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The Motor and the Brake of the Trailing Leg in Human Walking: Leg Force Control Through Ankle Modulation and Knee Covariance

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Abstract

Human walking is a complex task, and we lack a complete understanding of how the neuromuscular system organizes its numerous muscles and joints to achieve consistent and efficient walking mechanics. Focused control of select influential task-level variables may simplify the higher-level control of steady state walking and reduce demand on the neuromuscular system. As trailing leg power generation and force application can affect the mechanical efficiency of step-to-step transitions, we investigated how joint torques are organized to control leg force and leg power during human walking. We tested whether timing of trailing leg force control corresponded with timing of peak leg power generation. We also applied a modified uncontrolled manifold analysis to test whether individual or coordinated joint torque strategies most contributed to leg force control. We found that leg force magnitude was adjusted from step-to-step to maintain consistent leg power generation. Leg force modulation was primarily determined by adjustments in the timing of peak ankle plantar-flexion torque, while knee torque was simultaneously covaried to dampen the effect of ankle torque on leg force. We propose a coordinated joint torque control strategy in which the trailing leg ankle acts as a motor to drive leg power production while trailing leg knee torque acts as a brake to refine leg power production.

Keywords

Biomechanics; Locomotion; Motor Control; Robustness; Uncontrolled Manifold

Introduction

Steady-state human walking is a complex task that requires coordination of muscle activations, joint torques, and leg forces at various levels of neuromuscular control. Control of bipedal walking is likely simplified by exploiting the underlying dynamics (McGeer 1990; Garcia, Chatterjee et al. 2000; Collins, Ruina et al. 2005; Su and Dingwell 2007; Kurz, Judkins et al. 2008; Verdaasdonk, Koopman et al. 2009). Focusing higher-level control to a specific set of influential task parameters (e.g. leg force) during particular gait phases (e.g. double support) could reduce the number of variables and the duration over which

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control is required, thus simplifying the motor control problem (Bosco and Poppele 2000; Bosco, Poppele et al. 2000). Quantitative models of bipedal walking may suggest possible candidates for such controlled variables. Dynamic walking principles suggest that step-to-step transitions are critical periods of the gait cycle where much of the mechanical energetic demand originates (Kuo 2002; Donelan, Kram et al. 2002a; Donelan, Kram et al. 2002b). Negative work by the leading leg results in mechanical energy loss that must be re-supplied to the system with positive work generated by the trailing leg to maintain a steady, forward gait (Kuo 2002; Donelan, Kram et al. 2002a; Donelan, Kram et al. 2002b). Although forward musculoskeletal gait simulations also suggest significant muscle work is done in single support to raise the center of mass, they also corroborate the importance of mechanical work done by trailing leg muscles to propel the body forward and upward in late stance to redirect center of mass movement during the step-to-step transition (Neptune et al. 2004). Under steady walking conditions, achieving consistent trailing leg power production on each step may therefore be an implicit task goal of walking. How consistent leg power production is achieved despite inherent motor variability remains unclear. The purpose of this study was to identify a possible mechanism for generating consistent trailing leg power production despite intrinsic neuromuscular variability in steady state human walking.

Modulating trailing leg force on the ground likely contributes to consistent leg power generation. Leg power is determined by leg force and center of mass velocity (Eq. 1, see Donelan et al., 2002). The timing of trailing leg force application is important for achieving minimal energetic loss (Kuo 2002; Ruina, Bertram et al. 2005). Adjustments in leg force timing may therefore influence how trailing leg power is generated and provide a possible mechanism for stabilizing leg power. Our previous work demonstrated that joint torque variance was structured to modulate trailing leg vertical forces with each step in human walking (Toney and Chang 2013). Modulation of a particular variable may reflect step-to-step corrections made to achieve consistent execution of an alternative variable at a different hierarchical level (Shim, Latash et al. 2003; Gorniak, Zatsiorsky et al. 2007; Gorniak, Zatsiorsky et al. 2009). Modulation of force along the long axis of the trailing leg directly affects leg power and may contribute to consistent power generation from step to step. We hypothesized that force directed along the trailing leg would be most modulated (i.e., altered from step to step) when leg power is observed to be most consistent, indicating that the trailing leg makes step-by-step force corrections that act to stabilize leg power for more consistent energetics during step-to-step transitions (**H1**).

Leg forces can be modulated by joint torques in two ways: (i) through individual joint torque adjustments where each joint torque separately modulates leg force; or, (ii) through inter-joint coordination where joint torques act in concert to alter leg force production on each step. Using a modified uncontrolled manifold (UCM) analysis (Yen and Chang 2010), we can isolate the effect of each of these sources and determine their relative contribution to whole leg force control. Leg force modulation through regulation of a single joint torque would simplify the higher-level control required during steady state walking. The triceps surae muscle group is the largest contributor to trailing leg force production in walking (Kepple, Siegel et al. 1997; Neptune, Kautz et al. 2001), so step by step ankle torque modulation alone could effectively manipulate leg force. Relying on a single joint for motor

control, however, could limit one's ability to adjust to unexpected perturbations. Using another joint to counterbalance the power generating actions at the ankle would provide an additional level of control and enable more robust control of leg force. It has been suggested, for instance, that opposing forces in locomotion may have the beneficial effect of passively stabilizing the system while increasing maneuverability (Sefati et al., PNAS 2013). Previous work in cats has revealed neuromechanical coupling between ankle and knee action, suggesting that existing mechanisms for ankle-knee coordination may refine and stabilize leg force control during steady state walking (Nichols 1999; Wilmlink and Nichols 2003; Stahl and Nichols 2011). We hypothesized that individual control of ankle torques would be the greatest contributor to joint torque variance structure for modulating trailing leg force (**H2**), but that the ankle and knee would covary to provide a supplementary stabilizing effect on leg force (**H3**).

