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Humans robustly adhere to dynamic walking principles by harnessing motor abundance to control forces

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Abstract

Human walking dynamics are typically framed in the context of mechanics and energetics rather than in the context of neuromuscular control. Dynamic walking principles describe one helpful theoretical approach to characterize efficient human walking mechanics over many steps. These principles do not, however, address how such walking is controlled step-by-step despite small perturbations from natural variability. Our purpose was to identify neuromechanical control strategies used to achieve consistent and robust locomotion despite natural step-to-step force variability. We used the uncontrolled manifold concept to test whether human walkers select combinations of leading and trailing leg-forces that generate equivalent net-force trajectories during step-to-step transitions. Subjects selected leading and trailing leg-force combinations that generated consistent vertical net-force during step-to-step transitions. We conclude that vertical net-force is an implicit neuromechanical goal of human walking whose trajectory is stabilized for consistent step-to-step transitions, which agrees with the principles of dynamic walking. In contrast, inter-leg-force combinations modulated anterior–posterior net-force trajectories with each step to maintain constant walking speed, indicating that a consistent anterior–posterior net-force trajectory is not an implicit goal of walking. For a more complete picture of hierarchical locomotor control, we also tested whether each individual leg-force trajectory was stabilized through the selection of leg-force equivalent joint-torque combinations. The observed consistent vertical net-force trajectory was achieved primarily through the selection of joint-torque combinations that modulated trailing leg-force during step-to-step transitions. We conclude that humans achieve robust walking by harnessing inherent motor abundance of the joints and legs to maintain consistent step-by-step walking performance.

Keywords

Biomechanics; Locomotion; Motor control; Robustness; Uncontrolled manifold

Introduction

The overall energetic cost of walking can be minimized by selecting appropriate locomotion dynamics that minimize the energy dissipated between steps. Numerous models have described the relationship between legged locomotion dynamics and the measured metabolic

cost (Saunders et al. 1953; Cavagna et al. 1977; Hoyt and Taylor 1981; McGeer 1990; Alexander 1992; Minetti and Alexander 1997; Lee and Farley 1998; Garcia et al. 2000; Anderson and Pandy 2001; Kuo 2001). One popular model, dynamic walking, is “a theoretical approach to [describe] legged locomotion which emphasizes the use of simple dynamical models and focuses on behavior over the course of many steps, rather than within a single step” (Collins 2008). Dynamic walking principles propose that the primary metabolic cost of human walking results from the mechanical energy required to redirect the body’s center of mass (COM) during step-to-step transitions (Collins and Kuo 2010). Sequential single-limb stance phases are considered as independent inverted pendular arcs (Cavagna et al. 1977), but continuous, uninterrupted walking requires vertical redirection of the COM trajectory between these steps through coordinated actions of the leading and trailing legs (Fig. 1a). During these transition phases, mechanical energy is dissipated at heel strike (collision) of the leading leg and restored with propulsive work by the trailing leg (Collins and Kuo 2010; Donelan et al. 2002a, b; Kuo 2002, 2007; Kuo et al. 2005; Ruina et al. 2005). Dynamic walking principles therefore suggest that maintaining mechanically efficient step-to-step transitions are necessary for metabolically efficient walking. Motor control principles propose that variables critical for execution of a desired task remain consistent across many repetitions, while non-critical variables exhibit high variability. These patterns of directed variability reduction may reveal an organizational structure for movement control (Latash et al. 2002; Scholz and Schöner 1999; Schöner and Kelso 1988). The principles of dynamic walking therefore describe an optimal mean behavior for walking (Collins 2008), which implies consistent performance of some critical variables across many steps.

While accurately capturing mean dynamics and energetics of locomotion, dynamic walking principles do not address the natural kinetic deviations intrinsic to human joint-torques and limb forces with each step. The principles of dynamic walking do not explain, for example, how consistent center of mass redirection is achieved despite natural physiological variation in muscle-generated joint-torques and leg-forces experienced from one step to the next. It remains unclear how humans might robustly adhere to dynamic walking principles despite the effects of inherent step-to-step kinetic variability on net-force and resulting whole-body dynamics.

