The Role of Entrainment in Human Walking: Energy Minimization in Oscillating Environments

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Abstract

During locomotion, humans often entrain (i.e. synchronize) their steps to external oscillations: e.g. swaying bridges, tandem walking, bouncy harnesses, vibrating treadmills, exoskeletons. Previous studies have discussed the role of nonlinear oscillators (e.g. central pattern generators) in facilitating entrainment. However, the underlying benefits of entrainment are unknown. Given substantial evidence that humans prioritize economy during locomotion, we tested whether reduced metabolic expenditure accompanies human entrainment to vertical force oscillations, where frequency and amplitude were prescribed via a custom mechatronics system during walking. Although metabolic cost was not significantly reduced during entrainment, individuals who experienced negative work from oscillations had a higher cost than those who experienced positive work, and subjects generally selected phase relationships indicating the latter. It is possible that individuals use mechanical cues to infer energy cost and inform effective gait strategies. If so, an accurate prediction may rely on the relative stability of interactions with the environment. Our results suggest that entrainment is preferred over a wide range of oscillation parameters, though not as a direct priority for minimizing metabolic cost. Instead, entrainment may act to stabilize interactions with the environment, thus increasing predictability for the effective implementation of internal models that guide energy minimization.
Introduction

Human walking is an oscillating system where the body moves in cyclic patterns to traverse a substrate – often a static environment, e.g. a sidewalk. However, sometimes the environment behaves as a second oscillating system. In this case, the human and the environment together constitute a coupled oscillator system. For example, pedestrians sometimes spontaneously synchronize the frequency of their steps with that of a swaying bridge as they cross, and this frequency matching is referred to as entrainment. A similar phenomenon occurs in laboratory experiments where individuals are asked to walk on treadmills actuated with controlled oscillations in mediolateral and vertical directions. A recent study demonstrated human entrainment with periodic electrical stimulations of the medial gastrocnemius while walking on a conventional treadmill. Furthermore, during development, infants can learn to entrain their bouncing frequency with the resonance of an elastic harness.

Ahn and Hogan interpreted subject entrainment with an ankle exoskeleton as evidence that human locomotion is controlled, at least in part, by low level rhythmic nonlinear oscillators (e.g. central pattern generators). In their study, an actuator provided periodic torque profiles at the ankle joint independent of the subject’s actions. Over time, subjects learned to entrain with the periodicity of the exoskeleton and align muscle activation with that of the artificial system. It is unclear whether such behaviors represent a simple quirk of control mechanisms driving rhythmic gait, or if entrainment patterns are evidence of a more active process guiding effective locomotion in dynamic environments.

A longstanding perspective on gait recognizes that preferred movement patterns are largely consistent with energy minimization over a wide range of circumstances. There is strong empirical evidence that individuals naturally select walking parameters (step frequency, step length, step width, etc.) that minimize metabolic energy per distance travelled. Furthermore, it appears that internal models are continuously updated in real time to optimize energy output under novel circumstances.

Here, we test if entrainment to external oscillations is motivated by a reduction in metabolic expenditure. To accomplish this, we used a mechatronics oscillator system to provide periodic vertical forces (upward and downward) to the trunks of subjects as they walked on a treadmill (Fig. 1). As opposed to an exoskeleton strapped to a single joint, the oscillation system in this...
study is used to more directly influence the center of mass (CoM) and its dynamics – arguably a fundamental aspect of the task of locomotion\textsuperscript{16} – to directly assess locomotor control strategies driving interactions within a dynamic environment.

The system used two linear servomotors to tug on a pulley-cable system connected to a body harness worn by subjects (Fig. 1). An open loop current control was prescribed to the motors during experiments where the oscillation frequency and amplitude were fixed at different values for each trial condition. A more detailed description of the system can be found in the Supplementary Materials.

**Figure 1.** System schematic and images. (a) A schematic of the oscillator system is depicted in the sagittal plane. (b) Images of a subject walking in the system during a trial, from the side and from behind. Downward force came as the resultant of self-equalizing oblique cables. A curtain was used to blind the subject from any motion of the pulleys or motors, and headphones were used to play ambient noise to block out rhythmic sounds from the system. The headphones were also used to play a metronome beep during portions of the experiment. A more detailed description of the system can be found in the Supplementary Materials.

The experiment was divided into two phases while external oscillations were present (Fig. 2): first, subjects walked with a freely-chosen step frequency in response to the oscillations (i.e. individuals were allowed to entrain to the oscillations); second, individuals followed the beat of a metronome programmed to subject-specific baseline frequencies, measured \textit{a priori}. Both experiment phases lasted five minutes and allowed for a comparison of energetic
consumption during entrainment and non-entrainment. In addition, phase alignment of the force oscillations with the gait cycle were measured to characterize subject-preferred mechanical interactions with the oscillating environment.

Figure 2. Experimental protocol. (a) A generic trial condition is depicted with simulated step frequency data over time (magenta) and constant motor frequency (blue). Subjects walk with no oscillations during the first two minutes of the test. Motor oscillations begin at time zero and continue for five minutes while subjects freely interact with the system. Oscillations continue for another five minutes, but now a metronome directs individuals to step at their baseline preferred frequency ($f_p$) despite the external oscillation frequency ("frequency clamping"). The oscillations and metronome are terminated, and the subject is given fifteen additional seconds to prepare for the end of the trial. (b) Baseline conditions and oscillation parameters during experiment trials are shown: $\Delta f_m = 0, \pm 6\%$ and $A_m = 10, 30\%$ body weight (BW). Trial conditions were implemented randomly to reduce ordering effects.
Results

Subjects entrain to external oscillations

Figure 3 shows the median step frequency normalized to baseline preferred (magenta) as well as 25% and 75% quartiles (grey shaded region) for individuals who entrained their steps with external oscillations at least once during the indicated trial condition. Subjects generally preferred entrainment, overall. However, the level of entrainment varied between individuals; e.g. some only entrained in two trials while others entrained in five out of six total trials. The likelihood of subject entrainment largely depended on the oscillation parameters prescribed: frequency, $\Delta f_m$, expressed as a percent difference from subject baseline and amplitude, $A_m$, expressed as a percentage of subject body weight (BW) force (see Methods for details). For example, all ten subjects entrained when $\Delta f_m = -6, 0\%$ and $A_m = 30\%$ BW (Fig. 3b,d).

