (late) of adaptation. We computed the EMG ratio for each participant as the ratio of the average integrated EMG amplitude in late adaptation to early adaptation. An EMG ratio of one would indicate that there was no change in the average muscle activity during adaptation.

Statistical analysis. Repeated-measures ANOVA was used to test for significant differences in kinematic parameters and net metabolic power across all phases of the experiment (warm-up, slow baseline, fast baseline, early adaptation, late adaptation, early postadaptation and late postadaptation). When significant differences were observed, post hoc analyses were performed using Tukey’s HSD test. Student’s one-sample t test was used to test the null hypothesis that step length symmetry during late adaptation was not different from zero. We also used Student’s one-sample t test to test the hypothesis that the stance and swing phase EMG ratio came from a distribution with a mean of one, which would indicate that there was no change in muscle activity during the respective phase of the gait cycle (stance or swing).

Figure 2. Representative example of kinematic parameters recorded for a single participant during baseline walking at 0.5 m s\(^{-1}\), adaptation and postadaptation periods

The first and second dashed vertical lines delineate the transitions from baseline to adaptation and from adaptation to postadaptation, respectively. Data within each period were averaged using a five-step window. A, step length for each limb. During early adaptation, step lengths are markedly different between limbs, but gradually approach a similar value as adaptation progresses. B, the normalized difference in step length between limbs represented as step length symmetry. The observed changes in step length between limbs are captured by our measure of step length symmetry, which highlights the asymmetry during early adaptation and the gradual progression towards symmetry over the course of adaptation. C, step time for the fast and slow limbs. During early adaptation, step times are initially similar, but rapidly diverge as adaptation progresses. D, the normalized difference in step times represented as step time symmetry. Here, the divergence in step times during adaptation is evident by the fast increase in step time symmetry and a significant temporal asymmetry during late adaptation.
over the course of adaptation. In addition, we wanted
to determine whether changes in kinematics and EMG
were temporally correlated with the observed changes in
economy. To this end, we computed Pearson’s correlation
coefficients between the following parameters and the
net metabolic power for each participant: step length
symmetry; step time symmetry; and integrated EMG
amplitude. The first minute of metabolic power data
was omitted from the correlation analysis owing to the
transient change in power when going from baseline
walking to adaptation. We also determined whether the
magnitude of the observed reductions in metabolic power
was correlated with the magnitude of the changes in
each of our kinematic parameters using linear regression.
All statistical procedures were performed using Statistica
(Statsoft, Tulsa, OK, USA), and significance was set at the
5% level.

Results

Kinematic and metabolic changes during split-belt
adaptation

The perturbation in belt speeds during adaptation
produced robust changes in step length symmetry and
timing, as well as subsequent effects characteristic of motor
adaptation. An example from a single participant shows
step length symmetry (Fig. 4A) and step time symmetry
(Fig. 4B) recorded during all phases of the experiment.
During baseline walking, both step length symmetry and
step time symmetry remained near zero for the duration
of each period. However, these parameters varied in an
inverse manner over the course of adaptation. The change
in step length during adaptation was characterized by
a large initial asymmetry (approximately 10% of stride
length; Fig. 4A) and a gradual return to a baseline
value of approximately zero. In contrast, the difference
in step times became increasingly asymmetric, plateauing
at approximately 15% of the stride time (Fig. 4B). When
the belts were driven at the same speed during post-
adaptation, a large asymmetry in step length was observed
in the opposite direction of the initial asymmetry and was
gradually washed out over the course of postadaptation.
Likewise, the difference in step times during post-
adaptation was also characterized by an initial asymmetry
and gradual decline towards baseline.

Similar changes in step length symmetry and timing
were observed in the group data (Fig. 5A–D). We found a
significant effect of time period on step length symmetry
\( F_{6,60} = 45.04, \quad P < 0.001 \). Post hoc analyses revealed
that step length symmetry during early adaptation
was significantly different from late adaptation (early,
Split-belt adaptation reduces metabolic power

0.12 ± 0.02; and late, −0.002 ± 0.02; \( P < 0.001 \), but late adaptation was not different from zero (\( t_{10} = −0.099, P = 0.92 \)). This indicates that the participants returned to their baseline, symmetric walking pattern by the end of adaptation. Early postadaptation was characterized by a large asymmetry of similar magnitude but opposite direction to what was observed during early adaptation (0.10 ± 0.02). This asymmetry was gradually washed out, moving towards baseline values at the conclusion of the postadaptation phase (late postadaptation, 0.02 ± 0.01; and baseline, −0.01 ± 0.007; \( P = 0.37 \)). We also found a significant effect of time period on the difference in step times as measured by step time symmetry (\( F_{6,60} = 44.34, P < 0.001 \)). Step time symmetry gradually increased over the course of adaptation, and post hoc analyses revealed that step time symmetry was significantly greater during late adaptation than early adaptation (early, 0.06 ± 0.01; and late, 0.15 ± 0.008; \( P < 0.001 \)). This difference in step timing diminished rapidly during the first steps of postadaptation and continued to drop as the participants de-adapted.