Walking involves the use of more degrees of freedom than are strictly necessary to achieve a desired net-force. Current motor control theories suggest that humans harness this inherent motor abundance of elemental variables to maintain consistent and robust performance of task variables (Auyang et al. 2009; Bosco and Poppele 2000; Ivanenko et al. 2007, 2008; Scholz et al. 2000; Scholz and Schöner 1999; Yen et al. 2009; Yen and Chang 2010). For example, in bipedal walking, the sum of two leg-forces determine each net-force on the ground, so coordination of these individual leg-forces may minimize net-force deviations, thereby stabilizing (i.e., making more consistent) COM redirection for continuous walking without the need to minimize individual leg-force deviations. To simplify control of the complex task of walking, the human locomotor system may actively monitor and control a select few task variables that are most important for successful locomotion (Bosco and Poppele 2000; Ivanenko et al. 2007, 2008). Here, we define motor control as “the ability to regulate or direct the mechanisms essential to movement” (Shumway-Cook and Woollacott 2001). It is worth noting that this control can act to either stabilize (i.e., make more consistent) or modulate (i.e., make less consistent) a given variable, or “goal,” over many successive steps.

The uncontrolled manifold (UCM) analysis examines how the variance of system elements (e.g., individual leg-forces) is structured across cycles of periodic movements to minimize “error” in variables critical for task success (e.g., net-force) (Scholz and Schöner 1999; Yen

et al. 2009; Yen and Chang 2010). For example, a conductor may specify a particular volume level for a choir to perform. Rather than assigning a volume for each singer, which would yield an inconsistent ensemble volume, the conductor directs the ensemble volume, while each singer adjusts their own contribution to account for too loud or too soft singing of their neighbors. Like a choral conductor, the UCM analysis considers system elements (singers) that self-adjust to errors (reducing one singer's volume when another sings too loudly) to maintain a particular output (ensemble volume) (after Latash et al. 2003). Applying the UCM analysis across periodic walking cycles allows us to test whether humans exploit their many degrees of freedom to stabilize task variables in accordance with dynamic walking principles. Stabilization of net-force by alignment of elemental leg-force variance with the proposed manifold would suggest that net-force may be an implicit goal of human walking that is actively monitored and controlled by the locomotor system. Alternatively, the UCM analysis may reveal misalignment of the elemental variance structure from the manifold, thus indicating that net-force is not an implicit gait goal, but is instead modulated to stabilize another variable at a different hierarchical level (Gorniak et al. 2007, 2009; Shim et al. 2003). This analysis provides a method for testing whether or not variance of elemental variables project to align with hypothesized task goals. The UCM approach can therefore provide insight into what variables may serve as implicit neuromechanical gait goals since structured kinetic variance provides a window into nervous system's structure and function (Schöner and Kelso 1988).

The aim of this study was to test whether humans structure their inherent motor variability to stabilize the vertical net-force trajectory for consistent COM redirection across many steps during walking. Dynamic walking principles predict which variables are critical for efficient gait, providing a hypothesis for what locomotor task variables are likely stabilized through elemental variance structure. Initially, the COM of the body is directed forward and downward as it enters into a step-to-step transition (Fig. 1a). At the transition's conclusion, the COM is directed forward and upward as the body begins the next single leg support phase (Fig. 1a). Because only the vertical COM velocity changes direction, redirection of the COM trajectory during this step-to-step transition is solely determined by the net vertical force (F_v^{net}) generated by the legs. To ensure consistent COM redirections and a COM trajectory for minimal energy expenditure, a consistent F_v^{net} trajectory over many steps may be an implicit goal of human walking (Fig. 1b). We hypothesized that over many steps, walkers would generate leading and trailing leg-force combinations that would act to stabilize (i.e., make more consistent) the trajectory of the vertical component of net-force (F_v^{net}) during double support (Fig. 1d).

The anterior-posterior component of the center of mass velocity (v_{com}) remains oriented anteriorly (in the direction of progression) throughout the step-to-step transition. The v_{com} magnitude is adjusted using combinations of braking and propulsive forces from the leading and trailing legs, respectively (Fig. 1b). Walking on a treadmill requires one to maintain a constant average walking velocity, thus imposing an explicit speed goal. Maintaining a consistent, steady walking speed theoretically requires the COM velocity to be the same at the beginning and end of each transition phase, $|v_{\text{com}}^-| = |v_{\text{com}}^+|$ (Fig. 1a, b) (Kim and Park 2012; Kuo et al. 2005). Step-to-step transitions therefore also require balanced braking and propulsive forces but do not demand a specific target value for $F_{\text{ap}}^{\text{net}}$ across steps.