Conversely, no subjects entrained when $\Delta f_m = 6\%$ and $A_m = 10\%$ BW, thus only individual subject data are shown (Fig. 3e). In general, entrainment in conditions with higher motor frequencies and lower amplitudes was less stable and more transient. Note, the data for $\Delta f_m = 0$ end earlier than other trials since there was no metronome used (the oscillation frequency already matched baseline preferred, so was deemed unnecessary; Fig. 3c,d). However, individuals largely followed the metronome in other trials, as the median data quickly converged on a relative frequency of one at approximately 300 s into the trial.
Figure 3. Entrainment results. The median relative step frequency ($f_r$, step frequency divided by preferred step frequency in Baseline 2; magenta) of all subjects who entrained is plotted over each trial duration. 25% and 75% quartiles are used to indicate the distribution at every time point (grey shaded area). All trial conditions are shown, including: $\Delta f_m = -6\%$ in (a) and (b); $\Delta f_m = 0\%$ in (c) and (d); $\Delta f_m = 6\%$ in (e) and (f); $A_m = 10\% BW$ in (a), (c) and (e); $A_m = 30\% BW$ in (b), (d) and (f). The oscillations began at Time = 0 s and ended at approximately Time = 600 s. During 0 ≤ Time ≤ 300 s, subjects responded freely to the force oscillations. During 300 ≤ Time ≤ 600 s, subjects were directed to follow the cadence of the metronome at their predetermined baseline step frequency ("frequency clamping") even as the oscillations continued at a different frequency. There was no metronome used in trials where $\Delta f_m = 0$, since frequencies were already matched. As a result, these experiments ended after around Time = 300 s. Note, median data are only shown for individuals who entrained at least once throughout the trial. In the trial condition where $\Delta f_m = 6\%$ and $A_m = 10\% BW$, individual subject data are shown instead since no entrainment occurred.
In many instances, subjects exhibited transient entrainment – meaning their step frequency drifted in and out of the oscillation frequency throughout the trial (Fig. 4a). To better characterize how well subjects entrained their gait in the various trial conditions, two metrics were considered: entrainment step ratio ($ESR$, Fig. 4b) and average entrainment duration ($\Delta t_e$, Fig. 4c). The entrainment ratio is the proportion of steps within ±3 standard deviations (SD) of the motor frequency (1 SD determined from step frequency data in Baseline 2) during the first five minutes of exposure to oscillations in the experiment (i.e. no metronome). However, because this metric does not consider how bouts of transient entrainment are distributed throughout the trial, $\Delta t_e$ indicates the average time duration of all bouts in a given trial as a fraction of the 300 seconds time allotted. Thus, for both entrainment metrics, a value of zero means that no entrainment occurred while a value of one means that subjects entrained throughout the entire trial.

**Figure 4.** Entrainment is often transient. (a) Data from an example subject illustrates transient entrainment where relative step frequency (magenta) oscillates towards and away from the motor frequency (blue). Red data points indicate when the subject is considered entrained with the oscillator system (see Methods section for details on entrainment definition). (b) The entrainment step ratio ($ESR$; ratio of entrained steps to total steps taken during the first five minutes of oscillations in the experiment) and (c) the average entrainment duration ($\Delta t_e$; average time duration of bouts of entrainment) are shown as a function of oscillation amplitude and motor frequency, where each data point represents a subject’s level of entrainment during
each trial and box plots summarize the distribution. Linear mixed models were used to statistically test the effects of trial conditions on both entrainment metrics shown here (see Table S1 in the Supplementary Materials for full results).

Linear mixed models indicated that higher oscillation amplitudes increased both $ESR$ [fitted coefficient (95% confidence limits): $\beta = 2.267 (1.482, 3.052)$, $p < 0.001^*$] and $\Delta \tilde{e}$ [$\beta = 1.737 (0.958, 2.517)$, $p < 0.001^*$] while higher motor frequencies led to decreases in the entrainment metrics: [$\beta = -3.005 (-4.607, -1.402)$, $p < 0.001^*$] and [$\beta = -2.712 (-4.302, -1.121)$, $p = 0.001^*$], respectively. An interaction between motor frequency and oscillation amplitude was not significant ($p = 0.273$). In fact, this interaction was not significant in any of the models tested. Figures 4b and 4c illustrate higher levels of entrainment at larger amplitudes and lower motor frequencies, despite large inter-subject variation overall.

Entrainment does not reduce metabolic power

Metabolic power was compared for individuals in all trial conditions with the metronome turned off (subject allowed to entrain) versus with the metronome turned on (not allowed to entrain). Metabolic expenditure increased by 25.8% ($p < 0.001^*$) when subjects walked on the treadmill wearing the harness but with no active oscillations versus when they walked on the treadmill without the harness (Baselines 2 and 1, respectively; Fig. 5). When comparing trials with active oscillations, no significant differences were found, with the exception of one parameter combination: $\Delta f_m = -6\%$ and $A_m = 30\% BW$. This condition was more costly without the metronome compared to all other trials and baseline conditions. Still, metabolic cost did not differ significantly depending on the presence of the metronome (blue vs. green in Fig. 5) for any of the trial conditions tested. All in all, the metronome – and thus, the freedom of subjects to entrain – had no statistical effect on metabolic power. Importantly, this result did not change when controlling for the level of entrainment (e.g. $ESR$) in each trial condition.
Figure 5. Metabolic power does not depend on entrainment. Non-dimensional metabolic power was compared using a mixed linear regression stratified by trial condition and baseline type. A post hoc Tukey Honestly Significant Difference test was used to compare estimates of metabolic power in the model. Box plots are labelled with letters indicating conditions where power is not significantly different. Outliers are marked with “+”. See Table S2 in the Supplementary Materials for full results. Baseline 1 and 2 refer to walking on the treadmill without and with the harness, respectively. Box plots are shown for all metabolic data collected during the first five minutes of oscillations where the subject freely responded to the oscillation forces (i.e. metronome off). During the next five minutes of oscillations, a metronome guided subjects to step at their baseline preferred frequency (importantly, not matched to the oscillation frequency). This allowed for metabolic cost comparisons between entrained and non-entrained gait.
Subjects prefer to align peak forces at toe off

Figure 6a shows average tension forces measured in the harness for all subjects during Baseline 2. These forces act to pull vertically near the CoM of subjects as they walk on the treadmill. The red and blue curves indicate tension in the harness pulling up ($T_\uparrow$) and down ($T_\downarrow$), respectively, while the black curve is the summation of the two ($T_{\text{net}}$). Even though no active oscillations occur during the baseline test, there are still fluctuations in tension due to passive resistance of the system; these resistive forces largely occur due to the reflected inertia of the motors and associated hardware, as well as to damping effects. Given the alignment of these forces with the vertical velocity of the CoM (Fig. 6c), net negative power dominates the interaction (black shaded area in Fig. 6e, $P_{\text{net}}$) even as power of the cables pulling up ($P_\uparrow$, red) and down ($P_\downarrow$, blue) partly offset each other with both positive and negative power.

