FORCE CONTROL DURING HUMAN BOUNCING GAITS

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I think science has enjoyed an extraordinary success because it has such a limited and narrow realm in which to focus its efforts. Namely, the physical universe.

~*Ken Jenkins*

Physics isn't a religion. If it were, we'd have a much easier time raising money.

~*Leon Lederman*

The heavens declare the glory of God;
the skies proclaim the work of his hands.
Day after day they pour forth speech;
night after night they reveal knowledge.
They have no speech, they use no words;
no sound is heard from them.
Yet their voice goes out into all the earth,
their words to the ends of the world.

~*Psalms 19:1-4*

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In contrast to the confusing love-hate relationship that I had with this thesis work, there's nothing confusing about how much I appreciate the relationships formed during my time here. If anything, I'm confused why I didn't appreciate these relationships more in real-time. Looking back, I hope that I can capture at least some of it with words.

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SUMMARY

Every movement has a goal. For reaching, the goal is to move the hand to a specific location. For locomotion, however, goals for each step cycle are unclear and veiled by the automatic nature of lower limb control. What mechanical variables does the nervous system "care" about during locomotion? Abundant evidence from the biomechanics literature suggests that the force generated on the ground, or endpoint force, is an important task variable during hopping and running. Hopping and running are called bouncing gaits for the reason that the endpoint force trajectory is like that of bouncing on a pogo stick. In this work, I captured kinematics and kinetics of human bouncing gaits, and tested whether structure in the inherent step-to-step variability is consistent with control of endpoint force. I found that joint torques covary from step to step to stabilize only peak force. When two limbs are used to generate force on the ground at the same time, individual forces of the limbs are not stabilized, but the total peak force is stabilized. Moreover, passive dynamics may be exploited during forward progression. These results suggest that the number of kinetic goals is minimal, and this simple control scheme involves goals for discrete times during the gait cycle. Uncovering biomechanical goals of locomotion provides a functional context for understanding how complex joints, muscles, and neural circuits are coordinated.

CHAPTER I

INTRODUCTION

1.1 Motivation

Locomotion is critical for animal life. The ability to move from one place to another allows animals to search for food and avoid becoming food. For humans, the loss of the ability to walk or run represents a severe impediment to a healthy lifestyle. Locomotion is important for achieving higher behavioral goals, and it appears that locomotor control is 'easy' – we humans don't have to think about it. We can walk and hold a conversation with someone. A basketball player can run, dribble the ball, and plan the next strategic pass. The automatic nature of locomotor control is of great functional benefit.

However, the automaticity of locomotion obfuscates our understanding of its control. Similar to other motor tasks such as reaching, we make no conscious decision on which muscles to use and how much or when they should be activated. These computations are often executed by neural centers inaccessible to conscious thought. Therefore motor control research on the whole is a question of how the nervous system and musculoskeletal system work to execute motor tasks. However, unlike most other motor tasks, the automaticity of locomotor control also veils locomotor goals. Movements often involve biomechanical goals. When kicking a ball, the biomechanical goal of the lower limb is explicit: move the endpoint (foot) to the ball. Motor tasks are studied with an operating assumption of the task goal. But for locomotion, what physical variables of the lower limb are controlled to a specific value or range of values for each step? Unless task-specific constraints are applied, such as specific foot placements, biomechanical goals of each step are unclear. This gap in knowledge severely impedes our understanding of how the neuromechanical system and its parts work to generate locomotion. Progress for gait rehabilitation techniques and devices is also impeded because effective training should match the goals of the locomotor system.

The purpose of this dissertation is to uncover biomechanical goals implicit to control of locomotion. This introductory chapter is organized to give a brief overview of 1) the hierachical nature of locomotion as supported by electrical recordings of neural activity, 2) an endpoint force control hypothesis as suggested by biomechanics and robotics, and 3) a methodology derived from dynamical systems theory.

1.2 Hierarchical control of locomotion

1.2.1 Hierarchy of form

The neuroanatomy associated with locomotor control is distributed, and the organization can be conceptualized as a hierarchy (Pearson and Gordon, 2000). Located in the brain, "higher" centers are responsible for functions such as steering direction, speed, and initiation of locomotion (Armstrong, 1986; Grillner et al, 2008; Takakusaki et al, 2008). Located in the spinal cord, "lower" levels contain networks, or central pattern generators, that can autonomously generate cyclic muscle activation patterns for locomotion (Brown, 1911; Engberg and Lundberg, 1969; Rossignol and Dubuc, 1994; Grillner, 2006; Kiehn, 2006; McCrea and Rybak, 2008). Though most investigations on central pattern generators use animal models, evidence for these autonomous networks have been found in humans (Calancie et al, 1994; Dietz, 2003; Bradley, 2003; Hultborn and Nielsen, 2007). Although it is likely that supraspinal circuits exert some rhythmic influence on muscle activations (Garcia-Rill et al, 1983; Beloozerova and Sirota, 1993), especially in primates (Eidelberg et al, 1981), complex sequences of muscle activations are executed without "conscious" thought.

Spinal locomotor circuits can transform non-rhythmic input to rhythmically patterned output. In awake and freely moving cats, non-phasic electrical stimulation of the mesencephalic locomotor region in the midbrain induces rhythmic locomotion, and the intensity of stimulation modulates speed (Shik and Orlovsky, 1976). Moreover, sensory feedback of the cyclic limb movement is not necessary for sustaining rhythmic motor output (Grillner and Zangger, 1984). Also, a spinal cord isolated in a bath of neuromodulators generates rhythmic output (Kudo and Yamada, 1987; Kiehn and Kjaerulff, 1996). Finally, epidural stimulation over the spinal column of humans can facilitate locomotion (Minassian et al, 2004). Taken together, these pieces of evidence suggest that non-rhythmic input is sufficient for the lowest levels of the central nervous system to generate rhythmic output.

A hierarchical principle of a low-dimensional to high-dimensional transformation is supported by electromyographic recordings of muscle activity during human walking. Muscles of the lower limb may be activated in synergistic groups or modules (Ivanenko et al, 2004; Krouchev et al, 2006; Drew et al, 2008; Clark et al, 2010). These modules represent ways to transform low-dimensional commands to activations of multiple muscles, and these low-dimensional commands may correspond to limb-level or body-level mechanics such as limb orientation and body support (Ivanenko et al, 2005; Cappellini et al, 2006; Ivanenko et al, 2007; Neptune et al, 2009a).

Reflexes comprise the lowest level of neural control (Loeb et al, 1999). Sensory feedback reinforces patterned movement (Grillner and Zangger, 1984) and contributes to muscle activations during steady-state walking (Sinkjaer et al, 2000). During human hopping, muscle activity related to spinal reflexes is superimposed on feedforward activations of triceps surae muscles (Jones and Watt, 1971; Dyhre-Poulsen et al, 1991; Voigt et al, 1998b,a; Funase et al, 2001). Hopping is not a typical human gait, but when subjects practice hopping over many weeks, reliance on reflexes increases with no change in performance or movement patterns, suggesting automatic control can be delegated to levels further down the neuroanatomical hierarchy (Voigt et al, 1998a).

Sensory information may undergo high-dimensional to low-dimensional transformations as it ascends the hierarchy. Proprioceptive information, which includes state information of individual muscle fibers, tendons, and ligaments, arises from many sensors throughout the locomoting limb and body. Previous evidence suggests that multi-dimensional sensory information is weighted and summed to represent simple low-dimensional variables such as the center of mass (CoM) (Welch and Ting, 2008, 2009). In walking cats, the dorsal spinocerebellar tract may not encode separate joint information, but instead may transmit limb-level information such as limb orientation and limb force (Bosco et al, 2006). Thus supraspinal centers may operate on low-dimensional sensory information.

In summary, the organization of the central nervous system is hierarchical, with the higher levels sending low-dimensional commands to lower levels, and lower levels transforming these simple commands to a rhythmic and multi-dimensional motor output.

1.2.2 Hierarchy of function

Hierarchy of form motivates defining a hierarchy of function. Hierarchical control schemes not exclusive to locomotion have been proposed previously (for example, Schöner, 1995; Loeb et al, 1999; Todorov, 2004; Lockhart and Ting, 2007). Levels comprising hierarchical control schemes do not necessarily have to have one-to-one mappings with anatomical levels. Even without such a mapping, a control scheme is necessary for understanding functional coordination between motor elements such as individual muscles and neural circuits.

The high-level functional abstract thought of ‘run’ is transformed by the nervous system into a low-level functional pattern of muscle activations. The term functional implies that a goal is targeted. The highest and most explicit goal of locomotion

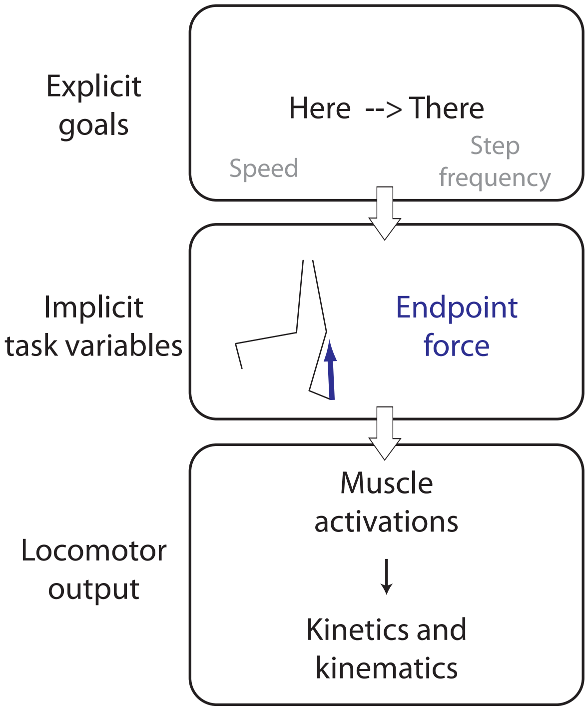

Figure 1: The locomotor task may be hierarchically partitioned into explicit and implicit task goals. The most obvious goal of locomotion is move the body from one location to another. Explicit goals may be added that modify the locomotor task, such as matching step frequency to a given beat. To accomplish given explicit goals, endpoint force trajectories may be targeted. These implicit force goals are carried out by activating muscles, resulting in joint kinetics and kinematics.

is to move the body from one location to another (figure 1A). Additional explicit goals may be added, such as matching the speed of a treadmill belt. But what are the goals of the detailed behavior of muscles and joints? Are there intermediate and implicit biomechanical goals targeted in each step cycle, or is the goal directly to move the body? The latter cannot be the case because there are many ways to move the body, and certainly not all are observed. Minimization of energetic costs may explain why behavior is constrained to a certain pattern (Roberts et al, 1997; Anderson and Pandy, 2001; Neptune et al, 2009b), but cannot fully explain small deviations away from the pattern. Biomechanical goals targeted in each step cycle are plausible and may help explain the inherent variability that is observed from step to step.

The overall purpose of this work was to identify biomechanical task goals implicit in locomotion. To narrow the scope of this work to testing one hypothesized, but likely, task variable, I review below previous studies on biomechanics of locomotion that seem to suggest that endpoint force is a task variable during hopping and running.

1.3 Bouncing gaits

Compared to walking, there is more agreement in the biomechanics literature on candidate task variables. During running, the CoM moves as if on a pogo stick. In the sagittal plane, CoM kinetic and gravitational potential energy fluctuate in phase (Cavagna et al, 1964). During the first half of the ground contact phase, the CoM slows down and reaches its lowest height in the gait cycle. Meanwhile, joints of the leg flex. In the second half of the ground contact phase, joints extend while the CoM position rises and velocity increases. This pattern is common across many species constituting a wide range of leg morphologies (Blickhan and Full, 1993; Farley et al, 1993). Therefore CoM dynamics are well-modeled as a simple point mass on a linear spring (Blickhan, 1989; McMahon and Cheng, 1990). In contrast, it is debatable whether to model the lower limbs as struts or springs for walking (compare Kuo et al

2005 with Blickhan et al 2007). For this reason, I focus on identifying task goals implicit to bouncing gaits, which includes human running and hopping. Endpoint force trajectories may be targeted during running and hopping to bounce the CoM and move it forward.

Generating a spring-like force during running may be important because it is an energetically efficient way to use the limb. Limb-level behavior reflects the behavior of its actuators: muscles and tendons. During running, these actuators behave like springs (Cavagna and Kaneko, 1977; Alexander and Bennet-Clark, 1977; Ker et al, 1987). This conserves energy by exchanging kinetic and gravitational potential energy with stored elastic energy. Despite detailed muscle-level changes across running speeds, however, energetic cost is proportional to limb-level forces (Sih and Stuhmiller, 2003), and inversely proportional to the time spent generating force on the ground (Kram and Taylor, 1990). Even without elastic components, a simple running model consisting of a point mass on telescopic legs produces a spring-like force to minimize energy use (Srinivasan and Ruina, 2006; Srinivasan, 2011). Therefore, generating a spring-like force takes advantage of the energy savings inherent in not only muscle-tendon properties but also inherent in the force trajectory itself.

Stability, or the ability to repeat the same movement each stride, may be another reason why forces are generated such that the CoM bounces. As ground impedance changes, human hoppers keep the CoM trajectory nearly consistent (Ferris and Farley, 1997; Moritz and Farley, 2003). This is observed even if the ground is more compliant than the leg, in which case, upon landing, the leg extends instead of flexes and muscle activations are significantly greater (Moritz and Farley, 2005). CoM dynamics are also consistent across joint loading conditions (Ferris et al, 2006; Chang et al, 2008), and a spring-like force is generated even when running over ground that has an unexpected drop in level (Daley and Biewener, 2006). Moreover, the successful implementation of the spring-mass template in control of legged robots (Chepponis et al, 1984; Saranli et al, 2001; Cham et al, 2002; Poulakakis and Grizzle, 2009) further demonstrates the importance of a spring-like leg force for stability.

In total, previous studies in biomechanics and robotics suggest that endpoint forces are generated to move the body in a stable and efficient manner. Therefore, I hypothesized that one goal implicit in bouncing gaits is achieving specific endpoint force trajectories from stride to stride. These specific trajectories may not be exactly like that of a linear spring. Linearity has merely been used as an approximate description of the resulting mechanics. The aforementioned biomechanical studies are limited to describing what the output force resembles. The hypothesis presented here is not proposing what the force trajectory is, but rather is proposing that there exists a targeted force trajectory.

It is possible, and likely, that other task variables exist in addition to endpoint force. One such variable may be limb stiffness (ratio of endpoint force and leg length). However, the mechanics of the leg are not always controlled to act like a linear spring. For example, when hopping on a damped surface, the lower limb performs positive net work to replace the energy lost by the damped surface and conserve the CoM motion (Moritz and Farley, 2003). Therefore, endpoint force control may explain observed CoM dynamics as a more general principle than control of limb stiffness.

1.4 Methodology

1.4.1 Coordination of motor elements

Dynamical systems or dynamic systems theory posits that elements (e.g., muscles, tendons, neurons) form coordinating structures specific to motor tasks (Saltzman and Kelso, 1987; Schöner and Kelso, 1988; Turvey, 2007). According to this theory, elements will covary and compensate for each other's fluctuations to ensure task-level dynamics are invariant. Put in another way, biological movements exhibit what Bernstein (1967) called "repetition without repetition" – upon repeated executions of the same motor task, individual degrees of freedom fluctuate more than task variables. Elemental covariation stabilizes task variables to targeted values across repetitions of a motor task.

Elemental covariation occurs throughout many levels of the motor system. Consider, for example, the ion channels of a neuron to be the elements that determine the aggregate electrical behavior of the neuron. Parameters of a neuron's membrane channels can covary to produce consistent spiking behavior of the neuron (Golowasch et al, 2002). At a higher anatomical level, synaptic strengths between neurons can covary to stabilize the behavior of a neural circuit (Prinz et al, 2004), such as a central pattern generator (Chiel et al, 1999) or cortical network (Carmena et al, 2005). At progressively higher levels, motor units fire asynchronously such that the force at the whole-muscle level is steady; muscles synergists around a joint can compensate for each other's behavior to keep the joint's behavior consistent (Misiaszek and Pearson, 2002); and finally, joints of a limb can covary for consistent behavior of the endpoint (Bernstein, 1967). Therefore covariation between elements seems to be a recurring theme in motor control.

Elemental covariation, especially at the joint and end-effector levels, has been documented across a variety of motor tasks. Consider multi-finger force production for example, in which there is a targeted total finger force value. Forces of the individual fingers are more variable than total finger force (Latash et al, 2001). Examples of other tasks that exhibit task-specific elemental coordination include speech (Kelso et al, 1984), grasping (Cole and Abbs, 1987), arm reaching (Haggard et al, 1995), pistol shooting (Scholz et al, 2000), pointing (Domkin et al, 2002), postural control (Krishnamoorthy et al, 2003), frisbee throwing (Yang and Scholz, 2005), and arm force production (Krishnamoorthy et al, 2007). These studies used explicit task variables, or variables that had task-specific values or trajectories as explicit goals. However, task variables specific to hopping and running are implicit and unknown, of which I aim to uncover through this work.

1.4.2 Uncontrolled manifold analysis

Uncontrolled manifold (UCM) analysis, a quantitative method developed by Scholz and Schöner (1999), tests whether variables are task variables. The method requires data from repeated movements of the same task and a linear mapping (matrix, or coordinate transformation) of elemental variables to the hypothesized task variable. The hypothesis may be supported if elemental variance across repetitions is preferentially constrained to the null space of the matrix, i.e. the manifold which represents any which way the elemental variables can vary (be "uncontrolled") without changing the value of the hypothesized task variable. Essentially, the UCM method tests whether the hypothesized task variable is more consistent across repetitions than the underlying elemental variables. Thus for locomotion, in which each step cycle can be considered a repetition, task constraints or task-specific experimental instructions should not change from step to step because true task variables may not be stabilized and not be detectable by this method. Therefore, I used steady-state locomotion and tested whether a goal is to stabilize the endpoint force trajectory from step to step.

To test whether endpoint force is a task variable, I used joint torques (net muscle-tendon moments about joints) as the elemental variables (figure 2). Joint torques represent the level of analysis just below endpoint force, and can be changed, albeit indirectly, by the nervous system. If joint torques covary within a force-equivalent manifold during steady-state hopping and running, then elements residing at further detailed levels, such as individual muscles or motor units, also vary in a way that stabilizes endpoint force.

One issue with the UCM method as originally proposed by Scholz and Schöner (1999) is that elemental variables do not necessarily need to covary to lie within the manifold. In other words, UCM results may not reflect covariation of elements. UCM

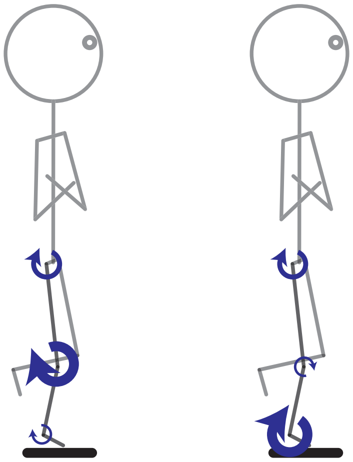

Figure 2: Idealized example of joint torque covariation. 2 hop cycles from the same subject are depicted. Both hops generate the same vertical force, but with different joint torque combinations. The hop cycle depicted on the left involves an above-average knee extensor torque and a below-average ankle extensor torque. The hop cycle depicted on the right involves a below-average knee extensor torque and a above-average ankle extensor torque. If such is the case, then the joint torques covary to stabilize vertical force. Vertical force may be a task variable, and such covariation in joint torques would represent evidence that vertical force is a task variable during hopping.

results may instead reflect heterogeneous distribution of variance across elements that vary independently. Variance of some elements may be less than variance of other elements for reasons other than stabilizing the hypothesized task variable. For example, the elemental variable that has the least amount of variance across repetitions may be a task variable, or variances of the elemental variables are explainable by signal-dependent noise (Harris and Wolpert, 1998).

This issue can also be explained by consideration of what happens when the UCM method is applied to a randomized or shuffled data set. A shuffled data set is a surrogate set, in which any putative elemental coordination is removed from the original experimental data set. This is done by combining one element's value from one repetition with other elements' values from different repetitions. If the elements covaried in the original data set, applying the UCM method to this surrogate data set should yield a different result than the original data set. The difference represents the effect of elemental covariation on the stability of the hypothesized task variable (Müller and Sternad, 2003). Therefore, I used this difference to test whether endpoint force is a task variable. Further explanation and mathematical proof are detailed in sections 3.2, 3.7, and 3.8 (Yen and Chang, 2010).

1.4.3 Experimental approach

During running, vertical and horizontal (fore-aft) endpoint forces have separate functional consequences on the CoM. An adequate vertical component needs to be generated to support body weight. Over many strides on level ground, the average vertical force is body weight, and during each stride, the vertical force follows a unimodal trajectory. Vertical force starts from zero, rises to a peak at mid-stance, and falls back to zero. Adequate horizontal forces need to be generated for the braking and acceleration that occurs during each stride. At a constant speed, the horizontal component averages zero, decelerating the CoM during the first half of stance phase and accelerating the CoM during the second half. Compared to sagittal plane forces, medio-lateral force and free moment about the vertical axis are small and previously not addressed in spring-mass models of human bouncing gaits. Therefore, this dissertation will focus only on sagittal plane (vertical and horizontal) forces.