Modulating the $F_{\text{ap}}^{\text{net}}$ trajectory with each step allows subjects to make step-to-step adjustments that counteract natural speed deviations and maintain the constant velocity required for treadmill walking. Consistent with previous work in hopping (Yen et al. 2009), we hypothesized that individual legs would coordinate braking and propulsive leg-forces to modulate $F_{\text{ap}}^{\text{net}}$ during step-to-step transition phases of walking and maintain the required

constant walking speed. Evidence of F_{ap}^{net} modulation to achieve a known explicit goal (constant walking speed) will provide support that the UCM analysis can successfully distinguish between stabilized and modulated variables.

Dynamic walking models typically consider both legs as rigid struts. In reality, individual joint-torques of the hip, knee, and ankle influence the net-forces that dictate COM dynamics by generating individual leg-forces (Fig. 1c). For a more complete picture of human locomotor control, we considered the role joint-torque combinations play in determining the individual leg-forces that then regulate net-force on the ground. We hypothesized that joint-torques would act in combinations that tend to stabilize individual leg-force components during step-to-step transitions. Residual variance in the two leg-forces can then be coordinated to regulate the net-force trajectory for consistent COM redirection as hypothesized above. Considering *intra*-leg-force control within the context of an *inter*-leg-force control model is consistent with a hierarchical structure of locomotion control (Gorniak et al. 2007, 2009; Loeb et al. 1999; Rybak et al. 2006; Shim et al. 2003).

Methods

Data collection

Nine healthy subjects (8 males, age: 34 ± 12.6 years, weight: 70.0 ± 11.6 kg, leg length: 93.8 ± 6.7 cm) gave informed consent as approved by the Georgia Institute of Technology Institutional Review Board. Each subject walked at a constant speed of 1.2 m/s for three 30-s trials. Ground reaction forces were collected independently for each limb as subjects walked on a custom dual-belt instrumented treadmill (1,080 Hz, Advanced Mechanical Technology Incorporated, Watertown, MA, USA). Subjects were familiar with treadmill walking, but were given as much time as desired to practice and rest prior to each trial. Simultaneous kinematics data were captured using a six-camera motion analysis system (120 Hz, VICON Motion Systems, Oxford, UK). Retroreflective markers were placed bilaterally on the anterior–superior iliac spine, posterior–superior iliac spine, thigh segment, knee joint center, shank segment, lateral malleolus, calcaneus, 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).

Uncontrolled manifold analysis

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 et al. 2009; Yen et al. 2009; Online Resource). Briefly, the UCM analysis partitions the total variability of redundant local variables into two components either parallel or perpendicular to a linearized estimate of the goal equivalent manifold. Comparing the relative magnitude of these orthogonal variance components can reveal whether elemental variables exhibit a non-random structure that aligns with a functional goal. The goal can be implicit as identified by theoretical models like dynamic walking, or they can be explicit due to task constraints or prescribed targets. The relationship between local elemental variables and the proposed goal variable is mathematically described within the Jacobian matrix ($\mathbf{J}$), which quantifies the effects of small local variable deviations on task variables. The null-space of $\mathbf{J}$ serves as a linearized

approximation of the manifold against which we can test our hypotheses about the structure of elemental variance. $\mathbf{J}$ is derived separately for each hypothesized combination of goal and local variables.

The UCM approach is a powerful tool for using variance as a window into the nervous system function, but like all statistical analyses, the UCM approach makes several assumptions that limit the scope of its applicability and interpretation. For example, we assume that elemental redundancy exists when applying the UCM approach (i.e., there are more available degrees of freedom than strictly necessary to achieve the task); however, no net joint-torque redundancy exists for a particular fixed limb configuration. The system's redundancy arises from the kinematic redundancy that exists from step-to-step as specific joint kinematics are never exactly repeated. To circumvent this limitation to study how the system utilizes step-to-step geometric redundancy and variability, we use a kinematic Jacobian that maps the corresponding joint-torques to end point force using an operational space formulation developed for controlling humanoid robots (Khatib 1987; Yen et al. 2009). This conversion therefore maintains kinetic consistency between elemental (joint-torques) and task variables (leg-force), which enables more direct analysis and interpretation of the underlying neuromechanical control. Using the UCM approach to investigate coordination of joint-torques for leg-force production therefore provides a necessary foundation from which to study the underlying neuromuscular structure and function more deeply. The requirement of redundancy also limits when in the gait cycle the UCM analysis can be used to evaluate kinetic redundancy. Because inter-leg kinetic redundancy exists only when both limbs generate force on the ground, we restricted the scope of our analysis to the double support periods when both feet are in contact with the ground. Our intent was to investigate how subjects account for natural deviations during step-to-step transitions through the use of inherent redundancy across the legs. Limiting our analysis to the double support period remains consistent with our purpose and provides a better understanding of the hierarchical organization of human locomotor control.