In Figure 6b, average tension forces are shown for subjects entrained with active oscillations in the system. Although the passive force peaks observed in Baseline 2 are still present in the entrained interaction (occurs in $T_\uparrow$ at around 0.80 of the step cycle), there is an additional upward peak (~0.35 in the step cycle) due to subjects’ preferred alignment of the active oscillations. This active force peak is further indicated by the motor phase selected by subjects during entrainment. The red histogram in Figure 6d characterizes the distribution of motor phase chosen by subjects during entrainment, where the average and standard deviation are given: $\bar{\phi} = 94 \pm 55^\circ$. This means that peak current is prescribed to the motor pulling up just after a quarter through the step cycle (approximately at toe off of the trailing leg). Due to system dynamics, this current peak shows up as a spike in tension force slightly later as the “active force peak”.

The preferred motor phase seems to imply a strategy of receiving positive power from the active oscillations, given peak active force approximately aligns with peak vertical CoM velocity (Fig. 6d). Despite this alignment, negative power still greatly outweighs any positive power received from the system. Since the resistive forces largely responsible for excess negative power relate to motion of the CoM (damping relates to velocity, inertial forces to acceleration), a 90% increase in vertical velocity amplitude may help to explain why net negative power still dominates subjects during entrainment, despite a preferred phase indicating the opposite.
Figure 6. Subjects prefer to align peak oscillation forces at toe off. The average harness tension is shown in (a) and (b), where the red and blue curves indicate cable tension pulling up ($T^\uparrow$) and down ($T^\downarrow$), respectively, and black indicates net tension ($T_{net}$). Average center of mass vertical velocity is shown in (c) and (d), while the red histogram in (d) indicates the distribution of motor phase chosen by subjects during entrainment. Average power from the cables pulling up ($P^\uparrow$, red) and down ($P^\downarrow$, blue) are shown in (e) and (f), while net power ($P_{net}$) is indicated with black shading. Panels (a), (c) and (e) indicate average curves measured during Baseline 2 (walking with the harness but no active oscillations), while panels (b), (d) and (f) indicate average curves measured during experiment trials. Snapshots of the walking step cycle are shown near the bottom to help orient the reader to the timing of events shown in plots. Zero in the step cycle corresponds with double stance while 0.5 corresponds with single stance.
Preferred phase lag varies by subject

Despite the entrainment strategy shown in Figure 6 representing the sample mean tested in the experiment, individual subjects displayed notable variance – for example, with respect to the work done by the oscillation forces on the CoM. Figure 7 shows the average tension force, CoM vertical velocity and mechanical power of three example subjects in trial conditions chosen to illustrate entrainment strategies resulting in moderate net positive work (Subject A), moderate net negative work (Subject B) and substantial net negative work (Subject C). A notable distinction of these subjects is the chosen phase alignment of motor forces. Subject A aligned the motor phase just after zero (median phase = 31°, or 0.087 in the gait cycle), and distinctive tension force humps were observed shortly thereafter (~0.25 in the gait cycle). Due to this phase, the net tension signal was locally shaped by active oscillation forces and approximately aligned with CoM velocity, thus resulting in net positive work ($W_c = 4.1$ J). Subject B preferred a slightly increased phase (64°, or 0.18). Although the resulting motor force hump was still relatively distinct, it was not robust enough to overcome resistive forces due to inertia and damping in the system, and net negative work was accumulated over the step ($W_c = -6.2$ J). Subject C preferred a relatively late motor phase (110.0°, or 0.32), and forces out of phase with the CoM velocity were exaggerated. Substantial net negative work was observed in this example ($W_c = -12$ J). Data from example subjects in Figure 7 imply that motor phase alignment had a prominent effect on the net mechanical work done on the CoM by the harness tension forces.
Figure 7. Subjects prefer a range of phase alignments, resulting in variable net power. Data from three subjects were chosen to demonstrate varying entrainment strategies. Average data for Subject A ($\Delta f_m = 6\%$, $A_m = 30\% BW$, 297 steps averaged) are shown in (a), (d) and (g), where motor phase alignment occurs at $\bar{\phi} = 0.087$ of the gait cycle. This strategy aligns peak tension forces with the center of mass (CoM) vertical velocity and thus, results in net positive work ($W_c = 4.1 J$). Average data for Subject B ($\Delta f_m = -6\%$, $A_m = 30\% BW$, 475 steps averaged) are shown in (b), (e) and (h) where motor phase alignment occurs at $\bar{\phi} = 0.18$ of the gait cycle. Since peaks in tension due to motor forces occur slightly later, positive power is relatively low and net negative work occurs ($W_c = -6.2 J$). Average data for Subject C ($\Delta f_m = -6\%$, $A_m = 30\% BW$, 444 steps averaged) are in (c), (f) and (i) where $\bar{\phi} = 0.32$ of the gait cycle, and mechanical power from the harness tension is dominated by resistive inertial forces, thus leading to substantial net negative work on the CoM ($W_c = -12 J$). Data points for subjects A, B and C are labelled in Figure 8b.
Net mechanical work determines metabolic power

Figure 8a shows how metabolic power and net mechanical work of the oscillations on the CoM vary due to phase lag of the active peak force pulling up. Minimum metabolic power is observed when active oscillations pull up on the body during toe off of the trailing leg ($\phi \approx 90^\circ$), and this corresponds to maximum net positive work from the oscillator forces (Fig. 8a). Although subjects interacting with the oscillator system mostly experienced net negative mechanical work overall, variation on the gait strategy chosen illustrated a range of work done [approximately $0.16 - 0.05 \ W kg^{-1}$] and a linear mixed model found a strong negative effect of net work on metabolic cost in individual subjects and trial conditions [$\beta = -4.201(-4.960, -3.442), p < 0.001^*$; see Fig. 8b]. In other words, more net positive work done by the harness tension meant a lower metabolic cost for subjects and more net negative work meant a higher cost. The oscillation amplitude also had an effect on metabolic power [$\beta = 0.088 (0.051, 0.125), p < 0.001^*$], showing an increase in cost at higher amplitudes, despite there being generally more entrainment in this condition. In fact, the level of entrainment was controlled for by including $ESR$ as a covariate in the model, and yet, this variable did not have a significant effect on metabolic power [$\beta = -0.004 (-0.013, 0.006), p = 0.488$]. An interaction term between motor frequency and oscillation amplitude was found to be insignificant after controlling for multiple hypothesis testing (see Table S1 in the Supplementary Materials for full results).
**Figure 8.** Positive mechanical work from the oscillator decreases metabolic power. Average data are shown for every subject in each trial condition during the first five minutes of oscillations when no metronome is present. (a) Net metabolic power is plotted versus the phase lag of peak upward force from the oscillations. A phase lag of 0° (or 360°) corresponds to peak upward force occurring at double stance while a lag of 180° corresponds to peak upward force occurring at midstance (i.e. when the center of mass passes over the stance foot). Net mechanical work done on subjects by the oscillation forces is also plotted versus the phase lag of peak upward force. Arbitrary sinusoidal functions are fit to these data to indicate the cyclical relationship between center of mass motion and oscillation forces. (b) Net metabolic power decreases as a function of net mechanical work done on subjects by the oscillation forces. A linear mixed model was used to assess the effect of net work on metabolic power (both variables non-dimensionalized; see results in Table S1 in the Supplementary Materials). Example data points from subjects A, B and C are labelled for comparison in plots of Figure 7. Blue and red data points correspond to trial conditions where $A_m = 10, 30\%\ BW$ respectively. Circles, squares and diamonds correspond to trial conditions where $\Delta f_m = -6, 0, 6\%$ respectively.
Discussion

Step frequency adaptations

Step frequency adaptations in the current study (±6%) are comparable to those of previous reports: approximately ±2–8% of preferred step frequency\(^{13-15,17}\). Even so, some subjects struggled to entrain with the oscillator system even in the most favorable conditions (e.g. preferred frequency, high amplitude). Similar variability in subject response has been noted in other studies\(^{14}\). Regardless, clear trends were identified; subjects displayed the most robust and stable entrainment during trials with high motor amplitudes and frequencies below the preferred step frequency measured at baseline.

