Rate-dependent control strategies stabilize limb forces during human locomotion

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A spring-mass model accurately predicts centre of mass dynamics for hopping and running animals and is pervasive throughout experimental and theoretical studies of legged locomotion. Given the neuromechanical complexity of the leg, it remains unclear how joint dynamics are selected to achieve such simple centre of mass movements consistently from step to step and across changing conditions. Human hopping is a tractable experimental model to study how net muscle moments, or joint torques, are coordinated for spring-mass dynamics, which include stable, or invariant, vertical ground forces. Subjects were equally able to stabilize vertical forces at all hopping frequencies (2.2, 2.8, 3.2 Hz) by selecting force-equivalent joint torque combinations. Using a hybrid-uncontrolled manifold permutation analysis, however, we discovered that force stabilization relies less on interjoint coordination at greater hopping frequencies and more on selection of appropriate ankle joint torques. We conclude that control strategies for selecting the joint torques that stabilize forces generated on the ground are adjusted to the rate of movement. Moreover, this indicates that legged locomotion may involve the differential regulation of several redundant motor control strategies that are accessed as needed to match changing environmental conditions.

Keywords: biomechanics; neuromechanics; UCM; hopping; spring-mass model; motor control

1. INTRODUCTION

A key feature of locomotion is the simplicity of the centre of mass dynamics despite the complexity embedded within a nonlinear time-varying neuromechanical system. In legged locomotion where bouncing gaits such as hopping and running are used, the centre of mass moves as if on a pogo stick. Whether observed in the locomotion of humans, dogs, cockroaches or crabs (Blickhan & Full 1993), the emergent mechanics from all these animals can be modelled as a simple linear spring—a ubiquitous phenomenon of terrestrial locomotion (Cavagna *et al.* 1977; Blickhan 1989; McMahon & Cheng 1990; Farley *et al.* 1993). Nonetheless, the presence of abundant degrees of freedom such as neurons, muscles and tendons within each leg introduced enough complexity to fuel decades of research on redundant motor systems starting with the seminal work of Bernstein (1967). How are such high-dimensional neuromechanical systems organized during locomotion so that the leg produces a simple, spring-like force trajectory consistently from step to step? Moreover, does this organization change if these steps are taken at increasingly faster rates?

One approach to understand how redundant degrees of freedom are controlled is to identify the structure of

variability across movement cycles (Scholz & Schöner 1999; Todorov & Jordan 2002). In a previous study on human hopping, we showed that the vertical ground reaction force was stable, i.e. varied little from hop to hop relative to how much the joint torques, or net muscle–tendon moments about joints of the leg varied (Yen *et al.* 2009). Kinetic redundancy of the joints was exploited such that, although many different seemingly random combinations of joint torques were used over successive hops, they yielded the same vertical ground reaction force over these same hops. In other words, joint torque variance was structured to make vertical force invariant from hop to hop.

The remaining question is addressed in this current study: does the control strategy used to structure joint torque variance depend on cycle frequency? A line of research by Full and colleagues supports the hypothesis that control strategy changes with locomotion speed (Full & Tu 1991; Ting *et al.* 1994; Full & Koditschek 1999; Kubow & Full 1999; Jindrich & Full 2002). However, this hypothesis has only been supported with mathematical models of arthropod locomotion. In this study, we aimed to directly test this hypothesis experimentally. We used human hopping in place because it is a tractable experimental model of bouncing gaits where the rate of movement can be manipulated reliably through the hopping frequency.

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There are two control strategies available that can structure joint torque variance to result in stable forces on the ground. The first strategy is to compensate for a change in one joint torque with a concurrent and counteracting change in another joint torque. For example, a deviation in ankle torque during a particular hop can be compensated by a deviation in knee torque so that the vertical ground reaction force remains unaffected from hop to hop. If this coordinated variation between joints is performed over many hops, then the vertical force variance should be significantly small relative to total joint torque variance. We call this first strategy a ‘covariation’ of the joints, following the work of Müller and Sternad (Müller & Sternad 2003, 2004).

The second control strategy that structures joint torque variance is to directly stabilize the individual joint (or joints) to which the generated force is most sensitive. In other words, it is possible that the ground force changes more in response to the variance of a specific joint or joints than in response to the variance of other joints. For hopping, ankle torque influences the vertical force applied to the ground more than knee or hip torques (Farley & Morgenroth 1999). Therefore, ankle torque stability has a larger role than hip or knee torque stability. Different amounts of variance among the different joints create a variance structure that can stabilize a task variable such as force (Schöner & Scholz 2007). We call this second strategy ‘individual variation’ to stress how the stabilization of one joint can directly stabilize force.

We hypothesized that, for human hopping in place, vertical force stabilization is accomplished through both covariation and individual variation of joint torques. To test this, we examined how joint torques varied from hop to hop to stabilize the vertical ground reaction force for three different hopping frequencies. We used the uncontrolled manifold (UCM) analysis method (Scholz & Schöner 1999; Latash *et al.* 2002) to test whether joint torque variance is generally structured to stabilize vertical ground reaction force at three different hopping frequencies as we had previously observed for only 2.2 Hz hopping (Yen *et al.* 2009). We then separated the contributions of the covariation strategy and individual variation strategy to this joint torque variance structure and found a rate-dependent shift from using more of the covariation strategy at low frequencies to using more of the individual variation strategy at greater hopping frequencies. Therefore, the roles of each individual degree of freedom in a redundant motor system such as the leg can change with task constraints. In addition to the mechanical redundancy associated with the joints of the leg, our findings indicate that a redundancy in control strategies can be exploited under changing task parameters, such as the rate of movement.