Inter-leg uncontrolled manifold analysis

In walking, forces applied by the leading and trailing legs on the ground determine the net-force (Eq. 1). This simple arithmetic relationship defines a two degree-of-freedom (2-DOF) system, and a 1×2 $\mathbf{J}$ matrix describes the influence of each individual leg-force on the net-force. We performed a 2-DOF uncontrolled manifold (UCM) analysis to quantify how inter-step leg-force variance is structured to generate consistent (i.e., stable) net-force values during step-to-step transitions (Scholz et al. 2000). The manifold describes a set of leg-force combinations that satisfy a single F^{net} value, so all leg-force deviations parallel to the manifold have no effect on F^{net} and are thus collectively called goal equivalent variance (GEV, Eq. 2). Leg-force deviations perpendicular to the manifold cause divergence from the desired F^{net} value, so this variance component is defined as non-goal equivalent (NGEV, Eq. 3), where C is the covariance matrix of leg-forces, d is the number of global degrees of freedom (1 net-force component), and n is the number of local degrees of freedom (2 leg-forces).

$$F^{\text{lead}} + F^{\text{trail}} = F^{\text{net}} \quad (1)$$

$$\text{GEV} = \frac{\text{trace}(\text{null}(\mathbf{J})^T \cdot C \cdot \text{null}(\mathbf{J}))}{n-d} \quad (2)$$

$$\text{NGEV} = \frac{\text{trace}((\mathbf{J} \cdot \mathbf{J}^T)^{-1} \cdot \mathbf{J} \cdot \mathbf{C} \cdot \mathbf{J}^T)}{d}. \quad (3)$$

We used the normalized difference between these two variance components, called the index of motor abundance (IMA, Eq. 4), to characterize the use of motor abundance to stabilize net-force at every 1 % of the gait cycle, where TOTV (Eq. 5) is the total measured leg-force variance (Yen et al. 2009).

$$\text{IMA} = \frac{(\text{GEV} - \text{NGEV})}{\text{TOTV}} \quad (4)$$

$$\text{TOTV} = \frac{\text{trace}(\mathbf{C})}{n}. \quad (5)$$

For inter-step behavior, each stride cycle was normalized to right heel strike. Transition phases were identified as periods of double support when both the right and left leg-forces exceeded 10 % of body weight (shaded region, Fig. 2). Average double support across all subjects was used to identify the transition phases for pooled data.

Intra-leg uncontrolled manifold analysis

We conducted a 3-DOF UCM analysis to quantify how joint-torque variance is structured to generate consistent (stable) leg-force components during transition phases. Derivation of $\mathbf{J}$ relating joint-torques to leg-force results from the dynamically consistent generalized inverse of the kinematic Jacobian relating joint angles to end point position (see Online Resource for additional detail) (Yen et al. 2009). For this intra-leg model, the ankle, knee, and hip joint-torques were the local variables, and the vertical and anterior–posterior force components of individual leg-forces (F_v^{lead} , $F_{\text{ap}}^{\text{lead}}$, F_v^{trail} , and $F_{\text{ap}}^{\text{trail}}$) were the tested goal variables. Similarly to the inter-leg analysis described above, the variance of intra-leg joint-torques was partitioned into GEV and NGEV components, and the IMA was used to characterize leg-force stabilization for each 1 % of the gait cycle. For this intra-leg analysis, each leg's stride cycle was normalized relative to its own heel strike (i.e., left leg data were normalized to left heel strike and right leg data to right heel strike). Self-normalized data from both legs were then pooled so the variance structure could be considered relative to leg function (leading or trailing) rather than by anatomical side.

Statistical analysis

Mean IMA trajectories across all subjects were evaluated for significant differences from zero using a one-tailed Student's t test ($\alpha = 0.005$). An IMA significantly greater than zero indicates the local variables (individual leg-forces or intra-leg joint-torques) were coordinated to generate the same net-force trajectory in each transition, which we interpret as stabilization of a controlled implicit neuromechanical goal of walking. In other words, a positive IMA indicates that only task-relevant deviations are reduced, which is consistent with a minimum intervention principle of motor control (Todorov and Jordan 2002). An IMA significantly less than zero indicates active modulation such that the local variables combined to produce a different net-force trajectory with each successive step, indicating that task-relevant deviations are not restricted, but instead contribute directly to net-force modulation. A negative IMA is therefore interpreted to mean that net-force is not an implicit gait goal, but is instead modulated to stabilize some alternative gait goal.

