Is conservation of center of mass mechanics a priority in human walking? Insights from leg-length asymmetry experiments

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ABSTRACT

Center of mass (COM) control has been proposed to serve economy- and stability-related locomotor task objectives. However, given the lack of evidence supporting direct sensing and/or regulation of the COM, it remains unclear whether COM mechanics are prioritized in the control scheme of walking. We posit that peripheral musculoskeletal structures, e.g. muscle, are more realistic control targets than the COM, given their abundance of sensorimotor receptors and ability to influence whole-body energetics. As a first test of this hypothesis, we examined whether conservation of stance-phase joint mechanics is prioritized over COM mechanics in a locomotor task where simultaneous conservation of COM and joint mechanics is not feasible: imposed leg-length asymmetry. Positive joint mechanical cost of transport (work per distance traveled; COT_{JNT}) was maintained at values closer to normal walking than COM mechanical cost of transport (COT_{COM}; $P<0.05$, $N=15$). Furthermore, compared with our measures of COM mechanics (COT_{COM}, COM displacement), joint-level variables (COT_{JNT}, integrated total support moment) also displayed stronger conservation (less change from normal walking) when the participants' self-selected gait was assessed against other possible gait solutions. We conclude that when walking humans are exposed to an asymmetric leg-length perturbation, control of joint mechanics is prioritized over COM mechanics. Our results suggest that mechanical and metabolic effort is likely regulated via control of peripheral structures and not directly at the level of the COM. Joint mechanics may provide a more accurate representation of the underlying locomotor control targets and may prove advantageous in informing predictive models of human walking.

KEY WORDS: Cost of transport, Locomotion, Inverted pendulum, Joint, Control, Prioritization

INTRODUCTION

Limbed terrestrial animals exhibit remarkably conserved center of mass (COM) mechanics during locomotion. Indeed, mammalian (including humans), avian, reptilian and even arthropod species adopt an inverted pendulum-style walking gait, characterized by an exchange between COM gravitational potential energy and kinetic energy (Blickhan and Full, 1987; Cavagna et al., 1977, 1976; Farley and Ko, 1997; Griffin et al., 2004; Griffin and Kram, 2000; Heglund et al., 1982; Rubenson et al., 2004). During faster locomotion, the spring–mass paradigm of running, characterized by in-phase fluctuations of COM gravitational potential energy and kinetic energy, is similarly ubiquitous (Blickhan, 1989; Cavagna et al., 1964; Geyer et al., 2006; Rubenson et al., 2004). Clinically focused studies have also demonstrated conservation of COM mechanics. Despite marked morphological differences, COM mechanical work during walking has been observed to be largely maintained between lower limb amputees walking with a prosthetic limb and able-bodied counterparts (Gitter et al., 1995), as well as between young and old adults (Ortega and Farley, 2007). Moreover, when COM mechanics are perturbed, limb mechanics are rapidly adjusted to restore a normal inverted-pendulum COM trajectory (Hof et al., 2010; Townsend, 1985).

Inverted-pendulum and spring–mass mechanics facilitate a reduction in the mechanical work of the COM and muscles, likely translating to a lower metabolic energy cost of walking (Cavagna et al., 1977; Cavagna and Kaneko, 1977). Accordingly, the stereotypical COM mechanics observed across animal species, including humans, may reflect a COM-level control scheme of legged locomotion aimed at minimizing COM mechanical work and cost of transport (COM work per distance traveled; COT_{COM}). For example, COM-level control has been observed in a classic series of running and hopping experiments, whereby peripheral limb stiffness is adjusted to account for changes in surface stiffness such that COM mechanics are relatively unaffected (Ferris et al., 1999, 1998; Ferris and Farley, 1997). Yet, despite the apparent COM control observed experimentally and adopted in modeling studies (Grimmer et al., 2008; Hof et al., 2005; Ruina et al., 2005; Srinivasan and Ruina, 2006; Townsend, 1985), it is not well established whether COM mechanics, and more specifically COT_{COM}, are a priority control target during walking [a 'target of control' is defined here as a variable that is sensed (either directly or indirectly) and regulated by the nervous system to achieve a locomotor task goal, e.g. economy].

From a sensorimotor perspective, it remains unclear how COM mechanics are regulated during locomotion (Bruijn and van Dieën, 2018). Integrated sensory input from peripheral structures such as muscles and joints may provide more direct control targets by which locomotor economy can be modulated. These peripheral structures provide well-documented neural sensors in the form of joint receptors, muscle spindles and Golgi tendon organs. Thus, COM mechanics, including COT_{COM}, may not be the principal control target prioritized for achieving locomotor economy but could instead serve as a sufficient proxy capturing the underlying proprioceptive control of movement in normal steady-state locomotion.

An understanding of COM versus peripheral-level control in locomotion is difficult to derive from the literature because disruptions in COM mechanics and joint/muscle mechanics often

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List of abbreviations

COM	center of mass
COT	cost of transport
COT_{COM}	center of mass mechanical cost of transport
COT_{JNT}	joint mechanical cost of transport
iTSM	integrated total support moment
W_{ext}	external mechanical work
W_{JNT}	joint work

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occur in parallel (Müller and Blickhan, 2010). Here, we devised an approach to more explicitly dissociate COM mechanical control and what we regard as a first approximation of lower-level peripheral control: joint mechanics. We generated a gait perturbation where simultaneous strong conservation of COM and joint mechanical parameters is not feasible, namely asymmetric leg-length walking. Our primary focus was on parameters affecting locomotor economy [e.g. COT_{COM} and stance-phase joint mechanical cost of transport (joint work per distance traveled; COT_{JNT}) and joint moments], where deviations from normal walking patterns have been found to increase metabolic cost (Gordon et al., 2009; Massaad et al., 2007). In the case of COM control prioritization, we expected COM mechanics to be more strongly conserved (less affected) between normal and perturbed walking at the expense of joint mechanics. Conversely, if stance-phase joint mechanics better represent the control priority for locomotor economy, they are more likely to maintain patterns more similar to normal walking during leg-length asymmetry perturbation, while COM mechanics will be disrupted. We hypothesized that stance-phase joint mechanics (COT_{JNT} and moments) would be more strongly conserved between normal and perturbed walking than COM mechanics (COT_{COM} and COM displacement). This hypothesis was motivated by prior work detailing the close association between joint-level mechanics and lower-limb muscle mechanics (Sasaki et al., 2009), and because of the high abundance of motor sensors at a muscle level. Additionally, joint and muscle mechanical behavior appears to be closely related to organismal energetics (Ellerby et al., 2005; Gordon et al., 2009; Selgrade et al., 2017a,b; Umberger and Rubenson, 2011), which further contributed to our hypothesis given the important role of energy minimization as a governing principle of locomotion (Alexander, 1989).

MATERIALS AND METHODS
Participants
Healthy adults (N=15: 8 females, 7 males; age 24.4±3.0 years; mass 71.8±11.3 kg; height 1.75±0.05 m; mean±s.d.) were included in this study. Participants were required to have no history of serious lower limb injuries in the past year, and no previously or currently diagnosed balance, stability or coordination diseases, disorders or conditions. They were also required to be within the shoe size range of US 7–11 (8.6±1.2) to accommodate the custom-made platform footwear (described below). Participants provided written informed consent for this study, which was approved by the Human Research Ethics Committee at the University of Western Australia (RA/4/1/7336).

Experimental design
Asymmetric walking was induced by having participants walk with a custom-manufactured ~90 mm platform shoe on their dominant limb only (equal to 9.7±0.4% of lower limb length). The shoe design is described in detail below. Participant gait mechanics were recorded during continuous walking on a force-plate-instrumented motorized treadmill under four conditions: (1) normal walking in standardized footwear; (2) walking in the asymmetrical footwear

using each participant's 'self-selected' technique; (3) walking in the asymmetrical footwear using an instructed 'crouching' technique (Fig. 1); and (4) walking in the asymmetrical footwear using an instructed 'vaulting' technique (described below; Fig. 1).