2. MATERIAL AND METHODS

2.1. Subjects

Five men and five women (26.1 ± 4.0 -year-old) volunteered to participate in this study. None of the subjects had a major injury or surgery that affected their ability to participate in any exercise activity. The body mass

and height of the subjects were 63.3 ± 8.2 kg and 170.8 ± 9.6 cm. All subjects gave informed consent to participate in this study, which was approved by the Georgia Institute of Technology Institutional Review Board.

2.2. Procedure

We briefly provide relevant details of our experimental protocol and UCM analysis, which is more thoroughly described in previous work (Auyang *et al.* 2009; Yen *et al.* 2009). Subjects hopped in place on their right legs matching the contact of the ground with the audible beat of a metronome. For each trial, the metronome was set to three different beats: 2.2, 2.8 and 3.2 Hz. Preferred frequency for human hopping (approx. 2.2 Hz) and higher frequencies yield linear spring-mass behaviour (Farley *et al.* 1991; Ferris *et al.* 2006). Subjects hopped for three 20–30 s trials at each of the three frequencies in random order for a total of nine trials with ample rest between every trial. An average of 167 ± 51 hops were analysed for each subject and frequency condition.

2.3. Data collection

We used a six-camera motion analysis system to record segment and joint kinematics (120 Hz, Vicon Motion Systems, Oxford, UK). We placed reflective markers on each subject’s second metatarsophalangeal joint, lateral malleolus, lateral condyle, anterior superior iliac spine, posterior superior iliac spine, shank segment and thigh segment. Subjects hopped on a force plate (1080 Hz, Advanced Mechanical Technology Incorporated, Watertown, MA, USA) providing ground reaction force data.

2.4. Data processing

We filtered marker and force data with a zero-phase lag fourth-order Butterworth low-pass filter with a 10 Hz cut-off frequency to calculate joint torques, or net moments of muscle–tendon forces about joints. We performed inverse dynamics to calculate torques about the ankle, knee and hip medio-lateral joint axes using sagittal plane kinematics and force data. Inertial properties of the foot, shank and thigh were estimated based on subject anthropomorphic measurements (Winter 1990). For analysis of ground reactions forces alone, we used the same filter but with a 25 Hz cut-off frequency. The data were cropped to include only stance phases, defined as ground contact time to take-off time. These times were identified by when vertical force crossed a threshold force of 32 N. We normalized and expressed the data as a percentage of stance phase.

2.5. Uncontrolled manifold analysis

For each 1 per cent time slice of stance phase, we investigated the variance structure of joint torques in relation to vertical force (F) variance. Control of vertical force was important for meeting the task objective of hopping at the prescribed frequency. We first derived a

linear relationship between vertical force and joint torques,

$$F \approx S(\theta) \cdot T \equiv [s_a \ s_k \ s_h] \cdot [\tau_a \ \tau_k \ \tau_h]^T. \quad (2.1)$$

The components of the joint torque column vector (τ) are the ankle (τ_a), knee (τ_k) and hip (τ_h) joint torques about the joints' medio-lateral axes. We derived S in a previous study (Yen *et al.* 2009). Briefly, S is a 3×1 matrix and is the transpose of a dynamically consistent generalized inverse of a kinematic Jacobian that relates changes in joint angles ($d\theta$) to a change in vertical endpoint position (Khatib 1987). S is derived using an operational space formulation, a current robotics technique for controlling forces in redundant manipulators (Khatib *et al.* 2004; Schaal & Schweighofer 2005). S takes into account leg segment inertias, and is a function of leg joint angles (θ) and the centre of pressure. The components of S , that is, the lower-case s 's, can be viewed as the individual sensitivities of vertical force to each joint torque (a, ankle; k, knee; or h, hip).

For each subject, hopping frequency condition and per cent of stance phase, we calculated variances of each joint torque and summed them to yield total joint torque variance. As with previous work (Yen *et al.* 2009), we used the UCM analysis method (Scholz & Schöner 1999) with equation (2.1) to separate total joint torque variance into two components: goal-equivalent (GEV) and non-goal-equivalent variance (NGEV). GEV represents joint torque hop-to-hop deviations that do not change the ground reaction force component under analysis. NGEV represents joint torque deviations that result in force component deviations, and is proportional to force variance. To compare GEV and NGEV, they need to be expressed as variance per degree of freedom. We defined TOTV as total joint torque variance per degree of freedom ($n =$ three local degrees of freedom: ankle, knee and hip joint torque), NGEV as non-goal equivalent variance per degree of freedom ($d =$ one global degree of freedom: vertical force magnitude) and GEV as goal-equivalent variance per degree of freedom ($n - d =$ two degrees of freedom).

$$\text{TOTV} = \frac{\text{trace}(C)}{n}, \quad (2.2)$$

$$\text{NGEV} = \frac{\text{trace}((S \cdot S^T)^{-1} \cdot S \cdot C \cdot S^T)}{d}, \quad (2.3)$$

$$\text{and GEV} = \frac{\text{trace}(\text{null}(S)^T \cdot C \cdot \text{null}(S))}{(n - d)}. \quad (2.4)$$

C is the covariance matrix of local variables, which are ankle, knee and hip joint torques. NGEV can be thought of as the projection of C onto the subspace of joint torque variations that result in force variation. GEV is the projection of C onto the subspace of joint torque variations that do not result in any force variation, i.e. the nullspace of S , which is spanned by the orthonormal column space of $\text{null}(S)$. The UCM analysis method was initially presented as a sequence of steps to partition TOTV into NGEV and GEV (Scholz & Schöner 1999). GEV and NGEV are encapsulated here for the first time in one-step linear algebraic forms while retaining generality for any number of global and local degrees of freedom. Expression in this

form allows for direct insight into the contributions from each element in S and C . In general, S is any linear mapping between local variables and the global performance variable.