Results

Joint moments and ground reaction forces

Across all subjects, the first double support step-to-step transition period occurred during 1–13 % (± 0.73 %) of the gait cycle. The second transition period began with contralateral heel contact at 50 % (± 0.29 %) and lasted until 62 % (± 0.69 %) of the gait cycle. The general trajectories of the recorded ground reaction forces and joint-torques were consistent with previously published work on human walking (Winter 1980; Nilsson and Thorstensson 1989). Despite the characteristic mean shapes of the trajectories, we observed a substantial amount of step-to-step variability in all force and joint-torque data for each subject (Fig. 2).

Inter-leg model for net-force control

Index of motor abundance (IMA) values for net vertical forces (F_v^{net}) were significantly greater than zero for 1–13 and 50–62 % of the normalized gait cycle, corresponding to each double support period (Fig. 3a, double support periods shaded). These results indicate that F_v^{net} is stabilized using leading and trailing leg-force variance structure to generate net-force equivalent combinations throughout step-to-step transitions. IMA values for net anterior–posterior forces ($F_{\text{ap}}^{\text{net}}$) were significantly less than zero from 7–13 and 56–61 % of the gait cycle (Fig. 3b). These results indicate that structure of braking and propulsive force variance resulted in net anterior–posterior forces that were highly inconsistent during the latter part of each step-to-step transition.

Intra-leg model for leg-force control

Index of motor abundance (IMA) values for leading leg vertical force (F_v^{lead}) were significantly greater than zero from 1–5 and 11–13 % of the complete gait cycle. In contrast, IMA values for the trailing leg vertical force (F_v^{trail}) were significantly less than zero from 56 to 60 % (Fig. 4a). For vertical forces, leading leg GEV exceeded NGEV throughout double support (Fig. 4c). Trailing leg vertical force modulation resulted from a dramatic increase in NGEV, while GEV remained relatively constant and small throughout double support (Fig. 4e). IMA values for leading leg anterior–posterior force ($F_{\text{ap}}^{\text{lead}}$) were significantly greater than zero from 1 to 7 % of the complete gait cycle, and IMA values for trailing leg vertical force ($F_{\text{ap}}^{\text{trail}}$) were significantly greater than zero from 50 to 61 % (Fig. 4b). Despite a slight increase in NGEV of the leading leg in late double support, GEV was greater than NGEV for both $F_{\text{ap}}^{\text{lead}}$ and $F_{\text{ap}}^{\text{trail}}$ (Fig. 4d, f).

Discussion

Appropriate coordination of joint-torques and leg-forces can lead to robust, stable walking behavior by harnessing inherent motor abundance to accommodate natural step-to-step inconsistencies. We applied the UCM analysis to test whether human walkers selected combinations of joint-torques and leg-forces that led to consistent locomotor goals. Positive IMA values indicate stabilization of the tested goal variable through the selection of net-force equivalent leg-force combinations to apply consistent net-force during each transition period. Negative IMA values, on the other hand, signify selection of leg-force combinations that result in variable net-force with each step to stabilize a different gait goal.

Inter-leg-forces stabilize net vertical force

We hypothesized that consistent vertical net-force trajectories would be necessary for maintaining the optimal step-to-step COM transitions suggested by dynamic walking

principles. Motor performance is naturally variable, so individual leg-forces will not be identical with each step, creating an apparent challenge to achieving stable net-forces. Our UCM analysis revealed that structure of F_v^{lead} and F_v^{trail} variance stabilized the F_v^{net} trajectory throughout each transition period. These results indicate that rather than generating identical vertical leg-forces with minimal variance across steps, humans exhibited considerable step-to-step variability while selecting combinations of lead and trail leg-forces that resulted in a consistent net-force trajectory. Because they are stabilized through these strategic leg-force combinations, a consistent vertical net-force trajectory during the step-to-step transition may therefore represent an implicit goal of walking that the human neuromuscular system is likely to monitor and control. Robust human gait as described by dynamic walking principles is thus accomplished by taking advantage of the flexible control enabled by inherent step-to-step leg-force variability to stabilize this implicit gait goal.