Comparison between conditions 1 and 2 was used to assess whether COM- or joint-level mechanics are more strongly conserved between normal walking and continuous self-selected walking with an asymmetric leg-length perturbation. (The terms 'conserved/conservation' here do not necessitate a total absence of change, but rather we use them to represent the degree to which variables deviate from normal walking.) The leg-length asymmetry intervention was used because it prevents simultaneous strong conservation of COM mechanics and joint mechanics relative to normal walking. A similar divergence in COM and joint work has been reported in symmetrical leg-length crouch walking (Gordon et al., 2009). While we did not specifically test muscle-level control, focusing on the joints allowed us to test a mechanism peripheral to COM mechanics that has direct proprioceptive feedback (Riemann and Lephart, 2002). Furthermore, although joint mechanics do not necessarily mirror muscle mechanics, they are known to be more closely associated with muscle mechanics than the whole-body COM (Sasaki et al., 2009).

Conditions 3 and 4 served as further assessment of whether COM or peripheral mechanics are more strongly conserved during a leg-length asymmetry perturbation. Our rationale was that the self-selected technique will result in stronger conservation of COM or joint mechanical variables compared with other plausible gait solutions if they are a priority control variable and represent the underlying control target. These two imposed conditions also provided the mechanical extremes of possible walking strategies, and thus allowed us to explore the spectrum of possible COM vertical displacement solutions.

It is important to stress that we were primarily concerned with the change between the perturbed and normal walking conditions (conservation of mechanics) rather than the discrete values of mechanical variables. For example, reducing COM displacement as much as possible has been found to be disadvantageous for locomotor
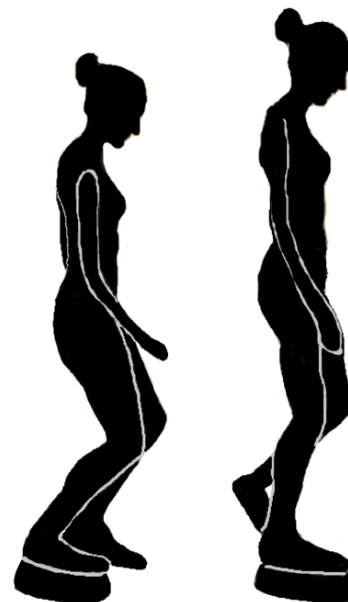

Fig. 1. Crouch (left) and vault (right) technique near midstance of the gait cycle.

economy (Massaad et al., 2007; Ortega and Farley, 2005). The ideal COM displacement might instead reside at some intermediate value (Kuo and Donelan, 2010), with deviations in either direction from this value being sub-optimal (Massaad et al., 2007).

All trials were conducted at 1.3 m s^{-1}, consistent with the average preferred walking speed of previous treadmill studies (Martin et al., 1992; Mohler et al., 2007; Panizzolo et al., 2013; Van Emmerik et al., 2005).

Testing protocol

Limb dominance (12 right, 3 left) was established by asking participants to stand on one leg, with the raised leg deemed dominant (Young et al., 2013). Subsequently, a series of retro-reflective markers were affixed to the participant's trunk and lower limbs in accordance with Besier et al. (2003). Three-dimensional kinematic data were collected using a 10-camera Vicon MX system (250 Hz; Oxford Metrics, Oxford, UK), synchronized to a split-belt (2×6 channel) instrumented treadmill (2000 Hz; Bertec Corporation, Columbus, OH, USA). In standardized footwear, participants completed a 3 min warm-up walk, followed by static and functional trials used to compute a joint coordinate system which included a functional hip joint center and mean helical knee axis (Besier et al., 2003). For this, participants moved their right and left feet (separately) into the following approximate positions whilst maintaining an extended knee: directly anterior (0 deg), 45 deg, 90 deg, 135 deg and directly posterior (180 deg), and completed five consecutive mid-range squats.

First, a 2 min walking trial in normal footwear was completed with the treadmill belt speed set to 1.3 m s^{-1} (the 'normal' condition). The dominant limb shoe (only) was replaced by a ~90 mm 'platform' shoe and the participant began a 3 min exploration period in which they were free to discover their preferred gait pattern under no instruction. A longer familiarization time was intentionally avoided to enable observation of the immediate prioritization response to the perturbation. At the end of the exploration, all participants were deemed, by observation, to have reached a 'consistent' technique; that is, displaying no major variation in stride-to-stride technique (e.g. foot strike pattern, vertical movement of the COM). A 2 min trial was collected to assess the self-selected technique when walking in the asymmetrical footwear. Following this, participants completed the two imposed techniques: 'crouching' and 'vaulting'.

For crouching, participants were asked to flex their knee as they walked over the platform shoe so that their peak hip height resembled that of normal walking. For vaulting, participants were asked to vault over the platform shoe, extending their knee as per midstance of normal walking. In this case, they were instructed that their peak hip height relative to their foot should be the same as that during normal walking (i.e. their peak hip height should equal normal walking peak hip height plus the height of the shoe platform). Crouching and vaulting conditions were completed independently, the order of which was reversed for each consecutive participant.

Data processing

Five representative strides from each condition were randomly selected from the recorded data. Marker trajectory and ground reaction force data were low-pass filtered using a zero-lag fourth-order Butterworth filter, with the same cut-off frequency of 15 Hz. Stride events (heel-strike and toe-off) were determined from the vertical ground reaction force. In all computations to follow, we define x, y and z directions as anteroposterior, vertical and mediolateral, respectively.

Computation of COM mechanical variables

We examined two variables across the stride: (1) positive and negative COT$_{COM}$, computed as the external COM work (W_{ext}; Eqns 1 and 2), normalized to body mass and distance traveled (J kg^{-1} m^{-1}), and (2) COM trajectory in the vertical and mediolateral directions (Eqns 7 and 8, respectively). These variables were computed from ground reaction force data. COM$_{COT}$ was analyzed as opposed to the COM work per step because differences in step frequency may arise between conditions and therefore work per distance will better represent the effect of gait on overall COM work requirements and thus locomotor economy. In computing W_{ext}, the combined limbs method was chosen to quantify the overall resultant COM work, exclusive of individual limb collision costs (Donelan et al., 2002). This method was specifically adopted in order to analyze the overall COM mechanics as opposed to limb-level mechanics. For values of $\overrightarrow{F_r} \cdot \overrightarrow{v_C} > 0$:

$$W_{ext}^+ = \int_{t_1}^{t_2} \overrightarrow{F_r} \cdot \overrightarrow{v_C}\, dt = \int_{t_1}^{t_2} (F_{rx}v_{Cx} + F_{ry}v_{Cy} + F_{rz}v_{Cz})dt; \quad (1)$$

and for values of $\overrightarrow{F_r} \cdot \overrightarrow{v_C} < 0$:

$$W_{ext}^- = \int_{t_1}^{t_2} \overrightarrow{F_r} \cdot \overrightarrow{v_C}\, dt = \int_{t_1}^{t_2} (F_{rx}v_{Cx} + F_{ry}v_{Cy} + F_{rz}v_{Cz})dt, \quad (2)$$

where F_r is the resultant ground reaction force, v_C is the resultant COM velocity, and t_1 and t_2 are initial and final time boundaries for the stride. The resultant force was computed as the instantaneous sum of the two treadmill force-plate recordings [the force-plate corresponding to the flat shoe limb (f) and the force-plate corresponding to the platform shoe limb (p); $F_{rx}=F_{fx}+F_{px}$, $F_{ry}=F_{fy}+F_{py}$ and $F_{rz}=F_{fz}+F_{pz}$]. The COM velocities (v_{Cx}, v_{Cy} and v_{Cz}) were computed by integrating the respective components of the combined force recordings and applying integration constants:

$$v_{Cx} = \int_{t_1}^{t_2} \frac{F_{fx} + F_{px}}{m}\, dt, \quad (3)$$

$$v_{Cy} = \int_{t_1}^{t_2} \frac{F_{fy} + F_{py} - m\boldsymbol{g}}{m}\, dt, \quad (4)$$

$$v_{Cz} = \int_{t_1}^{t_2} \frac{F_{fz} + F_{pz}}{m}\, dt, \quad (5)$$

where F_f and F_p are the force-plates corresponding to the flat and platform limbs, respectively, with force components denoted by x, y, z. Body mass and gravity (9.81 m s^{-2}) are represented by m and $\boldsymbol{g}$, respectively, while t_1 and t_2 are initial and final time boundaries of the stride (heel-strike to heel-strike). Integration constants were set according to Donelan et al. (2002). Briefly, the integration constant for v_{Cx} was computed by necessitating the mean v_{Cx} over a stride equaled the treadmill velocity and the integration constants for v_{Cy} and v_{Cz} were computed by necessitating the mean v_{Cy} and v_{Cz} over a stride equaled zero.