Stronger entrainment at lower frequencies

In general, subjects had an easier time entraining to oscillation frequencies below their preferred step frequency. The entrainment step ratio and the average entrainment duration were both found to be negatively affected by motor frequency (\(\beta = -3.005\) and -2.712, respectively) – meaning lower frequency conditions were associated with more consistent and robust entrainment and higher frequency conditions were associated with less consistent and robust entrainment. It is unclear why stronger entrainment was associated with lower oscillation frequencies, as other studies have not reported similar asymmetries\(^{13}\).

Metabolic cost of oscillator interaction strategies

Variation in metabolic power was not affected by entrainment but was instead strongly related to net mechanical work done on the subject by the harness tension. Specifically, receiving net positive work was associated with a lower energetic cost than with negative work. This result may be reasonable given: (1) zero net CoM work is required for steady, periodic gait (e.g. net positive oscillator work requires net negative muscle work, and vice versa) and (2) negative muscle work costs 4.8 times less metabolic energy than positive muscle work\(^{18}\). This logic assumes that no additional work is needed to compensate for extra force on the body, other than the net negative work needed to manage the energy balance. It is unclear if this assumption holds.
Ideally, the subject learns a strategy to receive positive power from the oscillator system in such a way that the leg muscles are unburdened from their typical function (e.g. Gordon & Ferris\(^{19}\)). Indeed, large amounts of positive mechanical power naturally occur due to push off forces during the step-to-step transition in the gait cycle, functioning to redirect the body from falling to rising with the next step\(^{20}\). Recent optimization models have identified a strategy for minimizing work while walking with an oscillating impulse applied to the CoM\(^{21}\). This strategy aligns upward oscillator forces with the step-to-step transition (motor phase = 0\(^\circ\)). The upward oscillator force does some work that the legs would normally do, thus minimizing cost in the model. Notably, this is a different strategy than what subjects preferred in the current study, where individuals largely aligned oscillation forces with CoM vertical velocity to maximize externally applied positive power (phase = 90\(^\circ\)). However, the model did not account for differential energetic costs of positive and negative muscle work, nor did it allow for negative work via passive dissipative mechanisms (e.g. collisions during foot-ground contact\(^{22-25}\), damping in soft tissue deformation\(^{26,27}\), etc.) which require near zero metabolic expenditure. Furthermore, the model did not account for swing leg dynamics and associated costs. These issues and others may be important for understanding subject preferences of increased positive mechanical power from the oscillations.

If the preferred strategy uses oscillation forces to replace positive muscle work, then the extent to which this strategy is energetically favorable likely relies on an individual downregulating leg work and associated muscle activity\(^{19}\). Yet subjects substantially increased the vertical excursion of their CoM when they entrained to motor oscillations compared to at baseline (an increase of 58.2\% or 125.5\% for \(A_m = 10\%\) or 30\% \(BW\), respectively). The increased body oscillation is likely evidence that subjects did not downregulate their push off during entrainment. Instead, it seems that subjects preferred to increase positive power from the system by aligning active force peaks approximately with toe off in the step cycle (Fig. 6b, 8a). Furthermore, subjects that leveraged the most positive power from the oscillations had the lowest metabolic cost (local minimum at \(\phi \approx 90^\circ\)). These results, however, should be treated with caution. Experiments presented here did not explicitly control or manipulate the motor phase, but rather, the phase variation depicted in Figure 8a represents subject preferences during the experiment with no metronome. Since subjects did not explore a full range of phase values in steady state, it is unclear if the preferred alignment centers on a global or local optimum. The grey dashed line in Figure 8a indicates a sine wave fit to the data, assuming a cyclical cost over phase. Extrapolation
of this fit beyond the relatively narrow range of data is questionable, and future studies could control motor phase explicitly to characterize fluctuations in cost.

Notably, the data show mostly net negative work in the sampled phase domain, despite maximal positive power expected in this region ($\phi \approx 90^\circ$). This bias may partially be explained by negative work associated with resistive forces due to reflected inertia of the motors and hardware, as well as damping in the system (e.g. back electromotive force). Increases in vertical excursion of the CoM during entrainment likely contributed to an exaggeration of these effects. Perhaps subjects prefer phase lags that maximize positive mechanical power from the oscillations in part to reduce dissipation in the system.

**Interactions with other active devices**

It is possible that the motor control system uses mechanical and/or physiological variables as a proxy for energetic cost, as other researchers have previously suggested\textsuperscript{28}. In this case, it appears that subjects prefer to maximize positive mechanical power from the oscillations. However, it is unclear if this preference is generalizable to mechanical interactions with other devices or if it is only relevant to the specific system discussed here. Ahn and Hogan\textsuperscript{7,8} found that subjects aligned ankle torques at push off with those from an ankle exoskeleton. Since the ankle generates high positive power during push off, the alignment likely means that individuals chose to leverage positive power from the device, similar to our subjects. A different study found that individuals prefer to align pulses of electrical stimulation to the plantar flexors either just before toe off or in advance of heel strike\textsuperscript{5}.

Experiments by Selinger et al.\textsuperscript{13} found subjects adjust their gait in response to resistive damping forces from a knee exoskeleton. While subjects could not possibly receive positive power from the device, they did actively adjust their gait to avoid negative power. Sánchez et al.\textsuperscript{29} investigated gait adaptation of subjects walking on a split-belt treadmill (a treadmill that contains separate belts moving at different speeds for each leg). The authors showed that when subjects are given sufficient time adapting to the system, they employ a step length asymmetry associated with net positive mechanical power from the treadmill and reduced metabolic output.
These examples provide some evidence of preferred subject interactions that involve either reducing net negative work or increasing net positive work from dynamic external devices. This strategy is consistent with our results that subjects prefer to align motor forces approximately with vertical CoM velocity. However, it is unclear if the ultimate objective is to increase positive power or to decrease metabolic expenditure, since the two are often correlated. Wong et al.\textsuperscript{30} showed that individuals do not adjust gait in exchange for higher levels of oxygen concentration fed to them through an air tube, even as they consciously acknowledge an increased effort from not adjusting their gait. Perhaps individuals are sensitive to positive mechanical power from external sources as an indirect sign of economical interactions with the environment.