Inter-leg-forces modulate net anterior–posterior force

Coordinated application of lead (braking) and trail (propulsive) leg-forces varied $F_{\text{ap}}^{\text{net}}$ trajectory from one step to the next. This modulation of $F_{\text{ap}}^{\text{net}}$ trajectory indicates that, as expected, consistent net anterior–posterior force application is not an implicit goal of treadmill walking and may instead contribute to the stabilization of a different goal (Gorniak et al. 2007, 2009; Shim et al. 2003). Changing the $F_{\text{ap}}^{\text{net}}$ trajectory with each step adjusts step-by-step COM accelerations that maintain the constant walking speed dictated by the treadmill. Requiring a particular walking speed in the experiment created an explicit goal of speed control that likely corresponds to an implicit goal of natural, overground walking.

Evidence of direct $F_{\text{ap}}^{\text{net}}$ trajectory modulation therefore provides some validation for the ability of the UCM analysis to identify and distinguish implicit locomotor goals from secondary variables that serve to stabilize other goals, such as speed.

Intra-leg joint-torques stabilize vertical leading leg-force and modulate trailing leg-force

Joint-torque variance is structured to control the vertical component of leg-force as required for leg function. Our results show that the F_v^{lead} trajectory is stabilized through the selection of force equivalent joint-torque combinations in steady state walking. Because the mechanics of a collision are by nature passive (Kuo et al. 2005), F_v^{lead} collisional forces are unpredictable. Lead limb forces generated on the ground during the step-to-step transition are, however, largely generated by muscular forces and therefore require some motor control. Our subjects negotiated the variability of each heel strike by stabilizing leading leg vertical force as much as possible, albeit imperfectly as some leg-force variance was retained. In contrast, trailing leg-force generation involves no collisional forces and is therefore more predictable, allowing the trailing leg to effectively respond to deviations in F_v^{lead} . We observed that trailing leg joint-torques coordinate to actively modulate the trajectory of F_v^{trail} during each step-to-step transition. Rather than trying to match the values of leading leg-forces, the modulation of the F_v^{trail} trajectory allows the trailing leg to make step-to-step adjustments that compensate for unexpected F_v^{lead} deviations, thereby maintaining a consistent F_v^{net} trajectory. Dynamic walking principles predict that the timing of trailing leg-force application is important for minimizing the energetic cost of walking (Collins and Kuo 2010; Kuo 2002; Ruina et al. 2005). Our UCM analysis of human walking further revealed that the trailing leg is also important for making step-to-step adjustments that stabilize the F_v^{net} trajectory, perhaps to ensure consistent COM transitions in the face of natural variability. These results provide evidence that the locomotor control system may

actively monitor and modulate trailing leg-forces in coordination with leading leg-force deviations to redirect the COM trajectory consistently between steps.

Intra-leg joint-torques stabilize anterior–posterior leg-forces

Leg-force equivalent combinations of intra-leg joint-torques generate consistent braking (F_{ap}^{lead}) and propulsive (F_{ap}^{trail}) force trajectories throughout step-to-step transitions. During step-to-step transitions, the leading leg provides anterior–posterior braking forces to slow the COM velocity. Propulsive forces generated by the trailing leg offset the kinetic energy lost during these braking impulses (Collins and Kuo 2010; Kuo 2002; Ruina et al. 2005).

The consistent F_{ap}^{lead} and F_{ap}^{trail} trajectories we observed agree with the dynamic walking prediction that propulsive forces will counterbalance leading leg braking forces in each transition. This leg-force stabilization is imperfect, however, and some small anterior–posterior leg-force deviations still occur. The resulting deviations in leg-forces then become the source of inter-leg-force variance that is structured to modulate the net anterior–posterior force for speed regulation.

Joint-torques influence net-force stability through locomotor control hierarchy

Considering intra-leg-force stabilization within the context of inter-leg net-force control implies a dependency of body-level force control on leg-level and joint-level variability (Fig. 5). Intra-leg joint-torques determine individual leg-forces, which are then coordinated to regulate net-force trajectories. Our results revealed how deviations at one level can be structured to attenuate or amplify the variability at another hierarchical level. Force equivalent joint-torque deviations, by definition, do not manifest as leg-force deviations and do not contribute to total inter-leg-force variability (Gorniak et al. 2007, 2009). In contrast, joint-torque deviations that are not force equivalent are directly transformed into leg-force deviations with each step. These remaining step-to-step deviations in leading and trailing leg-forces can be further structured through inter-leg coordination to directly affect the consistency of the net-force (Fig. 5). Directing variance into goal equivalent (GEV) or non-goal equivalent (NGEV) components at each hierarchical level allows the locomotor system to attenuate F_v^{net} and amplify F_{ap}^{net} trajectory variability with each step as required by the walking task.