To compute COM displacement (s_{Cx}, s_{Cy} and s_{Cz}), the v_{Cx}, v_{Cy} and v_{Cz} traces were further integrated:

$$s_{Cx} = \int_{t_1}^{t_2} v_{Cx} dt, \quad (6)$$

$$s_{Cy} = \int_{t_1}^{t_2} v_{Cy} dt, \quad (7)$$

$$s_{Cz} = \int_{t_1}^{t_2} v_{Cz}\,\mathrm{d}t, \qquad (8)$$

where t_1 and t_2 are initial and final time boundaries of the stride (heel-strike to heel-strike).

Computation of stance-phase joint mechanical variables

To characterize joint mechanics (ankle, knee and hip), we examined four sets of variables across stance phase: (1) joint angles; (2) net joint and total support moments normalized to body mass, and to body mass and distance traveled per step, respectively (N m kg^{-1} and N m kg^{-1} m^{-1}, respectively; Winter, 2009, 1980); (3) instantaneous body mass-specific joint power (W kg^{-1}); and (4) positive and negative COT$_{JNT}$, computed as joint work (W_{JNT}; Eqns 9 and 10) normalized to body mass and distance traveled (J kg^{-1} m^{-1}). Joint kinematic and inverse dynamics calculations were performed on both limbs ('flat' and 'platform') and computed with Vicon Nexus software (Vicon, Oxford Metrics, Oxford, UK). Inertial properties of the foot segment were input, taking into consideration the added mass of the footwear. A combined total value for positive joint work for values of $M\omega > 0$, where M represents the joint moment and ω is joint angular velocity, was computed as:

$$W_{JNT}^{+} = \int_{t_1}^{t_2} M_{Af}\omega_{Af} + \int_{t_1}^{t_2} M_{Kf}\omega_{Kf} + \int_{t_1}^{t_2} M_{Hf}\omega_{Hf}$$
$$+ \int_{t_1}^{t_2} M_{Ap}\omega_{Ap} + \int_{t_1}^{t_2} M_{Kp}\omega_{Kp} + \int_{t_1}^{t_2} M_{Hp}\omega_{Hp}, \qquad (9)$$

where values at the ankle, knee and hip are respectively denoted by Af, Kf and Hf for the non-platform shoe ('flat') and Ap, Kp and Hp for the platform shoe. t_1 and t_2 are initial and final time boundaries of the stance phase (heel-strike to toe-off).

The same procedure was applied for total negative joint work for values of $M\omega < 0$:

$$W_{JNT}^{-} = \int_{t_1}^{t_2} M_{Af}\omega_{Af} + \int_{t_1}^{t_2} M_{Kf}\omega_{Kf} + \int_{t_1}^{t_2} M_{Hf}\omega_{Hf}$$
$$+ \int_{t_1}^{t_2} M_{Ap}\omega_{Ap} + \int_{t_1}^{t_2} M_{Kp}\omega_{Kp} + \int_{t_1}^{t_2} M_{Hp}\omega_{Hp}. \qquad (10)$$

Supporting body weight has been demonstrated to affect the metabolic cost of locomotion (Kram and Taylor, 1990). The 'support moment' represents the total moment required to support the body weight and is composed of the antigravity moments at the individual joints (extension at the hip and knee and plantarflexion at the ankle; Winter, 2009, 1980). The support moment thus serves as a useful cost metric for the overall weight support during gait. The (pre-normalized) integrated net total support moment from each limb was computed and summed to produce a single combined support moment (Eqn 11), which was then normalized to body mass and distance traveled (iTSM; N m kg^{-1} m^{-1}):

$$\text{iTSM (pre-normalized)} =$$
$$\int_{t_1}^{t_2} (M_{Af} + M_{Kf} + M_{Hf}) + \int_{t_1}^{t_2} (M_{Ap} + M_{Kp} + M_{Hp}). \qquad (11)$$

The non-directional (absolute) percentage change from normal walking was calculated for vertical and mediolateral COM range,

positive and negative COT$_{COM}$, total positive and negative COT$_{JNT}$, and the iTSM.

Shoe design

The platform shoe was a modified version of the footwear worn in the normal condition (lightweight, zero heel-to-toe gradient, minimally cushioned with a rubber sole and canvas upper; Volley, Brand Collective, Australia). A block of semi-rigid foam, with a height of approximately 90 mm, was secured to the sole of the platform shoe via adhesive. The foam was crafted to mirror the shape of the sole. However, to increase the base of support and reduce the risk of a fall, 20 mm of additional width was provided at the point of treadmill contact (shoe–ground interface). The height of the foam block as a percentage of dominant limb length (916.2±31.9 mm), ranged from 9.1% to 10.2%. Shoe mass was standardized to ensure equal shoe mass in all four conditions. For the flat shoes, this was achieved by sewing small packages of lead fishing weights to the medial and lateral aspects of the canvas upper.

Statistical analyses

All data were screened for normality. To assess whether COM or joint mechanics were prioritized by our participants, we utilized two approaches. We determined whether significant changes between the four conditions (normal, self-selected, crouch, vault) existed for the collection of COM- and joint-level variables. Analysis of variance (ANOVA; parametric) and Friedman test (non-parametric) repeated-measures statistics were used accordingly, with alpha levels set at 0.05 for all analyses. Significance was followed up with *post hoc* comparisons; Bonferroni correction (parametric) or Wilcoxon tests (non-parametric) with appropriately adjusted significance ($P=0.0125$). We tested for differences in temporal parameters using similar ANOVA methods.

Those data that presented with non-normal distributions are indicated in Results with an asterisk; however, where no reference to normality is made, the data have been processed using parametric tests. SPSS 21.0 (Chicago, IL, USA) was used to perform all statistical analyses detailed above.

To further assess how COM and joint mechanical variables changed in the temporal domain between conditions, we performed a cross-correlation analysis ('xcorr' in-built function; Matlab 2018a, MathWorks, Natick, MA, USA) on each participant's mean curve for normal versus the asymmetrical conditions (self-selected, crouch and vault). These correlations assess the similarity in the shape of the variable versus time curve but do not consider differences in magnitude. We defined correlations between 1 and 0.8 as very strong, between 0.79 and 0.6 as strong, between 0.59 and 0.4 as moderate, between 0.39 and 0.2 as weak, and between 0.19 and 0 as very weak.

Note that while we present the non-directional percentage difference between the normal condition and the three asymmetrical leg-length conditions (self-selected, crouch, vault), no statistical analyses were run on these data.