Methods

Data Collection

Eight healthy subjects (6 male/2 female, 34.0 ± 12.6 years, weight: 81.5 ± 14.1 kg, leg length: 91.8 ± 4.7 cm) gave informed consent prior to participating in a protocol approved by the Georgia Institute of Technology Institutional Review Board. Four participants completed a six-minute walk test prior to data collection, three participants completed the test on a separate day after data collection, and one did not perform a six minute walk test ($660.2 \text{ m} \pm 56.0 \text{ m}$, ATS Statement: Guidelines for the Six-Minute Walk Test). Preferred walking speed ($1.29 \pm 0.10 \text{ m/s}$) was determined by allowing subjects to walk at a variety of speeds below their average walking speed during the six minute walk test, during which participants verbally indicated whether they would prefer the speed to be faster, slower, or if it was "just right." All participants walked on a custom-built, side-by-side dual-belt treadmill for two minutes at 75% of their preferred walking speed (PWS). Preliminary analysis on pilot subjects showed few notable differences in kinematics and kinetics data compared to data at preferred walking speed. Ground reaction forces were collected independently for each leg using mechanically isolated force plates (1080 Hz, Advanced Mechanical Technology Incorporated, Watertown, MA, USA) embedded beneath each custom-built treadmill (see Kram et al., JAP 1998). Simultaneous kinematics data were captured using a six-camera motion analysis system (120Hz, VICON Motion Systems, Oxford, UK). Retroreflective markers were placed bilaterally on the anterior superior iliac spine, posterior superior iliac spine, greater trochanter, thigh segment, knee joint center, shank segment, lateral malleolus, fifth metatarsal head, and second metatarsophalangeal joint.

Data Analysis

Marker and force data were filtered with a zero-phase lag fourth-order Butterworth low-pass filter with a 10 Hz cutoff frequency. Joint-torques were calculated in the sagittal plane using standard inverse dynamics calculations and estimated segment inertial characteristics based on subject specific anthropometrics (Winter 1980). Individual leg power was calculated as the dot product of the force recorded from that leg (leg force, F_{leg}) and center of mass (COM) velocity (v_{com} , Eq. 1). COM velocity was calculated with the integral of COM acceleration (a_{com}) as calculated from the product of subject mass (m) and net force

recorded from both legs (F_{net} , Eq. 2). The integration constants were zero for the vertical COM velocity component and treadmill speed in meters per second for the anterior-posterior COM velocity component. All data were time normalized starting from ipsilateral heel contact.

$$P = F_{leg} \cdot v_{com} \quad (\text{Eq. 1})$$

$$v_{com} = \int a_{com} dt = \int (F_{net}/m) dt \quad (\text{Eq. 2})$$

Uncontrolled Manifold Analysis

An Uncontrolled Manifold (UCM) analysis was performed using custom Matlab code. A detailed explanation of this technique as applied to vertical and anterior-posterior force components has been provided previously (Auyang, Yen et al. 2009; Yen and Chang 2010; Toney and Chang 2013). Briefly, the UCM analysis partitions total variability of elemental variables (e.g. joint torques) into two components either parallel or perpendicular to a linearized estimate of a goal equivalent manifold, where small joint-torque deviations do not affect the task goal (e.g. leg force). Comparing the relative magnitude of these orthogonal variance components over many steps can reveal whether elemental variables (joint-torques) exhibit a non-random structure over time that aligns with a hypothesized functional goal (leg force). The relationship between joint torques and the leg force is mathematically described within a Jacobian matrix (J), which quantifies the effects of small joint-torque deviations on the leg force. The null-space of J serves as a linearized approximation of the goal-equivalent manifold against which we test our hypotheses about the structure of elemental variance. Joint torque variance parallel to this manifold has no effect on leg force, so we term this parallel component goal-equivalent variance (GEV, Eq. 3), where n is the number of local degrees of freedom (3 joint torques), and d is the number of global degrees of freedom (1 leg force). We call joint torque variance perpendicular to the manifold non-goal equivalent variance (NGEV, Eq. 4) because it causes a deviation in the magnitude of leg force.

$$GEV = \frac{\text{trace} \left(\text{null} \left(J^T \right) \cdot C \cdot \text{null} \left(J \right) \right)}{n - d} \quad (\text{Eq. 3})$$

$$NGEV = \frac{\text{trace} \left(\left(J \cdot J^T \right)^{-1} \cdot J \cdot C \cdot J^T \right)}{d} \quad (\text{Eq. 4})$$

In each of these equations, C is the statistical covariance matrix of joint torques (Eq. 5), where σ_i^2 is individual variance of a single joint torque, σ_{ij} is covariance between two joint torques, and the subscripts denote a particular joint torque (a=ankle, k=knee, h-hip).