**Entrainment may stabilize interactions for internal models of gait**

Given that most subjects learned to entrain under a large range of oscillation parameters, it seems reasonable to conclude that individuals largely preferred a stable interaction with the environment in experiments detailed here. This could be interpreted as evidence of a feedforward gait control mechanism since unpredictability could impede effective implementation of internal models. Various studies have shown evidence of a dual-part locomotor control process, including a rapid response to external stimuli and a slower, more gradual, fine-tuning of the response\textsuperscript{31-33}. These findings are interpreted as evidence of an internal model used to make quick predictions (within seconds) regarding energetic cost based on state estimations and followed up with direct energy optimization occurring more slowly (within minutes). Other researchers have proposed that feedforward and feedback control mechanisms also play a role during gait adaptation to split-belt treadmills\textsuperscript{34} and lateral perturbation systems used to train individuals with incomplete spinal cord injury\textsuperscript{35}.

The experiments presented in the current study describe subject interactions that can be relatively volatile, at least before subjects converge on entrainment. In particular, inexperience with the oscillation system may require a prerequisite to the dual-part control of locomotion described previous: a stabilization phase. Here, stability does not necessarily refer to fall avoidance or balance, but rather to a state of relative consistency, where interactions with the environment are sufficiently repeatable over subsequent steps. A relatively stable interaction may be required before feedforward or feedback control can be successfully implemented, and entrainment could provide that stability.
Koban et al. explained a similar perspective in a slightly different context, with regards to individuals that entrain gait when walking side by side (i.e. interpersonal synchronization). They described a process by which entrainment occurs to reduce the perceived mismatch between an expectation about their companion’s motor behavior based on their own. An analogous principle could be adapted to the expectation of mechanical interactions with the environment, as mediated by the entrainment opportunities associated with the oscillator system described in this manuscript. In lieu of a direct metabolic motivation for entrainment, it may be possible that the motor control system prefers a relatively stable interaction with the environment so as to make feedforward predictions more precise and actionable.

Methods

Participants

A convenience sample of ten healthy university students (five males, five females) were recruited. The mean [± 1 standard deviation (SD)] subject height was 1.71 ± 0.07 m, leg length was 0.91 ± 0.06 m, weight was 65.7 ± 12.2 kg and age was 26.2 ± 2.9 years. Exclusion criteria for the experiments included any musculoskeletal injuries or neurological conditions affecting one’s gait or their ability to carry a heavy backpack. All participants provided informed consent to participate, and these studies were approved by an ethics review board at the University of Calgary (REB16-1517). All methods were performed in accordance with the relevant guidelines and regulations.

Measurements and analysis

Inertial measurement units, or IMUs (Xsens Technologies B.V., Enschede, The Netherlands) were placed at each ankle and the lower back. The ankle sensors were used to detect signal peaks and calculate step frequency as the inverse of the time period between peaks. The back sensor provided kinematics to approximate CoM motion (acquisition rate = 100 Hz). These data were integrated twice over time to get velocity and displacement, and a moving average (window set to stride time) was subtracted from the signal to adjust for low frequency drift error. A moving average filter (window of ±5 steps at each data point) was also applied to step frequency measurements to more clearly illustrate trends over time. Step frequency ($f_s$) was normalized
by the subject’s baseline frequency \( (f_p) \) measured while walking in the system with the motors inactive.

\[ f_r = \frac{f_s}{f_p} \]  

(1)

Custom in-line tension transducers were built with strain gauges (Micro-Measurements CEA-06-125UW-350, Wendell, NC, USA) configured in half-bridge circuits. The strain gauges were epoxied to C-shaped steel hooks and measured tension in cables pulling on the body harness during experiments (Fig. 1). The strain gauge signals were passed to a strain conditioning amplifier (National Instruments, SCXI-1000 with SCXI-1520 eight-channel universal strain gauge module connected with SCXI-1314 terminal block, Austin, Texas USA), digitized (NI-USB-6251 mass termination) and acquired in a custom virtual instrument in LabVIEW (National Instruments) at an acquisition rate of 100 Hz. The transducers were calibrated with known weights before every testing session using a least squares linear regression to quantify a conversion factor from volts to Newtons force \( (R^2 > 0.99) \).

At the beginning of each trial, a few seconds of data were collected where the subject stood still before starting the treadmill. During this time, the transducer signals measured force from the motors’ weight in the system plus nominal tension from the motors pulling the system taut. This initial tension was averaged over a ten second interval and subtracted from the subsequent signal in the trial.

Next, tension forces were multiplied by vertical velocity to calculate mechanical power acting on the CoM. Step cycles were distinguished by peaks in the vertical acceleration of the CoM (approximately indicating the middle of double stance). Tension forces, kinematics and mechanical power were all segmented into blocks of data comprising every step cycle identified in all trials. These data were interpolated at regular intervals matching the average resolution of the raw data collection (~55 data points per step).

Pulse signals were recorded in LabVIEW to mark the timing of peak current sent to the motors relative to the start time of a given step cycle \( (\Delta t_p) \). In addition to data synchronization, the pulse signals were used to calculate the phase lag of peak current relative to the step cycle \( (\phi) \).

\[ \phi = \Delta t_p f_s \cdot 360^\circ \]  

(2)

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Due to dynamics of the system, there was a slight delay from when peak current was driven to the motors to when tension spiked in the harness. The average delay, $\Delta \phi$, was calculated for all subjects and trials and phase data were shifted as appropriate: $\phi^* = \phi + \Delta \phi$.

Oxygen consumption and carbon dioxide elimination rates were measured using a commercial metabolic analysis system (TrueMax 2400, ParvoMedics, Salt Lake City, UT, USA). All trials lasted longer than five minutes, which allowed metabolic data to reach steady state conditions before mean and SD values were calculated (typically the remaining 2-3 minutes of each trial). Oxygen consumption rates in $ml O_2 s^{-1}$ were multiplied by a factor of 20.1 to convert to Watts. Gross metabolic rate was converted to net metabolic rate by subtracting baseline values during quiet standing. Net metabolic power was non-dimensionalized by dividing belt speed and subject BW (sometimes referred to as non-dimensional cost of transport). During all metabolics testing, the data were deemed acceptable if the respiratory exchange ratio remained below a value of 1.0.