RESULTS
Temporal data

Stride rate (non-normally distributed) was assessed for all conditions and presented with an ANOVA main effect. While crouching stride rate (1.00±0.10) exceeded normal stride rate [0.93±0.04; $P=0.012^*$, where the asterisk indicates non-normal distribution of data (see Materials and Methods)], self-selected stride rate (0.95±0.06; $P=0.002^*$) and vaulting stride rate

Table 1. Center of mass and joint mechanical variables

| Condition | COM trajectory range (m) | | COT$_{COM}$ (J kg^{-1} m^{-1}) | | COT$_{JNT}$ (J kg^{-1} m^{-1}) | | iTSM (N m kg^{-1} m^{-1}) |
	Vertical	Mediolateral	Positive	Negative	Positive	Negative	
Normal	0.052±0.01	0.046±0.005	0.407±0.063	−0.381±0.092	1.665±0.158	−1.079±0.104	0.802±0.218
Self-selected	**0.078±0.018***	0.05±0.006	**0.547±0.079***	**−0.551±0.11***	**1.933±0.222***	**−1.393±0.149***	**1.250±0.239***
Crouch	**0.053±0.016‡**	0.047±0.009	0.488±0.108	−0.482±0.131	**1.989±0.168***	**−1.535±0.192*,‡**	**1.754±0.292*,‡**
Vault	**0.116±0.011*,‡,§**	0.05±0.006	**0.766±0.126*,‡,§**	**−0.788±0.159*,‡,§**	**2.240±0.247*,‡,§**	**−1.671±0.24*,‡**	**1.142±0.206*,§**

COM, center of mass; COT$_{COM}$, center of mass mechanical cost of transport; COT$_{JNT}$, joint mechanical cost of transport; iTSM, integrated net total support moment. Data are means±s.d.
Bold indicates significance. *Significantly different from the normal condition. ‡Significantly different from the self-selected condition. §Significantly different from the crouch condition.

(0.92±0.06; P=0.001*), no other significant differences were present between the four conditions. Stance-phase duration of flat and platform shoe limbs across the four conditions produced an interaction effect. On the flat side, stance-phase duration of normal walking (0.68±0.03 s) exceeded that of the self-selected (0.65±0.04 s; P=0.017) and vault (0.64±0.04 s, P=0.044) conditions, and on the platform side, the crouch stance phase was shorter (0.63±0.05 s) than the stance phase of both the self-selected (0.67±0.05 s; P=0.024) and vault (0.71±0.05 s; P<0.001) techniques. While crouching produced equal stance durations, the platform-limb stance was longer than the flat-limb stance for both the self-selected and vault conditions (P<0.022).

COM mechanics
COM displacement
COM mechanical parameters are displayed in Table 1. A main effect of gait condition was detected for vertical COM displacement. This measure confirmed that our participants generated a range of COM vertical displacements across the self-selected, crouching and vaulting conditions (Fig. 2A). When compared with normal walking (0.05±0.01 m vertical COM displacement), the crouch condition was not significantly different (P>0.999). The self-selected and vault conditions, in contrast, displayed a far greater COM vertical range compared with normal walking (53% and 129% change, respectively; P<0.001). Self-selected asymmetric walking produced a higher COM vertical range than the crouch condition (P=0.009) but a lower range than the vault condition (P<0.001). The mediolateral COM range was also calculated; however, no significant differences were observed between the four conditions (P>0.216; Fig. 2B).

COT$_{COM}$
The positive COT$_{COM}$ (main effect of condition present) was elevated above normal walking during the self-selected condition (P<0.001). The positive COT$_{COM}$ was also elevated above normal walking in the vaulting condition, but to an even greater extent (P<0.001; Table 1, Fig. 3). Unlike the other two asymmetry conditions, the COT$_{COM}$ in the crouch condition was not statistically different from that during normal walking (P=0.135). The differences in negative COT$_{COM}$ exhibited a similar pattern to those of positive COT$_{COM}$ (non-normally distributed; Table 1, Fig. 3).

Joint mechanics
Stance-phase joint kinematic and kinetic gait profiles
Compared with normal walking, crouched walking was characterized by platform-limb flexed hip and knee joint postures throughout stance phase (Fig. 4). The near-isometric behavior of the knee joint was accompanied by an increased net knee extensor moment, deviating considerably from normal gait mechanics (Fig. 5). Conversely, vaulting appeared to utilize platform-limb knee and hip joint extension during the second half of stance phase to increase vertical COM displacement. As would be expected, the resulting kinematic traces in the vaulting stance leg closely mirror those of normal walking (Fig. 4). Furthermore, around the period of double-support, vertical ascent onto the platform shoe is assisted by an earlier onset of flat-limb positive ankle power, coupled with increased platform-limb positive hip power (Fig. 6). The self-selected condition was associated with midrange hip and knee extension relative to the imposed techniques. The large stance-phase knee moment and ankle power associated with crouching and vaulting, respectively, were avoided during the self-selected gait.
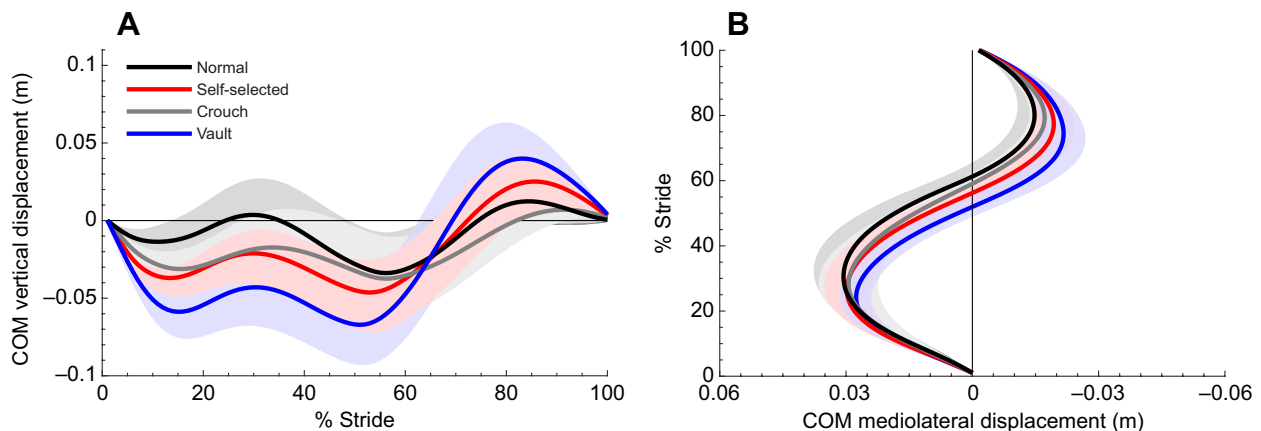

Fig. 2. Center of mass (COM) vertical and mediolateral displacement over the stride. (A) Vertical displacement; (B) mediolateral displacement. Data begin and end at the normal limb (non-platform shoe) heel-strike. Data are normalized to the center of mass position at initial heel-strike and are presented as means±s.d. (shaded regions) (N=15).
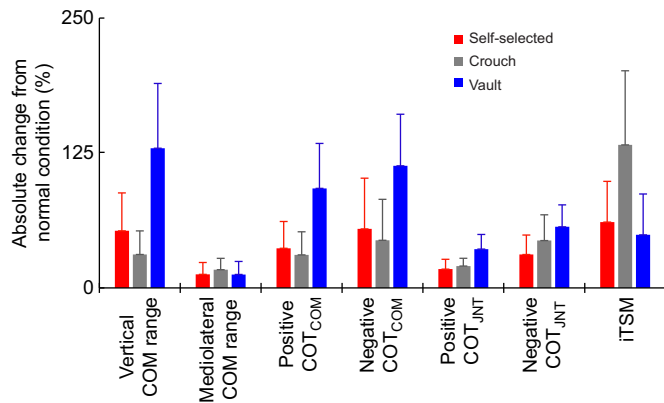
Fig. 3. Non-directional (absolute) percentage change from normal walking for self-selected, crouch and vault conditions. Data (means±s.d., N=15) include: vertical and mediolateral center of mass (COM) range (m), positive and negative center of mass cost of transport (COT_{COM}; J kg^{-1} m^{-1}), total positive and negative joint cost of transport (COT_{JNT}; J kg^{-1} m^{-1}) and integrated net total support moment (iTSM) normalized to body mass and distance traveled (N m kg^{-1} m^{-1}).