$$C = \begin{bmatrix} \sigma_a^2 & \sigma_{ka} & \sigma_{ha} \\ \sigma_{ak} & \sigma_k^2 & \sigma_{hk} \\ \sigma_{ah} & \sigma_{kh} & \sigma_h^2 \end{bmatrix} \quad (\text{Eq. 5})$$

The relative amount of GEV and NGEV reveals the overall effect joint torque variance has on the leg force trajectory. To quantify this effect and compare the organization of joint torque variance across individuals, we calculated a normalized metric of variance structure, the Index of Motor Abundance (IMA, Eq. 6), for each 1% of the gait cycle, where TotV is the normalized total joint torque variance (Eq. 7).

$$IMA = \frac{GEV - NGEV}{TotV} \quad (\text{Eq. 6})$$

$$TotV = \frac{\text{trace}(C)}{n} \quad (\text{Eq. 7})$$

The analysis used here differs only slightly from our previously published approach (Yen, Auyang et al. 2009; Toney and Chang 2013). Here we again use a kinematic Jacobian that maps the corresponding joint-torques to endpoint force using an operational space formulation developed for controlling humanoid robots (Khatib 1987; Yen, Auyang et al. 2009). However, rather than decomposing the leg force vector into globally referenced vertical and anterior-posterior components, we instead geometrically rotated the local reference frame to align with the leg orientation vector (center of pressure to ASIS marker). From this transformed data, we construct our geometrically derived Jacobian matrix to project joint torque variance into a task space aligned with the leg orientation vector. In this way, we analyze how joint torque deviations contribute to variance of the force generated along the long axis of the leg.

IMA trajectories were evaluated for significant differences from zero using a two-tailed Student's t-test ($\alpha=0.005$, Bonferroni corrected) to compare each percentage point of the gait cycle to zero. An IMA significantly greater than zero indicates the joint torque variance was structured to generate the same leg force at that point in the gait cycle with each step. A positive IMA means that task-irrelevant deviations were greater than task-relevant deviations, which is consistent with a minimal intervention principle of motor control (Todorov and Jordan 2002). We therefore interpret positive IMA values as an indication that leg force is stabilized, and is likely a controlled, implicit neuromechanical goal of walking at that point in the gait cycle. An IMA significantly less than zero indicates active modulation such that joint torques combined to produce a different leg force trajectory with each step. In this case, task-relevant deviations are not restricted, but instead enhanced and contribute directly to alter leg force. A negative IMA is therefore interpreted to mean that leg force is instead modulated to stabilize some alternative task variable (Shim, Latash et al. 2003; Gorniak, Zatsiorsky et al. 2007; Gorniak, Zatsiorsky et al. 2009).

Components of Index of Motor Abundance

Variance structure as indicated by the IMA metric can arise from two different sources: 1) individual control of joint torques and/or 2) covariance across joints torques. We used a modified UCM analysis to isolate the effect of these two possible sources (see Yen and Chang 2010). The UCM analysis uses a statistically derived covariance matrix (Eq. 5) to determine the underlying structure of the joint torques. Altering this covariance matrix allows us to isolate the effects of individual variance and covariance. Specifically, the variance of each joint torque relative to itself (individual variance) is contained within the diagonal elements of the covariance matrix and the off-diagonal elements are inter-joint covariances. To determine the effect of individual joint control of leg force, we removed the effects of inter-joint covariance by setting the off-diagonal elements to zero (C' , Eq. 8), and then re-calculated GEV' , $NGEV'$, and IMA' using C' .

$$C' = \begin{bmatrix} \sigma_a^2 & 0 & 0 \\ 0 & \sigma_k^2 & 0 \\ 0 & 0 & \sigma_h^2 \end{bmatrix} \quad (\text{Eq. 8})$$

The IMA value that results from using C' reflects the amount of joint torque variance structure that results from individual joint torque control, so we call this new metric INV ($=IMA'$). All remaining variance structure must then result from covariance between the joints. We therefore calculate the contribution of this coordination by subtracting the individual variance structure (INV) from the overall structure (IMA) (Eq. 9). In this way, we can determine whether the source of the overall joint torque variance structure is derived from an individual (INV) or coordinated (COV) joint torque variance control. It is important to note that the statistical covariance matrix (C) and COV metric indicate two different aspects of motor control. The covariance matrix reflects the statistical covariance between the elemental joint torques, while the COV metric indicates the effect this inter-joint covariance has on the stabilization of the leg force trajectory.

$$COV = IMA - INV \quad (\text{Eq. 9})$$

COV and INV trajectories were statistically evaluated and interpreted in the same way as IMA trajectories. We applied a two-tailed Student's t-test ($\alpha=0.005$, Bonferroni correction) to test for differences significantly different than zero. INV values greater than zero indicate that individual joint torque variance is organized to stabilize leg force output, while positive COV values indicate that covariance between joint torques have a stabilizing effect. Negative values for INV and COV indicate that joint torques are organized to modulate the leg force trajectory with each step through individual joint and coordinated joint control, respectively. To determine the similarity the COV and INV trajectories have to the IMA trajectory, we “fit” each trajectory to the IMA trajectory using the built-in Matlab function “corrcoef.” Larger resulting R^2 values indicate that either INV or COV account for a greater amount of inter-subject residual variance in the IMA trajectory (Bauman and Chang 2013). In other words, a larger R^2 value indicates a “better fit” of that component to the IMA trajectory.