I experimentally addressed vertical force generation in isolation by considering in-place hopping. Hopping and running are often considered mechanical analogues because both can be described by a spring-mass model. Human hopping in place has been used as an experimental model because of its tractability and potential to uncover principles applicable to other bouncing gaits such as running (Farley et al, 1987, 1991; Ferris and Farley, 1997; Farley and Morgenroth, 1999). Therefore the simplest bouncing gait to start with is hopping in place.

Chapter 2 (Yen et al, 2009) investigates hopping in place and tests whether joint torque redundancy may be utilized to control endpoint forces. I used the UCM analysis method developed by Scholz and Schöner (1999) to show that joint torque variability is not random. Chapter 3 (Yen and Chang, 2010) proceeds to investigate whether this non-random joint torque variability is a result of joint coordination or independent but differential joint torque variability. Through a modification of the UCM method, I show that it is a combination of both strategies, a combination that depends upon hopping frequency. Faster hopping frequencies result in more extended leg postures and shorter stance phase durations that may make joint coordination for hopping in place more difficult. Chapter 4 takes a closer look at the assumption taken in the previous chapters that endpoint force is a critical biomechanical variable that the nervous system cares about for hopping in place. To this end, I applied a series of experimental constraints on hopping to test alternative explanations of why joint torques covary. Chapter 5 builds on hopping in place by adding a horizontal force component to the locomotor task. It investigates forward hopping and running.

1.5 Significance

Knowledge of intended biomechanical goals during locomotion can provide a framework to understand compensatory behavior for injuries or other local deficits. As an example, a sprained ankle is accompanied by an adjustment of knee and hip behavior. This phenomenon may be explained by a consistent presence of a functional goal for the whole limb. A sprained ankle forces the limb to redistribute joint power production to the hip and knee to possibly conserve limb-level dynamics. Likewise, greater ankle torques compensate for fatigued thigh muscles during hopping (Orishimo and Kremenic, 2006). Results presented here may provide a framework that explains gait compensations within a reduced locomotor system and evaluates rehabilitation therapies (Latash and Anson, 2006). These results will also set a basis for investigating what neural or mechanical elements support multi-joint coordination. Finally, control principles of biological locomotion uncovered here may improve design of legged robots.

CHAPTER II

EXPLOITATION OF KINETIC REDUNDANCY FOR FORCE CONTROL DURING HOPPING IN PLACE

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2.1 Introduction

The center of mass dynamics of bouncing gaits such as human running and hopping are well modeled as a simple point mass on a linear spring (Blickhan, 1989; McMahon and Cheng, 1990; Farley et al, 1993). This suggests that the complex system of multiple muscles and joints of the leg are coordinated in a synergistic manner to achieve the simple behavior represented by the effective system stiffness, i.e. a ratio of ground reaction force to hip-to-toe leg length. In a previous study on human hopping we showed that leg length was controlled by coordinating the compensatory actions of joint kinematics (Auyang et al, 2009). In this study, we investigated how the seemingly invariant force patterns generated from cycle to cycle by the leg-spring are accomplished through the control of complex interjoint kinetics.

There are an infinite number of different ankle, knee, and hip joint torque combinations that result in the same total force produced by the leg. This concept is described by many terms such as motor redundancy, equifinality (Bernstein, 1967), and motor abundance (Latash, 2000). Redundancy in the leg allows an organism the opportunity for interjoint compensation and results in a more adaptable, robust locomotion. An increase in torque about one joint can compensate for the decrease in torque about an injured or weakened joint. For example, after muscles spanning the knee joint are fatigued, humans hop with increased hip and ankle torques to compensate for decreased knee torque (Orishimo and Kremenic, 2006). Interjoint compensation mechanisms are utilized for externally applied perturbations as well. The knee joint compensates for a resistive load applied around the ankle joint to produce the same peak ground reaction force as during hopping with no load (Chang et al, 2008).

Neuromechanical redundancy is exploited after a perturbation during locomotion, but is redundancy exploited during intact steady-state locomotion to stabilize global kinetic variables such as ground reaction force? We define "stability" as invariance across step cycles, which does not necessarily correlate with ability to resist tripping or falling (Dingwell and Cusumano, 2000), but is often used as a measure of skilled performance (Sekiya et al, 1997; Danion et al, 2003; Cusumano and Cesari, 2006). Even during controlled steady-state hopping, joint torques naturally vary from cycle to cycle, which could make the ground reaction force vary from cycle to cycle. Due to kinetic redundancy in the leg, however, it is possible that force is being stabilized through this joint torque variance if all the varying combinations of joint torques yield the same force, i.e. if the joint torques have goal-equivalent variance (GEV). This case would reflect the capacity of the system to reject perturbations in the form of joint torque deviations that are non-goal-equivalent (Scholz and Schöner, 1999).

The goal of the present study was to determine whether humans exploit joint kinetic redundancy during an unperturbed locomotion task. Hopping in place is an appropriate experimental model because it is a relatively simple locomotor behavior with easily identifiable task goals, i.e., leg force and leg stiffness. This contrasts with the more complex dynamics of walking. When hopping at a constant frequency, vertical force quickly becomes invariant, or stabilized, over time despite a wide range of possible force trajectories that could be used to meet the same hopping frequency (Cavagna et al, 1988; Blickhan, 1989; McMahon and Cheng, 1990; Farley et al, 1991; Rousanoglou and Boudolos, 2006). Impulse of vertical force is determined by variables that are constant: body mass and hop cycle period. To minimize energy expenditure, hoppers generally maximize duration of the vertical impulse while still maintaining a force trajectory proportional to center of mass position, as in a linear spring (Blickhan, 1989; McMahon and Cheng, 1990; Farley et al, 1991; Srinivasan and Ruina, 2006). Given that vertical force is stabilized, we asked if all joint torque variance is minimized (null hypothesis) to make the vertical force variance small, or if only those joint torque deviations that make vertical force vary from cycle to cycle are minimized (alternative hypothesis). If the alternative hypothesis is supported, then the executed joint torque combinations have GEV. Such a variance structure would indicate exploitation of kinetic redundancy, which is a non-trivial strategy for force stability.

We also tested whether kinetic redundancy is exploited for horizontal (fore-aft) ground reaction force production for hopping in place. To hop in place, control of horizontal force involves hop-to-hop corrections. If a positive horizontal force propels the body forward slightly, then a subsequent hop must produce a negative horizontal force to correct for the small drift in position. Therefore, to stay on average in the same place, the horizontal force trajectory must vary in both negative and positive directions from hop to hop. We define this type of purposeful cycle-to-cycle back-and-forth variation as force destabilization. To accomplish force destabilization, one trivial strategy is to equally increase variances of all joint torques. Yet, with this trivial strategy, some joint torque combinations will also act to stabilize horizontal force. Alternatively, motor redundancy can be exploited by structuring joint torque variance in a way to make all torque deviations destabilize horizontal force. As with vertical force stabilization, structuring joint torque variance for horizontal force destabilization is a non-trivial strategy.

We hypothesized that kinetic redundancy at the joint-level would be exploited to control limb-level force production during hopping in place at a constant frequency. Based on this general hypothesis, we predicted that joint torque variance would stabilize vertical force. In contrast, we predicted joint torque variance would destabilize horizontal force. Using the uncontrolled manifold (UCM) analysis method (Scholz and Schöner, 1999; Latash et al, 2002b), we tested if the majority of joint torque variance stabilizes vertical force and destabilizes horizontal force.

2.2 Methods

2.2.1 Subjects

Ten healthy subjects, 5 males and 5 females, with an average age of 26.1 years of age (SD 4.0), 63.3 kg body mass (8.2), and 170.8 cm height (9.6), gave informed consent to participate in this study that was approved by the Georgia Institute of Technology Institutional Review Board.

2.2.2 Procedure

Subjects hopped in place on their right legs following an audible beat of a metronome set at 2.2 Hz, which is approximately the preferred frequency for human hopping and exhibits spring-like behavior (Farley et al, 1991; Ferris et al, 2006). We instructed subjects to hop as comfortably as possible to avoid fatigue, to fold their arms across their chests and to comfortably flex their left knee to keep their left foot from touching the ground. Although many different leg stiffnesses and hop heights are possible, an energy minimizing strategy is observed to implicitly constrain subjects to hop with a consistent leg stiffness resulting in a consistent hop height (Cavagna et al, 1988; Blickhan, 1989; McMahon and Cheng, 1990; Farley et al, 1991; Rousanoglou and Boudolos, 2006). We also instructed subjects to hop in place, not look down at the ground, and to adjust any perceived horizontal drift with corrective hops. The dimensions of our force plate would allow subjects to drift up to 0.8 m horizontally (forward or backward) from starting position before they would land off the force plate. In practice, however, their foot placements did not vary by more than 0.1 m. Subjects practiced hopping until they felt comfortable matching the beat to their foot contact on the ground. To avoid fatigue, subjects hopped for three 2030 s trials with ample rest between every trial resulting in approximately 160 hops analyzed for each subject.

2.2.3 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 subjects 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 (1,080 Hz, Advanced Mechanical Technology Incorporated, Watertown, MA, USA) providing ground reaction force data.

2.2.4 Data analysis

We filtered marker and force data with a zero-phase lag fourth-order Butterworth low-pass filter with a 10 Hz cutoff frequency to calculate joint torques. We performed inverse dynamics to calculate torques about the ankle, knee, and hip joints using sagittal plane kinematics and force data. Inertial properties of the foot, shank, and thigh were estimated based on subject anthropomorphic measurements (Winter, 1990). The trials were cropped into individual stance times, defined as ground contact time to takeoff time using force data with a threshold of 32 N. We ignored aerial phase data because we were only interested in testing how joint torques act to generate a force on the ground. Standard deviations of stance phase times for all subjects at all frequency conditions were small (<24 ms). However, to analyze across hops, we normalized and expressed our data as a percentage of stance phase.

Time normalization is a uniform scaling of time for hops of different stance durations. The timing of peak values, however, can vary from hop to hop (Sadeghi et al. 2000). To also analyze the effects of timing variability, we applied in lieu of time normalization a time warping procedure based on the sequence of states method described by (Forner-Cordero et al, 2006). By defining the vertical force trajectory as a sequence of states, and acknowledging that the time between states is not uniform across hops, this algorithm shifted vertical force data points and their corresponding joint torque data points backward or forward in time to best match the average vertical force trajectory. We compared the final analysis results of time-warped data to our results of time-normalized data to identify the effects, if any, of timing variability.

To validate that time normalization did not introduce artificial timing variability, we employed a third method to analyze only a subset of hops that had the exact same number of raw samples. In this way, no time normalization or time warping was required because the nth time point of one hop could be compared to the nth time point of the other hops. We then compared the final analysis results of non-normalized subsets to our results of time-normalized whole data sets.

To investigate the variance structure of joint torques in relation to vertical force stabilization and horizontal force destabilization at each time slice, we derived two UCMs, or force-equivalent subspaces within the three-dimensional joint torque space. UCM_V represents all possible joint torque combinations that correspond to the average vertical force value for a time slice of stance phase. Likewise, UCM_H represents all possible joint torque combinations that correspond to the average horizontal force value. Each UCM was linearly approximated as the null space spanned by joint torque basis vectors ek that solve the general equation

$$0 = \left[\left(J \cdot M^{-1} \cdot J^{T} \right)^{-1} \cdot J \cdot M^{-1} \right] \cdot A \cdot \varepsilon_k \tag{1}$$

Both UCMs are two-dimensional ($k = 1, 2$). In other words, both UCMs are planes within a three-dimensional joint torque space. $0 = \left[\left(J \cdot M^{-1} \cdot J^T \right)^{-1} \cdot J \cdot M^{-1} \right]$, the transpose of the "dynamically consistent generalized inverse" of J (Khatib, 1987), yields endpoint force F_{end} when multiplied by segmental torques (see derivation in "Appendix"). M is the mass matrix of the full dynamical equation of motion

$$M(\theta) \cdot \ddot{\theta} + C(\theta, \dot{\theta}) + G(\theta) = \tau - J^T \cdot F_{end}, \tag{2}$$

where C is a coriolis and centrifugal force matrix and G is a gravitational force matrix. τ is the vector of calculated segmental torques, and A in Eq. (1) maps joint torques to segmental torques.

$$A = \begin{bmatrix} 1 & 0 & 0 \\ -1 & 1 & 0 \\ 0 & -1 & 1 \end{bmatrix} \tag{3}$$

J is the Jacobian of the equation relating segment angles (θ) to the vertical or horizontal component of the endpoint position, the hip joint center. F_{end} and ground reaction force are approximately equal for the task of hopping in place ($r^2 = 0.998$). Therefore, we applied this analysis to ground reaction force, which is directly related to center of mass movement. To map joint torques to vertical force, the Jacobian is

$$J = \begin{bmatrix} -l_1 cos(\theta_1) & -l_2 cos(\theta_2) & -l_3 cos(\theta_3) \end{bmatrix} \tag{4}$$

and to map joint torques to horizontal force, the Jacobian is

$$J = \begin{bmatrix} l_1 sin(\theta_1) & l_2 sin(\theta_2) & l_3 sin(\theta_3) \end{bmatrix} \tag{5}$$

The mass matrix M is the same in both cases.

$$M = \begin{bmatrix} l_1^2(m_2 + m_3) + I_1 & l_1(l_2 m_3 + m_2 l_2 d_2 cos(\theta_1 - \theta_2)) & l_1 m_3 l_3 d_3 cos(\theta_1 - \theta_3) \\ l_1(l_2 m_3 + m_2 l_2 d_2) cos(\theta_1 - \theta_2) & l_2^2 m_3 + I_2 & l_2 m_3 l_3 d_3 cos(\theta_2 - \theta_3) \\ l_1 m_3 l_3 d_3 cos(\theta_1 - \theta_3) & l_2 m_3 l_3 d_3 cos(\theta_2 - \theta_3) & I_3 \end{bmatrix} \tag{6}$$

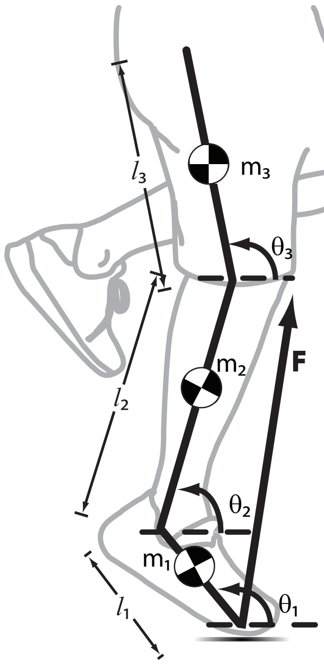

Figure 3: Schematic of our sagittal plane three-link rigid body model. The parameters of the model include lengths (l), masses (m), and angles (θ) of the foot (1), shank (2), and thigh (3) segments. These parameters were used to determine the relationship between ankle, knee, and hip joint torques and the ground reaction force (F).

The subscripts denote lower limb segment in a sagittal plane three-link model (foot = 1, shank = 2, thigh = 3). l is the calculated segment length. m is the segment mass. I is segment inertia for rotation about the segment's distal end, and d is the fractional distance from the segment's distal end to its center of mass estimated from an anthropometric model (Winter, 1990). θ is the angle formed between the segment and horizontal. Figure 3 is a schematic of these parameters. Only the mass of the hopping leg is included in our model because the rest of the body mass can be considered as the load the hopping leg must apply force against. By definition, ground reaction force acts at the center of pressure, which was calculated from force plate data. Therefore, for the J and M matrices, we defined the foot segment length l_1 to be from the ankle joint center to the center of pressure and not to the toe.

We performed the following variance analysis with respect to both of the UCMs (Scholz and Schöner, 1999; Scholz et al, 2001). We pooled together all hops across all three trials for each subject, and normalized stance phase time across all hops. For each 1% of stance phase, we calculated T^0, the average joint torque vector across hops. The elements of the vector are ankle, knee, and hip joint torques. For every 1% of stance phase of each hop we calculated a joint torque deviation vector $T_d = T^0 T$, which represented the difference of the average torque vector and the current hops torque vector. The UCM for each percent of stance phase was estimated by evaluating Eq. (1) with the current hop's leg posture and center of pressure. We resolved the deviation vector T_d into a component parallel to the UCM ($d_{//}$)

$$d_{//} = \sum_{k=1}^{2} \varepsilon_k^T T_d \varepsilon_k \tag{7}$$

and a component perpendicular to the UCM ($d_{\perp}$)

$$d_{\perp} = T_d - d_{//} \tag{8}$$

The variance per degree of freedom parallel to the UCM, which contributes zero variance to the force component, was defined as GEV

$$GEV = \frac{1}{N} \sum_{n=1}^{N} \frac{\left\| d_{//n} \right\|^2}{2} \tag{9}$$

The remaining component of variance per degree of freedom perpendicular to the UCM was defined as non-goal equivalent variance (NGEV)

$$NGEV = \frac{1}{N} \sum_{n=1}^{N} \frac{\left\| d_{\perp n} \right\|^2}{1} \tag{10}$$

N equaled the total number of hops from all trials of one subject, and was the squared magnitude.

To summarize, we separated joint torque variance into stabilizing (GEV) and destabilizing (NGEV) components with respect to vertical force, and repeated the analysis with respect to horizontal force. GEV and NGEV are measurements that are not directly comparable across subjects. Therefore, we used the index of motor abundance (IMA), which is the normalized difference between GEV and NGEV (Auyang et al, 2009), defined as

$$IMA = \frac{GEV - NGEV}{GEV + NGEV} \tag{11}$$

to quantify the degree of force stabilization with one normalized metric. IMA can range between -1 and 1. An IMA equal to 1 would indicate that all joint torque deviations for that time step resulted in the same force value, and that force was stabilized through exploitation of kinetic redundancy. An IMA equal to -1 would indicate that all joint torque deviations for that time step resulted in different force values, and that force was destabilized through exploitation of kinetic redundancy. An IMA equal to 0 would indicate that joint torque variance equally contributed to stabilizing and destabilized force; if force was stabilized or destabilized, it was not accomplished through a strategy that exploited kinetic redundancy.

To characterize force control during stance phase as a whole, we analyzed how variances of joint torque impulses related to variances of vertical and horizontal force impulses. We expected vertical impulse to be stabilized because constant frequency hopping dictates that vertical impulse should be constant, given that subjects hop to a consistent height. We also expected horizontal impulse to vary purposefully, or be destabilized, because positive and negative impulses should be used in variable fashion to stay on average in the same place. Without normalizing time, we integrated joint torques over stance phase time and decomposed the hop-to-hop torque impulse variance into stabilizing (GEV) and destabilizing (NGEV) components just as we did with joint torque trajectories. IMA metrics for vertical and horizontal force impulses were defined the same as in Eq. (11). The UCMs for torque impulses were the same as for torque trajectories (see Eq. (1)) except they were only evaluated once for the entire stance phase using the average posture of stance phase (see Eqs. (4)(6)). We verified that the choice of the average posture rather than the landing posture (most extended) or mid-stance posture (most flexed) was inconsequential. Among all subjects, the posture choice did not have any significant effect on the resulting IMA metrics ($P = 0.67$ for vertical, and $P = 0.30$ for horizontal). Therefore, using the average posture to approximate how torque impulses relate to force component impulses provided fair results.

2.2.5 Statistical analysis

Two IMA values, one for vertical force and one for horizontal force, were calculated for every 1% of stance phase. We predicted the IMA trajectory for vertical force to be greater than zero and the IMA trajectory for horizontal force to be less than zero throughout stance phase. We performed a Students one-tailed t test ($\alpha = 0.005$) at each 1% of stance phase to test whether IMA for vertical force was significantly greater than zero for vertical force, which is equivalent to testing whether GEV is significantly greater than NGEV. Likewise, we tested whether IMA for horizontal force was significantly less than zero ($\alpha = 0.005$).

2.3 Results

Within-subject variability of hopping frequency, position, joint torques, and force

Subjects exhibited accuracy and precision in meeting the beat of a metronome. All subjects hopped at a mean frequency within 0.7% of the prescribed 2.2 Hz. Standard deviation of hopping frequency was at most 3.6% of the prescribed frequency among all subjects.

In contrast, horizontal (fore-aft) position fluctuated significantly. Every hop resulted in a detectable change in horizontal position. The standard deviation of the toe marker at ground contact was as much as 0.10 m within a trial, and the maximum drift away from the initial position was 0.37 m. There were approximately as many forward hops as backward hops; the fraction of forward hops within a trial was 47.9% (SD 5.6), or nearly half.

Figure 4 shows a representative subjects general kinematics and kinetics. Subjects hopped with all joints flexing through the first half of stance phase and all joints extending through the second half (Fig. 4a). All three joints produced extensor torques throughout the stance phase (Fig. 4b). The time series of the vertical component of ground reaction force was unimodal in shape, and peaked during mid-stance (Fig. 4c). The horizontal component of ground reaction force fluctuated around 0 N (Fig. 4c).