As the participants adapted towards symmetric step lengths, they simultaneously reduced their net metabolic power despite the fact that the speeds of the treadmill belts did not change. An example of the net metabolic power for a single participant (Fig. 4C) shows an initial peak of 4 W kg\(^{-1}\) during early adaptation and a gradual reduction to slightly more than 2 W kg\(^{-1}\) after 5 min of walking. For this individual, metabolic power reduced with a gradual time course similar to that of step length symmetry and looked less like step time symmetry, which changed more rapidly early on (Fig. 4A). For the group, metabolic power was more strongly correlated with changes in step length symmetry than step time symmetry for a majority (8 of 11) of our participants (Table 1).

Overall, the restoration of symmetry during adaptation was associated with a reduction in metabolic power. We found a significant effect of period on metabolic power (\( F_{6,60} = 46.71, P < 0.001 \)). Post hoc analyses revealed that the metabolic power during late adaptation was significantly lower than during early adaptation (early, 3.80 ± 0.31 W kg\(^{-1}\); and late, 3.05 ± 0.24 W kg\(^{-1}\); \( P = 0.003 \); Fig. 5F). Although the average belt speed during adaptation (1 m s\(^{-1}\)) was equal to the speed during the warm-up, the net metabolic power during late adaptation was significantly greater than the power measured during warm-up (warm-up, 2.38 ± 0.07 W kg\(^{-1}\); and late adaptation, 3.05 ± 0.24 W kg\(^{-1}\); \( P = 0.01 \)). Therefore, although walking with symmetric step lengths was more economical than asymmetric walking, there was an additional power demand above what was required for walking with both belts moving at the mean speed of 1.0 m s\(^{-1}\).

The overall changes in metabolic power during adaptation were explained well by the reduction in step length asymmetry from early to late adaptation. Our between-subjects comparison revealed that the overall reduction in step length asymmetry during adaptation explained 58% of the variance in the reduction of metabolic power (Fig. 6). Subjects who experienced

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**Figure 4.** Step length symmetry (A), step time symmetry (B) and net metabolic power (C) for a single participant

Baseline, adaptation and postadaptation periods are each denoted at the top of the figure. Each data point represents a 10 s average for the respective variable. During adaptation, the time course of the decline in net metabolic power parallels the time course of step length symmetry adaptation.
Figure 5. Group data for the adaptation and postadaptation periods
Average adaptation and postadaptation curves for step length symmetry (A), step time symmetry (C) and net metabolic power (E). Shaded areas surrounding curves represent standard errors. Vertical boxes at the beginning of adaptation and postadaptation highlight the portion of the metabolic power data that was not included in the analysis. Average values of step length symmetry (B), step time symmetry (D) and net metabolic power (F) during all phases of the experiment. The numbers on the x-axis specify the belt speeds for baseline periods. Abbreviations: EA, early adaptation; LA, late adaptation; EP, early postadaptation; and LP, late postadaptation. *P < 0.05.

Figure 6. Reduction in metabolic power versus the change in step length symmetry (A) and step time symmetry (B) during adaptation
Positive values indicate a reduction in metabolic power for both plots. A, positive values on the horizontal axis indicate that step lengths were more symmetric during late adaptation relative to early adaptation. B, positive values on the horizontal axis indicate that step times were more asymmetric during late adaptation relative to early adaptation. The $r^2$ value and the $P$ value associated with each regression are shown on the figure.
the largest reductions in asymmetry from early to late adaptation typically had the largest reductions in metabolic power and vice versa. In contrast, there was a trend towards a negative relationship between the change in step time symmetry and the reduction in metabolic power (linear regression, $P = 0.07$). This suggests that increases in step time asymmetry oppose the increase in economy associated with reducing step length asymmetry.