Joint Torque Gain from the Jacobian Matrix

We further delineated the source of variance structure by quantifying the influence each joint torque has on leg force. Small deviations in each joint torque affect leg force variability differently depending on the leg's posture at that point in the gait cycle. For example, at the end of stance, small changes in ankle torque will have a larger impact on force along the leg than changes in knee or hip torque because the ankle is more flexed than either the knee or hip, maintaining a longer lever arm relative to the leg orientation vector. The geometric relationship between the joints and end point location is captured in the Jacobian matrix, where each element represents the gain on each joint torque at that point in the gait cycle. We determined the gain on each joint torque by comparing the Jacobian elements at the time of peak power for each subject. Differences in joint torque gain at this point in the gait cycle were evaluated by applying a repeated measures ANOVA and Scheffe's post-hoc multiple comparison test ($\alpha=0.05$).

Event Timing

We tested whether particular events related to leg power production occurred at similar times within the gait cycle. Specifically, we tested for differences in timing of peak power, local minimum of power variance, most negative IMA, most negative INV, maximum ankle torque variance, and maximum ankle torque rate of change. We applied a repeated measures ANOVA ($\alpha=0.05$) with a post-hoc Scheffe multiple comparison test to identify differences in timing of identified gait events.

We also reanalyzed data provided by Farris and Sawicki (2012) to determine whether a timing dependence existed between muscle fascicle performance and power output. These data included ultrasound recordings of medial gastrocnemius muscle fascicle length, rate of change, and power as well as calculated Achilles tendon forces for walking in 10 subjects at 0.75, 1.25, 1.75, and 2.00 m/s. We manually identified the time within the gait cycle that peak mean fascicle shortening acceleration, peak mean Achilles tendon force, and peak mean muscle tendon unit (MTU) power occurred for each subject. The linear relationship between peak tendon force, fascicle acceleration, and MTU power was determined with a first order polynomial fit using the built in Matlab command "polyfit."

Results

Joint torques and ground reaction forces

Individual leg forces and joint torque trajectories were consistent with previously published data (Winter 1980; Nilsson and Thorstensson 1989) when subjects walked comfortably at 75%PWS (Fig. 1). The first double support period when the leg of interest leads was initiated at ipsilateral heel strike and terminated at contralateral toe off, lasting from 1.0–15.8±1.4% of the gait cycle for all subjects. The second double support period from contralateral heel strike to ipsilateral toe off lasted from 51.1±0.8%–64.9±1.1% of the gait cycle (n=8).

Leg power

Leg power trajectories were also consistent with previously published data (Donelan, Kram et al. 2002a; Donelan, Kram et al. 2002b). Power was negative, meaning that power is absorbed by the leg, during the first double support period when the leg leads. Leg power is positive (generated) during the second double support period when the leg trails (Fig. 2). Variance of leg power across steps was relatively constant during single limb stance, but increased as power increased during the push off associated with the second double support period. Notably, variance of leg power demonstrated a local minimum ($58.4 \pm 1.0\%$ gait cycle) concurrently with the absolute maximum in leg power indicating some consistency of peak power generated across steps (Fig. 2, black arrow, $58.5 \pm 1.2\%$ gait cycle).

Intra-leg UCM analysis for leg force control

The index of motor abundance (IMA) was significantly greater than zero ($p < 0.005$) from 1–15% of the gait cycle, indicating that leg force was stabilized during the first double support period when the leg is leading (Fig. 3A). Leg force was modulated ($\text{IMA} < 0$, $p < 0.005$) in a small portion of the second half of single limb stance (at 44% gait cycle) and during double support when the leg trails (59–61% gait cycle). The time of most negative IMA ($58.9 \pm 1.5\%$ gait cycle) also occurred at the same time as maximal power production (Fig. 3, black arrow).

Contribution of individual and coordinated variance to intra-leg model for leg force control

The trajectories of INV and COV demonstrated different patterns throughout the gait cycle (Fig. 3B). Individual joint torque control generated INV values significantly greater than zero ($p < 0.005$) during the first part of double support when the leg leads (1–6% gait cycle). INV then fell to significantly less than zero during single limb support (26–45% gait cycle) and when the leg is trailing in the second double support period (57–63% gait cycle). Covariation between joint torques generated significantly positive COV values during the first double support and single limb stance (9–12% and 14–41% gait cycle) as well as throughout the second double support period when the leg trails (51–65% gait cycle). The INV trajectory accounted for 95% of the inter-subject residual variance in the IMA trajectory ($R^2 = 0.95$; $p < 0.005$). The COV trajectory, on the other hand, only accounted for 14% of the residual inter-subject variance in the IMA trajectory ($R^2 = 0.14$; $p = 0.002$).

Role of the ankle in leg force control

At the point in the gait cycle where peak leg power is generated, the Jacobian elements revealed a more than twofold greater gain on ankle torque (6.49 ± 0.73 gain) compared with that of either the knee (2.62 ± 0.64 gain) or hip (0.64 ± 0.43 gain) torques ($F = 162.9$, $p < 0.05$; Fig. 4).