**Test protocol**

During Baseline 1, subjects walked on the treadmill freely (i.e. without the body harness; Fig. 2b) for a five-minute duration. The treadmill speed ($v_b = 1.19 m s^{-1}$ on average) was programmed such that non-dimensional speed, $\tilde{v}$, equaled 0.4 during all testing.

$$v_b = \tilde{v}\sqrt{gL}$$

where $L$ is the subject’s hip height measured from the ground while standing. Speed was rounded to the nearest tenth of a km/hour, per the treadmill’s available resolution.

During Baseline 2, subjects walked while wearing the body harness connected to the pulley-cable system (Fig. 2b) for a ten-minute duration. Both actuators provided a constant nominal tension (approximately 10% BW) to reduce slack in the system, but the average net force on the body was zero since one cable pulled up while the others pulled down. Subjects also experienced added inertia from the motors and associated hardware connected in the system, as well as friction and damping. Each subject’s baseline preferred step frequency ($f_p$) was assessed and motor frequencies prescribed in testing conditions were determined relative to this baseline.
During experiments, subjects walked in the harness for two minutes with nominal motor current to avoid cable slack. Next, current oscillations were commanded to the motors at a constant frequency and amplitude, and the subject was instructed to respond freely (Fig. 2a). Five minutes later, subjects were asked to step to the beep of a metronome (matched to their baseline frequency, i.e. “frequency clamping”; Fig. 2a) even as oscillations continued at a different frequency. After another five minutes, the oscillations and metronome ceased, and the subject prepared to end the trial. Metabolic data was collected throughout this test to compare oxygen consumption while responding freely in the system (allowed to entrain) versus walking to the metronome (not allowed to entrain). This test was performed with various oscillation amplitudes ($A_m = 10, 30\% BW$) and motor frequencies relative to baseline step frequency ($\Delta f_m = 0, \pm 6\%$; see Fig. 2b).

\[ \Delta f_m = \frac{f_m-f_p}{f_p} \times 100\% \]  

(4)

In the case of trial conditions where $\Delta f_m = 0\%$, no metronome was played and the trial ended after five minutes of oscillations. Trial conditions were randomized to minimize any ordering effects.

During experiments, a curtain was used to blind subjects from any motion of the pulleys or motors (Fig. 1b). Ambient noise was played through headphones to help block out rhythmic sounds of the system. During trials, subjects were asked to walk in any manner that felt most natural or extracted minimal effort. However, subjects were encouraged to explore different aspects of their gait, including stride length. Note, a more detailed description of the oscillator system design and operation can be found in the Supplementary Materials.

Defining entrainment

Entrainment was defined with arbitrary thresholds: any step frequencies within $\pm 3$ SDs ($\approx \pm 0.02$ Hz) of the prescribed motor frequency for at least sixteen out of twenty (80%) consecutive steps. The SD of subjects was determined from the last minute of data from Baseline 2 (treadmill walking with the harness). Two metrics quantified the level of entrainment for a subject in each trial. The entrainment step ratio ($ESR$) is the ratio of entrained steps to total steps taken during experiment (without the metronome) while the average duration of
entrainment ($\Delta \bar{t}_e$) was used to estimate entrainment durations since subjects sometimes drifted in and out of the motor’s frequency.

Statistical analysis

Filtered relative step frequency data were interpolated at equal time intervals matching the data acquisition rate. Median values of the interpolated data were taken across all subjects who entrained at least once in the trial and at each time point, to represent skewed distributions more appropriately. Quartiles characterized the spread of the distribution for each time point at 25% and 75% levels.

Linear mixed models were used to assess various outcomes during experiments. The mixed model was chosen to control for repeated measurements among subjects participating in multiple trials each; subject was included in the models as a random effect. All statistical models were developed and evaluated in JMP (SAS Institute Inc., Cary, NC USA, version 14.1.0) using the restricted maximum likelihood method for parameter estimation and a compound symmetric covariance structure.

In three models, motor frequency ($\Delta f_m$) and amplitude ($A_m$) as well as an interaction between the two ($\Delta f_m \times A_m$) were added as fixed effects to test if the oscillation parameters contributed significantly to the various outcomes. The first two models tested the effect of oscillation parameters on the level of entrainment via $ESR$ and $\Delta \bar{t}_e$.

In order to assess metabolic power, a linear mixed model was stratified by trial condition, baseline type (wearing or not wearing the harness) and the metronome’s status (i.e. active or inactive) during data collection. A post hoc Tukey’s Honestly Significant Difference test was used to detect differences in estimates of metabolic power ($\alpha = 0.05$), while controlling for multiple hypothesis testing. Given the metronome’s status only indicates whether an individual has the capacity to entrain and not whether they actually did entrain, a separate model was used to test for the effect of entrainment level (via entrainment step ratio, $ESR$) as a covariate for metabolic power. $\Delta \bar{t}_e$ was not included to avoid collinearity. Mechanical work done by the harness tension was also included to assess any effect of the mechanical interaction on cost.

The significance of fixed model effects was evaluated with 95% confidence limits and post hoc $t$-tests where $p$ values were adjusted ($p_{adj}$) using the Bonferroni correction depending on how
many tests were performed in the model. Tests were considered significant if $p_{adj} < 0.05$.

Throughout the manuscript, unadjusted $p$ values are reported, and significance is indicated with asterisks. A summary of statistical model results is found in the Supplementary Materials.

References

1. Dallard, P. et al. London Millennium Bridge: Pedestrian-induced lateral vibration. Journal of Bridge Engineering 6, 412–417 (2001).

2. Peters, B. T., Brady, R. A. & Bloomberg, J. J. Walking on an oscillating treadmill: Strategies of stride-time adaptation. Ecological Psychology 24, 265–278 (2012).

3. Nessler, J. A., Heredia, S., Bélaire, J. & Milton, J. Walking on a vertically oscillating treadmill: Phase synchronization and gait kinematics. PLOS ONE 12, e0169924 (2017).

4. Tackett, E. The effect of noise on gait synchronization to a vertical oscillating treadmill. (2018).

5. Thorp, J. E. & Adamczyk, P. G. Mechanisms of gait phase entrainment in healthy subjects during rhythmic electrical stimulation of the medial gastrocnemius. PLoS ONE 15, e0241339 (2020).

6. Goldfield, E. C., Kay, B. A. & Warren, W. H. Infant bouncing: The assembly and tuning of action systems. Child Development 64, 1128–1142 (1993).

7. Ahn, J. & Hogan, N. Feasibility of dynamic entrainment with ankle mechanical perturbation to treat locomotor deficit. in 2010 Annual International Conference of the IEEE Engineering in Medicine and Biology Society, EMBC’10 3422–3425 (2010). doi:10.1109/EMBS.2010.5627892.

8. Ahn, J. & Hogan, N. Walking is not like reaching: Evidence from periodic mechanical perturbations. PLoS ONE 7, e31767 (2012).
9. Donelan, M., Kram, R. & Kuo, A. Mechanical and metabolic determinants of the preferred step width in human walking. *Proceedings of the Royal Society B: Biological Sciences* **268**, 1985–1992 (2001).