Joint torque variance and force variance for the representative subject are shown in Fig. 4d–f. We normalized stance time, and for each percentage of stance phase, we calculated the variances of all joint torques and force components. The variance trajectories of the ankle, knee, and hip torques were all unimodal during ground contact, reaching peaks at mid-stance (Fig. 4d). The sum of the variances for all three joints was also unimodal (Fig. 4e). Because joint torques directly affect the ground reaction force, it is reasonable to expect that the variances of vertical and horizontal forces would have also reached a peak at mid-stance phase. Horizontal force variance

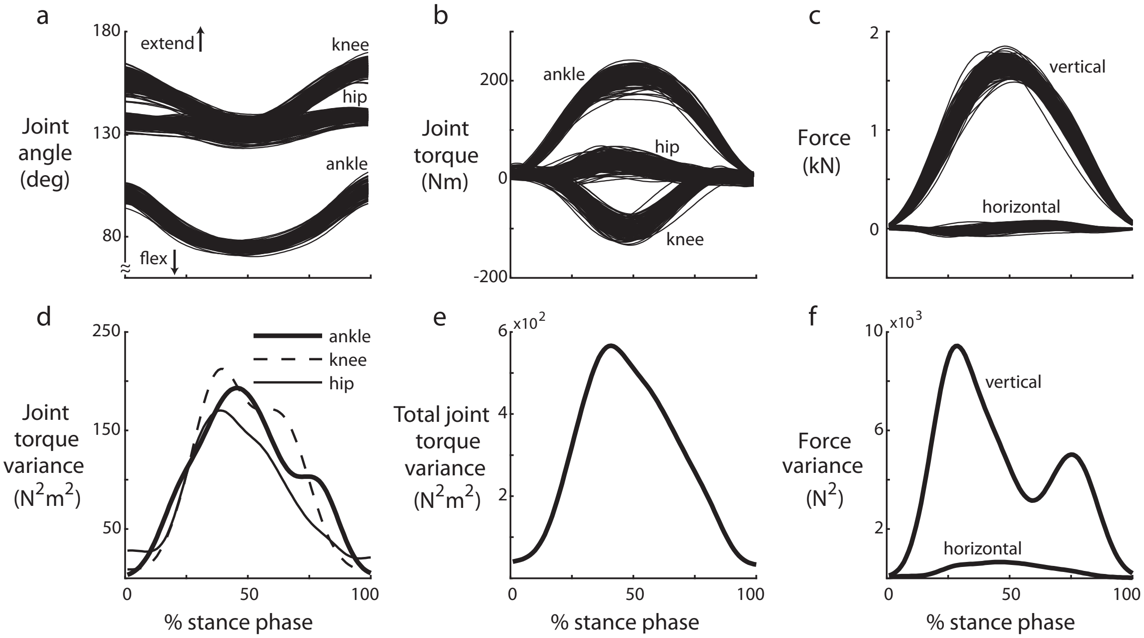

Figure 4: Sagittal plane kinematics and kinetics versus normalized stance time for 175 hops of a typical subject hopping on one leg at 2.2 Hz. **a** Hip, knee and ankle joint angle trajectories for all hops. An increase in joint angle through time corresponds to extension. **b** Hip, knee, and ankle joint torque trajectories for the same hops. A positive torque corresponds to a clockwise rotational acceleration of the distal segment around the joint. For the ankle and hip, a positive magnitude indicates an extensor torque, and for the knee, a negative magnitude indicates an extensor torque. **c** Corresponding vertical force and horizontal force for the same hops. **d** Unimodal joint torque variances of the ankle, knee, and hip. **e** Sum of the ankle, knee, and hip joint torque variances in **d** is a unimodal shape. **f** Bimodal trajectory of vertical force variance suggests that joint torques were coordinated to reduce vertical force variance during mid-stance

peaked near mid-stance, but vertical force variance reached peaks around 25 and 75% of stance phase when the rate of vertical force change was greatest (Fig. 4f). There was a notable attenuation of vertical force variance at mid-stance (Fig. 4f), suggesting that hop-to-hop compensation between joints must have lowered vertical force variance during mid-stance.

2.3.1 Vertical force

The structure of joint torque variance stabilized vertical force during the beginning, middle, and end of stance phase, but destabilized vertical force between these time periods, when the vertical force rate of change was greatest (Fig. 5a). Subjects exhibited a unimodal GEV trajectory that peaked at mid-stance. Recall that GEV for vertical force corresponds to the joint torque variance that does not lead to any cycle-to-cycle variance. In contrast, NGEV directly corresponds to vertical force variance. As expected, the NGEV trajectory was similar to the vertical force variance trajectory exhibiting a bimodal shape with a local minimum during mid-stance. GEV was larger than NGEV during the beginning, middle, and end of stance phase indicating there was more joint variance that stabilized vertical force than that which destabilized vertical force. The accompanying supplementary video (Animation 1) displays the changing distribution of the many joint torque combinations in 3D joint torque space relative to the 2D UCM for a representative subject. Joint torque variance structure changes throughout the stance phase. In particular, it increased in magnitude along the UCM to reduce vertical force variance during mid-stance.

To capture the relationship between GEV and NGEV with one metric, we took the difference between the two variance components. Then, to compare across subjects, we normalized the difference by the sum of the two, resulting in the metric IMA. A positive IMA for vertical force indicated exploitation of kinetic redundancy for vertical force stabilization. IMA for vertical force averaged across subjects was significantly

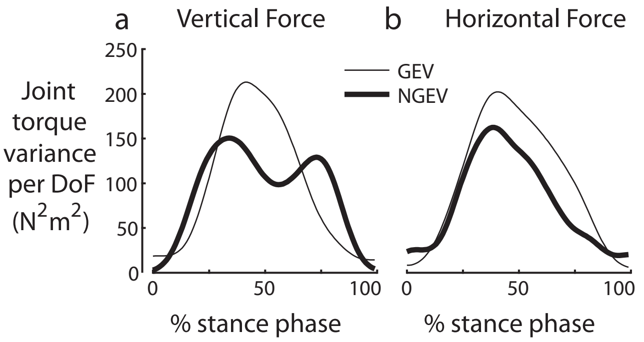

Figure 5: Representative subject's joint torque variance components per degree of freedom (DoF) with respect to vertical (**a**) and horizontal force (**b**). **a** GEV, the joint torque variance component that does not affect vertical force, is greater than NGEV, the component that leads to vertical force variance, during the beginning, middle, and end of stance phase. **b** NGEV for horizontal force is greater than GEV only at the beginning and end of stance phase.

greater than zero for 08, 3461, and 94100% of stance phase ($P < 0.005$; Fig. 6). In contrast, IMA for vertical force was negative for 1720 and 6985% of stance phase ($P < 0.005$; Fig. 6). These time periods of when joint torque variance destabilized vertical force corresponded to the time periods with highest rates of change in vertical force.

To investigate force stability on the whole, we considered how joint torques integrated over stance phase, or impulses, were controlled. Variations of joint torque impulses from hop to hop were structured to stabilize vertical force impulse. Torque impulse GEV was greater than NGEV for all subjects. IMA for vertical impulse was significantly greater than zero ($P = 3 \times 10^{-5}$) with an average value of 0.3 (SD 0.1).

2.3.2 Horizontal force

Horizontal force was destabilized through joint torque variance only at the beginning and end of stance phase. For all subjects, GEV and NGEV trajectories were both unimodal (Fig. 5b). We observed no trend across subjects indicating whether GEV or NGEV was the larger of the two components except at the beginning and end of stance phase. At the beginning and end of stance phase NGEV was greater than

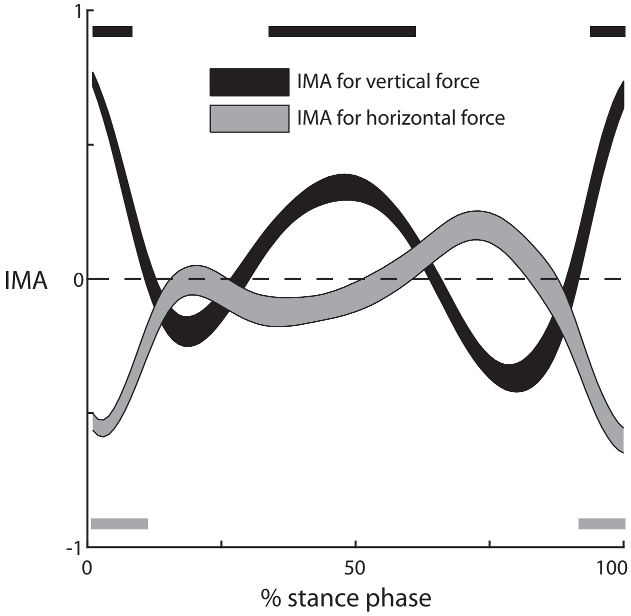

Figure 6: Index of motor abundance (IMA) for vertical and horizontal forces. The IMA metric is a measure of stabilization through structuring joint torque variance, i.e. making NGEV not equal to GEV. Data are mean values across subjects 1 SE related to either vertical force (black regions) or horizontal force (gray regions) performance tasks. Black horizontal bars indicate when IMA for vertical force is significantly greater than zero ($P < 0.005$) and gray horizontal bars indicate when IMA for horizontal force is significantly less than zero ($P < 0.005$).

GEV for all subjects. IMA for horizontal force averaged across subjects was not significantly different from zero for the majority of stance phase ($P > 0.005$, Fig. 6). Two exceptions occurred: at landing (011% of stance phase) and takeoff (92100% of stance phase). At landing and takeoff, IMA for horizontal force was significantly less than zero ($P < 0.005$), which corresponds to destabilization of horizontal force through structuring joint torque variance. In a third exception, IMA for horizontal force was significantly greater than zero only for a brief time between 70 and 74% of stance phase ($P < 0.005$). IMA for horizontal force impulse was not significantly different from zero ($P = 0.04$), and the average across subjects was -0.1 (SD 0.2).

2.3.3 Timing variability

Time periods around 25 and 75% of stance phase are characterized by the highest rates of change in vertical force (Fig. 4c). With high rates of change, a small error in timing from one cycle to the next (i.e., timing variability) will result in a large difference between the vertical forces of two cycles compared at a specific percent of stance phase. For a post hoc analysis of timing variability effects, we removed timing variability from our data through a modification of our analysis method. Instead of normalizing time across the hop cycle, we “warped” time (see data analysis in “Methods”) so that states such as peak force were matched together across hops.

Plotted as a function of 100 successive states (warped time) instead of normalized time, the peak vertical forces and peak joint torques were better phase-matched compared to when plotted against normalized time (Fig. 7a, b). Vertical force GEV was greater than NGEV throughout stance phase (Fig. 7c), which corresponded to an IMA always greater than zero (Fig. 7d). Compared to normalizing time, warping time increased IMA for vertical force throughout stance phase, with the greatest increases occurring near 25 and 75% of stance phase.

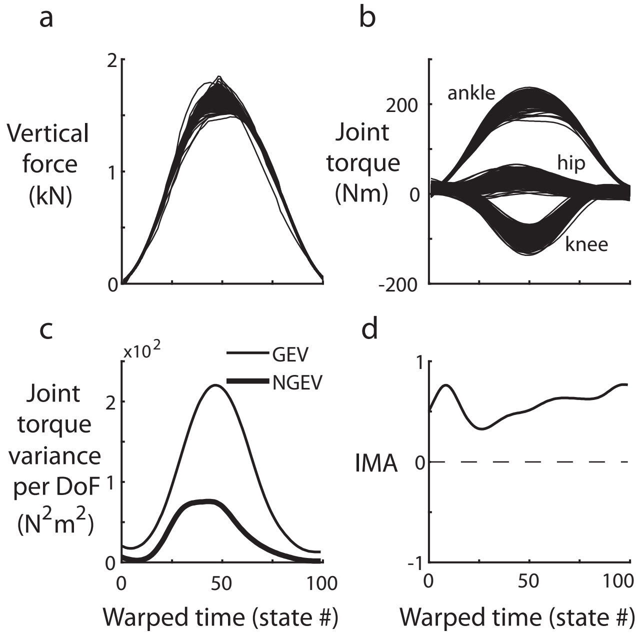

Figure 7: Representative subjects vertical force stabilization with timing variability removed. **a** The vertical force peaks across all 175 hops are more temporally aligned with one another, as are the joint torque peaks (**b**). **c** GEV for vertical force is always greater than NGEV when timing variability is removed. **d** IMA for vertical force in warped time is always greater than zero; vertical force is always stabilized through structured joint torque variance

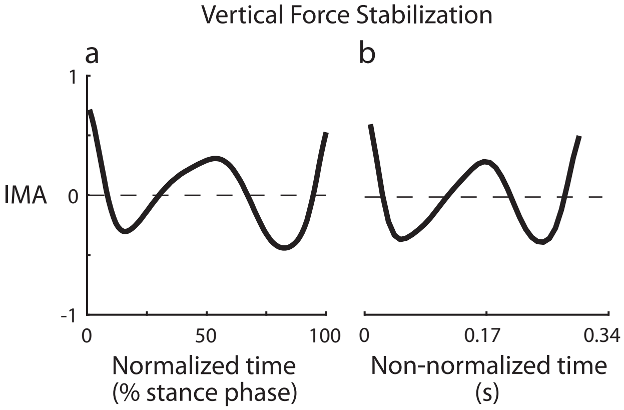

Figure 8: Representative subject's vertical force stabilization analyzed in normalized time (**a**) and in actual time (**a**). Only a subset of the representative subjects hops (54 of 175) was analyzed in **b**. The subset consisted of hops with the same number of time samples. Therefore, UCM analysis on this subset did not require time normalization. The vertical force stabilization metric (IMA) was similar in both analyses suggesting that time-normalization did not introduce artifacts into the results

As a test of whether time normalization introduced timing variability as an artifact, we analyzed a data subset that consisted of the same number of raw data samples for stance phase without warping or normalizing time, thereby preserving any real behavioral timing variability. The analysis in actual time yielded the same results as our analysis of all hops in normalized time (Fig. 8), suggesting that time normalization did not introduce any artifact.

2.3.4 Discussion

When hopping in place, small hop-to-hop joint torque fluctuations compensate for one another to accomplish the task goal of stabilizing the vertical force generated against the ground. While compensatory processes have been previously shown in large-scale perturbed locomotion, our present results suggest compensatory mechanisms between the joints are also utilized on a cycle-by-cycle basis during unperturbed steady-state locomotion. Compensation is possible because joint torques are redundant with respect to applying a force on the ground, and the results indicate that the locomotor system regularly utilizes this redundancy. During hopping in place, kinetic redundancy is exploited at landing, mid-stance, and takeoff for vertical force stabilization, and exploited at landing and takeoff for horizontal force destabilization (Fig. 6).

By analyzing joint-level variance during a locomotor task, this study extends previous work suggesting that motor redundancy is part of the solution to motor control (Gelfand et al, 1966; Latash, 2000) as opposed to being a problem that must be overcome (Bernstein, 1967). Exploitation of redundancy has been shown with the UCM method in other motor tasks such as sit-to-stand (Scholz and Schöner, 1999; Scholz et al, 2001), pistol shooting (Scholz et al, 2000), pointing (Domkin et al, 2002; Tseng et al, 2002), posture (Krishnamoorthy et al, 2003), and walking (Black et al, 2007). Experiments measuring finger forces gave insight into kinetic coordination (Latash et al, 2001; Shinohara et al, 2004; Shim et al, 2008; Zhang et al, 2008), but addressed coordination across appendages and not interjoint coordination within a single appendage. In this study, we are interested in the exploitation of motor redundancy for coordination between the joints, which is particularly relevant in locomotion.

2.3.5 Redundancy is exploited for vertical force stabilization

Preliminary analysis of our results suggests that joint torques are coordinated to stabilize vertical force during mid-stance. As extensor torques reach their maxima at mid-stance (Fig. 4b), so do their variances (Fig. 4d, e). This is expected because of signal-dependent motor noise, which predicts that torque variance increases as muscle force increases (Sutton and Sykes, 1967; Harris and Wolpert, 1998; Slifkin and Newell, 1999). However, vertical force variance approaches a minimum during mid-stance (Fig. 4f). Therefore, even though total torque variance is at a maximum at mid-stance, the majority of this joint-level “noise” is canceled out at the limb-level through compensatory coordination between the joints.

Our UCM analysis indicates that the joint torque variance component (NGEV) that leads to vertical force variance is reduced during mid-stance (Fig. 5a). This is consistent with previous results from models operating under optimal feedback control (Todorov and Jordan, 2002). Optimal feedback control predicts that only the deviations of joint variables that lead to deviations of the performance variable are minimized.

Our results suggest that landing, mid-stance, and takeoff are critical time points for vertical force stabilization (Fig. 6). Controlling force generation at landing, mid-stance, and takeoff during hopping is important for determining overall spring-mass dynamics that are characteristic of hopping. Meeting these forces consistently from hop to hop enables hoppers to keep a constant frequency while meeting physiological constraints. Avoiding large vertical force deviations at landing and takeoff are likely as important as stabilizing large forces at mid-stance. Impact force is a major source of energy lost in locomotion (Srinivasan and Ruina, 2006). Also, large impact force peaks could destabilize the vertical center of mass trajectory during the stance phase; likewise, fine control of the force as one is leaving the ground will provide any final corrections that determine the aerial phase center of mass trajectory. Vertical force may also be concurrently stabilized simply through minimizing total joint torque variance (Müller and Sternad, 2004; Cusumano and Cesari, 2006). Nonetheless, joint torque variance is structured to stabilize vertical force at landing, mid-stance, and takeoff suggesting that they are critical time points.

Vertical forces between landing, mid-stance, and takeoff times are not stabilized through the joint torque variance structure. This behavior is also consistent with previous results from models using optimal feedback control (Todorov and Jordan, 2002). In a model and experiment of a reaching task where the goal was to move the hand through a sequence of targets, Todorov and Jordan showed that hand position variance across multiple trials was lower at targets than the variance at midpoints between the targets. Feedback control was not exercised to stabilize the trajectory in between targets.

On the whole, the vertical force trajectory was stabilized as indicated by our analysis of vertical force impulse. Vertical force impulse was stabilized through structuring variance of joint torque impulses. To hop at a constant frequency, subjects kept vertical force impulse and hop height consistent from cycle to cycle. This means that the peak vertical force could have been varying inversely with contact time. However, peak vertical force variance during mid-stance was small (Fig. 4f), suggesting contact time variance was stabilized as well.

2.3.6 A combination of neural and mechanical processes may stabilize vertical force

Neural control in the form of force feedback has been shown to contribute to interjoint coordination (Nichols et al, 1999). For example, an increase in force produced by triceps surae muscles (ankle extensors) increases inhibition of quadriceps muscles (knee extensors). Thus more extensor torque around the ankle is compensated with less extensor torque around the knee. Inhibition also operates in the opposite direction, from quadriceps to triceps surae (Wilmink and Nichols, 2003). Furthermore, inhibition of the soleus muscle only appears at relatively high forces, which corresponds with our observation of coordinated compensation when the high forces of mid-stance are generated (Figs. 4e, f, 5a). These reflexes may play an important role in generating immediate alternative joint torque combinations that are force-equivalent.

In addition to neural processes, joints are linked through various mechanical structures such as multiarticular muscles, which can contribute to the joint coordination evident in our results. For example, the gastrocnemius is a biarticular muscle that can act concurrently as an ankle extensor and knee flexor. Extensor torques are positively correlated with the vertical force while flexor torques are negatively correlated. Therefore, with an above average muscle force produced by the gastrocnemius on a given hop, the resulting greater knee flexor torque may compensate to some degree the end-point force produced by the greater ankle extensor torque. Variances of multiarticular muscle forces contribute to variances at the joint level that may be diminished or canceled out at the limb level.

2.3.7 Timing variability destabilizes vertical force

Around 25 and 75% of stance phase, vertical force is not stabilized through structuring joint torque variance, as indicated by an IMA less than zero (Fig. 6). This is because of variability in the timing of force generation during the gait cycle. Timing variability is most likely to affect vertical force stability when vertical force has a high rate of change such that a small deviation in timing results in a large force fluctuation. The highest rates of force generation occurs around 25 and 75% of stance phase. We warped time to construct a hypothetical data set characterized by minimal timing variability. This allowed us to analyze equivalent states in the same time slice (Forner-Cordero et al, 2006). For example, peak vertical forces from each hop and the joint torques associated with them were analyzed as one time slice.

Warping time changed the joint torque variance structure to stabilize vertical force throughout stance phase (Fig. 7c, d). Mathematically, warping time necessarily reduces vertical force variance but does not necessarily change the structure of joint torque variance. Warping time could potentially reduce all joint torque variance equally (i.e., reduce both stabilizing (GEV) and destabilizing (NGEV) components equally) without changing the structure. Nonetheless, warping time did change the structure by reducing vertical force NGEV more than GEV. The greatest change was at 25 and 75% of stance phase (cf. Fig. 5a), when the rate of change in vertical force was greatest. Positive correlation between rate of change in force and the destabilizing variance component has also been observed in finger force production (Latash et al, 2002a). Our results go beyond correlation and quantify how much timing variability affects force stability and joint torque variance structure.

Timing variability is an actual behavioral phenomenon of hopping. UCM analysis in actual time, without normalization or warping, yields the same results as with time normalization (Fig. 8). Therefore time normalization did not introduce any artifact. Because warping time removes timing variability, the difference between warped time and normalized time provides insightful estimation of the magnitude of destabilization that timing variability introduces into force control.