It is possible that the overall reduction in metabolic power could be biased by individuals who walked at the fast speed ($1.5 \text{ m s}^{-1}$) immediately prior to adaptation (e.g. Fig. 3A). Our post hoc analysis revealed that a greater net metabolic power was associated with walking at the fast speed relative to the slow speed (fast, $3.42 \pm 0.1 \text{ W kg}^{-1}$; and slow, $1.57 \pm 0.07 \text{ W kg}^{-1}$, $P < 0.001$), which might result in a higher initial power during early adaptation. We did not find a significant effect of baseline order on the change in metabolic power from early to late adaptation ($F_{1,9} = 2.61$, $P = 0.14$), though subjects who walked at the slower speed immediately prior to adaptation tended to have a larger reduction in metabolic power (fast prior, $-0.44 \pm 0.23 \text{ W kg}^{-1}$; and slow prior, $-0.91 \pm 0.18 \text{ W kg}^{-1}$). Importantly, 10 of 11 subjects clearly reduced metabolic power over the course of adaptation.

**Changes in muscle activity during adaptation**

Changes in muscle activity throughout the gait cycle were consistent with the observed reduction in net metabolic power during adaptation. Average normalized EMG traces for a representative participant during early and late adaptation illustrate this change (Fig. 7). For many of the muscles, most notably LG and TA of the fast limb and TA of the slow limb, there is a reduction in muscle activity in late adaptation (grey lines with black shading) relative to early adaptation (black lines with grey shading). This observation was confirmed in the group averages of the EMG ratio in each muscle (Fig. 8). Here, stance phase muscle activity (Fig. 8A and C) was reduced in all but one of the muscles (BF of the slow limb) during late adaptation relative to early adaptation (single-sample t tests, all $P < 0.05$). The largest reductions in stance phase EMG activity were observed in TA (17 ± 5%) and LG (29 ± 8%) of the fast limb and TA (35 ± 7%) and VL (14 ± 5%) of the slow limb. These reductions did not appear to result from reduced agonist–antagonist co-contraction over the course of adaptation. During the period of peak activity in LG of the fast limb, its antagonist, TA, was minimally active (Fig. 7). Likewise, during the period of peak activity in TA of the slow limb, LG was relatively quiescent. For the swing phase (Fig. 8B and D), muscle activity was reduced in all muscles during late adaptation relative to early adaptation (single-sample t tests, all $P < 0.05$). The largest reduction in EMG was observed in TA of the slow limb (25 ± 9%), while the reduction in other muscles ranged from 8 to 20%.

The time course of changes in EMG amplitude during adaptation was also consistent with the time course of the observed reduction in net metabolic power. The integrated EMG amplitude during stance and swing for all muscles was gradually reduced over the course of adaptation (Fig. 9). We computed correlation coefficients between the time series of EMG amplitude and net metabolic power for each participant to determine whether these measures were reduced at similar rates (Table 2). Although significant correlations between muscle activity and metabolic power were observed for most muscles, the strongest correlations for both the fast and slow limbs were found for TA (fast, $r = 0.50 \pm 0.02$; and slow, $r = 0.48 \pm 0.01$) and LG (fast, $r = 0.45 \pm 0.02$; and slow, $r = 0.53 \pm 0.09$) The presence of temporal correlations between muscle activity and net metabolic power provides evidence that a gradual reduction in muscle activity is likely to drive the observed reduction in metabolic power.

**Discussion**

Our results demonstrate that the reduction of step length asymmetry during split-belt treadmill adaptation is associated with a reduction in the metabolic power associated with walking. This reduction in power is temporally correlated with changes in step length symmetry, and the size of this reduction is strongly correlated with the magnitude of the improvement in step length asymmetry during split-belt adaptation.
Figure 7. Average EMG traces during early and late adaptation for a representative subject. Each trace is the average rectified EMG of five consecutive steps of the fast limb (left side) or slow limb (right side). For each muscle, EMG amplitude is expressed as a percentage of the peak activity for the respective muscle during fast baseline walking. Stance phase was normalized to 0–60% of stride time and swing was normalized to 60–100% of stride time. Horizontal bars at the beginning of each stride indicate a normalized EMG amplitude of zero. Black lines with grey shading denote early adaptation, while grey lines with black shading denote late adaptation. Shading represents standard errors. Abbreviations: BF, biceps femoris; LG, lateral gastrocnemius; TA, tibialis anterior; and VL, vastus lateralis.