Time of power, motor control, and ankle torque events

The time of maximum ankle torque variance and maximum ankle torque rate of change (Fig. 5) occurred significantly later than any tested leg power (time of peak power, time of minimum power variance) or motor control (time of minimum IMA, time of minimum INV) event ($F = 147.292$, $p < 0.005$, Fig. 6). While these observed differences were statistically

significant, the absolute timing differences are likely not discernable by the nervous system. On average, maximum ankle torque variance occurred $2.1 \pm 0.7\%$ and maximum ankle torque velocity occurred $1.4 \pm 0.6\%$ later in the gait cycle than the average timing of the power and motor control events. A two percent difference equates to approximately 20ms in real time, which is faster than the time required for a timing error to be sensed by the nervous system and a reactionary force to be developed (Granata et al., Archives Phys Med Rehab 2000). It is also notable that ankle torque variance exhibits a local minimum at the time of peak ankle torque magnitude, indicating that relatively consistent amplitudes of peak ankle torque were generated with each step.

Achilles tendon properties and leg force

The time at which peak Achilles tendon force occurred during walking correlated well with when in the gait cycle peak muscle tendon unit (MTU) power was achieved ($R^2 = 0.64$, Fig. 7A). The slope of this relationship between peak Achilles tendon force and peak MTU power was close to unity (0.98), and the tendon reached peak force at a consistent time before peak power (intercept = 6.89% gait cycle). In contrast, the time of peak gastrocnemius fascicle shortening acceleration was not as well correlated with when peak MTU power was achieved ($R^2 = 0.397$, $y = 0.35x + 39.12$, Fig. 7B).

Ankle-knee covariance

The magnitude of ankle-knee covariance as determined from the coefficients of the covariance matrix, **C** (Eq. 8), was greater than ankle-hip or knee-hip covariance at the time of peak power ($F=28.28$, $p<0.05$, Fig. 8). Positive ankle-knee covariance at the time of peak power means that the knee tends to generate a flexion torque when the ankle generates a plantar-flexion torque, reducing the translation of ankle plantar-flexion torques directly to leg force.

Discussion

We investigated the functional contribution of individual (INV) and coordinated (COV) joint torque control of leg force during leg power generation in steady state walking. We found that maximal modulation of leg force coincided with the time of peak leg power production and a minimum in leg power variance, which suggests that step-to-step corrections in leg force leads to consistent power generation (**H1**). Leg force modulation was achieved primarily through timing adjustments in ankle torque production rather than by modulating peak ankle torque magnitude (**H2**). We propose that the nervous system may control and structure these ankle torque timing adjustments by modulating when elastic recoil of the Achilles tendon is initiated. We also demonstrated that knee torque plays a key role in controlling leg force output by attenuating and counterbalancing the effect of ankle torque deviations on leg force (**H3**).

Trailing leg force is modulated to maintain consistent leg power

In steady state walking, the locomotor system adopts efficient and repetitive walking mechanics, so we expected variables with a large impact on the consistency of step-to-step transitions to be similar with each step. We expected trailing leg power generation to be

consistent because modeling studies have demonstrated the substantial influence the trailing leg has on steady-state walking efficiency (Kuo 2002; Ruina, Bertram et al. 2005). Agreeing with our prediction (**H1**), our empirical findings show peak trailing leg power generation reaches a consistent magnitude at a consistent time in the gait cycle (Fig. 2). A local minimum in trailing leg power variance occurs concurrently with peak power production and indicates that peak power is more consistent than any surrounding time point.

Our UCM analysis revealed that joint torque variance was most structured to modulate leg forces ($\text{IMA} < 0$, $p < 0.05$) at the same point in the gait cycle when leg power reaches its peak (Fig. 3A). In other words, joint torques combined to apply a different trailing leg force each time leg power was maximized in each step. Modulation of a particular task variable may indicate that this particular variable may be making corrections with each step to stabilize another variable at a different organizational level (Shim, Latash et al. 2003; Gorniak, Zatsiorsky et al. 2007; Gorniak, Zatsiorsky et al. 2009). Leg power is determined by force along the leg and center of mass velocity (Eq. 1), so modulation of leg force will directly affect the leg power profile. Our finding of negative IMA at the same instance as peak power generation suggests that joint torques are organized to generate a different leg force with each step, which results in the maintenance of consistent peak power production during step-to-step transitions. The influence of leg force timing on walking mechanics has been established in robotic systems and mathematical representations (Kuo 2002; Ruina, Bertram et al. 2005) and the importance of step-by-step adjustments in ankle push off work has been shown to have an important influence on mediolateral foot placement and overall metabolic energy cost of stabilizing balance (Kim and Collins, 2015). This is the first time a similar relationship has been established in human walkers as it relates to how the joints coordinate to result in consistent mechanical power production over many steps.