Stance-phase COT_{JNT}

Total positive (normally distributed) and negative (non-normally distributed) stance-phase COT_{JNT} is presented in Table 1. Main effects were detected for both measures. *Post hoc* analyses revealed increases in positive and negative COT_{JNT} in all leg-length asymmetry conditions when compared with values of normal walking ($P<0.003$). The self-selected technique produced total COT_{JNT} closest to normal walking, with an absolute change of 17% and 31% in positive and negative COT_{JNT}, respectively (Fig. 3). These differences were further exaggerated in the crouch (positive: 20%, negative 44%) and vault (positive: 36%, negative 57%) conditions (Fig. 3). Total positive COT_{JNT} was greater when

vaulting than in both the self-selected and crouch trials ($P<0.009$), which were not significantly different from one another ($P=0.959$). Total negative COT_{JNT} was lower for the self-selected than for both the crouch and vault techniques ($P<0.006*$), whilst the two imposed conditions did not vary significantly ($P=0.088*$).

Work distribution between joints

The distribution of positive and negative COT_{JNT} across the joints throughout stance phase did not differ substantially when walking with the leg-length asymmetry perturbation compared with normal walking (Table 2). In the normal condition, ankle, knee (non-normal distribution) and hip joint positive COT_{JNT} contributions of 35.9±4.1%, 22.9±5.7% and 41.2±4.9% to the total mechanical COT of the limbs (the sum of the COT_{JNT} in each joint from both limbs) were observed, respectively. The ankle, knee and hip (non-normal distribution) joint negative COT_{JNT} accounted for 32.9±8.8%, 43.4±9.2% and 23.7±8.3%, respectively (for the percentage COT_{JNT} contribution in the other conditions, see Table 2). Significance testing revealed the ankle positive COT_{JNT} contribution was greater in the normal condition than in the vault condition ($P=0.002$). This was the only percentage COT_{JNT} contribution (including both positive and negative values) to deviate significantly from normal walking across all measured joints.

iTSM

Stance-phase support moment parameters are displayed in Table 1. A main effect of gait condition was detected for iTSM. All asymmetrical gaits produced greater iTSM than normal walking ($P<0.001$), with no significant difference detected between self-selected and vault conditions ($P=0.139$). Both the self-selected and the vaulting asymmetry techniques, however, displayed significantly ($P<0.05$) lower iTSM than the crouching condition. The absolute percentage change between the asymmetry
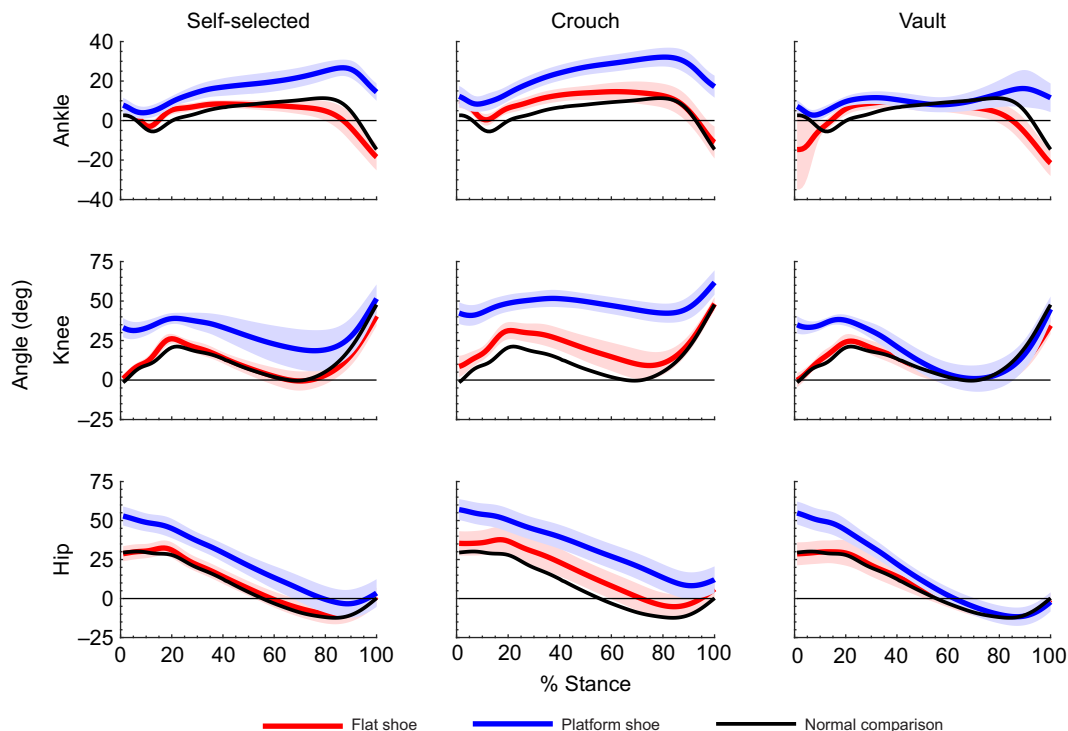

Fig. 4. Joint angles during stance phase for the flat and platform limb. A normal walking trace is included for comparison. The traces begin at heel-strike and end at toe-off of the respective limb. Data are presented as means±s.d. (shaded regions) (N=15).

Table 2. Percentage COT$_{JNT}$ distribution between the ankle, knee and hip joints

Condition	Positive COT$_{JNT}$ (%)			Negative COT$_{JNT}$ (%)		
	Ankle	Knee	Hip	Ankle	Knee	Hip
Normal	35.90±4.08	22.92±5.74	41.18±4.39	32.89±8.84	43.39±9.18	23.73±8.31
Self-selected	31.31±6.57	23.47±6.61	45.22±5.99	31.84±6.53	44.10±6.04	24.05±5.57
Crouch	32.01±7.19	22.44±7.76	45.55±7.82	29.00±5.92	46.45±6.90	24.55±6.81
Vault	**30.36±4.46**[*]	23.45±5.33	46.20±5.33	**44.16±8.82**[‡,§]	**34.53±7.60**[‡,§]	21.31±5.25

Data (means±s.d.) are the average between the two limbs during stance phase.
Bold indicates significance. [*]Significantly different from the normal condition. [‡]Significantly different from the self-selected condition. [§]Significantly different from the crouch condition.

conditions and normal walking was 61%, 132% and 49% for the self-selected, crouch and vault conditions, respectively (Fig. 3).

Cross-correlation
Cross-correlations of the normal condition versus each asymmetrical gait condition (self-selected, crouch and vault) are presented in Table 3. COM trajectories produced strong (>0.7) to very strong (>0.8) correlations for each condition. The cross-correlation of most joint variables was also strong to very strong across conditions, but some weak correlations were also exhibited (Table 3). Overall, the strongest correlations existed between normal walking and the self-selected perturbed condition.