2.3.8 Redundancy is exploited for horizontal force destabilization only at landing and takeoff

The data support our hypothesis that joint torque variance is structured to destabilize horizontal force (i.e., make horizontal force purposefully vary from hop to hop). Subjects hop back and forth to stay on average in the same place. Horizontal force is controlled to vary so that the different horizontal forces produced from hop to hop correct for one another over time. However, significant structuring of joint torque variance to destabilize horizontal force occurs only at landing and takeoff (Fig. 6). This suggests that landing and takeoff are critical time points when the locomotor system uses horizontal force to make hop-to-hop positional corrections.

The positive IMA for horizontal force around 75% of stance phase is contrary to our hypothesis; joint torque variance stabilized horizontal force for part of the hop cycle. This may be a vestige of the control strategy that occurs for forward hopping and running. The peak force for forward propulsion occurs at around 75% of stance phase during running (Munro et al, 1987; Chang and Kram, 1999). Stabilization of horizontal peak force would be critical for maintaining a constant forward speed, just as the stabilization of peak vertical force is critical for constant step rate. Antiphasic alternation between vertical and horizontal force control may be required during steady state running to stabilize respective peak force components and appears during hopping in place as a remnant of this strategy. A task alternation strategy between vertical and horizontal force control may be important when stabilization of both force components is required as in forward running.

Our data show that stabilization of vertical force through structuring of joint torque variance correlates with destabilization of horizontal force. This suggests an anti-phasic relationship between vertical and horizontal force stabilization (Fig. 6). The orientations of the UCM_V and UCM_H planes in joint torque space are nearly perpendicular to each other. Leg posture dictates the orientations of the UCM planes because the planes are functions of joint angles and center of pressure (Eqs. (4)(6)). For the representative subject, the average angle across time between the two UCM planes is 86° and ranges between 73 and 90° through stance phase. If the joint torque variance is structured to be parallel to one UCM plane, then the joint torque variance could automatically be structured to be perpendicular to the other UCM plane. Therefore, it is possible that only vertical force is actively controlled during hopping in place, with horizontal force destabilization as a mathematical byproduct of vertical control. If this were the case, we could still conclude that joint torque variance is structured and redundancy exploited to accomplish both vertical and horizontal task goals of hopping in place.

Yet, it is important to point out that simultaneous stabilization of both vertical and horizontal force is possible; joint torque variance can be structured along the line of intersection of the two UCM planes. This line represents a one-dimensional force-equivalent subspace that the neuromechanical system can exploit to simultaneously stabilize both vertical and horizontal force components. A similar multi-task control strategy has been successfully employed in robotics (Khatib et al, 2004). Therefore, joint torque variance that stabilizes vertical force does not necessitate horizontal force destabilization. For example, the data show that during mid-stance vertical force is stabilized while horizontal force is not destabilized (Fig. 6). This supports the hypothesis that destabilization of horizontal force at landing and takeoff may be a result of active control of the horizontal force component. Comparison with other hopping tasks where the horizontal task goal is experimentally manipulated is needed to further test this hypothesis.

Possible limitations of the current study are the estimations involved with inverse dynamics calculations. These estimations introduce uncertainties in joint torque values. While previous studies have examined the magnitude of joint torque uncertainties for walking and running (McCaw and DeVita, 1995; Pearsall and Costigan, 1999; Riemer et al, 2008), none have estimated uncertainties during hopping. Uncertainties consist of artificial cycle-to-cycle noise (decreased precision) and biases (decreased accuracy). However, only the portion of uncertainties resulting from decreased precision influences our results, which are only based on hop-to-hop variances. To our knowledge, no study has estimated the amount of additional artificial variance. It is generally accepted that calculated hip torque has the greatest uncertainty. We note in our data set, however, that hip torque variance is on par with knee and ankle torque variances (Fig. 4d), supporting the reliability of our calculated hip torque variance.

2.4 Conclusion

Vertical force stabilization and horizontal force destabilization are specific task goals of hopping in place, and joint torque variance was structured to accomplish these goals. Thus our results support the general principle that kinetic redundancy is exploited to accomplish functional locomotor task goals. This strategy represents how complex joint-level behavior is controlled to yield the simple and invariant behavior at the limb-level that is described by the spring-mass model of bouncing gaits. The locomotor control system has an inherent property of joint-level compensation via use of redundancy to accomplish task goals. It remains to be seen how this cycle-to-cycle compensation strategy relates to compensation strategies used during chronically perturbed or injured locomotion.

2.5 Acknowledgments

The authors thank Dr. Lena Ting and members of the Neuromechanics Laboratory. We also thank Dr. T. Richard Nichols and the members of the Comparative Neuromechanics Laboratory for helpful comments in preparing the manuscript. This work was funded by National Science Foundation IGERT DGE-0333411 and National Science Foundation GRFP fellowship awarded to JTY.

2.6 Appendix

Following Khatib (1987), the goal of this section is to derive a matrix J^{-T} that maps torques T to endpoint force F_{end}.

$$J^{-T}T = F_{end} \tag{12}$$

Given F_{end}, and supposing we already have J^{-T} , there are infinite number of torques that satisfy the Eq. (12). The general solution is

$$T = J^T F_{end} + [I - J^T J^{-T}]T_0, \tag{13}$$

where T_0 is any arbitrary torque vector and J^{-T} can be one of an infinite number of possibilities for the pseudo-inverse of J^T . The term $[I - J^T J^{-T}]T_0$ lies in the null space of J^{-T}, and represents torques that do not affect F_{end}. Comparing Eq. (13) to Eq. (2), $[I - J^T J^{-T}]T_0$ represents the dynamics and gravity effects of the linked segments, or

$$[I - J^T J^{-T}]T_0 = M\ddot{\theta} + C + G \tag{14}$$

Indeed, in a static case without gravity, the relationship between torques and endpoint force via the principal of virtual work is

$$T = J^T F_{end} \tag{15}$$

where J^{-T} is the transpose of the kinematic Jacobian relating displacements of segment angles to endpoint position x.

$$\partial x = J \cdot \partial\theta \tag{16}$$

In the dynamic case with gravity, torques $[I - J^T J^{-T}]T_0$ that do not affect the endpoint force in Eq. (13) must satisfy the following dynamical constraint (see Lemma).

$$[I - J^T J^{-T}]T_0 = 0 \tag{17}$$

This constraint is satisfied by only one particular pseudo-inverse of J^T, namely

$$J^{-T} = [JM^{-1}J^T]^{-1}JM^{-1} \tag{18}$$

Plugging Eq. (18) into the left-hand side of Eq. (17), we verify that the dynamical constraint is satisfied with this particular choice of J^{-T}.

$$JM^{-1}[I - J^T[JM^{-1}J^T]JM^{-1}]T_0 \Rightarrow JM^{-1}T_0 - JM^{-1}J^T[JM^{-1}J^T]^{-1}JM^{-1}T_0 \tag{19}$$

$JM^{-1}J^T$ is a square matrix. Therefore multiplying it by its inverse $[JM^{-1}J^T]^{-1}$ yields the identity matrix and Eq. (19) is further reduced to

$$JM^{-1}T_0 - IJM^{-1}T_0 \tag{20}$$

which equals zero and satisfies the dynamical constraint of Eq. (17).

2.6.1 Lemma

The following proof is adapted from (Khatib, 1980). An endpoint force F_0 that is associated with torques from system dynamics and gravity has the following relationship with those torques:

$$J^T F_0 = M\ddot{\theta} + C + G \Rightarrow \ddot{\theta} = M^{-1}[J^T F_0 - C - G] \tag{21}$$

where we rearranged to solve for segment angle accelerations. Taking the double derivative of Eq. (16) with respect to time, we note that

$$\ddot{x} = J\ddot{\theta} + \dot{J}\ddot{\theta} \tag{22}$$

Plugging Eq. (21) into Eq. (22), we have

$$\ddot{x} = \Lambda^{-1}F_0 - JM^{-1}C - JM^{-1}G + \dot{J}\dot{\theta} \tag{23}$$

where

$$\Lambda = [JM^{-1}J^T]^{-1} \tag{24}$$

represents the effective system mass as seen from the endpoint. We now rearrange Eq. (23) to solve for F_0.

$$F_0 = \Lambda[\ddot{x} - \dot{J}\dot{\theta} + JM^{-1}C + JM^{-1}G] \tag{25}$$

Using Eq. (22) once again, Eq. (25) simplifies to

$$F_0 = \Lambda[J\ddot{\theta} + JM^{-1}C + JM^{-1}G] \tag{26}$$

Factoring out JM^{-1}, Eq. (26) can be rewritten as

$$F_0 = \Lambda[JM^{-1}(M\ddot{\theta} + C + G)] \tag{27}$$

It is clear from this reformulation that F_0 will non-trivially be zero, i.e. the system dynamics and gravitational torques will not move the endpoint or contribute to a contact force at the endpoint, if the torques are constrained such that

$$JM^{-1}(M\ddot{\theta} + C + G) = 0 \tag{28}$$

CHAPTER III

RATE-DEPENDENT CONTROL STRATEGIES FOR HOPPING IN PLACE

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3.1 Introduction

A key feature of locomotion is the simplicity of the center of mass dynamics despite the complexity imbedded within a non-linear time-varying neuromechanical system. In legged locomotion where bouncing gaits such as hopping and running are used, the center of mass moves as if on a pogo stick. Whether observed in the locomotion of humans, dogs, cockroaches or crabs (Blickhan and Full, 1993), the emergent mechanics from all these animals can be modeled as a simple linear spring a ubiquitous phenomenon of terrestrial locomotion (Cavagna et al, 1977; Blickhan, 1989; McMahon and 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 and Schöner, 1999; Todorov and 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 and Tu, 1991; Ting et al, 1994; Full and Koditschek, 1999; Kubow and Full, 1999; Jindrich and 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.

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 Muller and Sternad (Müller and 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 compared to variance of other joints. For hopping, ankle torque influences the vertical force applied to the ground more than knee or hip torques (Farley and 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 and 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 (Latash et al, 2002b; Scholz and Schöner, 1999) to test if 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 rate of movement.

3.2 Methods

3.2.1 Subjects

5 males and 5 females (26.1±4.0 years 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 that was approved by the Georgia Institute of Technology Institutional Review Board.

3.2.2 Procedure

We briefly provide relevant details of our experimental protocol and Uncontrolled Manifold (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 3 different beats: 2.2, 2.8, and 3.2 Hz. Preferred frequency for human hopping (approximately 2.2 Hz) and higher frequencies yield linear spring-mass behavior (Farley et al, 1991; Ferris et al, 2006). Subjects hopped for three 20-30 second trials at each of the three frequencies in random order for a total of 9 trials with ample rest between every trial. An average of 16751 hops were analyzed for each subject and frequency condition.

3.2.3 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) providing ground reaction force data.

3.2.4 Data processing

We filtered marker and force data with a zero-phase lag fourth-order Butterworth low-pass filter with a 10 Hz cutoff 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 cutoff frequency. The data were cropped to include only stance phases, defined as ground contact time to takeoff 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.

3.2.5 Uncontrolled Manifold analysis

For each 1 percent 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.

$$F \approx S(\theta) \cdot T \equiv \begin{bmatrix} s_a & s_k & s_h \end{bmatrix} \cdot \begin{bmatrix} \tau_a & \tau_k & \tau_h \end{bmatrix}^T . \tag{29}$$

The components of the joint torque column vector (T) 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 ($\partial\theta$) 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 and 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 and Schöner, 1999) with equation (29) 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).

$$\mathrm{TOTV} = \frac{\mathrm{trace}\,(C)}{n}, \tag{30}$$

$$\mathrm{NGEV} = \frac{\mathrm{trace}\left(\left(S \cdot S^T\right)^{-1} \cdot S \cdot C \cdot S^T\right)}{d}, \tag{31}$$

$$\mathrm{GEV} = \frac{\mathrm{trace}\left(\mathrm{null}\,(S)^T \cdot C \cdot \mathrm{null}\,(S)\right)}{n-d}. \tag{32}$$

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 null(S). The UCM analysis method was initially presented as a sequence of steps to partition TOTV into NGEV and GEV (Scholz and 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 and Scholz (2005), to quantify and compare across subjects the degree of force stabilization (equation (33)),

$$\mathrm{IMA} = \frac{\mathrm{GEV} - \mathrm{NGEV}}{\mathrm{TOTV}}. \tag{33}$$

3.2.6 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,

$$\mathrm{CoV} = \mathrm{IMA} - \mathrm{InV} \tag{34}$$

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).

3.2.7 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).

3.3 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 9a). The resulting ground reaction force had a vertical component trajectory that was unimodal with a maximum near mid-stance (figure 9b). 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 10). As subjects hopped more quickly, variances of the joint torques decreased, particularly the ankle torque variance (figure 10a). 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 10b).

Vertical force variance was most sensitive to ankle torque variance and least sensitive to hip torque variance (figure 11). 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

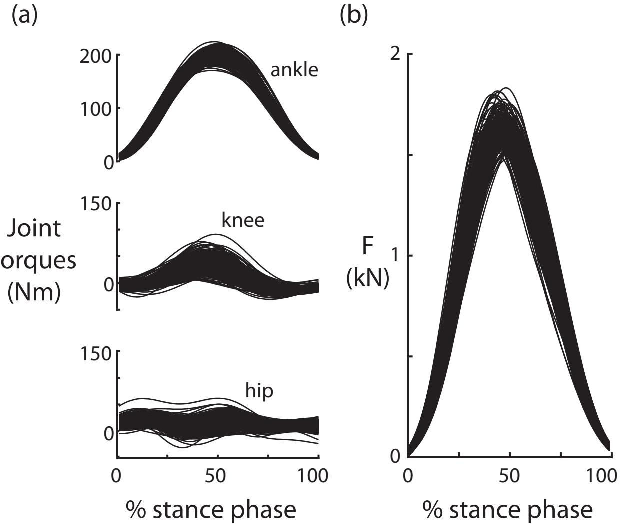

Figure 9: Sagittal plane kinetics versus normalized stance time for 175 hops of a representative subject hopping on one leg at 2.8 Hz. (a) Hip, knee and ankle joint torque trajectories for all hops. A positive joint torque corresponds to an extensor torque. (b) Corresponding vertical ground reaction force (F) for the same hops.

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 11). All mean torque sensitivities were significantly different between the three joints ($p \ll 0.001$), 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 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 12a). The three peak IMA values corresponding to the beginning, middle and end of stance did not change significantly as

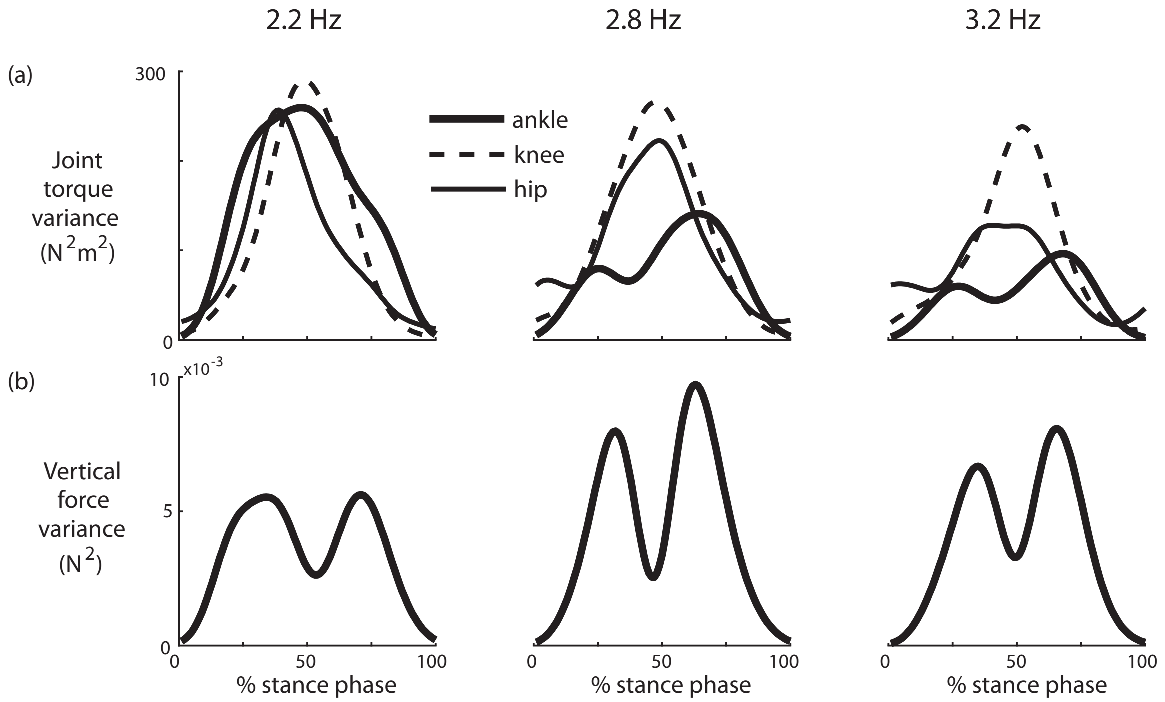

Figure 10: A representative subject's kinetic variance across hops at each hopping frequency condition. (a) Ankle, knee and hip joint torque variances across hops. The magnitude and shape of the ankle torque variance trajectory changed as frequency increased. Thick line, ankle; dashed line, knee; thin 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.

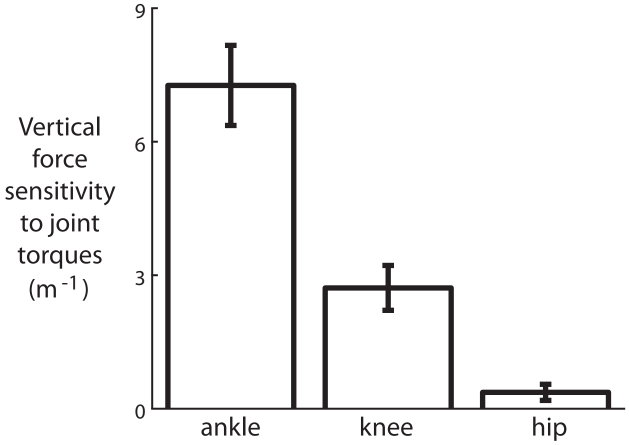

Figure 11: Mean (±s.d.) sensitivities of vertical force variability to each of the joints' torque variability for a representative subject across stance time and hopping frequencies. All means were significantly different between the three joints ($p \ll 0.001$).

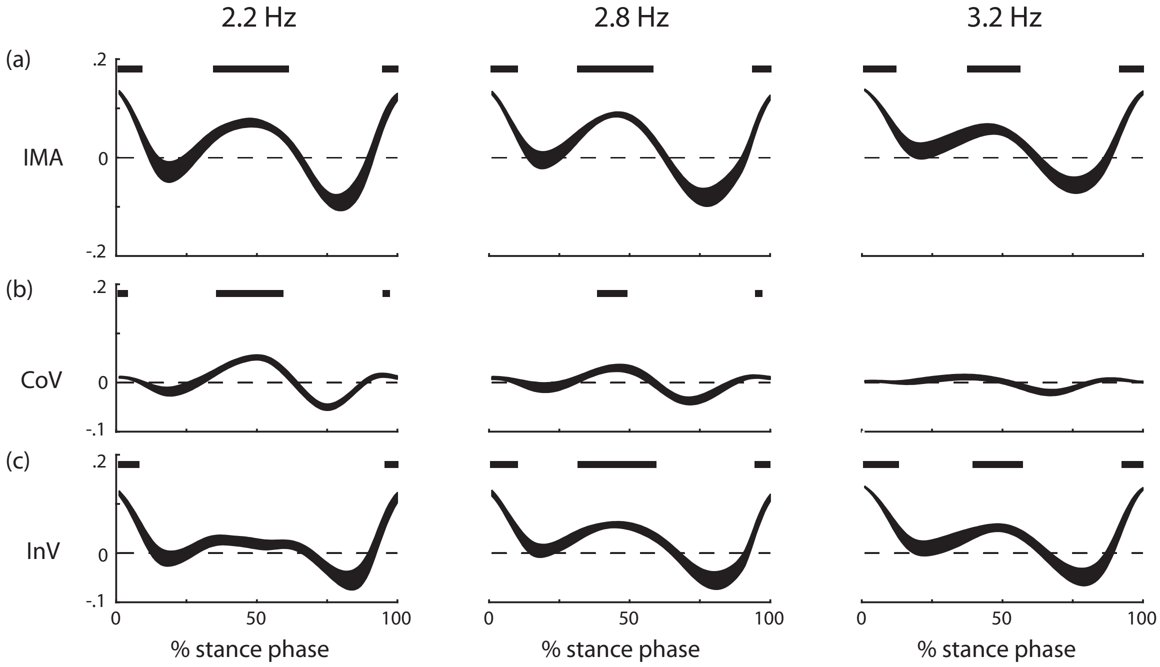

Figure 12: (a) Index of motor abundance (IMA), (b) contributions from coordinated variation (CoV), and (c) individual variation (InV) strategies for 2.2, 2.8 and 3.2 Hz hopping. Data are means across all subjects (±1 s.e.m.) related to vertical force. Stabilization of vertical force occurred when IMA 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).