10. Bertram, J. E. A. Constrained optimization in human walking: cost minimization and gait plasticity. *Journal of Experimental Biology* **208**, 979–991 (2005).

11. Bertram, J. E. A. & Ruina, A. Multiple walking speed–frequency relations are predicted by constrained optimization. *Journal of Theoretical Biology* **209**, 445–453 (2001).

12. Kuo, A. D. A simple model of bipedal walking predicts the preferred speed-step length relationship. *Journal of Biomechanical Engineering* **123**, 264–269 (2001).

13. Selinger, J. C., O’Connor, S. M., Wong, J. D. & Donelan, J. M. Humans can continuously optimize energetic cost during walking. *Current Biology* **25**, 2452–2456 (2015).

14. Selinger, J. C., Wong, J. D., Simha, S. N. & Donelan, J. M. How humans initiate energy optimization and converge on their optimal gaits. *Journal of Experimental Biology* **222**, jeb198234 (2019).

15. Simha, S. N., Wong, J. D., Selinger, J. C. & Donelan, J. M. A mechatronic system for studying energy optimization during walking. *IEEE Transactions on Neural Systems and Rehabilitation Engineering* **27**, 1416–1425 (2019).

16. Croft, J. L., Schroeder, R. T. & Bertram, J. E. A. The goal of locomotion: Separating the fundamental task from the mechanisms that accomplish it. *Psychonomic Bulletin and Review* **24**, 1675–1685 (2017).

17. Wong, J. D., Selinger, J. C. & Donelan, J. M. Is natural variability in gait sufficient to initiate spontaneous energy optimization in human walking? *Journal of Neurophysiology* **121**, 1848–1855 (2019).

18. Margaria, R. Positive and negative work performances and their efficiencies in human locomotion. *Int. Z. angew. Physiol. einschl. Arbeitsphysiol* **25**, 339–351 (1968).

19. Gordon, K. E. & Ferris, D. P. Learning to walk with a robotic ankle exoskeleton. *Journal of Biomechanics* **40**, 2636–2644 (2007).
20. Donelan, J. M., Kram, R. & Kuo, A. D. Simultaneous positive and negative external mechanical work in human walking. *Nature* 35, 117–124 (2002).

21. Schroeder, R. T. & Bertram, J. E. Minimally actuated walking: Identifying core challenges to economical legged locomotion reveals novel solutions. *Frontiers in Robotics and AI* 5, (2018).

22. Ruina, A., Bertram, J. E. A. & Srinivasan, M. A collisional model of the energetic cost of support work qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. *Journal of Theoretical Biology* 237, 170–192 (2005).

23. Bertram, J. E. A. & Hasaneini, S. J. Neglected losses and key costs: Tracking the energetics of walking and running. *Journal of Experimental Biology* 216, 933–938 (2013).

24. Kuo, A. D. Energetics of actively powered locomotion using the simplest walking model. *Journal of Biomechanical Engineering* 124, 113–120 (2002).

25. Lee, D. v, Comanescu, T. N., Butcher, M. T. & Bertram, J. E. A. A comparative collision-based analysis of human gait. *Proceedings of the Royal Society B: Biological Sciences* 280, 20131779 (2013).

26. Zelik, K. E. & Kuo, A. D. Human walking isn’t all hard work: Evidence of soft tissue contributions to energy dissipation and return. *Journal of Experimental Biology* 213, 4257–4264 (2010).

27. Riddick, R. C. & Kuo, A. D. Soft tissues store and return mechanical energy in human running. *Journal of Biomechanics* 49, 436–441 (2016).

28. Snaterse, M., Ton, R., Kuo, A. D. & Donelan, J. M. Distinct fast and slow processes contribute to the selection of preferred step frequency during human walking. *Journal of Applied Physiology (Bethesda, Md. : 1985)* 110, 1682–90 (2011).

29. Sánchez, N., Simha, S. N., Donelan, J. M. & Finley, J. M. Taking advantage of external mechanical work to reduce metabolic cost: the mechanics and energetics of split-belt treadmill walking. *The Journal of Physiology* 597, 4053–4068 (2019).
30. Wong, J. D., O’connor, S. M., Selinger, J. C. & Donelan, J. M. Contribution of blood oxygen and carbon dioxide sensing to the energetic optimization of human walking. *Journal of Neurophysiology* **118**, 1425–1433 (2017).

31. Snaterse, M., Ton, R., Kuo, A. D. & Maxwell Donelan, J. Distinct fast and slow processes contribute to the selection of preferred step frequency during human walking. *Journal of Applied Physiology* **110**, 1682–1690 (2011).

32. O’Connor, S. M. & Donelan, J. M. Fast visual prediction and slow optimization of preferred walking speed. *Journal of Neurophysiology* **107**, 2549–2559 (2012).

33. Pagliara, R., Snaterse, M. & Donelan, J. M. Fast and slow processes underlie the selection of both step frequency and walking speed. *Journal of Experimental Biology* **217**, 2939–2946 (2014).

34. Mawase, F., Haizler, T., Bar-Haim, S. & Karniel, A. Kinetic adaptation during locomotion on a split-belt treadmill. *Journal of Neurophysiology* **109**, 2216–2227 (2013).

35. Wu, M., Brown, G. & Gordon, K. E. Control of locomotor stability in stabilizing and destabilizing environments. *Gait & Posture* **55**, 191–198 (2017).

36. Koban, L., Ramamoorthy, A. & Konvalinka, I. Why do we fall into sync with others? Interpersonal synchronization and the brain’s optimization principle. *Social Neuroscience* **14**, 1–9 (2019).

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Author contributions

J.E.A.B. and R.T.S. conceived the project and experiment. R.T.S. performed all data collection and analysis, design and development of the mechatronics system, and composed the initial manuscript. R.T.S., J.E.A.B. and J.L.C. all contributed to subsequent manuscript revisions.

Competing interests

The authors declare no competing interests.