GEV and NGEV are not directly comparable across subjects. Therefore, we used the index of motor abundance (IMA), similar to Tseng & Scholz (2005), to quantify and compare across subjects the degree of force stabilization (equation (2.5)),

$$\text{IMA} = \frac{\text{GEV} - \text{NGEV}}{\text{TOTV}}. \quad (2.5)$$

2.6. Separation of covariation and individual variation

It is possible that a joint torque variance structure can arise from unequal variances among the three joint torques, i.e. individual variation, and not necessarily from hop-to-hop deviations of joint torques that compensate for one another, i.e. covariation. To isolate the effects of the individual variation strategy, and as a point of departure from previous implementations of UCM analysis, we first found InV, which is the IMA value of a surrogate dataset that had all measurable evidence of covariation removed. A surrogate dataset was formed from joint torque permutation among all hops of a subject and hopping frequency condition. For example, if 150 hops were collected from a subject hopping at a given frequency, then the surrogate dataset consisted of 150^3 hops. Each ankle torque from the original 150 hops was combined with every measured knee and hip joint torque in all possible combinations. The surrogate dataset had joint torque pair-wise covariation values exactly equal to zero, and the variances of the three joint torques were the same as the original dataset (appendix A). Thus the surrogate dataset can be represented by the same covariance matrix C as the original dataset but with the non-diagonal terms replaced with zeros. Moreover, we verified that each of the joint torque variances was normally distributed using the Lilliefors test for normality (Conover 1980). Therefore, UCM analysis on this surrogate dataset revealing stabilization of force was only sensitive to inequality between variances of the joint torques. If the variances of the joint torques had been equal, or if force had been equally sensitive to variances of all joint torques, then InV would have been 0, which would have corresponded to no effect of individual variation of joint torques on force (see proof in appendix B). An InV greater than 0 would indicate that the joint torque to which the force is most sensitive to has the least amount of variance (appendix B).

To calculate the amount of force stabilization or destabilization caused by the covariation strategy alone, we took the difference between the IMA value of the original dataset and the InV value as described above to find CoV,

$$\text{CoV} = \text{IMA} - \text{InV}. \quad (2.6)$$

Analogous to the InV metric, the CoV metric considers only the effects of the covariances of the joint torques

on the variance of the force component and represents a minimum of the amount of interjoint coordination used to stabilize force (appendix A).

2.7. Statistical analysis

For each of the three variance metrics (IMA, InV, CoV) at each of the three hopping frequencies (2.2, 2.8, 3.2 Hz), we performed a Student's two-tailed *t*-test ($\alpha = 0.01$) at each 1 per cent of stance phase to test whether the metric averaged across subjects was significantly different from zero. A positive IMA indicates that torque variance was structured to stabilize force, and a negative IMA indicates that torque variance was structured to destabilize force. An IMA of zero would indicate an absence of structure in joint torque variance. The same applies to the InV and CoV metrics, but InV and CoV consider only the contribution of the individual variation strategy and covariation strategy, respectively. We ran a one-way repeated measures analysis of variance (ANOVA) to test whether hopping frequency affected force stabilization (IMA).

3. RESULTS

All subjects hopped within 5 per cent of the prescribed frequency for all the three frequency conditions. For all conditions, the ankle, knee and hip joint torques were extensor torques for the majority of stance phase (figure 1*a*). The resulting ground reaction force had a vertical component trajectory that was unimodal with a maximum near mid-stance (figure 1*b*). The following results pertain to intra-subject variances of ankle, knee and hip joint torques at each per cent of stance phase and how they relate to control of ground reaction forces.

Although vertical ground reaction force variance was consistent across hopping frequencies, joint torque variance changed (figure 2). As subjects hopped more quickly, variances of the joint torques decreased, particularly the ankle torque variance (figure 2*a*). Furthermore, the ankle torque variance changed from a unimodal trajectory at 2.2 Hz to a bimodal trajectory at 2.8 and 3.2 Hz. In contrast, the vertical force variance trajectory was consistently bimodal for all frequencies (figure 2*b*).

Vertical force variance was most sensitive to ankle torque variance and least sensitive to hip torque variance (figure 3). The dynamically consistent model we used to map joint torques to vertical force was parameterized by segment inertias, lengths and angles. The parameters resulted in a map (*S*) that weighed the influence of the ankle joint torque on force the greatest among the three joints. Averaged across stance phase time and hopping frequencies, a representative subject's vertical force was 63.3 (± 2.2) per cent less sensitive to knee torque and 95.3 (± 1.0) per cent less sensitive to hip torque than to ankle torque (figure 3). All mean torque sensitivities were significantly different between the three joints ($p < 0.001$), and the small s.d.'s across time and frequencies indicated consistent primary force sensitivity to ankle torque variance. Ankle torque sensitivity was greater than knee and hip torque sensitivities throughout

Figure 1. Sagittal plane kinetics versus normalized stance time for 175 hops of a representative subject hopping on one leg at 2.8 Hz. (a) Hip, knee and ankle joint torque trajectories for all hops. A positive joint torque corresponds to an extensor torque. (b) Corresponding vertical ground reaction force (*F*) for the same hops.

stance phase for all hopping frequencies. Therefore, it is possible that reduction of only the ankle torque variance, i.e. individual variation, can structure total joint torque variance for stabilization of force.

Stabilization of vertical force through structuring of joint torque variance was robust across all subjects and the three frequencies tested. For all hopping frequencies, the IMA was significantly positive for isolated periods during the beginning, middle and end of stance phase ($p < 0.01$; figure 4*a*). The three peak IMA values corresponding to the beginning, middle and end of stance did not change significantly as subjects hopped more quickly ($p = 0.41, 0.10$ and 0.43 , respectively).

At 2.2 Hz, both covariation and individual variation strategies contributed to vertical force stabilization. Covariation stabilized vertical force during mid-stance (figure 4*b*), while individual variation stabilized vertical force at the beginning and end of stance phase (figure 4*c*). Covariation at mid-stance explains why vertical force variance reached a minimum at mid-stance despite all three joint torque variances having reached a maximum at mid-stance (figure 2, 2.2 Hz).