Variable timing of peak ankle plantar-flexion torque leads to leg force modulation

The strong agreement between INV and IMA trajectories (Fig 3) indicates that leg force control was mostly determined by a strategy of controlling individual joint torque variability throughout the gait cycle. At the instance when peak power occurs, ankle torque gain has a greater influence on leg force deviations as compared to knee and hip deviations (Fig 4). In other words, at the time of peak power production, small adjustments in ankle torques will manifest as larger changes in leg force compared to similar adjustments in knee or hip torque. Ankle torque therefore exercises the largest influence in modulating leg force and is largely responsible for the joint torque variance structure observed during the power generation phase at the end of stance (**H2**). As a result, leg force modulation at the end of stance is likely achieved by individually controlling ankle torque rather than through coordination of all three intra-leg joint torques as has been seen in human hopping or in other phases of the gait cycle (Yen, Auyang et al. 2009; Yen and Chang 2010; Toney and Chang 2013). Although we did not consider it in our analysis here, the influence of the lead leg force on the control of the trailing leg could also play an important role. As observed in this study, joint torque variance structures tend to stabilize the lead leg force and they tend to modulate the trail leg force. In our previous work, we also saw that the lead and trail leg forces are coordinated to stabilize whole body dynamics (Toney and Chang 2013). This suggests that the trail leg force would tend to counteract any small deviations in lead leg

force. It would be worthwhile to investigate the influence of an interlimb neural pathway between the leading and trailing legs given the importance of their mechanical relationship in gait.

Direct investigation of the ankle torque trajectory revealed that the magnitude of peak ankle plantar-flexion torque is highly consistent across strides, but there is greater variability as ankle torque decreases rapidly at the end of push-off (Fig. 5). Leg force is most modulated (IMA most negative) and leg power is maximal at nearly the same time that the ankle torque is exhibiting high variability and decreasing rapidly (Fig. 5, Fig. 6). In congruence with the high gain on ankle torque variability at this time, these data suggest that trail leg force is largely modulated by ankle torque timing variability at push-off. At its peak, the magnitude of ankle torque has a high tolerance for timing deviations due to its shallow slope, but periods of rapid torque change can result in greater sensitivity to timing variability (Latash, Scholz et al. 2002; Yen et al., 2009). As a result, small timing adjustments in ankle torque result in larger leg force deviations as plantar-flexion torque changes rapidly in the trailing leg during push off. Thus, peak ankle plantar-flexion torque magnitudes are achieved consistently, but the timing at which these peaks occur is varied. Taken in sum, these results suggest that adjustments in the timing of a stereotyped ankle torque trajectory are important for leg force modulation and, ultimately, leads to consistent leg power generation. The large influence of ankle torque on leg force output may not be surprising as the ankle has been shown to be a primary source for propelling the body forward in walking (Kepple, Siegel et al. 1997; Neptune, Kautz et al. 2001). This is the first study, however, to demonstrate the influence of stride-to-stride changes in ankle joint torque on stride-to-stride variability of leg force and power. In particular, the work presented here indicates that, while power magnitude may be determined by ankle torque magnitude, small timing adjustments in the ankle torque trajectory contribute to generating consistent leg power with each step during steady walking.

Potential passive mechanism for modulating trailing leg forces

Our analysis revealed that the timing of ankle torque production was varied to generate consistent leg power. This evidence suggests that humans generate a consistent load with the ankle plantarflexor muscle tendon unit on each step, but vary the timing of this force production. An analogous mechanism has been described in jumping frogs, where an “inertial catch” influences peak power production of the leg through slow loading of passive, series elastic structures in the ankle plantarflexors, followed by rapid elastic recoil and energy release (Roberts 2002; Roberts and Marsh 2003; Roberts and Azizi 2011). This catapult mechanism is able to decouple muscle fiber shortening from whole body movements because passive structures are stretched while muscle fascicles remain at a near constant length, which leads to an amplified peak power output with very little energetic demand required by cross bridge cycling to initiate movement (Roberts and Marsh 2003). A similar decoupling of muscle fascicle shortening and Achilles tendon lengthening has been observed in human walking (Ishikawa, Komi et al. 2005; Farris and Sawicki 2012; Cronin, Avela et al. 2013), and may explain the ability to decouple the time when ankle torque is most effective at modulating leg force from when the torque reaches peak magnitude. Peak ankle torque is directly related to peak muscle-tendon unit force and it appears that both are

generated consistently from step to step based on the low variability in peak ankle torque magnitude (Fig. 5A). The time of peak leg power output, however, did not coincide with when peak ankle torque occurred. Instead, peak leg power corresponded with the rapid unloading phase of push off when ankle torques were most variable from step to step (Fig. 5A). The high variance in submaximal ankle torque is related to its high rate of change during push off (Fig. 5B), when small adjustments in ankle torque timing can have a large effect on leg force output (Fig. 3). Although recent work points to the influence of muscle activation onset timing on mechanical power output of a muscle-tendon unit (Sawicki, Robertson et al JEB 2015), our results also point to the importance of the timing of muscle deactivation. Utilizing the Achilles tendon in this way would allow human walkers to employ a passive structure to control propulsive power and achieve more efficient step-to-step transitions. In fact, mathematical simulations reveal that series elasticity at the ankle can aid walking economy by reducing the energy lost in leading leg collisions, consistent with dynamic walking principles and suggestive of a mechanical advantage to utilizing the Achilles tendon in this same manner (Zelik, Huang et al. 2014).