Figure 8. Electromyogram ratio for the average muscle activity during stance and swing phases. A, stance phase EMG ratio for the fast limb. B, swing phase EMG ratio for the fast limb. C, stance phase EMG ratio for the slow limb. D, swing phase EMG ratio for the slow limb. The horizontal dashed lines represent a value of one. Values less than one indicate that the average muscle activity during late adaptation was less than the activity measured during early adaptation. Abbreviations are as for Fig. 7. Asterisks denote a significant difference from early to late adaptation at the $P < 0.05$ level.
Split-belt adaptation reduces metabolic power

Although motor adaptations occur in a variety of contexts, the reasons why the nervous system elects to restore certain aspects of movements have yet to be established. In the upper limb, there are conflicting views on the role of energetic optimization during force field adaptation. One study demonstrated that individuals were unable to adapt their freely selected hand paths to follow the minimal energy path as defined by end-point work (Kistemaker et al. 2010), but this study did not measure metabolic power. In contrast, a more recent study found that there are indeed measurable reductions in metabolic power during force field adaptation (Huang et al. 2012); however, the changes in power occurred over a much longer time scale than the changes in reaching error and muscle activity. Thus, it appears that motor learning and energy use are not temporally coupled in the context of reaching. In the present study, we not only demonstrated that metabolic power is reduced during locomotor adaptation, but we have also shown that the time course of this reduction parallels the time course of changes in both step length symmetry and muscle activity. This, along with the correlation between the magnitude of step length symmetry improvement and the reduction in metabolic power, suggests that it is the systematic, stride-by-stride changes in interlimb co-ordination that drive the observed reduction in power. Therefore, it is possible that an energy-minimization process drives split-belt locomotor adaptation.

Energy reduction during motor learning of novel skills has been demonstrated previously (Childs et al. 2002; Lay et al. 2002; Galna & Sparrow, 2006). However, unlike short-term motor adaptation, skill learning often involves long-term practice over multiple days and, once the skill is learned, it can immediately be used in the appropriate context (Bastian, 2008). Reductions in metabolic power and muscle activity have also been observed over multiple days of adaptation to an assistive torque provided by a powered ankle exoskeleton (Sawicki & Ferris, 2008). Although changes in metabolic power over multiple days have been associated with reductions in muscle activity (Lay et al. 2002; Sawicki & Ferris, 2008), the long time scale necessary to observe these changes would not predict that metabolic power would be reduced during a single session of motor adaptation.

**Kinematic contributions to metabolic power reduction**

Although step length symmetry is used as our measure of error during adaptation, it is not clear whether symmetry
itself or other kinematic changes drive the reduction in metabolic power. Split-belt adaptation involves both spatial and temporal changes in the walking pattern (Malone & Bastian, 2010), and each of these is likely to influence the economy of walking. The step length asymmetry present during early adaptation is gradually reduced by shortening the slow step and lengthening the fast step. Collisional models and experimental data demonstrate that metabolic power should increase non-linearly as steps are lengthened and decrease as steps are shortened (Donelan et al. 2002; Kuo, 2002). Thus, the observed changes in step length are likely to oppose one another, and the change in net metabolic power will depend on the relative magnitude of the individual changes in step length.

Likewise, metabolic power scales non-linearly with the frequency of leg swing (Doke et al. 2005), which is inversely proportional to step time. During early adaptation, the step times diverge, with the slow step time increasing and the fast step time decreasing. This trend continues throughout adaptation, leading to opposing effects on the net metabolic power. Like step length, the change in metabolic power due to changes in step time will depend on the difference in magnitude of these changes between limbs. Given these non-linear interactions between step length and step time, further research is necessary to quantify the contributions of spatial and temporal adjustments to economy during split-belt adaptation.

Ultimately, the observed reduction in metabolic power is likely to be driven by muscle contraction, and our EMG data provide insight into which muscles may be driving this change in power. Over the course of adaptation, the average integrated muscle activity was reduced in nearly all of the muscles that we investigated. This reduction was most evident during late stance for the lateral gastrocnemius of the fast limb and during early stance for tibialis anterior of the slow limb. It was previously demonstrated that these muscles were more active during split-belt walking relative to walking with the belts moving at the same speeds (Dietz et al. 1994), but the authors did not indicate whether this activity changed as participants adapted to walking on the treadmill.

There are multiple factors which may contribute to the change in muscle activity throughout adaptation. During early adaptation, the leg on the fast belt is extended more rapidly and further than expected, resulting in two potential consequences. First, this could cause a large impact at slow heel strike, potentially resulting in stretch-induced activity in the slow TA during early stance. This collision might also require a higher level of ankle extension torque to restore the energy lost during the step-to-step transition (Kuo, 2001; Donelan et al. 2002). As the slow step length is reduced, the impact at slow heel strike would gradually be reduced and the fast leg would be in a more optimal, less extended position at preswing, thereby requiring less ankle extension torque. On the slow limb, the high level of TA activity could be interpreted as an attempt to stabilize the ankle joint during the single support phase. Although we did not observe heightened co-contraction of the gastrocnemius during this period, it is possible that other muscles which we did not record, such as soleus, were recruited to maintain stability during early adaptation. As the participants learned the task dynamics, this stabilization strategy may have become unnecessary.