Even though overall vertical force stabilization was consistent across frequencies (figure 4*a*), subjects increasingly relied on the individual variation strategy (InV) and less on the covariation strategy (CoV) to stabilize vertical force as they hopped more quickly (figure 4*b,c*). Covariation for vertical force stabilization (CoV) averaged across subjects was significantly greater than zero at the beginning, middle and end of stance for 2.2 Hz hopping (0–4, 36–59, 95–97% stance phase; $p < 0.005$). At 2.8 Hz, only the middle and end of stance phase exhibited significant stabilization from covariation (39–49, 95–97% stance phase; $p < 0.005$). For 3.2 Hz hopping, we did not find any significant contribution from covariation at any point during stance phase ($p > 0.02$; figure 4*b*). In contrast, individual variation for vertical force stabilization (InV) at mid-stance was not significantly greater than zero for

Figure 2. A representative subject's kinetic variance across hops at each hopping frequency condition. (a) Ankle, knee and hip joint torque variances across hops. The magnitude and shape of the ankle torque variance trajectory changed as frequency increased. Thick line, ankle; dashed line, knee; thin line, hip. (b) Variance trajectory of the vertical component of the ground reaction force. The shape and magnitude near mid-stance of the vertical force variance trajectory was consistent across hopping frequencies.

Figure 3. Mean ($\pm$ s.d.) sensitivities of vertical force variability to each of the joints' torque variability for a representative subject across stance time and hopping frequencies. All means were significantly different between the three joints ($p \ll 0.001$).

2.2 Hz ($p > 0.005$), but was significant for the higher frequencies ($p < 0.005$; figure 4c).

4. DISCUSSION

Joint torque variance was structured consistently across hopping frequencies to stabilize vertical force. However, the strategy used to structure joint torque variance changed as a function of frequency (figures 4 and 5). At slow frequencies, hoppers used interjoint coordination, or covariation, to cancel out small mid-stance joint torque fluctuations between joints from hop to hop. At high frequencies, hoppers used individual variation, or minimization of ankle torque variance to

stabilize vertical force. The UCM analysis with the permutation method as performed here provides an effective tool for quantifying the changing role of interjoint coordination in achieving seemingly invariant motor behaviour across changing conditions. Further, our results underscore the importance of stabilizing particular joints in a redundant system to achieve stability of the performance variable.

The individual joint torque variances and the vertical force variance suggest that the joint-level control strategy changed across hopping frequencies to maintain the same limb-level force stability (figure 2). At 2.2 Hz, even though the variances of all three joint torques peaked near mid-stance, the vertical force variance reached a local minimum. This suggests that mid-stance joint torques were coordinated to counteract each other's fluctuations from hop to hop, so that vertical force variance was reduced. At 2.8 and 3.2 Hz, approximately the same low mid-stance vertical force variance was achieved but through direct minimization of ankle joint torque variance. At 2.8 and 3.2 Hz, the vertical force variance trajectory followed the ankle torque variance trajectory: bimodal with a local minimum at mid-stance. This observation suggests that vertical force variance is most sensitive to ankle torque variance. As subjects hopped more quickly, the variance of the ankle torque was reduced more than the other joint torque variances. One would expect a concomitant reduction in vertical force variance with a reduction in ankle torque variance. However, hoppers also used less covariation (less interjoint coordination) to stabilize vertical force. As a result, vertical force stability was consistent as frequency increased because hoppers use less covariation strategy and more individual variation strategy in the form of reduced ankle torque variance.

Our analysis quantified the sensitivity of the force variance to each of the individual joint torque variances

Figure 4. (a) Index of motor abundance (IMA), (b) contributions from coordinated variation (CoV), and (c) individual variation (InV) strategies for 2.2, 2.8 and 3.2 Hz hopping. Data are means across all subjects (± 1 s.e.m.) related to vertical force. Stabilization of vertical force occurred when IMA was greater than zero. Black horizontal bars indicate when IMA, CoV or InV is significantly greater than zero ($p < 0.005$). IMA was generally consistent across hopping frequencies (a). The contribution of the joint torque covariation strategy to vertical force stabilization decreased as subjects hopped more quickly (b). The contribution of the individual variation strategy to vertical force stabilization increased as subjects hopped more quickly (c).

Figure 5. Relative roles of the two control strategies that stabilize vertical ground reaction force during human hopping. At slow hopping frequencies, interjoint torque coordination (covariation) is the dominant strategy, while at faster hopping frequencies, stabilization of ankle torque (independent variation) is the dominant strategy. The additive force-stabilizing effect of the two strategies is constant across hopping frequencies.

(figure 3). Our results are in agreement with other hopping studies that indicate control of the ankle joint is most important for the spring-mass dynamics of human hopping (Farley *et al.* 1998; Farley & Morgenroth 1999). Despite the importance of the ankle joint, other joints can contribute to counteracting loads applied only at the ankle (Chang *et al.* 2008). Because the sensitivities to each of the joints is dependent on limb posture and the limb posture changed during stance phase, it is possible that the ankle joint torque may not always be the most important joint for vertical force production. However, by quantifying the sensitivities to each joint at every time point, we empirically verified that the ankle joint is always the most important joint for hopping at the conditions tested in this study. The results also confirm that vertical force is sensitive to knee and hip joint torques although these are relatively small compared with the sensitivity to ankle torque. Significant sensitivities to all three joints correspond to a redundant system in

which coordinated variation may be used to stabilize the performance variable.