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 12b), while individual variation stabilized vertical force at the beginning and end of stance phase (figure 12c). 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 10, 2.2 Hz).

Even though overall vertical force stabilization was consistent across frequencies (figure 12a), 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 12b,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 (04, 3659, 9597% stance phase; $p < 0.005$). At 2.8 Hz, only the middle and end of stance phase exhibited significant stabilization from covariation (3949, 9597% 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 12b). In contrast, individual variation for vertical force stabilization (InV) at mid-stance was not significantly greater than zero for 2.2 Hz (p >0.005), but was significant for the higher frequencies ($p < 0.005$; figure 12c).

3.4 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 12 and 13). 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 10). 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

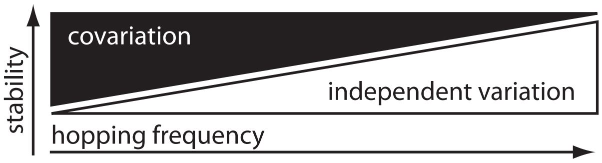

Figure 13: Relative roles of the two control strategies that stabilize vertical ground reaction force during human hopping. At slow hopping frequencies, interjoint torque coordination (covariation) is the dominant strategy, while at faster hopping frequencies, stabilization of ankle torque (independent variation) is the dominant strategy. The additive force-stabilizing effect of the two strategies is constant across hopping frequencies.

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 11). 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 and 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 and 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 midstance 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 and 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 and 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 (Full and Koditschek, 1999; Jindrich and 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 and 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 and 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 and 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.

3.5 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 and 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.

3.6 Acknowledgements

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3.7 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 $x_1, x_2, ..., x_n$. X varies over N trials and determines the task variable through a map S, which is a single row matrix consisting of elements $s_1, s_2, ..., s_n$. Equation (35) 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

$$\text{NGEV} = \frac{\mathbf{S} \cdot \text{cov}\left(\mathbf{X}\right) \cdot \mathbf{S}^T}{\mathbf{S} \cdot \mathbf{S}^T}, \tag{35}$$

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

$$\begin{aligned} \text{NGEV} &= \frac{\begin{bmatrix} s_1 & \cdots & s_n \end{bmatrix} \begin{bmatrix} \sigma_1 & \cdots & \sigma_{1,n} \\ \vdots & \ddots & \vdots \\ \sigma_{1,n} & \cdots & \sigma_n \end{bmatrix} \begin{bmatrix} s_1 \\ \vdots \\ s_n \end{bmatrix}}{\begin{bmatrix} s_1 & \cdots & s_n \end{bmatrix} \begin{bmatrix} s_1 \\ \vdots \\ s_n \end{bmatrix}} \\ &= \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} s_i s_j \sigma_{i,j}^2}{\sum_{i=1}^{n} s_i^2} \\ &= \frac{\sum_{i=1}^{n} s_i^2 \sigma_i^2 + \sum_{i=1}^{n} \sum_{j=1}^{n;j\neq i} s_i s_j \sigma_{i,j}^2}{\sum_{i=1}^{n} s_i^2} \end{aligned} \tag{36}$$

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 $n-1$,

$$\mathrm{V} = \sum_{i=1}^{n} \sigma_i^2 \tag{37}$$

$$\begin{aligned} \mathrm{GEV} &= \frac{\mathrm{V} - \mathrm{NGEV}}{n-1} \\ &= \frac{\left(\sum_{i=1}^{n} s_i^2\right)\left(\sum_{i=1}^{n} \sigma_i^2\right) - \sum_{i=1}^{n} s_i^2 \sigma_i^2 - \sum_{i=1}^{n} \sum_{j=1}^{n; j \neq i} s_i s_j \sigma_{i,j}^2 .}{(n-1) \sum_{i=1}^{n} s_i^2} \end{aligned} \tag{38}$$

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 (38) involve only individual variances and the third term involves only covariances.

We now perform a permutation on the vector set $\left\{\mathbf{X}_k\right\}$ to obtain the product set $\left\{x_{1,k}\right\} \times \left\{x_{2,k}\right\} \times \cdots \times \left\{x_{n,k}\right\}$. For example, if $\left\{x_{1,k}\right\}$ 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 $\left\{\mathbf{X}_k\right\}$ (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 and Sternad, 2003). In contrast, the product of the permutated vector set has exactly zero covariation and the same individual variances as the original vector set, as proved below.

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

$$\sigma_i^2 = \frac{1}{N} \sum_{k=1}^{N} \left(x_{i,k} - \overline{x}_i\right)^2 . \tag{39}$$

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

$$\begin{aligned}
{}^{P}\sigma_i^2 &= \frac{1}{N^n} \sum_{k1=1}^{N} \sum_{k2=1}^{N} \cdots \sum_{kn=1}^{N} \left(x_{i,kn} - \overline{x}_i\right)^2 \\
&= \frac{1}{N} \sum_{k1=1}^{N} \frac{1}{N} \sum_{k2=1}^{N} \cdots \frac{1}{N} \sum_{kn=1}^{N} \left(x_{i,kn} - \overline{x}_i\right)^2 \\
&= \frac{1}{N} \sum_{k1=1}^{N} \frac{1}{N} \sum_{k2=1}^{N} \cdots \sigma_i^2 \qquad\qquad\qquad . \\
&\vdots \\
&= \frac{1}{N} \sum_{k1=1}^{N} \sigma_i^2 \\
&= \sigma_i^2
\end{aligned} \tag{40}$$

Therefore, upon permutation, the variances of the local variables remain unchanged. The covariance of the ith and jth local variables in the product set is

$$\begin{aligned}
{}^{P}\sigma_{i,j}^2 &= \frac{1}{N^n} \sum_{k\_1=1}^{N} \sum_{k\_2=1}^{N} \cdots \sum_{k\_(n-2)=1}^{N} \sum_{l=1}^{N} \sum_{m=1}^{N} \left(x_{j,l} - \overline{x}_j\right) \left(x_{i,m} - \overline{x}_i\right) \\
&= \frac{1}{N^n} \sum_{k\_1=1}^{N} \sum_{k\_2=1}^{N} \cdots \sum_{k\_(n-2)=1}^{N} \sum_{l=1}^{N} \left(\left(x_{j,l} - \overline{x}_j\right) \cdot \sum_{m=1}^{N} \left(x_{i,m} - \overline{x}_i\right) \right) \\
&= \frac{1}{N^n} \sum_{k\_1=1}^{N} \sum_{k\_2=1}^{N} \cdots \sum_{k\_(n-2)=1}^{N} \sum_{l=1}^{N} \left(\left(x_{j,l} - \overline{x}_j\right) \cdot 0 \right) \\
&= 0.
\end{aligned} \tag{41}$$

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

$$
{}^{P}\mathrm{NGEV} = \frac{\displaystyle\sum_{i=1}^{n} s_i^2 \sigma_i^2}{\displaystyle\sum_{i=1}^{n} s_i^2}, \tag{42}
$$

$$
{}^{P}\mathrm{GEV} = \frac{\left(\displaystyle\sum_{i=1}^{n} s_i^2\right)\left(\displaystyle\sum_{i=1}^{n} \sigma_i^2\right) - \displaystyle\sum_{i=1}^{n} s_i^2 \sigma_i^2}{(n-1)\displaystyle\sum_{i=1}^{n} s_i^2}. \tag{43}
$$

3.8 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. GEV - NGEV >0), then local variance is structured to stabilize the task variable. The difference GEV - 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 (36) and (38), the difference GEV - NGEV can be expanded out as

$$
\mathrm{GEV} - \mathrm{NGEV} = \frac{\left(\displaystyle\sum_{i=1}^{n} s_i^2\right)\left(\displaystyle\sum_{i=1}^{n} \sigma_i^2\right) - n\displaystyle\sum_{i=1}^{n} s_i^2 \sigma_i^2 - n\displaystyle\sum_{i=1}^{n}\sum_{j=1}^{n;j\neq i} s_i s_j \sigma_{i,j}^2}{(n-1)\displaystyle\sum_{i=1}^{n} s_i^2}. \tag{44}
$$

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

$$ {}^{P}\mathrm{GEV} -{}^{P}\ \mathrm{NGEV} = \frac{\left(\sum_{i=1}^{n} s_i^2\right)\left(\sum_{i=1}^{n} \sigma_i^2\right) - n\sum_{i=1}^{n} s_i^2\sigma_i^2}{(n-1)\sum_{i=1}^{n} s_i^2}. \tag{45} $$

Equation (45) 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 (45) 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

$$ \left(\sum_{i=1}^{n} s_i^2\right)\left(\sum_{i=1}^{n} \sigma_i^2\right) = n\sum_{i=1}^{n} s_i^2\sigma_i^2. \tag{46} $$

Equation (46) is satisfied if $s_i^2 = s^2$ for all $i = 1, 2, \cdots, n$, 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 (46), we have

$$ \begin{aligned} \left(\sum_{i=1}^{n} s_i^2\right)\left(\sum_{i=1}^{n} \sigma_i^2\right) &= \\ \left(\sum_{i=1}^{n} s^2\right)\left(\sum_{i=1}^{n} \sigma_i^2\right) &= \\ n \cdot s^2 \left(\sum_{i=1}^{n} \sigma_i^2\right) &= \qquad\qquad . \\ n\sum_{i=1}^{n} s^2\sigma_i^2 &= \\ &= n\sum_{i=1}^{n} s_i^2\sigma_i^2 \end{aligned} \tag{47} $$

Likewise, equation (46) is satisfied if $\sigma_i^2 = \sigma^2$ for all $i = 1, 2, \cdots, n$, which corresponds to all local variables having the same variance

$$\begin{aligned}
\left(\sum_{i=1}^{n} s_i^2\right)\left(\sum_{i=1}^{n} \sigma_i^2\right) &= \\
\left(\sum_{i=1}^{n} s_i^2\right)\left(\sum_{i=1}^{n} \sigma^2\right) &= \\
\left(\sum_{i=1}^{n} s_i^2\right) n \cdot \sigma^2 &= \qquad\qquad . \\
n \sum_{i=1}^{n} s_i^2 \sigma^2 &= \\
&= n \sum_{i=1}^{n} s_i^2 \sigma_i^2
\end{aligned} \tag{48}$$

CHAPTER IV

VERTICAL FORCE CONTROL FOR HOPPING IN PLACE

4.1 Introduction

Human hopping has been used in previous biomechanics studies as a mechanical analogue of running (Farley et al, 1987, 1991; Ferris and Farley, 1997). In both hopping and running, the lower limb acts like a linear spring. Therefore, the body can be modeled as a point mass on a spring (Blickhan, 1989; McMahon and Cheng, 1990). Hopping in place is the simplest bouncing gait because there is no leg swing, forward progression, or production of braking or horizontal forces. It represents a tractable experimental model in which modulation of parameters such as hop height or hopping frequency have predictable consequences on other descriptive parameters (Blickhan, 1989).

However, as simple as hopping may be, it is not known what the task variables are. A task variable, such as hand position during reaching tasks, is often known for a particular task because it is made explicit. In motor control studies, a known task variable provides a functional context in which to understand the neural and musculoskeletal mechanisms behind the movement. Without knowledge of task variables, functional significance of component behavior are unclear and often conjectural.

The first aim of this current study was to test whether joint torque covariation can serve as evidence that a particular kinetic variable is a task variable for hopping. To do so requires a hopping task in which a kinetic variable is an explicit task variable. During steady-state hopping, vertical force impulse generated over a hop cycle is explicitly constrained if hoppers are instructed to land in synchrony with a metronome beat (timed hopping). Vertical force impulse is not constrained when hopping without a metronome beat (un-timed hopping). Joint torque covariation that stabilizes vertical force impulse was hypothesized to appear during timed hopping and not appear during un-timed hopping.

During hopping in place, vertical force applied on the ground may be an implicit task variable because it determines center of mass (CoM) movement. Based on biomechanics literature, which shows a seemingly ubiquitous phenomenon of the CoM bouncing during hopping and running (Cavagna et al, 1964; Full et al, 1991; He et al, 1991; Moritz and Farley, 2005; Daley and Biewener, 2006; Chang et al, 2008), I previously assumed force was a task variable for hopping (Chapters 2 and 3). When hopping in place on one leg at a comfortable frequency of 2.2 Hz, vertical force is not explicitly constrained by the task. Nonetheless, joint torques covaried from hop to hop to stabilize peak vertical force (Yen et al, 2009; Yen and Chang, 2010). Thus peak vertical force may be a task variable for hopping in place.

However, it is unclear whether the observed joint torque covariation was the result of a centrally-derived peak force goal or was merely a consequence of the hopping mechanics. For example, even if variations in muscle activations are random, non-random joint torque variations can occur because of mechanical joint coupling, especially through muscle-tendon units that span multiple joints. Musculature of the cat hindlimb constrains the direction of force production despite random muscle activation patterns (Bunderson et al, 2010). Likewise, peak force generated by a single limb during mid-stance of human hopping may exhibit less variations than joint torques from hop to hop strictly because of mechanical constraints. Furthermore, peak force stabilization may be a consequence of hopping like a linear spring-mass system. During hopping in place at 2.2 Hz, lower limb behavior is like that of a linear spring (Farley et al, 1991). A relatively stable peak force may emerge from this simple mechanical behavior. Thus it is possible that joint torque covariation represents a correlation with stable peak force that is unrelated to a task goal of peak force stabilization.

The second aim of this current study was to test whether force-stabilizing joint torque covariation is strictly determined by hopping mechanics. Hopping mechanics of the lower limb, in terms of the general pattern of flexion and then extension of joints during stance phase, are similar between one- and two-legged hopping. If joint torques necessarily covary because of mechanics, then it is likely that the same intralimb covariation of joint torques should be observed in both one- and two-legged hopping. However, if peak force stabilization is a task goal because of its direct relationship to CoM movement during one-legged hopping, then during two-legged hopping, total (left plus right limb) peak force should be stabilized through interlimb joint torque covariation. Moreover, if intralimb joint torque covariation is not merely a consequence of mechanics, then intralimb covariation should not be observed to stabilize an individual limb's peak force during two-legged hopping because the individual limb's force does not fully determine CoM movement. I therefore compared steady-state hopping on one leg with steady-state hopping on two legs. Furthermore, I compared one- and two-legged hopping when subjects alternated between the two tasks within the same trial. This was to test whether intralimb joint torque covariation can change from a hop-to-hop basis, which would represent further evidence that joint torque covariation is driven at least in part by a centrally-derived force goal. Finally, I tested whether peak force stabilization can be disassociated from linear spring-like mechanics of the lower limb by having subjects hop in place on one leg at 1.2 and 1.7 Hz. These low frequencies have been shown to elicit non-spring-like behavior (Farley et al, 1991). For all hopping tasks, I hypothesized that joint torques would covary to stablize total peak force regardless of the mechanics involved.

One can argue that joint torque covariation during hopping in place may not be a result of purposeful stabilization of vertical force. Rather, biomechanical linkages between joints dictate that the joints have to covary in a certain way, and this certain way only happens to result in relatively low vertical force variance. This argument leads to a specific prediction that can be tested experimentally. Specifically, if biomechanical coupling always results in joint torque covariation stabilizing vertical force, then one should see this covariation with every hopping task. However, I offer here an example, two-legged hopping, that does not confirm this prediction.

One may also argue that vertical force must necessarily be consistent across cycles during rhythmic hopping. In theory, this is not true. Previous studies have shown that, for a given hopping frequency, hoppers can generate different vertical forces. Different vertical forces are generated when subjects are instructed to change hop height (Farley and Morgenroth, 1999) and duty cycle (Voigt et al, 1998b). Therefore, hoppers can theoretically generate these different forces from hop to hop while hopping at a constant frequency. However, this has not been experimentally shown. Here I show that net force generated on the ground changes from hop to hop as subjects alternate between one- and two-legged hopping within the same trial.

Yet another argument can be made that force stabilization is a consequence of hopping like a linear spring-mass system. This argument predicts that if hoppers do not exhibit linear spring-mass dynamics, then vertical force would not be stabilized. Here, this prediction is also falsified. I examined hopping in place at frequencies less than preferred frequency (low-frequency hopping) because it has previously been shown that low-frequency hopping does not exhibit linear spring-mass dynamics (Farley et al, 1991). Despite this non-linear behavior, hoppers stabilized vertical force.

During hopping in place, vertical force applied on the ground may be a task variable because it determines center of mass (CoM) movement. Based on biomechanics literature, which shows a seemingly ubiquitous phenomenon of the CoM bouncing during hopping and running (Cavagna et al, 1964; Full et al, 1991; He et al, 1991; Moritz and Farley, 2005; Daley and Biewener, 2006; Chang et al, 2008), I previously assumed force was a task variable for hopping (Chapters 2 and 3; Yen et al, 2009; Yen and Chang, 2010). In this chapter, I tested this assumption through investigation of a series of hopping conditions.

These hopping conditions were designed to test alternative explanations for the joint torque covariation observed in Chapter 3. When hopping in place on one leg at a comfortable frequency of 2.2 Hz, joint torques covaried between hops in such a way as to not affect vertical force variance. This may have been because vertical force was a task variable. Alternatively, vertical force stability may have been a byproduct of simple physics or simple linear spring-mass dynamics. Also, joint torques may have covaried because biomechanical linkages between joints dictate that the joints have to covary in a certain way, and this certain way only happens to stabilize vertical force.

Before testing these alternative explanations, I first tested if joint torque covariation can serve as evidence that a kinetic variable is important to a task. Vertical force impulse generated over a hop cycle is explicitly constrained during steady-state hopping with a metronome beat. I compared this task to hopping without a metronome beat and predicted that joint torque covariation changes in response to a force impulse constraint.

A multi-jointed limb with muscles that span multiple joints may always exhibit a joint variance structure regardless of a controller that targets a peak vertical force. To test this alternative hypothesis, I compared 1-legged and 2-legged hopping in place. During 2-legged hopping, the force generated by an individual limb is not directly pertinent to overall performance, whereas total (left plus right limb) force is. Therefore I predicted that joint torques do not covary to stabilize the force of an individual limb. Noting that total (left + right limb) force applied on the ground was different between the two conditions, I also tested if they remained different when subjects alternated between one- and two-legged hopping within a single bout of hopping (i.e., a in-place hopscotch-like pattern). If the total forces are different between one- and two-legged hopping, then simple physics cannot explain force stability.

Finally, I tested if force stability is a consequence of hopping like a linear spring-mass system. It has previously been shown that one-legged hopping in place at frequencies less than preferred frequency does not exhibit linear spring-mass dynamics (Farley et al, 1991). Therefore low-frequency hopping represents a substantial behavioral variation from typical bouncing gaits. I predicted that forces are still stabilized during low-frequency hopping.

4.2 Methods

4.2.1 Subjects

Two groups of subjects volunteered to participate in this series of hopping experiments. Group A consists of 6 males and 5 females (26.0±3.9 years old; body mass 63.4±7.7 kg; height 170.6±9.4 cm). Group B consists of 7 males and 4 females (24.4±3.0 years old; body mass 61.3±7.3 kg; height 173.2±4.6 cm). The two groups were not compared with one another. One groups performed a subset of the hopping tasks, and the other group performed the other hopping tasks as explained in the next section. None of the subjects had a major injury or surgery that affected their ability to participate in any exercise activity. All subjects gave informed consent to participate in this study that was approved by the Georgia Institute of Technology Institutional Review Board.

4.2.2 Hopping Tasks

Subjects hopped in place without looking down at the ground and with arms folded across the chest. Subjects were required to rest a minimum of 2 minutes between trials to avoid fatigue. There were 7 different task conditions: 1) hop without a metronome, 2) hop with a metronome at their preferred frequency, 3) hop at 1.2 Hz, 4) hop at 1.7 Hz, 5) hop at 2.2 Hz, 6) hop on two legs at 2.2 Hz, and 7) alternate between one-legged and two-legged hopping at 2.2 Hz. Conditions 1 - 5 are hopping on one leg (right lower limb). Group A performed conditions 5 and 6 in random order. Group B performed the remaining five conditions. They performed condition 1 first, then the rest of the conditions were performed in random order. Of group B, all subjects performed conditions 1 and 2, ten of them performed conditions 3 and 4, and eight of them performed condition 7. Before performing each condition, subjects were required to practice the condition for a minimum of one trial until they felt comfortable. Trial durations and other specifics are described below.

4.2.2.1 Hopping with and without a metronome (conditions 1 and 2)

To validate ability to detect a kinetic task variable, I used a hopping condition that had an explicit constraint of a kinetic variable. When hopping comfortably to the beat of a metronome, the average vertical force impulse generated over one hop cycle is constrained to body weight divided by the metronome frequency. To determine the frequency of the metronome, I first instructed subjects to hop comfortably on their right leg without a metronome. Three trials of 25 trials each with no metronome were collected, and the preferred frequency was calculated from the data of the three trials pooled together. Each subject then hopped for another set of three trials of 50 hops each to the beat of an audible metronome set to their preferred frequency. Therefore, both conditions had the same average vertical force impulse, but the with-metronome condition explicitly specified the average vertical force impulse.