Interactions between step-to-step joint-torque and leg-force deviations describe a hierarchical organization for locomotor control of human walking. In our walking data, non-force equivalent joint-torque variance (NGEV) is present in the intra-leg control of all leg-level task variables (Fig. 4c–f, thick lines). For stabilized leg-force trajectories

(F_v^{lead} , F_{ap}^{lead} , F_{ap}^{trail}), GEV exceeds NGEV to result in IMA values greater than zero, but some deviations in each of these leg-forces inevitably remain. The large amount of joint-torque NGEV in the trailing leg (Fig. 4e, thick dashed line) results in F_v^{trail} modulation. The resulting negative IMA (Fig. 4a, dashed line) indicates that the trailing leg makes leg-force adjustments from one step to another to counteract unexpected deviations in the leading leg-force. Such coordination of leg-force deviations ultimately stabilizes the F_v^{net} trajectory for consistent COM redirection (Fig. 5, thick dashed line). Modulation of the F_{ap}^{net} trajectory is similarly achieved by coordinating leg-force deviations that remain after F_{ap}^{lead} and F_{ap}^{trail} stabilization. These results delineate a hierarchical locomotor control strategy for stabilizing implicit (e.g., consistent F_v^{net} trajectory) and explicit (e.g., constant walking speed) locomotor goals. This hierarchical strategy attenuated kinetic deviations from joint-torques to leg-force and ultimately minimized vertical net-force deviations. This same strategy

specifically amplified the cascade of deviations that modulated net anterior–posterior force to control walking speed.

Potential mechanisms for stabilization of hierarchical forces

The evidence presented here supports a hierarchical organization of human locomotor control, but the mechanisms governing control within this organization remain less clear. Passive mechanics could account for some of the observed force stabilization. Dynamic walking principles use simple dynamical models (Collins 2008) that have guided the construction of passive robots requiring no active control to walk down an incline (Garcia et al. 1998; McGeer 1990). Though they demonstrate the potential for walking to be driven solely by passive mechanics, these robots only walk successfully over a limited range of initial conditions. For example, Garcia et al. (1998) found that simple walkers with rigid struts for legs were stable only on slopes less than 0.019 rad ($<1.1^\circ$). More sophisticated robot walkers that include a knee joint still only demonstrate “stable, persistent walking” on slopes with less than 6 degrees of decline (Garcia et al. 2000). Even on acceptably shallow slopes, stability of these robots remains highly sensitive to initial conditions. While they can establish the minimal requirements for locomotor control, passive dynamics alone do not explain the scope of adaptability and robust performance across the range of typical conditions observed in human walking. Unlike passive robots, human walkers must negotiate joint-torque and leg-force interactions that are not rigidly coupled and coordinate multiple active degrees of freedom to achieve consistent vertical net-force trajectories across large time scales. Negotiating these complicated interactions suggests contribution from some neuromuscular controller.

While the observed vertical net-force stabilization and anterior–posterior net-force modulation could be due to some inherent mechanical properties of the biomechanical system, passive mechanics are unlikely to be the sole determinant of human walking stability. Previous work has shown that following peripheral nerve injury, hip-to-toe leg length, and leg orientation parameters are preserved despite disruption of normal joint angle trajectories, suggesting that neural circuits exist to coordinate joint-level local variables to maintain whole limb-level function (Bauman and Chang 2013; Boeltz et al. 2013; Chang et al. 2009). Leg length trajectories are, however, not preserved following the disruption of central neural circuits despite intact biomechanical connections (Stahl and Nichols 2011). The central nervous system may, therefore, also be required to maintain the coordination of joint-level variance structure that stabilizes limb-level performance across step cycles.

Inherent properties of the neuromuscular system may contribute to achieving consistent, stable leg- and net-force production. Heterogenic reflex pathways mediate intra-leg coordination of joint-torques and may contribute to joint-torque adjustments in response to small perturbations, resulting in consistent leg-force production (Nichols et al. 1999; Wilmink and Nichols 2003). Recent investigations demonstrate that humans adapt temporal-spatial parameters and muscular activation patterns to achieve inter-leg symmetry when forced to walk with an asymmetric walking pattern (Dietz et al. 1994; Reisman et al. 2005; Prokop et al. 1995). Such inter-leg coupling, coordination, and control may be informed by load receptors (Jensen et al. 1998) and achieved through central inhibitory pathways active during bilateral but not in unilateral tasks (Ting et al. 1998). Actions of multi-articular muscles and/or interaction torques could also contribute to maintaining consistent leg-forces through passive mechanics (Cabel et al. 2001; Kurtzer et al. 2006; Sangani et al. 2007). For example, adopting a more extended leg posture leads to stable leg-force production despite high joint-torque variability in hopping tasks (Yen and Chang 2010). Although the aforementioned pathways may regulate the coordinated intra- and inter-leg action during gait, identification of the relevant mechanisms requires further study and focused investigation. Nevertheless, the results presented here support the idea that human walkers

use a hierarchical strategy to harness inherent motor variance to achieve flexible and robust control of bipedal locomotion.