Todorov & Jordan (2002) proposed that biological controllers minimize variations only in joints that lead to variability in the performance variable; variations in joints that do not lead to variability in the performance variable are left untouched or unrestricted. Since the mechanical system that Todorov and Jordan used had joints that equally influenced the performance variable, the variations that were minimized were spread and coordinated among all the joints (covariation strategy). However, if the system is configured such that the performance variable is largely sensitive to only one joint, then minimization of that one joint's variance can be an important task stabilization strategy. In the present study, vertical force in human hopping is most sensitive to the ankle torque. At high frequencies, hoppers minimized ankle torque variance to achieve the same overall force stability as at low frequencies. At mid-stance of 2.2 Hz hopping, subjects minimized joint torque combinations that lead to vertical force variance through an interjoint coordination strategy (Yen *et al.* 2009).

This present study is the first to employ a hybrid method to separate and consider the contributions from both covariation and individual joint variation in the stabilization of a limb movement. Müller and Sternad focused on only covariation (Müller & Sternad 2003) and used permutation of experimental data to quantify the effects of covariation. Schöner and Scholz noted that the permutation method does not take into account individual variation, i.e. 'different amounts of variance in the different elemental variables' (Schöner & Scholz 2007). UCM analysis takes into account both covariation and individual variation, and adds the

contributions of the two into a metric that quantifies how much the structure of joint variance stabilizes or destabilizes the performance variable. However, studies employing the UCM analysis method have stressed covariation in the interpretation of their results (Scholz *et al.* 2000; Tseng *et al.* 2003; Black *et al.* 2007; Hsu *et al.* 2007; Zhang *et al.* 2008; Auyang *et al.* 2009; Yen *et al.* 2009).

Our results are consistent with a number of other locomotion studies that also suggest locomotor-control strategy changes with speed (Ting *et al.* 1994; Full & Koditschek 1999; Jindrich & Full 2002). Another way to distinguish control strategies for locomotor stability is consideration of feed-forward and feedback processes. Full and colleagues hypothesized that slow-moving locomotion is actively stabilized using feedback control via neural reflex pathways. With the more rapid leg movements at greater speeds, they suggest that rapid locomotion is passively stabilized along with feed-forward neural control because feedback processes would involve too large a time delay to be effective (Full & Koditschek 1999). Considering the dynamics of a bouncing gait such as running, hopping and galloping as that of a simple mass-spring system (Blickhan 1989; McMahon & Cheng 1990; Farley *et al.* 1993), the effective stiffness of the legs can be tuned *a priori* so that the effective leg spring can immediately absorb the energy of an unexpected perturbation and return the body to the desired locomotor cycle (Jindrich & Full 2002). However, joints can have differential roles for energy absorption (Daley *et al.* 2007), which is consistent with our finding that the most distal joint, the ankle, is used for stability at the highest hopping frequencies. Although an interesting area for further study, it remains to be tested whether the covariation we found for slow-frequency hopping is a product of feedback processes between muscles crossing different joints, and whether the individual variation we found at higher frequency hopping is the product of a feed-forward process controlling joints independently.

5. CONCLUSION

We now have experimental evidence that supports the existence of more than one limb-control strategy for stabilizing a bouncing gait, and that selection of these strategies depends on rate of movement. As such, it is not surprising to find recent evidence that different neural networks in the spinal cord can be activated for different speeds of the same locomotor mode as opposed to merely turning the excitation of the same neural network up or down (El Manira & Grillner 2008; McLean *et al.* 2008). A redundancy of limb-control strategies would allow locomoting animals to select an amalgamation that is most energetically and computationally efficient, and also allows for the greatest behavioural plasticity in a changing, unpredictable environment.

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APPENDIX A

Proof: By permutation of a set of local variables (e.g. joint torques), individual variation effects are isolated from covariation effects on the structure of local variance.

We demonstrate that individual variances of local variables and their covariations have analytically separable effects on local variance structure. It must be shown that GEV and NGEV, the two measures that determine local variance structure, can each be expressed as a sum of two terms; one term represents individual variation and the other term represents covariation. Then, applying the expressions to a surrogate dataset that is composed of all possible combinations of local variables across all movement cycles, we show that the covariation term becomes zero, and GEV and NGEV are dependent only on the individual variances of the local variables.

First we define the elements of vector $\mathbf{X}$ as n local variables $x_1, x_2, \dots, x_n$. $\mathbf{X}$ varies over N trials and determines the task variable through a map $\mathbf{S}$, which is a single row matrix consisting of elements $s_1, s_2, \dots, s_n$. Equation (A 1) is an example of such a mapping. The variance of the projection of $\mathbf{X}$ on $\mathbf{S}$ across N trials yields NGEV (Zhang *et al.* 2008), and can be compactly written as

$$\text{NGEV} = \frac{\mathbf{S} \cdot \text{cov}(\mathbf{X}) \cdot \mathbf{S}^T}{\mathbf{S} \cdot \mathbf{S}^T}, \quad (\text{A } 1)$$

where $\text{cov}(\mathbf{X})$ is the $n \times n$ covariance matrix of the vector set $\{\mathbf{X}_k\}$ for $k = 1, 2, \dots, N$. The diagonal terms of $\text{cov}(\mathbf{X})$ are the individual variances of the local variables, σ_i^2 for $i = 1, 2, \dots, n$. The off-diagonal terms are the pair-wise covariances of the local variables, $\sigma_{i,j}^2$ for $i = 1, 2, \dots, n$ and $j = 1, 2, \dots, n$ and $i \neq j$. The expression for NGEV can be expanded out as

$$\begin{aligned} \text{NGEV} &= \frac{\begin{bmatrix} s_1 & \cdots & s_n \end{bmatrix} \begin{bmatrix} \sigma_1 & \cdots & \sigma_{1,n} \\ \vdots & \ddots & \vdots \\ \sigma_{1,n} & \cdots & \sigma_n \end{bmatrix} \begin{bmatrix} s_1 \\ \vdots \\ s_n \end{bmatrix}}{\begin{bmatrix} s_1 & \cdots & s_n \end{bmatrix} \begin{bmatrix} s_1 \\ \vdots \\ s_n \end{bmatrix}} \\ &= \frac{\sum_{i=1}^n \sum_{j=1}^n s_i s_j \sigma_{i,j}^2}{\sum_{i=1}^n s_i^2} \\ &= \frac{\sum_{i=1}^n s_i^2 \sigma_i^2 + \sum_{i=1}^n \sum_{j=1, j \neq i}^n s_i s_j \sigma_{i,j}^2}{\sum_{i=1}^n s_i^2}. \end{aligned} \quad (\text{A } 2)$$

The first summand in the numerator is a weighted sum of the individual variances of the local variables, and the second summand is a weighted sum of the covariances of the local variables. The entire numerator is equal to the variance of the task variable. Including the denominator effectively changes the units from units of the task variance to units of the local variance. Therefore, it is clear how NGEV can be expressed as the sum of individual variances and covariances.