4.2.2.2 One- versus two-legged hopping (conditions 5 and 6)

To test whether biomechanics dictate that joint torques should covary in a certain way, I compared hopping on one and two legs because the importance of an individual limb's force is different between the two conditions yet both are well-controlled hopping tasks. Subjects hopped on their right leg for three 30-second trials, and on both legs for another three 30-second trials. In both conditions, subjects were instructed to hop to the beat of an audible metronome set at 2.2 Hz. 2.2 Hz is approximately the average preferred frequency when hopping on two legs (Farley et al, 1991). In total, subjects hopped approximately 200 times for each of these two conditions.

4.2.2.3 One- and *two-legged hopping ('hopscotch', condition 7)*

Again, subjects hopped to the beat of a metronome set at 2.2 Hz. They were instructed to perform the following pattern: hop on one leg (right lower limb) two times, hop on two legs two times, repeat. Subjects performed this pattern for two trials of 100 hops each.

4.2.2.4 Slow-frequency hopping (conditions 3 and 4)

To test whether forces are stabilized when the lower limb does not act like a linear spring, I instructed subjects to hop with a metronome beat set at frequencies below the typically preferred hopping frequency of 2.2 Hz. Farley et al (1991) also investigated slow-frequency hopping and instructed subjects to execute each hop with one smooth motion of the CoM. Here, I did not include that instruction to avoid explicitly defining a biomechanical goal. Subjects hopped at 1.2 Hz for five 30-hop trials, and at 1.7 Hz for four 38-hop trials.

4.2.3 Data collection and processing

As described in previous chapters, ground reaction forces and joint motion data were recorded while subjects hopped in place. Inverse dynamics was used to calculate sagittal plane torques about the ankle, knee, and hip (Winter 1990). Times when subjects made contact with the ground and left the ground were identified by when vertical force crossed a threshold force of 25 N. Only stance phase data are considered because no forces are generated on the ground during the aerial phase. The data are time-normalized and expressed as a percentage of stance phase.

4.2.4 Analysis

4.2.4.1 Variance

Kinetic variance and covariance quantities were calculated in this study. These quantities refer to within-subject and within-hopping condition fluctuations about a mean across hop cycles. Often, these variances are trajectories. For example, the variance of vertical force during stance phase is a trajectory because the vertical force is a trajectory.

4.2.4.2 Joint torque covariation (CoV)

As described in the previous chapter (Yen and Chang, 2010), I used the covariation metric CoV (equation (34)) to quantify how much joint torques were coordinated to stabilize vertical force from hop to hop.

Here I briefly review how CoV was calculated. For a given time slice, the 3x3 joint torque covariance matrix was projected onto the null space of a 1x3 matrix (equation (32)). This 1x3 matrix maps joint torques to vertical force, and is the dynamically-consistent inverse of the Jacobian relating changes in joint angles to changes in vertical endpoint position. The projection of the covariance matrix was repeated but onto the range space instead of the null space (equation (31)). The difference of these two projections, normalized by total joint torque variance per degree of freedom (TOTV, equation (30)), yields an Index of Motor Abundance (IMA, equation (33)). These pair of projections and normalization were repeated for the same covariation matrix but with the off-diagonal elements set to zero (which is the equivalent of permutating through all joint torque combinations of the data set or randomly shuffling the data an infinite amount of times), yielding Independent Variation (InV). The difference between IMA and InV is CoV (equation (34)).

An equivalent method that involves less steps but algebraically yields the same CoV value is first taking the original covariation matrix and setting the diagonal elements to TOTV. This effectively zeros out any contributions from InV (see section 3.8. This step allows isolation of how much joint torque covariation does affect vertical force variance (non-goal-equivalent covariance, NGEV) and does not affect vertical force variance (goal-equivalent covariance, GEV) by projecting this adjusted covariation matrix onto the range and null space, respectively. The normalized difference of these components directly yields CoV. These NGEV and GEV components are guaranteed to be positive, as variance measures should always be because they are squared differences about a mean.

CoV is bounded between -3 (all joint torque covariation leads to vertical force variance) to 1.5 (all joint torque covariation leads to zero vertical force variance). CoV > 0 indicates that the majority of joint torque covariance does not affect vertical force variance (i.e., stabilizes vertical force), and CoV < 0 indicates that the majority of joint torque covariance does affect vertical force variance (i.e., destabilizes vertical force). CoV $= 0$ indicates no correlation between joint torque covariation and vertical force variation.

For each hopping condition, the CoV metric was calculated for each time slice of stance phase in which the average vertical force applied on the ground was more than half of body weight. This effectively precluded analysis of joint torques generated at the time points of ground contact and liftoff. For these time points, vertical force was always at or just above the 25 N threshold, which defines contact and liftoff events. Therefore, CoV for these time points are artificially inflated because the force is consistent at these time points by definition. Moreover, these forces were small and did not affect body movement nearly as much as the rest of the force trajectory. The first few and last few time points that were not analyzed accounted for a total of no more than 5% of force impulse generated over a stance phase for any of the hopping conditions.

In addition to generating a CoV trajectory to test which parts of the force trajectory were stabilized, a CoV metric was also calculated to quantify how much joint torque impulses were coordinated to stabilized vertical force impulse (analogous to methods section 2.2.4). The impulse is the integral of force or torque over one stance phase. Because integrating over stance phase yields one number as opposed to a time series, CoV for vertical impulse was not performed for each time slice of stance phase but already captured all of the stance behavior in one number.

The CoV metrics described in the above paragraphs pertain to *intralimb* joint torque coordination, but I also calculated a CoV metric for *interlimb* joint torque coordination in the case of two-legged hopping. This interlimb CoV metric quantifies to what degree six joints (ankles, knees, and hips) are coordinated to stabilize total (left plus right) vertical force. Interlimb CoV is calculated the same way as intralimb CoV except that a 6x6 covariance matrix is projected onto a 1x6 matrix, which is a row-concatenation of two 1x3 matrices representing each limb. Therefore, this concatenation assumes neglible direct influences from joint torques of one limb to the other limb's vertical force. CoV for interlimb joint torque coordination can range from -6 to 1.2.

4.2.4.3 Leg stiffness

Vertical force is related to vertical displacement of the CoM. If the lower limb acts perfectly like a linear spring, then this relationship is linear. The slope of a linear fit between vertical force and vertical CoM displacement (double integration of vertical force divided by body mass) was used as an estimate of leg stiffness. R-squared values of these linear fits pertain to the linearity of the force-displacement relationship.

4.2.4.4 Statistics

A Student's one-tailed t-test ($\alpha = 0.005$) was performed to test whether the CoV metric averaged across subjects was significantly greater than zero. A positive CoV

Table 1: Comparison of variability (within subject standard deviations) when hopping with and without a metronome beat. Values in bold indicate significant decrease from the without metronome condition ($p < .05$). Values are across-subject averages (s.d.). The force impulse values F_{imp} are normalized by body weight.

	cycle duration msec	max hip height mm	$F_{imp,peak}$ msec	$F_{imp,whole}$ msec
w/o metronome	16 (8)	9 (3)	30 (5)	16 (2)
w/ metronome	**12 (2)**	8 (3)	27 (6)	**11 (1)**

Table 2: Comparison of variance when hopping with and without a metronome beat. The CoV value in bold indicates significant increase from the without metronome condition ($p < .05$). The other dependent measures did not significantly decrease with the metronome on ($p > .05$). Values are across-subject averages (s.d.).

	TOTV $msec^2$	GEV $msec^2$	NGEV $msec^2$	CoV	CoV >0 p-value
w/o metronome	53 (29)	18 (9)	16 (11)	.11 (.21)	.03
w/ metronome	45 (14)	16 (5)	12 (4)	**.26 (16)**	$<10^{-3}$

indicates that joint torque covariance was structured to stabilize vertical force.

4.3 Results

4.3.1 Hopping with vs. without a metronome beat

While hopping in place on one leg, subjects exhibited hop-to-hop variability. In response to hopping with a metronome beat set at their preferred frequency, subjects did not change their hopping frequency (2.13 ± .18 hops per second, $p = .97$), but variability of some parameters decreased more than other parameters when the metronome was turned on (Table 1). Variability of cycle duration and of vertical force impulse generated over a whole cycle ($F_{imp,whole}$) decreased ($p = 0.03, p = 0.01$, respectively). Variability of peak height of the hip marker and vertical force impulse generated from landing to time of peak force ($F_{imp,peak}$) did not decrease ($p = .28, p = .21$, respectively).

Joint torque variance was similar between hopping with and without a metronome beat (Table 2). Total (ankle + knee + hip) variance of joint torque impulses (TOTV) decreased slightly but not significantly with the metronome on ($p = .13$). TOTV components, GEV and NGEV, also decreased but not significantly ($p = .12$). However the two components did not decrease by the same amount. The component that affected vertical force impulse (NGEV) decreased significantly more than the component that did not affect vertical force impulse (GEV) ($p = .01$).

To evaluate whether the metric CoV is sensitive to the explicit task constraint of hopping to a metronome, I compared CoV between hopping with and without a metronome (Table 2). CoV for vertical force impulse significantly increased with the metronome turned on ($p = .05$). Here, CoV is the normalized difference between joint torque impulse covariance that did not affect and did affect vertical force impulse variance. CoV was greater than zero for both hopping conditions, but at different significance levels (table 2). CoV for 9 out the 11 subjects increased with the metronome turned on. The other 2 subjects had the greatest CoV values among all subjects for hopping without a metronome (.34 and .32).

Between hoppping with and without a metronome beat, joint torques covaried similarly in terms of stability of the vertical force trajectory (figure 14). The variance of the peak force did not change (without metronome: .02 ± .02, with metronome: .01 ± .01 body weights^2; $p = .10$), nor did the sum (ankle + knee + hip) of joint torque variances at the time of peak force generation change ($p = .18$). Also, the timing of the peak force did not change (without metronome: 48 ± 4, with metronome: 47 ± 2% of stance phase; $p = .68$), and CoV at the time of peak force generation did not change (without metronome: .52 ± .4, with metronome: $.54 \pm .3; p = .89$). The time during stance phase in which CoV was significantly positive ($p < .005$) was also similar (without metronome: 34-56, with metronome: 34-63% stance phase).

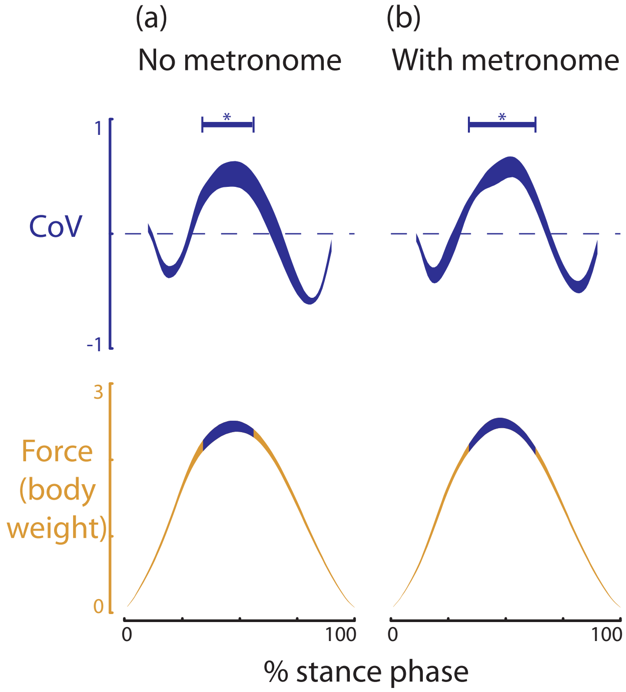


Figure 14: Vertical force stabilization during hopping (a) without and (b) with a metronome. Positive CoV values represent stabilization of vertical force through joint torque covariation. Blue horizontal bars above CoV traces indicate when CoV is significantly greater than zero ($p < .005$). The blue-shaded regions of the normalized vertical force trajectories also indicate when CoV is significantly greater than zero. Data are across-subject averages (±1 s.e.m.).

Table 3: Parameter differences of the right lower limb between one- and two-legged hopping. Values are for the right lower limb and are across-subject averages (s.d.). Stiffness is normalized by body weight times sum of the three lower limb segment lengths, and peak force is normalized by body weight. Joint angles are evaluated at the time of peak force production. Except for R^2 and hip angle, all metrics are different between one- and two-legged hopping, as indicated by * ($p < .005$).

	R^2	Stiffness	Peak force	Ankle ang.(○)	Knee ang.(○)	Hip ang.(○)
1L	.95 (.10)	20.1 (2.8)	2.59 (.22)	101 (3)	133 (3)	166 (2)
2L	.96 (.01)	14.4 (1.9)*	1.76 (.18)*	96 (3)*	129 (4)*	166 (2)

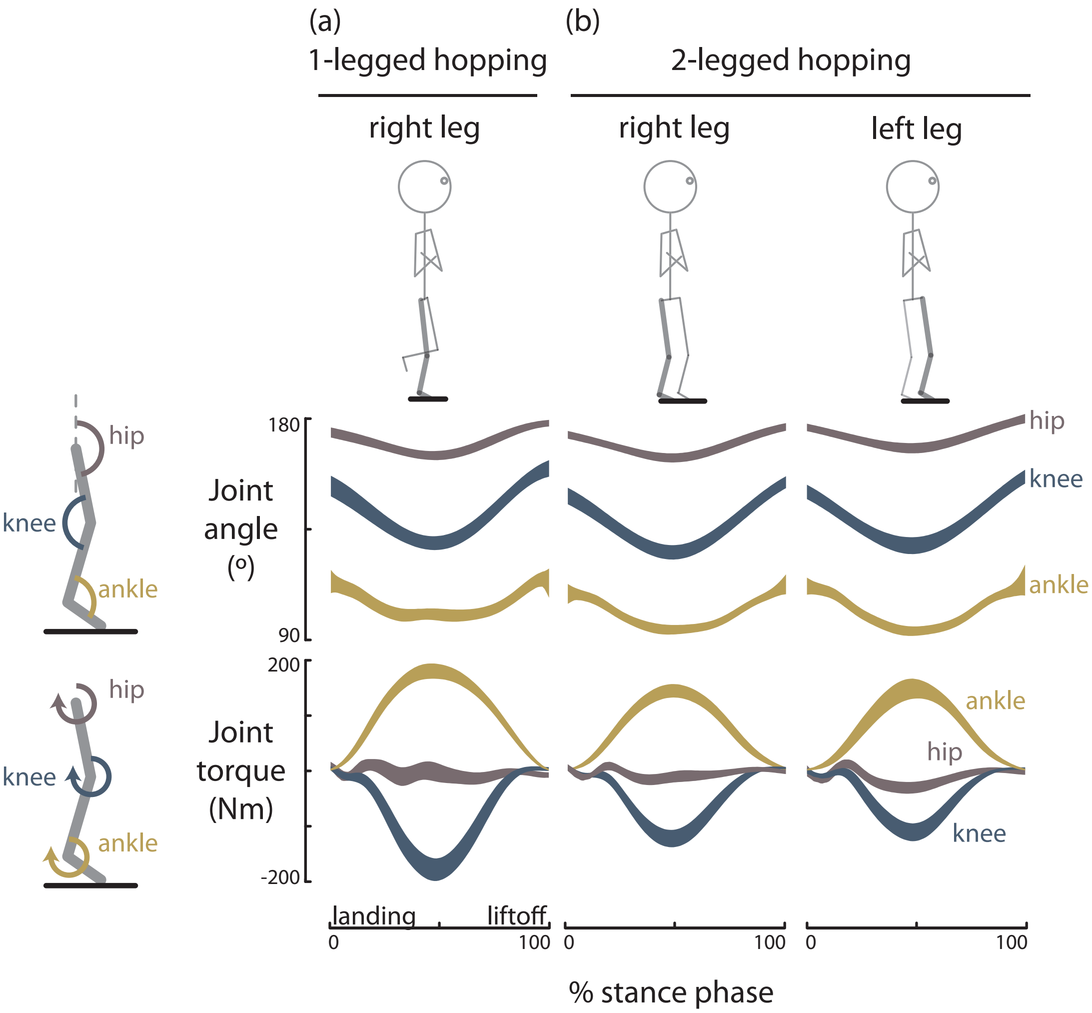


Figure 15: Example joint angles and torques during one- and two-legged hopping. Data are across-hop averages (± s.e.m.) for one subject hopping on (a) one leg and (b) two legs. One-legged hopping data are from experimental trials distinct from two-legged hopping trials. In both conditions, subjects hopped to the beat of a metronome set at 2.2 Hz.

4.3.2 One- vs. two-legged hopping

The lower limbs had qualitatively similar behavior between one-legged (1L) and two-legged (2L) hopping. During both conditions the right limb acted like a linear spring. The R^2 values of the linear relationship between the right limb's vertical force and center of mass (CoM) displacement were high and did not significantly change between conditions (table 3; $p = .72$). For both conditions, the joints flexed during the first half of stance phase and extended during the second half of stance phase (figure 15).

Lower limb behavior was quantitatively different between 1L and 2L hopping (table 3). The stiffness (slope of the force-CoM displacement relationship) of the right lower limb was significantly smaller during 2L than during 1L ($p < 10^{-6}$). Compared to 1L, 2L peak force of the right limb significantly decreased ($p < 10^{-8}$). During 2L, for most subjects, the lower limbs did not generate force symmetrically (left peak force $= 1.58 \pm .21$ body weight; $p < 10^{-3}$), with an average difference in peak force of $16.9 \pm 11.0\%$. Peak force was not different between the right and left limbs for only two of the eleven subjects ($p > .58$). The R^2 value of a linear fit between force and CoM displacement was not significantly different between the left and right leg (left: $.96 \pm .02$, right: $.96 \pm .01$, $p = .04$). Ankle and knee joints of the right limb were slightly more flexed during 2L compared to during 1L, whereas the hip did not change (table 3). Subjects generated less ankle, knee, and hip extensor torques in 2L than 1L (figure 15; $p < 10^{-3}, 10^{-5}, 10^{-3}$, respectively).

Although the shape of the total joint torque variance trajectory was similar between 1L and 2L hopping, the shape of the vertical force variance trajectory was different. (figure 16). For both conditions, during the first half of stance phase, subjects landed and lowered their CoM while increasing joint torques through time. The variance of joint torques also increased through the landing phase toward a maximum around mid-stance. During 1L hopping, the maximum joint torque variances coincided with a local minimum in vertical force variance. This was not the case

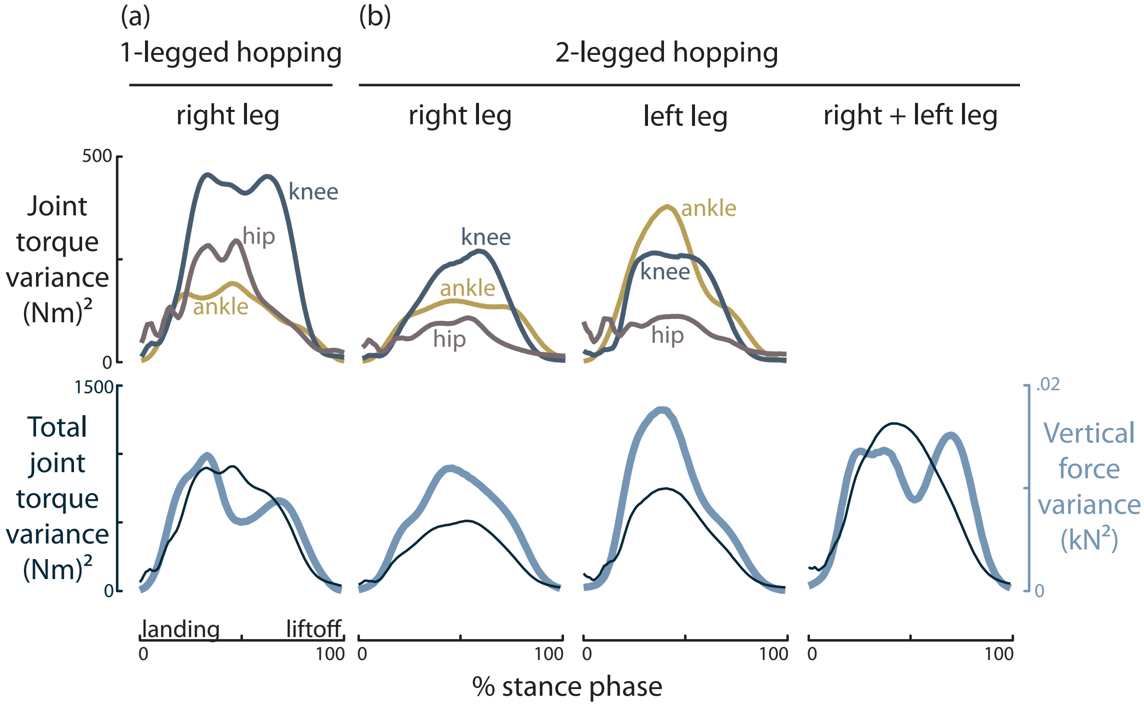


Figure 16: Example joint torque variance and force variance during 1- and 2-legged hopping. Data are across-hop variances for one subject hopping on (a) one leg and (b) two legs. One-legged hopping data are from experimental trials distinct from two-legged hopping trials. In both conditions, subjects hopped to the beat of a metronome set at 2.2 Hz. Note that in both the one- and two-legged results, the variance of the total force at mid-stance reaches a local minimum while total joint torque variance reaches a maximum.

for either the right or left limb during 2L hopping, in which case the vertical force variance reached a maximum in parallel with joint torque variance. Variance of peak force (normalized by body weight) for the right limb was significantly greater during 2L than during 1L (1L: 0.013 ± 0.005, 2L: 0.026 ± 0.011; $p < 10^{-3}$). However, analogous to 1L hopping, variance of total (right + left) peak force reached a local minimum during mid-stance during 2L hopping.