Conclusion

We studied dynamic walking principles in human subjects within the general framework of the uncontrolled manifold concept to identify implicit control targets the neuromuscular system may actively monitor and control to achieve robust walking. The results presented here collectively demonstrate that human locomotor control harnesses step-to-step kinetic variability to achieve robust, steady state walking. Human walkers take advantage of their inherent motor abundance by structuring joint- and leg-level variance to stabilize implicit intra- and inter-leg hierarchical goals. Because dynamic walking principles make predictions about individual leg power and work, future studies should also test these as potential goal variables within the framework already constructed here. Future investigation may also explore how these implicit goals are adapted in response to changing environmental conditions or neuromuscular pathologies.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1.

When considering naturally variable human walking, we consider steps as a cumulative behavior and not in isolation. **a** In dynamic walking, leading and trailing leg-forces act together to consistently transition the center of mass from one pendular arc to the next (v_{com}^- at the beginning of a transition period to v_{com}^+ at the end). **b** Individual vertical leg-forces sum to F_v^{net} while braking leading leg-forces are balanced by propulsive trailing leg-force to determine F_{ap}^{net} . **c** Intra-leg joint-torques at the ankle (τ_1), knee (τ_2), and hip (τ_3) determine individual vertical and anterior–posterior leg-force components. **d** Behavior within each step can vary as long as behavior over time leads to the mean behavior described by dynamic walking. For example, vertical leg-forces can vary while making adjustments to maintain consistent step-to-step F_v^{net} trajectory for consistent COM transitions

Fig. 2.

Sagittal plane kinetics as a percent of the gait cycle for each step (*thin, gray lines*) and mean behavior across all steps (*thick, black lines*) from one representative subject. Body weight normalized vertical and anterior-posterior ground reaction forces (GRF) (*left panel*) for a complete gait cycle and joint-torques (*right column*) during stance are shown. Shaded areas depict transition periods where the first occurs from 1 to 13 % (± 0.80 %) of the total gait cycle as the right leg (*solid lines*) leads and the second from 51(± 0.71)–61 % (± 0.83 %) as the left leg (*dashed lines*) leads

Fig. 3. Inter-limb stabilization of net vertical force (*top*) and modulation of net anterior–posterior force (*bottom*). IMA values (*solid*) significantly greater than zero (*horizontal bar, black line shading*) indicate that net vertical force (*dashed*) is stabilized during inter-step transitions due to selection of net-force equivalent leg-force combinations. IMA values significantly less than zero (*horizontal bar, black line shading*) indicate that leading and trailing leg anterior–posterior forces are coordinated to vary net anterior–posterior forces with each step

Fig. 4.

Intra-limb variance structure selectively modulates trailing leg vertical forces. IMA values for the vertical **a** and anterior-posterior **b** components of leg-forces when the leg is leading (*solid line*) or trailing (*dashed*) during the transition phase. Note that the transition period for the trailing leg begins at 50 % and ends at 62 % of the complete gait cycle, while leading leg transition begins at 1 % and ends at 13 %. During each transition, one leg leads while the other trails, so each of these behaviors occur simultaneously during each transition phase. The GEV (*thin line*) and NGEV (*thick*) components of variance for the transition phase when the leg is leading (**c-d**) and trailing (**e-f**)

Fig. 5.

Postulated hierarchical control to achieve robust walking as described by the dynamic walking model. Intra-leg joint-torque combinations modulate F_v^{trail} . Different F_v^{trail} values with each transition inflate leg-level NGEV, dominating the inter-leg variance available for inter-leg coordination to stabilize F_v^{net} , an implicit goal of human gait. A similar structure also holds for $F_{\text{ap}}^{\text{net}}$ modulation, where leg-level NGEV is equally small in the leading and trailing legs and variable step-to-step $F_{\text{ap}}^{\text{net}}$ is achieved through timing differences in leg-force application