DISCUSSION
The current study questioned whether the COM or peripheral structures, in this case joint mechanics, reflect targets of control prioritized by the central nervous system during human walking. This was assessed indirectly by quantifying the efficacy with which COM and joint mechanical costs were conserved (i.e. how much/little they changed relative to normal walking) when humans were exposed to a continuous asymmetrical perturbation in the form of uneven leg-length (footwear heights). Additionally, we imposed two alternative techniques for negotiating the perturbation, namely 'crouching' and 'vaulting', which spanned the spectrum of possible COM vertical displacement solutions. Our hypothesis that conservation of joint-level mechanics would be stronger than conservation of COM mechanics was supported. During stance phase, the self-selected technique minimized joint-level disturbances compared with those at the COM. This finding indicates objectives other than the literal control of the whole-body COM may be given precedence in the neuromuscular control scheme for economical walking, at least during steady-state
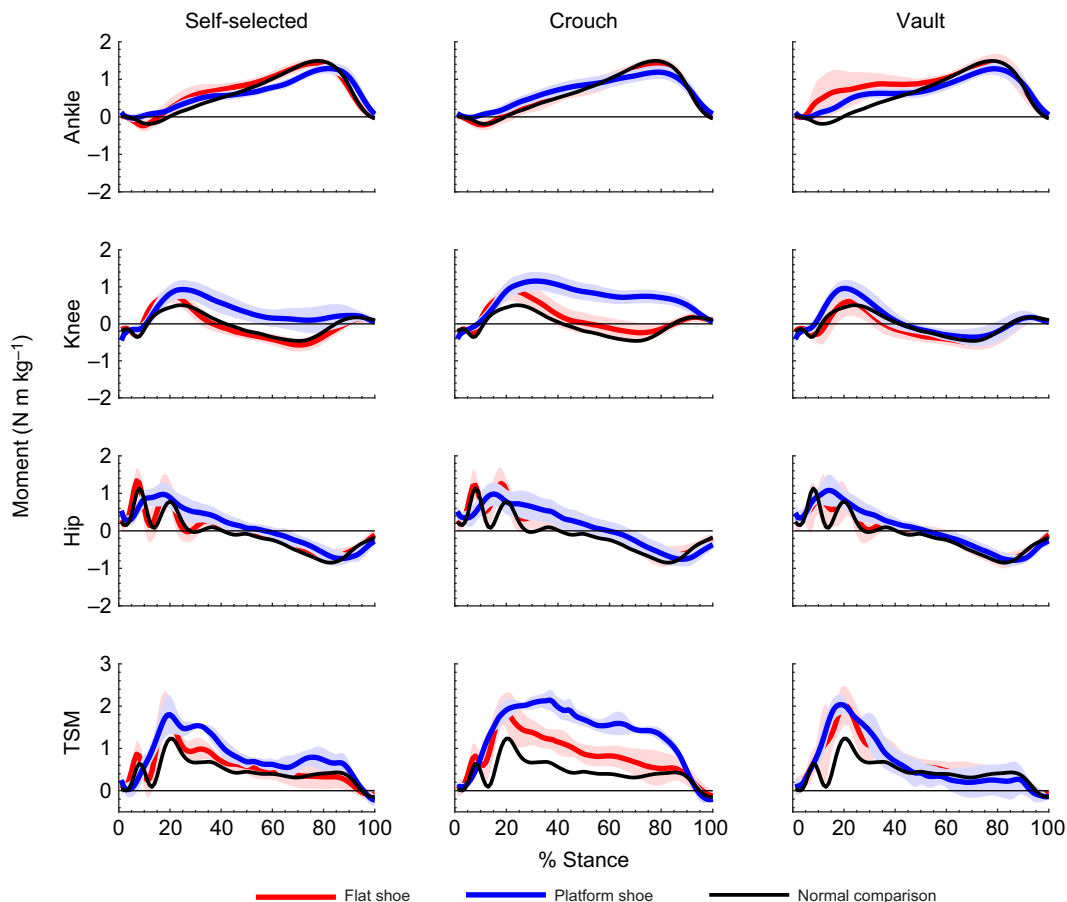

Fig. 5. Net mass-specific joint moments during stance phase for the flat and platform limb. A normal walking trace is included for comparison. The traces begin at heel-strike and end at toe-off of the respective limb. Data are presented as means±s.d. (shaded regions) (N=15). TSM, total support moment.
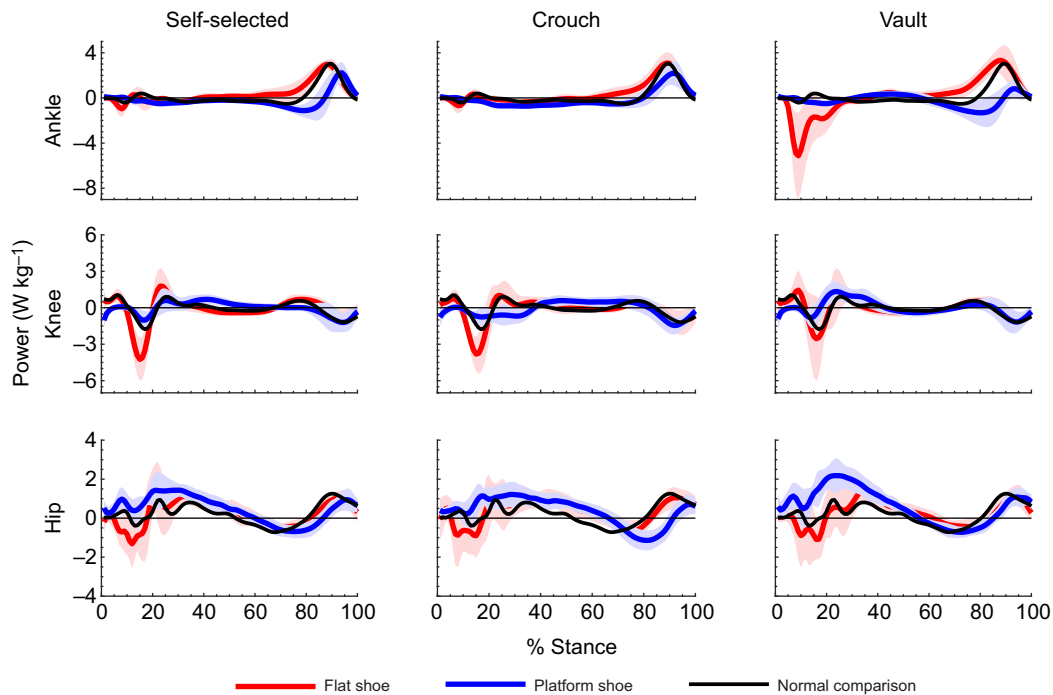
Fig. 6. Net mass-specific joint power during stance phase for the flat and platform limb. A normal walking trace is included for comparison. The traces begin at heel-strike and end at toe-off of the respective limb. Data are presented as means±s.d. (shaded regions) (N=15).

locomotion and prior to longer-term motor learning. It must be noted that our findings do not conclusively point to the joints as the specific target of control, nor do we propose there is a direct sensor for COT_{JNT} or overall support moments. Rather, the stronger conservation of joint mechanics observed here is interpreted to reflect a general peripheral-level control scheme for economical locomotion arising from joint and/or muscle feedback.

COM versus peripheral (joint) mechanical conservation
Studies specifically comparing COM- and peripheral-level control are sparse and offer conflicting findings. It has been suggested that variation in joint mechanics is a strategy to conserve higher-level mechanics including whole-limb trajectories and power generation, and COM motion. For example, during postural balance tasks, humans have been observed to regulate COM-related behavior through coordination of lower-level structures including joints and muscles (Nashner, 1977; Nashner and McCollum, 1985; Ting and Macpherson, 2005; Torres-Oviedo et al., 2006). Joint-mediated control of whole-limb mechanics (which are closely linked to COM mechanics) has also been observed both in unperturbed human walking (conserved limb power; Toney and Chang, 2016) and after peripheral nerve injury in walking cats and rodents (conserved limb trajectories; Bauman and Chang, 2013; Chang et al., 2009). Panizzolo et al. (2017) likewise showed that individual joint mechanics (ankle, knee, hip) adapt to various unanticipated terrain disturbances in ways that maintain total positive mechanical work of the lower limb, irrespective of the type of perturbation. Albeit not directly studying walking gait, a pivotal series of running and hopping studies have also shed light on central versus peripheral mechanical conservation. Several groups have shown that humans maintain their COM mechanics by adjusting leg stiffness across various conditions including running speed, hopping frequency and surface stiffness (Chang et al., 2008; Ferris et al., 1998; Ferris and Farley, 1997; Yen et al., 2009).

Taken together, the aforementioned studies indicate the nervous system may prioritize conservation of COM rather than joint-level mechanics. This conclusion is seemingly in contrast with findings of the current study. The previous studies did not, however, directly asses COM- or joint-level costs in the form of mechanical work or COT. This is an important consideration because, as this study shows, even altered joint kinematic and kinetic profiles do not necessarily impair COT_{JNT} (see below for further discussion). It is not clear, therefore, whether the conservation of higher-level mechanics, including the COM, in the previous studies necessarily rules out control of lower-level costs at joints and/or muscles, despite the observed changes in the measured joint mechanics. The current study is arguably less ambiguous with regard to COM- versus joint-level control, in part because it was designed specifically to limit simultaneous strong conservation of COM- and joint-level costs. It is also worth noting that many human subject tests have specific requirements which restrict technique (e.g. hop at a set frequency or set height). These instructions might influence how the subject perceives the task goal and thus might artificially impart conservation of COM- and/or joint-level mechanics. The present study was careful to minimize any instruction in the self-selected condition.