The work presented here identifies an additional functional role for this catapult mechanism: controlling when elastic recoil is initiated through muscle deactivation can modulate leg force output for consistent power production in step-to-step transitions. Modulating the timing of ankle torque generation requires sensory feedback to make appropriate adjustments and account for ever-present motor variability. Distal limb motor control is suggested to be largely regulated by force sensory feedback (Nielsen and Sinkjaer 2002; Daley and Biewener 2006; Faist, Hoefer et al. 2006; Daley, Felix et al. 2007; Af Klint, Mazzaro et al. 2010). Further, Golgi tendon organs have been implicated in regulating timing of the gait cycle (Capaday 2002), making them a likely sensor for modulating initiation of Achilles tendon recoil. We reanalyzed ultrasound data from Farris and Sawicki (2012), which revealed a good correlation between the timing of peak Achilles tendon force and peak medial gastrocnemius muscle tendon unit (GM-MTU) power (Fig. 7A). In contrast, we observed a much weaker correlation between the time of maximum change in fascicle shortening velocity (i.e., time of greatest fascicle acceleration) and GM-MTU power (Fig. 7B). The time when the rate of fascicle shortening (or acceleration) reaches a peak should correspond to a substantial change in muscle shortening dynamics (e.g., a change from isometric to shortening activation). These results suggest that the Achilles tendon loading inherent to the catapult mechanism may be facilitated by force feedback. If present, force facilitation within the triceps surae group would increase muscle stiffness and provide an anchor from which the Achilles tendon can stretch as the limb is loaded in stance phase. Ankle load reduction at the end of stance would then result in a decrease of force-mediated facilitation and possibly result in a complete reversal to force-mediated inhibition (Faist, Hoefer et al. 2006). Our data (Fig. 5B) indicate that peak leg power occurs during a period of maximum rate of change in ankle torque during push-off, which signifies a rapid decrease in muscle-tendon unit force at the end of stance. Regulating when the triceps surae muscle group is deactivated may therefore play a critical role in controlling step-to-step leg power consistency by determining when Achilles tendon recoil is initiated. While this potential mechanism is speculative, our data agree with other previously published work and provide

an interesting framework for future investigations to test the mechanism controlling the timing of ankle torque production in human walking.

Role of the knee to mediate ankle torque deviations

While independent control of the ankle dominates step-to-step variability of leg force output and, ultimately leg power generation, covariation (COV) between the joints remains present and functionally significant throughout the gait cycle (Fig. 3B). The contribution of COV is largely positive throughout the gait cycle, contrasting the aforementioned destabilizing effect of the ankle. Controlling leg force output in the trailing leg with ankle torque alone would be challenging, similar to driving a car with only a gas pedal and no brake. The knee may serve as an ancillary controller that adjusts the extent to which ankle torque deviations are translated up the leg to influence COM movement by regulating leg force and stabilizing leg power generation. In fact, at the time of peak leg power production, the ankle and knee covary such that plantar-flexion torques at the ankle are balanced by flexion torques at the knee (Fig. 8). In other words, the knee is able to counteract deviations in ankle plantar-flexion torque in a way that tends to lessen the effect of the ankle on leg force. In this way, the ankle acts as the primary motor for leg power generation, but the knee may act as a brake to attenuate the effect ankle torque deviations can have on the leg (**H3**). Mutually opposing forces are common in animal locomotion and have been indicated to be a mechanism to simplify neural control by passively stabilizing movement while simultaneously increasing maneuverability (Sefati, et al., PNAS 2013). The knee adds an additional layer of control and could allow for more robust regulation of leg force.

It remains unclear whether ankle-knee covariance results from biomechanical connections or is an active reflex mechanism to help mediate ankle torque deviations up the leg. Intra-leg and inter-muscular reflex mechanisms may contribute to the monitoring and control of ankle torque generation (Wilmink and Nichols 2003; Stahl and Nichols 2011). However, the inherent stiffness of medial and lateral gastrocnemius couples the knee and ankle, resulting in inter-joint stability (Nichols 1999), so a passive or structural mechanism for ankle-knee coupling is also possible. Ishikawa et. al. (2005) also demonstrated different functional behaviors between the bi-articular medial gastrocnemius and the mono-articular soleus muscles, suggesting that various muscles may be regulated via different mechanisms during human walking. A combination of neural and/or biomechanical ankle-knee coupling is, therefore, also possible. While the exact mechanism for ankle-knee covariation remains unclear, we have shown that the knee appears to coordinate with the ankle to mediate the effects of distal torque deviations as they translate proximally up the leg and influence center of mass mechanics.

A potential limitation of this work is that we assumed a rigid, non-deformable foot in our analysis. Recent work has shown that inclusion of a deformable foot can provide a significant source of damping mechanics within the leg (Zelik, Takahashi, Sawicki, 2015). The simple analysis we employed here ignores this important feature of the foot, which may have an influence over the interjoint coordination and control of the leg and deserves further study.

Conclusion

We studied the motor control of trailing leg force generation to determine how consistent step-to-step leg power production may be achieved in steady state walking. Our results demonstrate that human walkers modulate trailing leg forces primarily through variable timing of peak ankle plantar-flexion torque in order to make step-to-step leg force adjustments that maintain consistent peak leg power production. Variable timing of peak ankle torque generation may be regulated by controlled initiation of Achilles tendon elastic recoil. Utilization of the Achilles tendon in this way would not only regulate peak power output and reduce the energetic demand of power production, but may also simplify motor control to regulation of a single task: timing of muscle-tendon unit unloading and Achilles tendon recoil. Our subjects maintained robust leg force control by coupling knee and ankle function. Knee torques were coordinated to attenuate the effect of ankle torque deviations on leg force, providing an additional layer of control and allowing more refined modification of leg force. Our results emphasize the important roles of individual ankle control, sensory feedback, and ankle-knee coupling have in achieving consistently powered steady walking. These results in healthy adults further highlight possible physiological sources of pathological gait deviations in individuals with impaired ankle function (e.g. amputation, stroke, trauma, etc.) and provide potential areas for focused improvement for the control and design of walking robots and powered prosthetic devices.