GEV is total local variance (V) minus NGEV and normalized by the dimension of the null space of S , which is $n - 1$,

$$V = \sum_{i=1}^n \sigma_i^2 \quad (\text{A } 3)$$

$$\begin{aligned} \text{GEV} &= \frac{V - \text{NGEV}}{n - 1} \\ &= \frac{\left(\sum_{i=1}^n s_i^2 \right) \left(\sum_{i=1}^n \sigma_i^2 \right) - \sum_{i=1}^n s_i^2 \sigma_i^2 - \sum_{i=1}^n \sum_{j=1}^{n:j \neq i} s_i s_j \sigma_{i,j}^2}{(n - 1) \sum_{i=1}^n s_i^2}. \end{aligned} \quad (\text{A } 4)$$

Similar to NGEV, GEV can also be expressed as a sum of individual local variance effects and covariance effects. The first two terms in the numerator in equation (A 4) involve only individual variances and the third term involves only covariances.

We now perform a permutation on the vector set $\{\mathbf{X}_k\}$ to obtain the product set $\{x_{1,k}\} \times \{x_{2,k}\} \times \dots \times \{x_{n,k}\}$. For example, if $\{x_{1,k}\}$ is the set of all ankle joint torque values measured, then each ankle torque value is combined with every knee and every hip torque value measured. If we had simply scrambled the vector set $\{\mathbf{X}_k\}$ (i.e. have had an ankle torque value combined with only one random knee torque and one random hip torque), then the resulting set may retain some covariation (Müller & Sternad 2003). In contrast, the product of the permuted vector set has exactly zero covariation and the same individual variances as the original vector set, as proved below.

The individual variance of the i th local variable in the original vector set is

$$\sigma_i^2 = \frac{1}{N} \sum_{k=1}^N (x_{i,k} - \bar{x}_i)^2. \quad (\text{A } 5)$$

The individual variance of the i th local variable in the product set is the same,

$$\begin{aligned} {}^p\sigma_i^2 &= \frac{1}{N^n} \sum_{k1=1}^N \sum_{k2=1}^N \dots \sum_{kn=1}^N (x_{i,kn} - \bar{x}_i)^2 \\ &= \frac{1}{N} \sum_{k1=1}^N \frac{1}{N} \sum_{k2=1}^N \dots \frac{1}{N} \sum_{kn=1}^N (x_{i,kn} - \bar{x}_i)^2 \\ &= \frac{1}{N} \sum_{k1=1}^N \frac{1}{N} \sum_{k2=1}^N \dots \sigma_i^2 \\ &\vdots \\ &= \frac{1}{N} \sum_{k1=1}^N \sigma_i^2 \\ &= \sigma_i^2. \end{aligned} \quad (\text{A } 6)$$

Therefore, upon permutation, the variances of the local variables remain unchanged. The covariance of

the i th and j th local variables in the product set is

$$\begin{aligned} {}^p\sigma_{i,j}^2 &= \frac{1}{N^n} \sum_{k1=1}^N \sum_{k2=1}^N \dots \sum_{k,(n-2)=1}^N \sum_{l=1}^N \sum_{m=1}^N (x_{j,l} - \bar{x}_j)(x_{i,m} - \bar{x}_i) \\ &= \frac{1}{N^n} \sum_{k1=1}^N \sum_{k2=1}^N \dots \sum_{k,(n-2)=1}^N \sum_{l=1}^N \\ &\quad \times \left((x_{j,l} - \bar{x}_j) \cdot \sum_{m=1}^N (x_{i,m} - \bar{x}_i) \right) \\ &= \frac{1}{N^n} \sum_{k1=1}^N \sum_{k2=1}^N \dots \sum_{k,(n-2)=1}^N \sum_{l=1}^N ((x_{j,l} - \bar{x}_j) \cdot 0) \\ &= 0. \end{aligned} \quad (\text{A } 7)$$

Therefore, upon permutation, all covariances of the local variables go to zero. Furthermore, NGEV and GEV of the permuted dataset depend only on the individual variances of the local variables

$${}^p\text{NGEV} = \frac{\sum_{i=1}^n s_i^2 \sigma_i^2}{\sum_{i=1}^n s_i^2}, \quad (\text{A } 8)$$

$${}^p\text{GEV} = \frac{\left(\sum_{i=1}^n s_i^2 \right) \left(\sum_{i=1}^n \sigma_i^2 \right) - \sum_{i=1}^n s_i^2 \sigma_i^2}{(n - 1) \sum_{i=1}^n s_i^2}. \quad (\text{A } 9)$$

APPENDIX B

Proof: The variance structure of local variables (e.g. joint torques) is not affected by individual variation if the local variables have equal variances or if the task variable is equally sensitive to variances of all local variables.