Work on cursorial ground birds which, similarly, do not take instruction on their adopted movement behavior, paints a more complex picture of COM versus joint control strategies. In a comprehensive series of studies on running guinea fowl negotiating both anticipated and unanticipated perturbations, Daley and colleagues provide observations which contradict COM dynamics as the direct target of control (Birn-Jeffery et al., 2014; Daley et al., 2006; Daley and Biewener, 2006). While the authors show that the overall limb-loading magnitude is consistent with spring–mass dynamics, the COM dynamics are not maintained relative to unperturbed gait. This body of work disputes the notion that COM dynamics are strongly conserved, and instead suggests some aspects of limb or joint loading are more likely to be the direct targets of

Table 3. Cross-correlation results from COM data, and kinematic and kinetic joint data

Condition	COM displacement		Ankle angle		Knee angle		Hip angle		Ankle moment		Knee moment		Hip moment		Ankle power		Knee power		Hip power	
	Vertical	Mediolateral	Flat shoe	Platform shoe	Flat shoe	Platform shoe	Flat shoe	Platform shoe	Flat shoe	Platform shoe	Flat shoe	Platform shoe	Flat shoe	Platform shoe	Flat shoe	Platform shoe	Flat shoe	Platform shoe	Flat shoe	Platform shoe
Normal vs self-selected	0.83±0.12	0.96±0.04	0.79±0.17	0.64±0.31	0.95±0.05	0.84±0.09	0.97±0.06	0.90±0.10	0.98±0.01	0.97±0.02	0.89±0.06	0.30±0.35	0.87±0.08	0.86±0.07	0.81±0.09	0.49±0.32	0.71±0.13	0.33±0.27	0.63±0.15	0.71±0.10
Normal vs crouch	0.81±0.22	0.96±0.04	0.88±0.08	0.66±0.26	0.90±0.10	0.75±0.15	0.89±0.18	0.77±0.15	0.98±0.01	0.97±0.02	0.70±0.25	−0.15±0.39	0.78±0.24	0.78±0.09	0.84±0.11	0.77±0.17	0.65±0.21	0.19±0.37	0.50±0.31	0.43±0.26
Normal vs vault	0.72±0.26	0.88±0.10	0.62±0.20	0.47±0.31	0.92±0.06	0.84±0.07	0.98±0.02	0.97±0.06	0.89±0.10	0.96±0.03	0.73±0.28	0.69±0.18	0.80±0.14	0.87±0.05	0.57±0.21	0.12±0.25	0.56±0.17	0.37±0.19	0.53±0.20	0.68±0.14

Data are means±s.d.

control (Daley et al., 2006; Daley and Biewener, 2006). Full and Koditschek (1999) similarly suggest that any substantial shift in COM behavior from the original 'template' indicates that COM mechanics are not a 'literal control target for the musculoskeletal system' (Full and Koditschek, 1999). Other experiments provide indirect support for a joint-level control scheme. For example, Kao et al. (2010) showed that unexpected reductions in the ankle joint torque delivered by a powered exoskeleton are accommodated by biological (muscle) moments so that the total moment generation is remarkably similar between perturbed and non-perturbed walking.

The present study indicates that conservation of COM mechanics is not always prioritized during human locomotion, and further challenges the notion that the COM is the principal target of control. There are several lines of evidence suggesting conservation of lower-level peripheral factors, as indicated by joint mechanical costs, are prioritized over conservation of COM costs after induced leg-length asymmetry, as detailed below.

Mechanical COT conservation

First, we demonstrated that positive COT_{JNT} is more strongly conserved (changed less relative to normal walking) than positive COT_{COM} during a gait perturbation in which simultaneous conservation of both forms of work is not easily achievable. This is especially important considering that minimization of mechanical work, and work-derived metabolic energy predictions, have been an underlying basis for a COM control strategy (Srinivasan, 2010; Srinivasan and Ruina, 2006). The conservation of COT_{JNT} over COT_{COM} work has a mechanistic explanation if energy cost is, in fact, a locomotor objective. Joint work, unlike COM work, accounts for simultaneous positive and negative work at the joints (Zatsiorsky, 2002), similar to how the individual-limb COM work approach captures simultaneous positive and negative work of the left and right limbs (Donelan et al., 2002). As a result, COT_{JNT} is more strongly associated with muscle mechanical energy (Sasaki et al., 2009) and therefore better captures global (organismal) metabolic energetics compared with COT_{COM} (Gordon et al., 2009; Umberger and Rubenson, 2011). However, it remains unclear whether the nervous system senses and regulates directly at the level of the joints. While sensory feedback from joints exist, muscle-level targets of control (such as muscle fiber strain, force or activation) might instead dictate the preferred gait solution, with joint work conservation occurring because it is more strongly coupled to muscle function than the COM. The observed conservation of joint mechanics might thus reflect the nervous system optimizing whole-body energy costs based on correlates that are more rapidly sensed than COT_{JNT} (Wong et al., 2017).

It should be noted that minimization of COT_{COM} does not minimize metabolic energy (Gordon et al., 2009; Massaad et al., 2007; Ortega and Farley, 2005), and therefore we did not expect that COM work should be as low as possible even if it is a target of control. Rather, we would expect that the change in COT_{COM} between normal and asymmetric walking conditions should be minimal. This is because deviations in COT_{COM}, both above and below normal walking values, increase the energy cost of walking (Massaad et al., 2007). In contrast, however, our results provide evidence that controlling COT_{COM} – in particular, avoiding deviations in COT_{COM} from that of normal walking – is not prioritized during human walking if it degrades other potentially stronger control targets (e.g. joints and/or muscle mechanics).

It is also important to acknowledge that in recent perturbed walking experiments, improved gait symmetry in various biomechanical parameters (e.g. step length) may conserve

COM and/or joint mechanics relative to normal walking, but does not necessarily result in energetic optimality (Sánchez et al., 2017). Therefore, it remains possible that COT_{JNT} may have been conserved irrespective of any link to energetic task goals. If this were the case, other joint-level optimality criteria, for example joint stress (Alessandro et al., 2018), might have factored into the observed regulation of gait behavior. Identifying the relative contribution of energetic and mechanical determinants of joint mechanical conservation is challenging but will prove important to further uncover underlying control objectives in human locomotion.

Gait technique selection

Second, only strong conservation of joint mechanical costs was specific to the self-selected gait solution; COT_{JNT} and support moment were minimized in the self-selected condition (Table 1, Fig. 3). This was also reflected to a degree in cross-correlation analyses, which showed the strongest correlation of joint variables between the normal and the self-selected conditions (Table 3). In contrast, stronger conservation of COM costs occurred in the imposed (non-preferred) crouch condition; positive and negative COT_{COM}, and vertical COM range, were significantly lower in magnitude, and closer to normal walking values, during crouch walking compared with the self-selected asymmetric gait (Table 1, Fig. 3). In fact, unlike the self-selected asymmetric gait, there were no statistical differences in the parameters between normal walking and crouch walking. Similarly, cross-correlations were very strong (>0.8) between normal walking and not only the self-selected condition but also the crouch condition (Table 3; although in general it should be noted that the shape of the COM trajectory appears less impacted by the perturbation than the overall magnitude of COT_{COM}).

These results offer evidence that direct, purposeful conservation of COM mechanics is not a predictable characteristic of steady-state human gait in which energetic minimization is likely an important objective. Instead, peripheral structures are arguably the more plausible control targets that are sensed and regulated during walking in order to satisfy the task objective of economical gait.