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Figure 1.

Representative subject resultant leg force (left panel) and corresponding joint torques (right column). Gray lines represent leg force and joint torque values for each step, while the thick black lines represent the mean trajectory. Double support when the leg is leading ($1-14.4 \pm 0.7\%$ gait cycle) and when the leg is trailing ($50.8 \pm 1.0\% - 63.2 \pm 1.2\%$ gait cycle) are bounded by the vertical lines. Gait cycles are defined from heel contact (0%) to ipsilateral heel contact (100%)

Figure 2.

Trailing leg power is consistent. Mean and inter-subject standard deviation of leg power (solid line) and leg power variance (dashed line) for one leg of each subject throughout the gait cycle. Peak leg power occurs simultaneously a local minimum in leg power variance (large arrow). In other words, maximal leg power production is highly consistent.

Figure 3.

Individual joint-torques modulate trailing leg force profiles to make leg power consistent. A) Mean and standard deviation of Index of Motor Abundance of (IMA) across subjects for one leg throughout the gait cycle. Note that IMA is calculated only when the task level variable (ground reaction force) is generated when the leg is on the ground. Hip, knee, and ankle joint torques combine to stabilize leg force ($IMA = 0$, $p < 0.005$, bars and asterisks) when the leg is leading ($1-15.8 \pm 1.4\%$ Gait Cycle) and modulate leg force ($IMA = 0$, $p < 0.005$) when the leg is trailing in double support ($51.1 \pm 0.8\% - 64.9 \pm 1.1\%$ GC). B) Variability due to individual joint torque variance structure (INV, solid line) and co-variation among joint torques (COV, dashed line). Co-variation among the joints is present throughout the gait cycle ($COV = 0$, $p < 0.005$, dashed bars and asterisks), but individual variation of joint torques appears to dominate the overall structure of joint torque variance ($INV = 0$, $p < 0.005$, solid bars and asterisks): the trace of INV is more similar to the trace of IMA ($R^2 = 0.95$) than the trace of COV compared to IMA ($R^2 = 0.14$).

Figure 4.

Gain of each joint torque to leg force deviations at the instance of maximum leg power. A larger gain indicates that deviations in that joint torque manifest as leg force deviations to a greater degree than joints with smaller gains. At the instance of maximum leg power generation, ankle torque deviations have a greater gain, and therefore a greater influence on leg force modulation, than either the knee or the hip (rmANOVA: $F = 162.9$, $p < 0.05$).

Figure 5.

A) Mean and inter-subject standard deviation of normalized ankle torque profiles (solid line) and variability of these profiles across all steps (dashed line) for all subjects. Note that the instance of maximum plantar-flexion torque corresponds with a local minimum of ankle torque variability. In other words, maximum ankle plantar-flexion torque magnitude is more consistent than other instances in the gait cycle. B) Mean and standard deviation of rate of change of ankle plantar-flexion torque (blue).

Figure 6.

Bar and whisker plot representing the timing of identified gait events within the gait cycle: (from L to R) peak power, local minimum in leg power variance, most negative IMA value, most negative INV value, local maximum in ankle torque variance, absolute maximum in ankle torque velocity. In each box, the central line represents the median, the edges are the 25th and 75th percentiles, and the whiskers extend to the most extreme data points. A repeated measures ANOVA analysis with Scheffe post-hoc multiple comparisons revealed that maximum ankle torque variance and maximum ankle torque velocity occurred significantly later in the gait cycle ($2.1 \pm 0.7\%$ and $1.4 \pm 0.6\%$ respectively) than the other gait events. These significant timing differences, however, are likely not a large enough delay to be detected by the nervous system.

Figure 7.

Data reproduced with permission from Farris and Sawicki (2012). Each data point indicates the time at which each event occurs for mean data of each subject. A) The time (% Gait Cycle) at which the Achilles tendon force is maximum is well correlated ($R^2 = 0.640$) with when peak muscle tendon unit (MTU) power occurs. This correlation holds across various slow and fast walking speeds. B) The time (% Gait Cycle) at which medial gastrocnemius fascicle shortening acceleration (i.e., change in velocity) was the greatest was not as well correlated with the time of peak MTU power ($R^2 = 0.397$) across various walking speeds.

Figure 8.

Mean and inter-subject standard deviation of covariation between ankle-knee, ankle-hip, and knee-hip joint torques at the time of peak power. The amount of covariation between joint torques depends on leg posture at each point the gait cycle. Ankle-knee torque covariation is significantly greater than either knee-hip or ankle-hip covariance (rmANOVA, $F = 28.275$, $p < 0.05$). A positive relationship between ankle and knee joint torques indicates that when the ankle generates a plantar-flexion torque, the knee tends to generate a flexion torque, leading to minimally altered leg force. Ankle-knee covariation therefore likely most influence the COV contribution to leg force stabilization.