Figures and Tables

Figure 1. System schematic and images. (a) A schematic of the oscillator system is depicted in the sagittal plane. (b) Images of a subject walking in the system during a trial, from a side view and from behind. Downward force came as the resultant of self-equalizing oblique cables. A curtain was used to blind the subject from any motion of the pulleys or motors, and headphones were used to play ambient noise so as to block out rhythmic sounds from the system. The headphones were also used to play a metronome beep during portions of the experiment. Additional details regarding the oscillator system design and operation can be found in the Supplementary Materials.
Figure 2. Experimental protocol. (a) A generic trial condition is depicted with simulated step frequency data (magenta) over time and constant motor frequency (blue). There are no oscillations during the first two minutes of the test. Motor oscillations begin at time zero and continue for five minutes while subjects freely interact with the system. Next, oscillations continue for another five minutes and the metronome directs individuals to step at their baseline preferred frequency ($f_p$) despite the external oscillation frequency (“frequency clamping”). The oscillations and metronome are terminated, and subject is given fifteen additional seconds to approach the end of the trial. (b) Baseline conditions and oscillation parameters during experiment trials are shown: $\Delta f_m = 0, \pm 6\%$ and $A_m = 10, 30\%$ body weight (BW). Trial conditions were implemented randomly to reduce ordering effects.
Figure 3. Entrainment results. The median relative step frequency ($f_r$, step frequency divided by preferred step frequency in Baseline 2; magenta) of all subjects who entrained is plotted over the trial duration. 25% and 75% quartiles are used to indicate the distribution at every time point (grey shaded area). All trial conditions are shown, including: $\Delta f_m = -6\%$ in (a) and (b); $\Delta f_m = 0\%$ in (c) and (d); $\Delta f_m = 6\%$ in (e) and (f); $A_m = 10\% \text{ BW}$ in (a), (c) and (e); $A_m = 30\% \text{ BW}$ in (b), (d) and (f). The oscillations began at $\text{Time} = 0 \text{ s}$ and ended at approximately $\text{Time} = 600 \text{ s}$. During $0 \leq \text{Time} \leq 300 \text{ s}$, subjects responded freely to the force oscillations. During $300 \leq \text{Time} \leq 600 \text{ s}$, subjects were directed to follow the cadence of the metronome at their predetermined baseline step frequency (“frequency clamping”) even as the oscillations continued at a different frequency. There was no metronome used in trials where $\Delta f_m = 0$, since frequencies were already matched. As a result, these experiments ended after around $\text{Time} = 300 \text{ s}$. Note, median data are only shown for individuals who entrained at least once throughout the trial. In the trial condition where $\Delta f_m = 6\%$ and $A_m = 10\% \text{ BW}$, individual subject data are shown instead since no entrainment occurred.
Figure 4. Entrainment is often transient. (a) Data from an example subject illustrates transient entrainment where relative step frequency (magenta) oscillates towards and away from the motor frequency (blue). Red data points indicate when the subject is considered entrained with the oscillator system (see Methods section for details on entrainment definition). (b) The entrainment step ratio ($ESR$; ratio of entrained steps to total steps taken during the first five minutes of oscillations in the experiment) and (c) the average entrainment duration ($\Delta \bar{t}_e$; average time duration of bouts of entrainment) are shown as a function of oscillation amplitude and motor frequency, where each data point represents a subject’s level of entrainment amplitude and box plots summarize the distribution. Linear mixed models were used to statistically test the effects of trial conditions on both entrainment metrics shown here (see Table S1 in the Supplementary Materials for full results).
Figure 5. Metabolic power does not depend on entrainment. Non-dimensional metabolic power is compared between all trial conditions and baseline tests. A Tukey Honestly Significant Difference test was performed on least squares mean values for all conditions. Box plots are labelled with letters indicating conditions where power is not significantly different. Outliers are marked with “+”. See Table S2 in the Supplementary Materials for full results. Baseline 1 and 2 refer to walking on the treadmill without and with the harness, respectively. Box plots are shown for all metabolic data collected during the first five minutes of oscillations where the subject freely responded to the oscillation forces (i.e. metronome off). During the next five minutes of oscillations, a metronome guided subjects to step at their baseline preferred frequency (importantly, not matched to the oscillation frequency). This allowed for metabolic cost comparisons between entrained and non-entrained gait.
Figure 6. Subjects prefer to align peak oscillation forces at toe off. The average harness tension is shown in (a) and (b), where the red and blue curves indicate cable tension pulling up ($T^\uparrow$) and down ($T^\downarrow$), respectively, and black indicates net tension ($T_{\text{net}}$). Average center of mass vertical velocity is shown in (c) and (d), while the red histogram in (d) indicates the distribution of motor phase chosen by subjects during entrainment. Average power from the cables pulling up ($P^\uparrow$, red) and down ($P^\downarrow$, blue) are shown in (e) and (f), while net power ($P_{\text{net}}$) is indicated with black shading. Panels (a), (c) and (e) indicate average curves measured during Baseline 2 (walking with the harness but no active oscillations), while panels (b), (d) and (f) indicate average curves measured during experiment trials. Snapshots of the walking step cycle are shown near the bottom to help orient the reader to the timing of events shown in plots. Zero in the step cycle corresponds with double stance while 0.5 corresponds with single stance.
Figure 7. Subjects prefer a range of phase alignments, resulting in variable net power. Data from three subjects were chosen to demonstrate varying entrainment strategies. Average data for Subject A ($\Delta f_m = 6\%$, $A_m = 30\% BW$, 297 steps averaged) are shown in (a), (d) and (g), where motor phase alignment occurs at $\bar{\phi} = 0.087$ of the gait cycle. This strategy aligns peak tension forces with the center of mass (CoM) vertical velocity and thus, results in net positive work ($W_c = 4.1 J$). Average data for Subject B ($\Delta f_m = -6\%$, $A_m = 30\% BW$, 475 steps averaged) are shown in (b), (e) and (h) where motor phase alignment occurs at $\bar{\phi} = 0.18$ of the gait cycle. Since peaks in tension due to motor forces occur slightly later, positive power is relatively low and net negative work occurs ($W_c = -6.2 J$). Average data for Subject C ($\Delta f_m = -6\%$, $A_m = 30\% BW$, 444 steps averaged) are in (c), (f) and (i) where $\bar{\phi} = 0.32$ of the gait cycle, and mechanical power from the harness tension is dominated by resistive inertial forces, thus leading to substantial net negative work on the CoM ($W_c = -12 J$). Data points for subjects A, B and C are labelled in Figure 8b.
**Figure 8.** Positive mechanical work from the oscillator decreases metabolic power. Average data are shown for every subject in each trial condition during the first five minutes of oscillations when no metronome is present. (a) Net metabolic power is plotted versus the phase lag of peak upward force from the oscillations. A phase lag of 0° (or 360°) corresponds to peak upward force occurring at double stance while a lag of 180° corresponds to peak upward force occurring at midstance (i.e. when the center of mass passes over the stance foot). Net mechanical work done on subjects by the oscillation forces is also plotted versus the phase lag of peak upward force. Arbitrary sinusoidal functions are fit to these data to indicate the cyclical relationship between center of mass motion and oscillation forces. (b) Net metabolic power decreases as a function of net mechanical work done on subjects by the oscillation forces. A linear mixed model was used to assess the effect of net work on metabolic power (both variables non-dimensionalized; see results in Table S1 in the Supplementary Materials). Example data points from subjects A, B and C are labelled for comparison in plots of Figure 7. Blue and red data points correspond to trial conditions where $A_m = 10, 30\% \text{ BW}$ respectively. Circles, squares and diamonds correspond to trial conditions where $\Delta f_m = -6, 0, 6\%$ respectively.