Given the COM displayed a mechanical profile most similar to that of normal walking in the crouch condition, why did participants avoid a crouched gait when selecting their preferred technique? This can be understood when examined in context with joint mechanics. Whilst crouching best maintained COM costs, it was also found to produce an iTSM that deviated substantially from normal walking values (Fig. 3). A crouched gait and the concomitant elevation in iTSM are expected to incur a considerable increase in muscle activation and force, (Abitbol, 1995; Biewener, 1989; Carey and Crompton, 2005; Hicks et al., 2008; Hsu et al., 1993; Perry et al., 1975; Steele et al., 2013, 2010) and, by extension, locomotor energetics (Kram, 2000; Kram and Taylor, 1990; Roberts et al., 1997). Rather than adopting a COM-conserving gait (crouch), subjects instead preferred a gait solution that minimized the increase in both COT_{JNT} and joint moments at the expense of COM mechanics.

Conserved distribution of joint work

Finally, the distribution of work between joints across normal walking and the asymmetric walking conditions provide further evidence that joint mechanics are largely conserved in response to a leg-length asymmetry perturbation. Whereas total positive COT_{JNT} was found to increase in all conditions relative to normal walking, the distribution of positive COT_{JNT} remained largely unchanged between the normal, self-selected and crouch

techniques. Only the ankle showed a statistical difference between the normal and vault conditions. In general, decreases in the ankle contribution to positive COT_{JNT} on the platform shoe side were compensated for by increases on the normal shoe side, allowing the ankles to continue to contribute ~36% to total work.

Are joint kinematics and kinetics both conserved after induced leg-length asymmetry?

It is conceivable that overall support moments and COT_{JNT} are optimally conserved after perturbation, whilst joint kinematics (angles) are altered. Compensation of joint kinematics, for example, has been suggested to be a control strategy by which higher-level gait features, including whole-limb kinematics, are maintained following neuromuscular injury (Bauman and Chang, 2013; Chang et al., 2009). Our analyses of individual joint kinematics, moments and powers provide insight into the extent of joint-level conservation. Similar to Chang et al. (2009), we observed modification of all joint angles during the self-selected gait solution to induced leg-length asymmetry, both for the limb on the platform shoe side and for the limb on the unaltered (flat) shoe side. Unlike joint moments and COT_{JNT}, these joint kinematic modifications were not minimized in the self-selected condition; the smallest deviation in joint angles was observed in the vaulting condition (Fig. 4). Thus, motor redundancy of joint kinematics may aid in the conservation of joint kinetic variables (work and moments). It is important to note, however, that whilst there is clearly a larger offset in joint angle (posture change) in the self-selected gait compared with vaulting, the angular excursions and velocities over the stance phase are greater during vaulting. This can contribute to both the increase in the moments and COT_{JNT} required at the joints during the vaulting gait (Figs 5 and 6). When comparing individual joint moment and power, some deviation is evident during the self-selected gait condition compared with normal walking. Nevertheless, these deviations are smallest overall in the self-selected condition compared with the two imposed conditions (crouching and vaulting), a finding reflected by the stronger cross-reactions of most joint moment and power traces between normal and self-selected conditions. This observation is consistent with the overall smallest effect on COT_{JNT} and net support moments in the self-selected condition.

Is the COM a direct target of control that is sensed?

Several lines of inquiry suggest COM mechanics are a target of neuromuscular control during walking. The view that controlling COM mechanics is important for economical locomotion is often supported by modeling studies, many of which capture salient features of limbed locomotion when using COM mechanical energetics (or metabolic energetics derived from COM mechanics) as their objective function (Alexander, 1980; Ruina et al., 2005; Srinivasan and Ruina, 2006). For instance, in an attempt to determine why humans select walking and running gaits from the myriad of possible biomechanical variations, Srinivasan and Ruina (2006) utilized a basic bipedal pendular model onto which they imposed the goal of minimizing the mechanical COT. This simple model, even when devoid of elastic properties, discovered walking (inverted pendulum) and running (impulsive bouncing) gait solutions at low and high velocities, respectively. Others have proposed that COM control is central to gait stability, which may, in turn, influence locomotor economy (Donelan et al., 2004; Ijmker et al., 2013). Several studies indicate that human limb mechanics are adjusted to maintain a desirable COM kinematic state (Aminiaghdam et al., 2017; Grimmer et al., 2008; Hof et al., 2010, 2005; Townsend, 1985). These COM control schemes, based largely on COM position and velocity, help explain stabilization after

perturbations, but also stability during steady-state locomotion (Wang and Srinivasan, 2014).

Under these mechanisms of COM control, the COM state must be either sensed directly or estimated indirectly through other sensory modalities. It is conceivable that the vestibular or visual system, intestinal sensors, proprioceptive feedback or some combination of these provides the necessary sensory input. How plausible these mechanisms are as a sensor for the COM mechanical state has recently been reviewed (Bruijn and van Dieën, 2018), but as the authors point out, whether these sensory modalities are, in fact, mapping COM kinematics and kinetics during gait remains unexplored. Some authors have even proposed that stable steady-state walking can occur in the absence of neural feedback (Garcia et al., 1998; McGeer, 1990).

The current study does not directly test whether the COM mechanical state is sensed. Thus, we cannot definitively discount the COM as a target of control, responsible for the observed mechanical patterns of normal and leg-length asymmetry walking. However, our finding that COM mechanics are not prioritized when they are pitted against joint mechanics provides initial support for a non-COM-based control scheme. Our results are indicative of peripheral control, which we postulate resides at the joint and/or muscle level and suggest that stereotypical COM mechanics may be a derived characteristic. Whether our results generalize to other forms of gait perturbation or normal unperturbed walking is not known. Further experiments that determine more directly whether joint/muscle targets of control indeed dictate observed COM mechanical patterns will prove important for understanding the motor control of walking.

Limitations

This study considers the primary task objective to be energetic cost minimization. Energy minimization is pervasive in steady-state locomotion. However, other task objectives such as stability, musculoskeletal (fatigue/injury avoidance) and psychological (comfort, pain avoidance) factors may also have motivated the self-selected gait mechanics we observed. In the extreme case, the COM may have been the principal control target for a different task objective (e.g. stability) where the self-selected COM mechanics may be the optimally stable solution. This interpretation, however, lacks clear evidence. Although speculative, we also cannot rule out that the preferred gait solution does not reflect any specific task-goal objective (or combination of objectives). This might occur if the preferred gait arises through a feedback-mediated central pattern generator encoding joint mechanics.

No asymmetrical footwear familiarization was provided to participants prior to attending the laboratory and was only minimally provided prior to testing. Limited familiarization allowed us to determine acute control responses, which was our intended objective. However, future work could consider the effect of adaptation to identify shifts in control with training. Finally, a consideration of swing-phase joint mechanics when walking with induced leg-length asymmetry may also provide a more complete understanding of control strategies.

For the current study, we held speed constant in order to compare magnitudes across key variables from each condition, and to present a speed-independent conclusion. It is possible, however, that our COM and joint mechanics were influenced by the experimental speed selected. For example, increased walking speed has been associated with increased vertical and decreased mediolateral COM displacement (Orendurff et al., 2004). An interesting future direction may be to administer the same experiment but allow all conditions to be performed at the subject's preferred walking speed unique to that condition.

Despite these limitations, our finding that conserved joint mechanics are prioritized is consistent with a neuromuscular control scheme of walking defined by targeted control at a peripheral musculoskeletal level rather than the COM.

Conclusions

In summary, COM mechanics serve as a useful metric capturing fundamental features of legged locomotion. However, we propose that the priority for conserving joint mechanics indicates that control targets most likely reside in peripheral musculoskeletal structures as opposed to the COM. We suggest that joint mechanics are a better proxy for the underlying peripheral control of walking. Thus, joint mechanical constraints and/or cost functions may offer advantages over those applied to the COM when modeling human locomotion. The results from this study also have implications for understanding both normal and pathological gait, as well as for bio-inspired robots and wearable technologies (e.g. exoskeletons) where locomotor control is a critical design feature.

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