Figure 9. Average adaptation curves for the integrated EMG amplitude during each stride
Each curve represents the group average, with standard errors indicated by shading. For each muscle, the EMG amplitude is expressed as a percentage of the maximal EMG integrated over a full stride for the respective muscle during fast baseline walking (MIBA). The vertical scale bar adjacent to the slow TA is for this muscle only; for all other muscles, the scale bar is adjacent to the slow VL. Horizontal bars at the beginning of each trace indicate a normalized EMG amplitude of 80%. Abbreviations are as for Fig. 7.
Reducing metabolic power: a goal or a byproduct of adaptation?

It remains to be determined whether the economy of walking is directly optimized during split-belt adaptation or if the observed reduction in metabolic power is an indirect consequence of another, possibly error-driven, optimization process. When individuals are initially exposed to walking on a split-belt treadmill, it is not obligatory that people would desire to or be able to directly to optimize the economy of walking. The only clear requirement of the task is to select a pattern of co-ordination that keeps the body upright while perhaps providing some margin of safety. Outside of this goal, people could pursue any combination of additional goals. For example, it has been proposed that adjustments to rapid changes in treadmill speed include a fast, pre-programmed response driven by prior experience and a slower, more gradual change, potentially involving direct optimization of energy expenditure (Snaterse et al. 2011). For split-belt adaptation, it is possible that the rapid changes associated with step timing and the gradual changes in step lengths reflect similar mechanisms. Alternatively, error-driven processes based on step length asymmetry or other kinematic parameters may inherently result in a more economical walking pattern.

Split-belt adaptation, like other forms of error-based motor learning, is a cerebellum-dependent process. The cerebellum is critically important for practice-dependent, predictive adjustment of movements (Lang & Bastian, 2002; Maschke et al. 2004; Smith & Shadmehr, 2005), and damage to the cerebellum impairs split-belt treadmill adaptation (Morton & Bastian, 2006). However, the role of the cerebellum in reducing energy expenditure during adaptation has yet to be established. One possibility is that the cerebellum is only involved in adjusting for kinematic prediction errors and the observed reduction in energy expenditure is simply a byproduct of this process. Other possibilities require the cerebellum to have access to some estimate of effort or energy expenditure, which could be provided using a combination of somatosensory feedback (Sanes & Shadmehr, 1995), afferent feedback from chemoreceptors (Heymans, 1963; Gestreau et al. 2010) or an efference copy of motor commands (Miall et al. 1993). Thus, the cerebellum could be used to minimize the error between the expected effort needed to walk at the perceived speed and the effort sensed through central and peripheral signals. Lastly, the cerebellum may be involved in direct minimization of energy expenditure by developing a systematic representation of the relationship between changes in motor commands and estimated changes in effort or energy expenditure.

Broader implications for the recovery of locomotor function

One issue that has yet to be addressed is how our findings relate to the processes that drive locomotor recovery following injury or disease. For example, walking asymmetry is commonly observed after physical injury (e.g. amputation) or neurological injury (e.g. unilateral stroke). Over the course of recovery, it is possible that these patients adapt to the loss of biomechanical and/or neural control options and adopt the most economical gait pattern given these constraints. Alternatively, the damage to the nervous system resulting from stroke could disrupt the circuits responsible for energetic optimization, thereby resulting in a suboptimal gait.

For both amputees and stroke survivors, it is also conceivable that the goal of economy is superseded by constraints on maintaining a stable gait that reduces the likelihood of falling. Additional studies are necessary to determine how these factors influence the recovery process.

The relationship between symmetry and economy following stroke remains an open question that may be important for guiding the rehabilitation process. Stroke survivors are capable of improving symmetry through training on a split-belt treadmill (Reisman et al. 2007, 2009), and these changes can be maintained with repeated exposures to the treadmill (Reisman et al. 2010). What remains to be seen is whether symmetry improves economy in these individuals. This is important because if an abnormally high rate of energy expenditure limits the self-selected walking speed for stroke survivors, then an increase in economy may promote faster walking.

References


**Author contributions**

All experiments were performed in the laboratory of J.S.G. All authors contributed to the conception and design of the study. J.M.F. and J.S.G. collected data for the study. All authors contributed to the analysis and interpretation of the data and the drafting of the manuscript. The final version of the manuscript was approved by all authors.

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