Joint torques of the right lower limb covaried substantially differently between 1L and 2L hopping (figure 17). As with hopping to the metronome set at subjects' preferred frequencies, hopping to the metronome set at 2.2 Hz on one leg also resulted in a positive CoV during midstance (38-53% stance phase, $p < .005$). In contrast, joint torques of the same limb (right limb) did not covary to stabilize force of the right limb at any point in time during 2L hopping. Joint torques of the left limb also did not covary to stabilize force during 2L hopping. At the time of peak force, CoV for left limb only was not significantly different from CoV for the right limb only (right: -.30 ± .38, left: -.31 ± .37; $p = .86$). Nonetheless, as indicated by a significantly positive CoV for right and left limbs considered together, joint torques across both limbs covaried to stabilize total (right + left) vertical force during mid-stance (44-58% stance phase, $p < .005$). Total peak force during 1L was generated by the right limb only, and total peak force during 2L was generated by right and left limbs together. Total peak force (normalized by body weight) was different between the two conditions (1L: 2.59 ± 0.22, 2L: 3.33 ± 0.37 body weight; $p \ll .005$), but was stabilized by joint torque covariation in both conditions.

4.3.3 Hopscotch

When subjects hopped on one and two legs in an alternating fashion within the same trial (hopscotch pattern), joint torques covaried in the same way as when hopping on one and two legs in separate trials (figure 17). Joint torques within the right limb

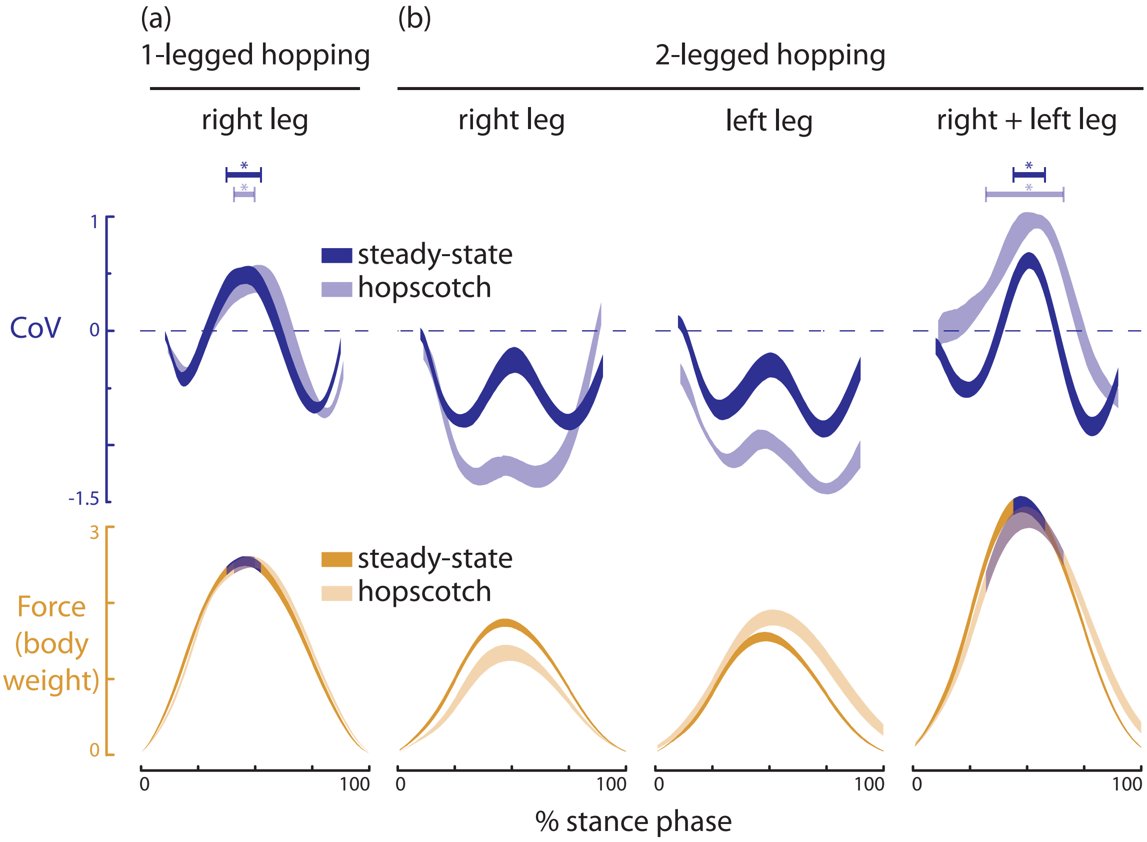


Figure 17: Vertical force stabilization through joint torque covariation during (a) 1-legged and (b) 2-legged hopping. Positive CoV values represent stabilization of vertical force through joint torque covariation. The first two columns (right leg, left leg) of (b, 2-legged hopping) represent results from analyzing joint torque covariation within one limb. The last column (right + left leg) represents results from analyzing joint torque covariation across both limbs. In other words, it is a different analysis of the same data as in the first two columns of (b). Blue horizontal bars above CoV traces indicate when CoV is significantly greater than zero ($p < .005$). The blue-shaded regions of the normalized vertical force trajectories also indicate when CoV is significantly greater than zero. Data are across-subject averages (±1 s.e.m.). In all panels, the darker trajectories are results from subjects hopping on one and two legs in separate trials (steady-state). The lighter trajectories are results from subjects alternating between one- and two-legged hopping within the same trial (hopscotch).

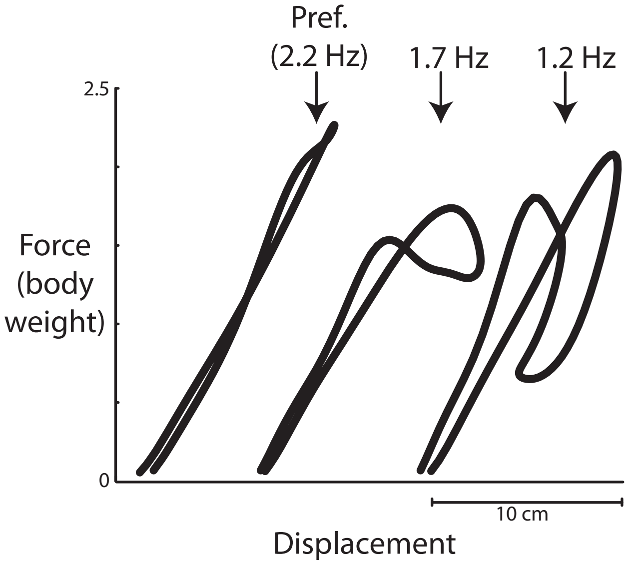


Figure 18: Example force-displacement relationship during slow-frequency hopping. Convention is such that displacement increases as center of mass moves downwards. Curves are labeled according to the beat of the metronome that the subject hopped in synchrony with. Data are from one subject, averaged across hops, and are of the vertical components only.

covaried to stabilize vertical force during mid-stance of hopping on one leg (42-50% stance phase, $p < .005$), but the joint torques did not covary to stabilize force of the right limb at any point when hopping on two legs. Joint torques across both limbs covaried to stabilize total (right + left) peak force (32-66% stance phase, $p < .005$). Total peak forces (normalized by body weight) were significantly different between one- and two-legged hopping (one-legged: 2.56 ± 0.23, two-legged: 3.20 ± 0.42; $p \ll .005$).

4.3.4 Slow frequency hopping

Subjects did not behave like a spring-mass system when hopping at frequencies below their preferred hopping frequency (figure 18). Vertical force was not a linear function of vertical CoM displacement for the slow hopping frequencies (1.7 and 1.2 Hz). As subjects hopped more slowly, the R^2 value of a linear fit between force and displacement decreased significantly (preferred: $.98 \pm .01$, 1.7 Hz: $.85 \pm .15$, 1.2 Hz: .54

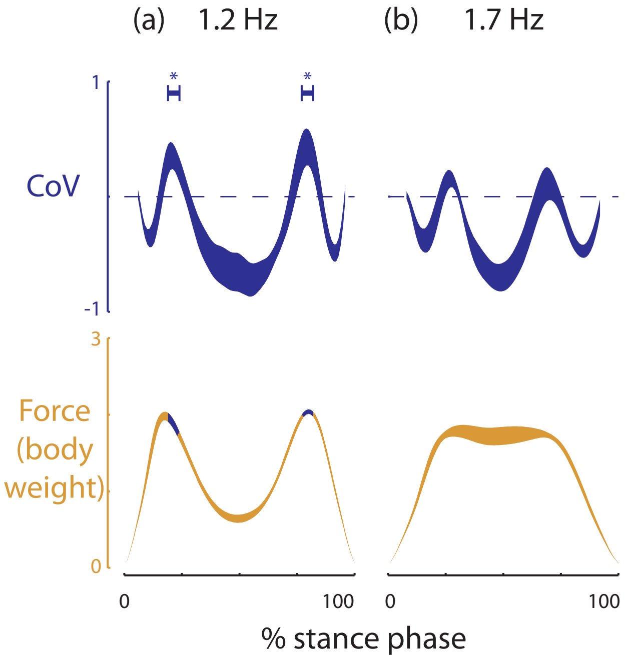


Figure 19: Vertical force stabilization during (a) 1.2 Hz and (b) 1.7 Hz hopping. Positive CoV values represent stabilization of vertical force through joint torque co-variation. Blue horizontal bars above CoV traces indicate when CoV is significantly greater than zero ($p < .005$). The blue-shaded regions of the normalized vertical force trajectories also indicate when CoV is significantly greater than zero. Data are across-subject averages (±1 s.e.m.).

± .15; $p < 10^{-6}$). If the lower limb acted like a spring, then the force would have increased as the CoM moved downwards. However, during landing at the slow frequencies, the force decreased as the CoM was still moving downwards. Also, during liftoff, some subjects increased force generation as the CoM move upwards.

Joint torques covaried to stabilize the peak forces generated during 1.2 Hz hopping (figure 19a). For all subjects, the average vertical force trajectory across hops had two peaks. The first and second halves of stance phase considered as separate phases were not spring-like. The R^2 value of a linear fit between vertical force and CoM displacement was .51 ± .18 for the first half of stance phase, and .63 ± .14 for the second half of stance phase. The two vertical force peaks coincided with the two times during stance phase in which CoV was significantly greater than zero (18-24 and 77-82% stance phase, $p < .005$). CoV at the times of each subject's generation of peak

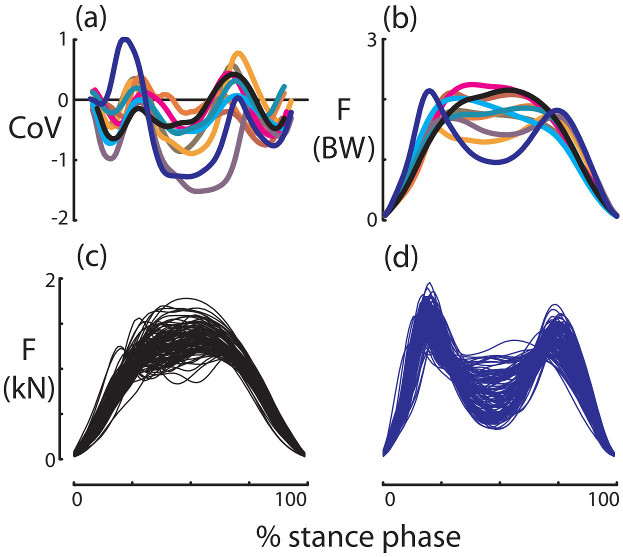


Figure 20: Intersubject variability of vertical force stabilization during 1.7 Hz hopping. (a) Positive CoV values represent stabilization of vertical force through joint torque covariation. (b) Vertical force averaged across hop cycles. (a, b) Each subject's data is shown. (c, d) Vertical force of all hop cycles for two example subjects. Consistent across panels, each color corresponds to an individual.

forces was significantly greater than zero (first peak: $0.44 \pm 0.31, p < 10^{-3}$; second peak: $0.55 \pm 0.35, p < 10^{-3}$). CoV for vertical force impulse was not significantly greater than zero ($0.07 \pm 0.47, p = 0.33$).

Joint torques did not covary to stabilize the vertical force trajectory during 1.7 Hz hopping (figure 19b). Averaged across subjects, CoV was not significantly greater than zero for any time point ($p > .005$). CoV for vertical force impulse was not significantly greater than zero ($-0.23 \pm 0.47, p = 0.92$). The CoV for force trajectories varied considerably between subjects (figure 20a), as did the force trajectories averaged across hop cycles (figure 20b). Some subjects on averaged generated two peak forces (double bouncers), and some subjects on averaged generated one peak force (single bouncers). Some subjects single bounced on some hops and double bounced on other hops. As an example, force trajectories generated from one subject (figure 20c) had one peak for 34% of the hops, two peaks for 62% of the hops, and three peaks for 4% of the hops. In contrast, one subject consistently produced two peak forces during each hop cycle (figure 20d).

4.4 Discussion

4.4.1 Summary

Results presented here suggest that peak vertical force is a task variable. As opposed to stabilizing joint torques patterns or the force trajectory, humans may only stabilize peak force. This was supported by the relatively low variance of peak force and relatively high variance of joint torques (figure 16), and by joint torque covariation during steady-state hopping (figures 14, 17, and 19). I discuss below how joint torque covariation can indicate what task variables are, and then how alternative explanations for joint torque covariation fail to explain results obtained in this study.

4.4.2 Joint torque covariation as evidence of kinetic task goals

The method used here of analyzing joint torque covariation was sensitive to an explicit task constraint, and thus may be used to uncover implicit task variables of unconstrained tasks. A positive value of the covariation metric CoV potentially supports a hypothesized task variable as a true task variable. Positive results of analogous metrics have been shown for tasks in which a task variable was made explicit, i.e. there was an experimentally specified value of a mechanical variable for subjects to target (for example, Müller and Sternad, 2003). Here, the average vertical force impulse of one hop cycle was specified through the constant beat of a metronome. Subjects could have generated force impulses that varied around this average and still have kept the beat by varying hop height. A constant target for hop height in addition to a metronome beat would have made force impulse an explicit task variable. Nonetheless, subjects hopped to a consistent height during steady-state hopping. I observed that when the metronome is turned on, the force impulse variance decreases (table 1). This decrease in force impulse variance was accompanied by an increase in the CoV metric (table 2), suggesting that CoV can be used to detect kinetic task variables.

It was possible that even without the metronome, vertical force impulse was an implicit task variable for some subjects. The two subjects with the largest CoV metrics for hopping without a metronome showed a CoV trend opposite of the other subjects. When the metronome was turned on, CoV for these two subjects decreased. When hopping to a metronome, timing errors between foot strike and metronome beat may have been detected and compensated with fluctuations in the opposite direction, thus increasing impulse variance and decreasing CoV. When hopping at the same frequency but without an audible metronome, timing errors do not exist because there is no metronome and subjects do not fluctuate force impulse further to compensate for previous hops.

4.4.3 Alternative explanations of kinetic variability

4.4.3.1 Stabilization as definition of steady-state

Steady-state hopping, by intuition, suggests consistency of biomechanical variables from step to step. Therefore, the trivial result would have been low joint torque variance and low force variance. Instead, joint torque variance was relatively high compared to the force variance. This non-trivial result can be explained by coordination of joint torques for stabilization of peak force (figures 14, 17, and 19). Moreover, when alternating between one- and two-legged hopping, subjects switched between intralimb joint coordination and interlimb joint coordination to stabilize two different net peak force magnitudes (figure 17).

4.4.3.2 Physics

Consistent peak forces also cannot be explained by simple physics. Physics did not dictate that peak forces must be invariant to hop at a constant frequency. This was clearly not the case for when subjects alternated between hopping on one leg and two legs. For this hopping task, peak force alternated between two magnitudes (figure 17).

This refutes that simple physics determined the consistency of peak forces. To hop at a constant frequency and generate the consistent vertical force impulses, subjects can vary peak force and duration of stance phase. The hopping task did not explicitly require that peak forces be stabilized. Rather, peak force stabilization was likely a task goal implicitly generated by the locomotor system.

4.4.3.3 Signal-dependent noise

Force variance reported here is not directly explained by signal-dependent noise (Harris and Wolpert, 1998), because force variance reached a local minimum at mid-stance even though extensor torques, muscle activations (Dyhre-Poulsen et al, 1991; Moritani, 1991; Funase et al, 2001), and force reached a maximum (figure 16). Smaller forces and smaller muscle activations, which occur at times other than mid-stance (around 25 and 75% of stance phase), actually generated greater force variability. Thus it is not likely that the low peak force variance was a consequence of random noise.

4.4.3.4 Biomechanics

Was the structure of joint torque variance observed here an artifact of passive biomechanics? Ordered locomotor behavior can emerge from properties of a mechanical structure (for example, McGeer 1990b; Collins et al 2005; Cruse et al 2007; Pfeifer et al 2007; Rieffel et al 2010; Bunderson et al 2010). If this were the primary explanation, then the repeated flexion and extension of joints, which are mechanically linked through multiarticular muscles and connective tissue, would nave covaried in similar fashion across all bouncing gaits. On the contrary, joint torques within a limb covaried differently between one- and two-legged hopping (figure 16). Intralimb joint torque covariance stabilized the limb's force during one-legged hopping but not during two-legged hopping (figure 17), perhaps because the limb's force was not as critical to overall performance during two-legged hopping as it was during one-legged hopping.

Therefore, mechanics alone likely did not dictate force-stabilizing joint covariation, but instead the importance of a single limb's force to the specific locomotor task likely determined whether or not the force was stabilized. This comparison between one- and two-legged hopping suggests an intended goal of peak force stabilization.

It may be argued that comparing the mechanics of one- and two-legged hopping is not valid because the posture of the limb was different between the two conditions. During two-legged hopping, the limb was slightly more flexed during mid-stance compared to one-legged hopping (table 3). Based on results from Chapter 3 (Yen and Chang, 2010), we would have predicted an increase in intralimb joint torque coordination with more flexed postures if posture was the primary determinant of joint torque covariation. However, intralimb joint torque coordination decreased with the more flexed posture of two-legged hopping (figure 17b). Further work is required to tease out the effects of posture, hopping frequency, and force magnitudes. Nevertheless, posture alone cannot explain the observed joint torque behavior. The most parsimonious explanation is that total force, and not individual limb force, is a task variable.

4.4.3.5 Rate of force change

Can low rates of force production explain stabilization of peak force? Peak force coincided with a low rate of change in force. Any timing variability would have had minimal affect on variability within time slices that coincide with low rates of change, and timing variability would have amplified magnitude variability within a time slice with high rates of change. Therefore stabilization of peak force and not of other parts of the force trajectory may be accounted for by timing variability (Gutman and Gottlieb, 1992; Latash et al, 2002a). In the discussion section of chapter 2 (Yen et al, 2009), I attributed force destabilization during landing and liftoff to timing variability, but the time warping method may not have isolated timing variability as asserted.

To test whether low rates of force change always show stability, I investigated kinetics for hopping at the slow frequency of 1.2 Hz. When subjects hopped at 1.2 Hz, a force is produced during mid-stance that has a low rate of force change and is not a peak force (figure 19). These forces were not stabilized, thus showing that forces with low rates of change are not necessarily stabilized.

4.4.3.6 Spring-mass dynamics

Is force stabilization merely a consequence of hopping like a spring-mass system? Results here indicate that this is not the case. When subjects hopped at frequencies below their preferred frequency (1.7 and 1.2 Hz), the lower limb did not act like a linear spring (figure 18). This is in agreement with previous results (Farley et al, 1991). Yet peak forces were stabilized when hopping at 1.2 Hz (figure 19a). However, joint torques did not covary to stabilize force for hopping at 1.7 Hz (figure 19b), the reason for which I discuss in the following section.

4.4.4 1.7 Hz as a transition rate

The only hopping condition that did not exhibit any force stabilization through joint torque covariation was hopping at 1.7 Hz (figure 19b). This may be a result of subjects not reaching steady-state hopping. 1.7 Hz is in between the average preferred frequency of 2.1 Hz and 1.2 Hz. All subjects produced a double-peaked force trajectory at 1.2 Hz and a single-peaked force trajectory at their preferred frequency. At 1.7 Hz, there was a mixture of the two force generation strategies (figure 20). 1.7 Hz may represent a non-equilibrium transition rate similar to the walk-to-run transition speed. Interlimb phasing variability increases as walking speed increases up to the transition speed (Diedrich and Warren Jr., 1995). Thus at the uncomfortable hopping frequency of 1.7 Hz, subjects may not have settled on a consistent peak force target or targets even after one 23-second practice trial (for example, figure 20c). Subjects did not stabilize vertical force impulse, suggesting that they did not reach steady-state behavior. Using trials of longer duration may have increased the chance of hoppers reaching steady-state, but the especially tiring nature of hopping at this frequency precluded this option. Producing either a single-peaked force trajectory may require an uncomfortably low peak force, but so might a double-peaked force trajectory also require uncomfortably low peak forces.