If there is more GEV than NGEV (i.e. $\text{GEV} - \text{NGEV} > 0$), then local variance is structured to stabilize the task variable. The difference $\text{GEV} - \text{NGEV}$ serves as a metric of the local variance structure. We demonstrate that the local variance structure is not dependent on individual variances either (i) when the individual joint variances are equal to each other, or (ii) when the task variable is equally sensitive to each joint torque. Using equations (A 2) and (A 4), the difference $\text{GEV} - \text{NGEV}$ can be expanded out as

$$\begin{aligned} \text{GEV} - \text{NGEV} &= \\ &= \frac{\left(\sum_{i=1}^n s_i^2 \right) \left(\sum_{i=1}^n \sigma_i^2 \right) - n \sum_{i=1}^n s_i^2 \sigma_i^2 - n \sum_{i=1}^n \sum_{j=1}^{n:j \neq i} s_i s_j \sigma_{i,j}^2}{(n - 1) \sum_{i=1}^n s_i^2}. \end{aligned} \quad (\text{B } 1)$$

As shown in appendix A, by operating on a permuted dataset, we isolate the contribution of individual variances from the contribution of covariances on local variation structure.

$${}^P\text{GEV} - {}^P\text{NGEV} = \frac{\left(\sum_{i=1}^n s_i^2\right)\left(\sum_{i=1}^n \sigma_i^2\right) - n \sum_{i=1}^n s_i^2 \sigma_i^2}{(n-1) \sum_{i=1}^n s_i^2}. \quad (\text{B } 2)$$

Equation (B 2) quantifies the local variance structure that is a result of individual variances. There is no structure (i.e. individual variances do not contribute to local variance structure) if equation (B 2) evaluates to zero. This zero structure condition is non-trivially satisfied if the two terms in the numerator are equal to each other, i.e. if

$$\left(\sum_{i=1}^n s_i^2\right)\left(\sum_{i=1}^n \sigma_i^2\right) = n \sum_{i=1}^n s_i^2 \sigma_i^2. \quad (\text{B } 3)$$

Equation (B 3) is satisfied if $s_i^2 = s^2$ for all $i = 1, 2, \dots, n$, which corresponds to the variance of the task variable being equally sensitive to variances of all local variables. Starting with the left-hand side of equation (B 3), we have

$$\begin{aligned} \left(\sum_{i=1}^n s_i^2\right)\left(\sum_{i=1}^n \sigma_i^2\right) &= \\ \left(\sum_{i=1}^n s^2\right)\left(\sum_{i=1}^n \sigma_i^2\right) &= \\ n \cdot s^2 \left(\sum_{i=1}^n \sigma_i^2\right) &= \\ n \sum_{i=1}^n s^2 \sigma_i^2 &= n \sum_{i=1}^n s_i^2 \sigma_i^2. \end{aligned} \quad (\text{B } 4)$$

Likewise, equation (B 3) is satisfied if $\sigma_i^2 = \sigma^2$ for all $i = 1, 2, \dots, n$, which corresponds to all local variables having the same variance

$$\begin{aligned} \left(\sum_{i=1}^n s_i^2\right)\left(\sum_{i=1}^n \sigma_i^2\right) &= \\ \left(\sum_{i=1}^n s_i^2\right)\left(\sum_{i=1}^n \sigma^2\right) &= \\ \left(\sum_{i=1}^n s_i^2\right)n \cdot \sigma^2 &= \\ n \sum_{i=1}^n s_i^2 \sigma^2 &= n \sum_{i=1}^n s_i^2 \sigma_i^2. \end{aligned} \quad (\text{B } 5)$$

REFERENCES

- Auyang, A. G., Yen, J. T. & Chang, Y. H. 2009 Neuromechanical stabilization of leg length and orientation through interjoint compensation during human hopping. *Exp. Brain Res.* **192**, 253–264. (doi:10.1007/s00221-008-1582-7)
- Bernstein, N. I. 1967 *The coordination and regulation of movements*. Oxford, UK: Pergamon.
- Black, D., Smith, B., Wu, J. & Ulrich, B. 2007 Uncontrolled manifold analysis of segmental angle variability during walking: preadolescents with and without Down syndrome. *Exp. Brain Res.* **183**, 511–521. (doi:10.1007/s00221-007-1066-1)
- Blickhan, R. 1989 The spring-mass model for running and hopping. *J. Biomech.* **22**, 1217–1227. (doi:10.1016/0021-9290(89)90224-8)
- Blickhan, R. & Full, R. J. 1993 Similarity in multilegged locomotion: bouncing like a monopode. *J. Comp. Physiol. A* **173**, 509–517. (doi:10.1007/BF00197760)
- Cavagna, G. A., Heglund, N. C. & Taylor, C. R. 1977 Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.
- Chang, Y. H., Roiz, R. A. & Auyang, A. G. 2008 Intralimb compensation strategy depends on the nature of joint perturbation in human hopping. *J. Biomech.* **41**, 1832–1839. (doi:10.1016/j.jbiomech.2008.04.006)
- Conover, W. J. 1980 *Practical nonparametric statistics*. Hoboken, NJ: John Wiley & Sons, Inc.
- Daley, M. A., Felix, G. & Biewener, A. A. 2007 Running stability is enhanced by a proximo-distal gradient in joint neuromechanical control. *J. Exp. Biol.* **210**, 383–394. (doi:10.1242/Jeb.02668)
- El Manira, A. & Grillner, S. 2008 Switching gears in the spinal cord. *Nat. Neurosci.* **11**, 1367–1368. (doi:10.1038/nn1208-1367)
- Farley, C. T. & Morgenroth, D. C. 1999 Leg stiffness primarily depends on ankle stiffness during human hopping. *J. Biomech.* **32**, 267–273. (doi:10.1016/S0021-9290(98)00170-5)
- Farley, C. T., Blickhan, R., Saito, J. & Taylor, C. R. 1991 Hopping frequency in humans: a test of how springs set stride frequency in bouncing gaits. *J. Appl. Physiol.* **71**, 2127–2132.
- Farley, C. T., Glasheen, J. & McMahon, T. A. 1993 Running springs: speed and animal size. *J. Exp. Biol.* **185**, 71–86.
- Farley, C. T., Houdijk, H. H., Van Strien, C. & Louie, M. 1998 Mechanism of leg stiffness adjustment for hopping on surfaces of different stiffnesses. *J. Appl. Physiol.* **85**, 1044–1055.
- Ferris, D. P., Bohra, Z. A., Lukos, J. R. & Kinnaird, C. R. 2006 Neuromechanical adaptation to hopping with an elastic ankle-foot orthosis. *J. Appl. Physiol.* **100**, 163–170. (doi:10.1152/jappphysiol.00821.2005)
- Full, R. J. & Koditschek, D. E. 1999 Templates and anchors: neuromechanical hypotheses of legged locomotion on land. *J. Exp. Biol.* **202**, 3325–3332.
- Full, R. J. & Tu, M. S. 1991 Mechanics of a rapid running insect: two-, four- and six-legged locomotion. *J. Exp. Biol.* **156**, 215–231.
- Hsu, W.-L., Scholz, J. P., Schöner, G., Jeka, J. J. & Kiemel, T. 2007 Control and estimation of posture during quiet stance depends on multijoint coordination. *J. Neurophysiol.* **97**, 3024–3035. (doi:10.1152/jn.01142.2006)
- Jindrich, D. L. & Full, R. J. 2002 Dynamic stabilization of rapid hexapedal locomotion. *J. Exp. Biol.* **205**, 2803–2823.
- Khatib, O. 1987 A unified approach to motion and force control of robot manipulators: the operational space

- formulation. *IEEE J. Robot. Autom.* **3**, 43–53. (doi:10.1109/JRA.1987.1087068)
- Khatib, O., Sentis, L., Park, J. & Warren, J. 2004 Whole-body dynamic behavior and control of human-like robots. *Int. J. Hum. Robot.* **1**, 29–43. (doi:10.1142/S0219843604000058)
- Kubow, T. M. & Full, R. J. 1999 The role of the mechanical system in control: a hypothesis of self-stabilization in hexapedal runners. *Phil. Trans. R. Soc. Lond. B* **354**, 849–861. (doi:10.1098/rstb.1999.0437)
- Latash, M. L., Scholz, J. P. & Schöner, G. 2002 Motor control strategies revealed in the structure of motor variability. *Exerc. Sport Sci. Rev.* **30**, 26–31. (doi:10.1097/00003677-200201000-00006)
- McLean, D. L., Masino, M. A., Koh, I. Y., Lindquist, W. B. & Fetcho, J. R. 2008 Continuous shifts in the active set of spinal interneurons during changes in locomotor speed. *Nat. Neurosci.* **11**, 1419–1429. (doi:10.1038/nn.2225)
- McMahon, T. A. & Cheng, G. C. 1990 The mechanics of running: how does stiffness couple with speed? *J. Biomech.* **23**(Suppl. 1), 65–78. (doi:10.1016/0021-9290(90)90042-2)
- Müller, H. & Sternad, D. 2003 A randomization method for the calculation of covariation in multiple nonlinear relations: illustrated with the example of goal-directed movements. *Biol. Cybern.* **89**, 22. (doi:10.1007/s00422-003-0399-5)
- Müller, H. & Sternad, D. 2004 Decomposition of variability in the execution of goal-oriented tasks: three components of skill improvement. *J. Exp. Psychol. Hum. Percept. Perform.* **30**, 212–233. (doi:10.1037/0096-1523.30.1.212)
- Schaal, S. & Schweighofer, N. 2005 Computational motor control in humans and robots. *Curr. Opin. Neurobiol.* **15**, 675–682. (doi:10.1016/j.conb.2005.10.009)
- Scholz, J. P. & Schöner, G. 1999 The uncontrolled manifold concept: identifying control variables for a functional task. *Exp. Brain Res.* **126**, 289–306. (doi:10.1007/s002210050738)
- Scholz, J. P., Schöner, G. & Latesh, M. L. 2000 Identifying the control structure of multijoint coordination during pistol shooting. *Exp. Brain Res.* **135**, 382–404. (doi:10.1007/s002210000540)
- Schöner, G. & Scholz, J. P. 2007 Analyzing variance in multi-degree-of-freedom movements: uncovering structure versus extracting correlations. *Motor Control* **11**, 259–275.
- Ting, L. H., Blickhan, R. & Full, R. J. 1994 Dynamic and static stability in hexapedal runners. *J. Exp. Biol.* **197**, 251–269.
- Todorov, E. & Jordan, M. I. 2002 Optimal feedback control as a theory of motor coordination. *Nat. Neurosci.* **5**, 1226–1235. (doi:10.1038/nm963)
- Tseng, Y. W. & Scholz, J. P. 2005 The effect of workspace on the use of motor abundance. *Motor Control* **9**, 75–100.
- Tseng, Y. W., Scholz, J. P., Schöner, G. & Hotchkiss, L. 2003 Effect of accuracy constraint on joint coordination during pointing movements. *Exp. Brain Res.* **149**, 276–288. (doi:10.1007/s00221-002-1357-5)
- Winter, D. A. 1990 *Biomechanics and motor control of human movement*. New York, NY: John Wiley & Sons.
- Yen, J. T., Auyang, A. G. & Chang, Y. H. 2009 Joint-level kinetic redundancy is exploited to control limb-level forces during human hopping. *Exp. Brain Res.* **196**, 439–451. (doi:10.1007/s00221-009-1868-4)
- Zhang, W., Scholz, J. P., Zatsiorsky, V. M. & Latash, M. L. 2008 What do synergies do? Effects of secondary constraints on multidigit synergies in accurate force-production tasks. *J. Neurophysiol.* **99**, 500–513. (doi:10.1152/jn.01029.2007)