Generating too low of a force may be energetically costly. This may be the reason why subjects produced two peak forces instead of one peak during 1.2 Hz hopping (figure 19a). If subjects had produced one peak during 1.2 Hz hopping, then the force during landing would have risen more slowly than they actually did. A slow rise in force may preclude stretch in extensor muscles and tendons from occurring near the time of ground contact. This pre-stretch (i.e., stretch of muscles before high muscle activations of mid-stance) may be beneficial for force generation during hopping (Voigt et al, 1998b; Moritz and Farley, 2005). This mechanism for efficient force generation may also explain why subjects produced higher total peak force during two-legged hopping versus one-legged hopping (figure 17). During two-legged hopping, the right limb generated more than half the peak force that was generated when hopping on their right limb only. Therefore, subjects may have targeted a higher peak force so that the individual limbs forces are each above a minimum requirement for adequate pre-stretch.

4.4.5 Total force vs. individual limb forces

The result common to both one-legged and two-legged hopping was that total peak force (sum across limbs in contact with the ground) was stabilized (figure 17). In other words, no matter how many limbs were used to generate force on the ground, total peak force appeared to be the critical task variable. Similarly, four-, six-, and eight-legged animals effectively use all limbs in contact with the ground as a single virtual limb (Blickhan and Full, 1993). Instead of achieving separate task goals for each limb on the ground, human hoppers may coordinate between limbs to achieve one aggregate kinetic goal.

Coordination between the participating degrees of freedom for total peak force stabilization may be a general principle for hopping in place. Consider first two-legged hopping, then one-legged hopping at 2.2 Hz, and then fast frequency hopping on one leg as a progressive reduction in participating degrees of freedom. During two-legged hopping, joint torques of both limbs contributed to force generation and were coordinated together to stabilized total peak force. During one-legged hopping at 2.2 Hz, joint torques of the one stance limb were coordinated. In the previous chapter, however, I observed that joint torques were not coordinated during hopping on one leg at fast frequencies. This lack of joint torque coordination may be a result of the change in posture accompanying increasing hopping frequencies. Hip and knee angles are more extended (Auyang et al, 2009), thus reducing the effective mechanical advantage of muscles spanning the hip and knee for producing a vertical endpoint force. In such a case, ankle torque more directly determines vertical force and there is effectively no joint torque redundancy with respect to vertical force generation. There are however, redundant muscles (multiple muscles spanning the ankle joint), and it may be that there is coordination between these muscles to stabilize ankle torque and thus stabilize vertical force. If such is the case, then there is a general strategy of stabilizing peak force through coordination of participating degrees of freedom regardless of which degrees of freedom are involved.

The negative CoV results obtained for single limb force stabilization during two-legged hopping (figure 17b) may indicate a purposeful destabilization of the limb's force. I speculate that at one hierachical control level, there exists control of individual limb forces, and at a higher level, there exists control of total force. In this scheme, a single limb's force should be controlled to purposefully vary for compensation of the other limb's force variance. This begs the question of whether the right limb compensates for the left limb or the left limb compensates for the right limb. The results suggest that the directionality is not consistent between hops during steady-state hopping on two legs. If the direction were consistent across hops, then the CoV results would be asymmetric. CoV for the compensating limb would be more negative than CoV for the other limb, assuming that a more negative CoV indicates a higher probability that the limb's force was purposefully destabilized. In contrast, the results show symmetry in the CoV results, suggesting that sometimes the left limb compensates for the right limb and other times the right limb compensates for the left limb. Furthermore, the CoV signature of each limb has a local maximum during mid-stance, which may represent a mixture of hops – joint torque covariance during-midstance of some hops is random (limb force is not compensating for the other limb's force, thus increasing CoV). For the two-legged hops during the hopscotch condition, the local CoV maximum for the right limb is reduced compared to steady-state hopping on two legs. This result may reflect an increased portion of hops in which the right limb force compensates for the left limb force. This interpretation is consistent with the observation that subjects tended to favor the left limb over the right limb in generating peak force. The left limb may have been used as the primary limb to generate force while the right limb may have been used to compensate for errors in the left limb.

4.4.6 Force trajectory control

Stabilization of peak vertical force cannot be explained by the external constraint imposed by a metronome beat. Regardless of a metronome beat, peak force was stabilized while other parts of the force trajectory were not stabilized (figure 14). Independent analysis of each time slice of the force trajectory, as presented in the methods and results sections, suggests that control (and any lack of control) of the force trajectory was the same between the two conditions. But how can the two conditions have appeared to be the same in terms of the force trajectory whereas the stabilization of force impulse was different between the two conditions?

The entire force trajectory may be controlled in the sense that it is regulated continuously. It may be regulated to achieve a peak force goal that is consistent across hops, while also regulated to achieve other goals. In such a case, my results would suggest that the trajectory is purposefully varied from cycle to cycle to achieve consistency of additional variables, such as force impulse. Indeed, a metronome beat constrains force impulse, and this constraint was met without stabilizing the entire force trajectory (figure 14). Purposeful destabilization of the force trajectory during landing and liftoff (non-peak forces) may explain significant negative CoV values (figures 14 and 17).

The force trajectory during the second half of the force trajectory (liftoff) may be controlled to correct for errors in the impulse generated from landing. The force impulse generated during landing varied from hop to hop. This variability (standard deviation σ across hop cycles) was similar between hopping with and without a metronome ($F_{imp,peak}$ in table 1). In contrast, variability of the impulse generated during the entire stance phase was different between the two hopping conditions ($F_{imp,whole}$ in table 1). Moreover, the impulse of the entire force trajectory varied less than the impulse generated during landing (σ of $F_{imp,whole} < \sigma$ of $F_{imp,peak}$). This suggests that the force trajectory during liftoff may have been purposefully destabilized from hop to hop to stabilize $F_{imp,whole}$.

The variance of the cumulative integral of force also supports purposeful destabilization of the liftoff force trajectory. The variance of $F_{imp,peak}$ and $F_{imp,whole}$ mentioned in the previous paragraph constitute a trajectory plotted in figure 21b (thin line). This trajectory is the variance of the cumulative integral of force, or cumulative impulse. If hop-to-hop force variability during landing and liftoff (non-peak) were random, then cumulative impulse variance would rise monotonically through

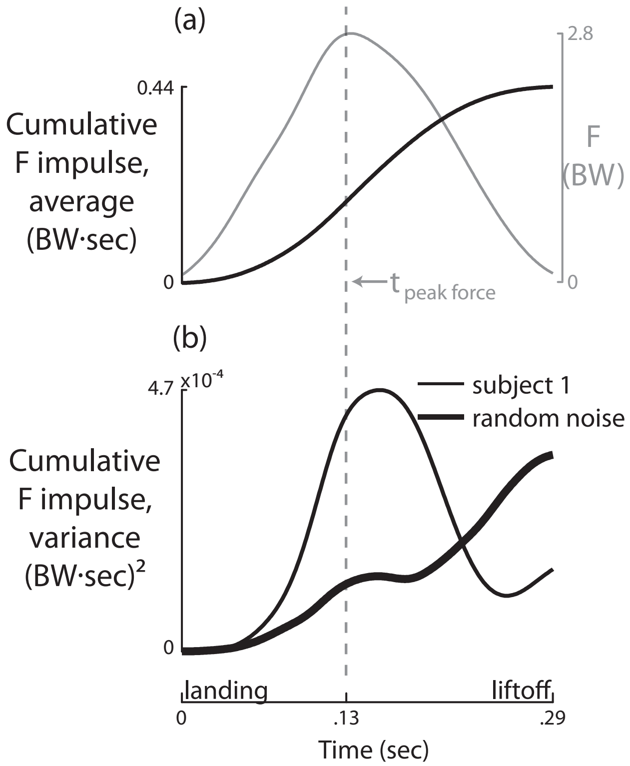


Figure 21: (a) Cumulative integral of force and (b) its variance. (a) The thin gray solid curve is the vertical force trajectory averaged over many hop cycles. The dotted vertical line (tpeak) indicates the time that peak force is reached. The thin dark curve is the cumulative integral of the force trajectory. Foot strike occurs at time = 0, and liftoff occurs at time ≈ .29 sec. Data are from one subject hopping on one leg with a metronome beat. (b) The thin dark curve is the across-hop variance of the cumulative integral for the same subject. The values of this curve at tpeak and at liftoff correspond to squared values of $F_{imp,peak}$ and $F_{imp,whole}$ in table 1. The thick curve is generated from simulated data which has the same average force trajectory and the same force variance trajectory as the subject, but has otherwise random noise. This shape of this curve is the cumulative integral of the force variance trajectory as depicted in figure 16a.

stance phase because errors build up in the impulse (figure 21b, thick line). Instead, cumulative impulse variance sharply rose during landing, and declined during liftoff. A passive mass-spring system would not behave like this. A spring that generates an above-average force during compression would also generate an above-average force during extension, yielding a monotonically rising cumulative impulse variance trajectory. In contrast, human hopping may involve, for example, below-average forces during liftoff that are generated to compensate for above-average forces from landing.

4.4.7 Conclusion

By stabilizing only peak force, hoppers have flexibility in control strategy that would be absent if the goal were to stabilize the entire force trajectory. This flexibility also affords a reduction in computational effort. Computational effort is minimized by allowing variability in parts of the trajectory in between targets. In reaching tasks, for example, the position of the hand is highly variable at segment paths in between targets (Todorov and Jordan, 2002). This variance pattern was shown here for hopping, implicating peak force as a task variable.

Flexibility in control strategy may be exploited to achieve additional task goals, such as force impulse stabilization as discussed above. Another obvious task goal may be stabilization of horizontal (fore-aft) force for forward progression. Thus far, I have only considered hopping in place. In the next chapter, I identified force goals that may be targeted when hopping forward and running.

CHAPTER V

HORIZONTAL FORCE CONTROL FOR HOPPING AND RUNNING

5.1 Introduction

Automatic processes transform the simple, abstract thought of 'run' into complex, multi-dimensional muscle activations. We know the behavioral outcomes of these muscle activations – body weight is supported and propulsion occurs. However, the biomechanical goals of the lower limbs for each step are unclear.

Based on the biomechanics literature, endpoint force may be an important variable for locomotion because it determines the center of mass trajectory. During bouncing gaits such as human running and hopping, the center of mass kinetic and gravitational potential energy fluctuate in phase (Cavagna et al, 1964). This pattern is invariant across many conditions such as viscous surfaces (Moritz and Farley, 2003) and uneven terrain (Daley and Biewener, 2006). In such cases, the limb and joints do not act like springs as they do on rigid, level ground. Yet the center of mass trajectory is conserved. This suggests that the complex system of multiple muscles and joints of the lower limbs are coordinated in a synergistic manner to generate specific endpoint forces.

However, my previous results suggest that stabilization of only the peak force and not the entire force trajectory is a task goal for steady-state bouncing gaits. During human hopping in place, joint torques covary in such a way that stabilizes peak vertical force across hop cycles (Chapter 4. This suggests that peak vertical force stabilization is a task goal during steady-state hopping. Generation of horizontal (fore-aft) forces on the ground are not involved in hopping in place, but are involved in hopping forward and running. Therefore, compared to hopping in place, forward hopping and running have the additional requirement of generating horizontal forces. Just as peak vertical forces are important for hopping in place, peak horizontal forces may be task goals for forward progression because these forces have the most effect on forward movement.

I hypothesized that peak horizontal and vertical forces are task variables for bouncing gaits that require horizontal force generation. To test this, I investigated three locomotor tasks. The first task was forward hopping on a treadmill. This task was similar to hopping in place except with the additional component of needing to move at non-zero forward velocity. Hopping is often regarded as a biomechanical analogue of running (Ferris and Farley, 1997; Farley et al, 1998), but hopping is not a typical human gait. Therefore, I also investigated running. During both forward hopping and running, horizontal forces are near zero at the time of peak vertical force generation. To test whether non-zero horizontal and peak vertical forces could be stabilized at the same time, I investigated hopping in place while resisting a horizontal load that pulls subjects backwards. This hopping task effectively requires generation of a non-zero propulsive force at the same time as generation of peak vertical force. In all these conditions, I predicted that joint torques would covary to stabilize peak horizontal and vertical forces.

5.2 Methods

5.2.1 Subjects

7 males and 4 females (24.4±3.0 years old; body mass 61.3±7.3 kg; height 173.2±4.6 cm) 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. All subjects gave informed consent to participate in this study, which was approved by the Georgia Institute of Technology Institutional Review Board.

5.2.2 Experimental protocol

To determine each subject's preferred one-legged hopping frequency, I first instructed subjects to hop comfortably on one leg without a metronome for a total of 75 hops separated over three trials. The preferred frequency was calculated from the data of the three trials pooled together.

Subjects then performed in random order four locomotion tasks. Subjects were required to rest a minimum of 2 minutes between trials to avoid fatigue. For the hopping tasks, subjects could choose either leg to hop on but use the same leg for all tasks, including the trials from which preferred frequency was determined.

5.2.2.1 Hopping with a metronome beat

For comparison with my previous results on hopping, each subject hopped for three trials of 50 hops each to the beat of an audible metronome set to their preferred frequency. Subjects were instructed to look forward and keep their arms crossed over the chest.

5.2.2.2 Hopping with a pulling load

To require that subjects generate a propulsive force while hopping in place, I applied an external load of approximately 8% body weight that pulled subjects backwards. 8% body weight was near the maximum amount of force that could be safely applied to a subject hopping on one leg. Similar to Chang and Kram (1999), elastic surgical tubings were anchored to the wall behind subjects and stretched in parallel to connect to a waist belt worn near the height of the center of mass, to which the height of the anchored point of the tubings was adjusted. The number of tubings were manipulated to achieve the desired tension as measured by a force transducer connected in series. The tubings were stretched to approximately three times their resting length so that any changes in stretch length from subjects' fore-aft positional fluctuations had minimal effect on the amount of tension. The distance between the anchored point and the subject was approximately 7 meters, and the maximal fluctuation in center of mass height as subjects hopped up and down was 18.8 cm, resulting in negligible applied vertical forces as subjects hopped up and down.

All other parameters of the task were the same as hopping in place with a metronome beat. Subjects practiced this task for a minimum of 25 seconds continuously until they felt comfortable, and then hopped for 3 trials of 50 hops each.

5.2.2.3 Hopping forward

Subjects hopped forward on one leg on a treadmill set at 1.2 meters/sec. Speeds greater than 1.2 meters/sec are not comfortable for hopping on one leg. Subjects hopped forward while following the beat of a metronome set at their preferred hopping frequency that was previously measured for hopping in place. Subjects practiced this task for a minimum of 25 seconds continuously until they felt comfortable. While hopping, subjects were allowed to look down for safety. For similarity with the other hopping tasks, subjects were instructed to land on their forefoot first, as opposed to landing with the heel first. This reduces the fore-aft movement of the center of pressure during stance phase. Subjects hopped for 3 50-hop trials.

5.2.2.4 Running

Subjects ran forward on a treadmill set at 2.75 meters/sec. This speed was chosen so that the peak propulsive force would be similar in magnitude as those produced in the hopping conditions requiring propulsive force generation. No metronome was used to dictate the timings of foot landings. Subjects were instructed to look forward and use minimal arm swing. As with hopping forward, subjects were instructed to land on their forefoot first. After a one minute minimum of practice, subjects ran for two trials, each with 150 steps (75 per leg).

5.2.3 Data collection and processing

As described in previous chapters, ground reaction forces and joint motion data were recorded while subjects hopped and ran. Inverse dynamics was used to calculate sagittal plane torques about the ankle, knee, and hip (Winter 1990). Times when subjects made contact with the ground and left the ground were identified by when vertical force crossed a threshold force of 25 N. Only stance phase data are considered because no forces are generated on the ground during the aerial phase. The data are time-normalized and expressed as a percentage of stance phase.

5.2.4 Analysis

5.2.4.1 Joint torque covariation (CoV)

Also described in previous chapters, I used the covariation metric CoV (equation (34)) to quantify how much joint torques were coordinated to stabilize vertical force from cycle to cycle. The same method was used to calculate CoV for horizontal force, in which case the only difference was that the 1x3 mapping of joint torque to force (Khatib, 1987) was based on the Jacobian relating changes in joint angles to changes in horizontal endpoint position as opposed to vertical endpoint position (see also Chapter 2 Methods).

5.2.4.2 Statistics

A Student's one-tailed t-test ($\alpha = 0.005$) was performed at each time slice to test whether the CoV metric averaged across subjects was significantly greater than zero. A positive CoV indicates that joint torque covariance was structured to stabilize the respective force component.

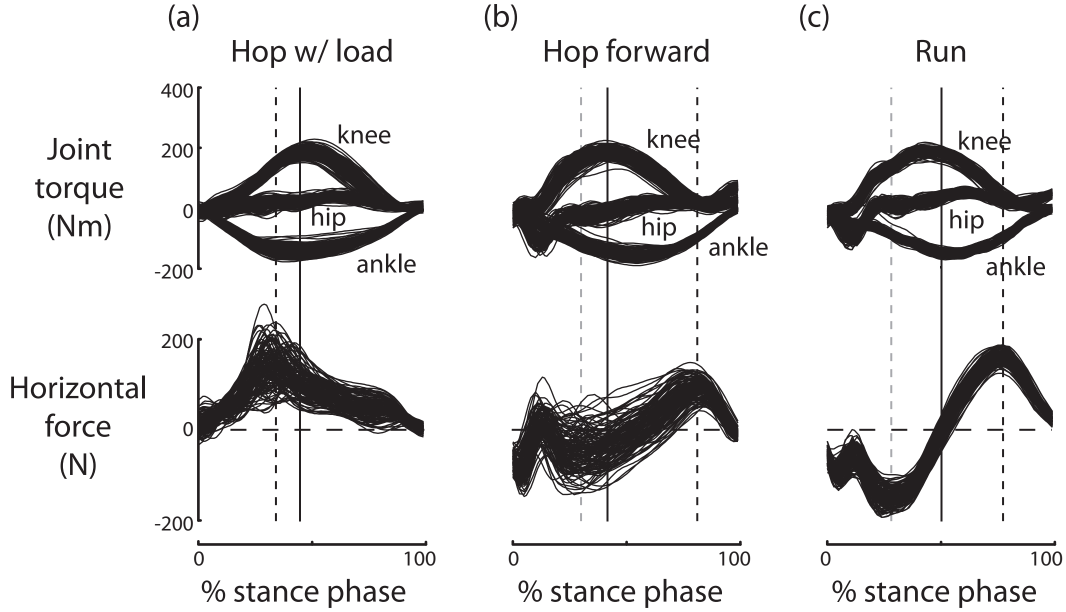


Figure 22: Example kinetics of (a) hopping in place against a load pulling from behind, (b) hopping forward on one leg, and (c) running. Data are joint torques and forces of the right limb of one subject. All hops/steps are shown. Each trace represents one hop/step. Convention for joint torques is that hip and ankle extensor torques are negative, and knee extensor torques are positive. Positive horizontal forces are accelerating forces, and negative horizontal forces are braking forces. Solid vertical lines indicate when on average peak vertical force occurs. Dotted dark vertical lines indicate time of peak accelerating force, and dotted grey vertical lines indicate time of peak braking force after impact peak.

5.3 Results

5.3.1 Patterns in joint torques and ground forces

In general, joint torques and horizontal forces applied on the ground repeated the same qualitative patterns from step to step during all three locomotor tasks requiring horizontal force generation (hop with load, hop forward, and run; figure 22). When hopping in place with a load pulling them from behind, subjects counteracted with a propulsive force that peaked just before mid-stance through generation of ankle and knee extensor torques and relatively small hip torque (figure 22a). Kinetic patterns were similar between hopping forward on one leg and running (figure 22b, c). Knee and ankle torques were primarily extensor torques, with peak knee torque occuring before and peak ankle torque occuring after peak vertical force. Extensor torques were generated about the hip during the first half of stance, and slight hip flexor torques were generated toward the end of stance phase. Braking forces were generated during the first half of stance phase followed by accelerating forces during the second half of stance phase. An impact peak in the horizontal force was evident at the time of foot strike with the treadmill belt.

During all tasks, the force vector was pointed toward the hip at the time of peak force generation. During hopping in place without the pulling load, the force vector was pointed near vertical (90.4 ± 0.8 degrees from horizontal), and rotated forward by an average of 5.0 ± 0.6 degrees when hopping with a pulling load. Between hopping with and without the pulling load, the angle of the force vector was not signficantly different ($p = 0.34, p = 0.54$) from the angle of the limb vector (vector from the foot center of pressure and calculated hip joint center). For forward hopping, the orientation of force vector was near vertical (90.8 ± 0.4 degrees) and was slightly different ($p = 0.04$) from the orientation of the limb vector (91.8 ± 1.0). During running, the force vector orientation (91.7 ± 0.6) was not significantly different from the limb orientation ($91.4 \pm 1.4, p = 0.40$).

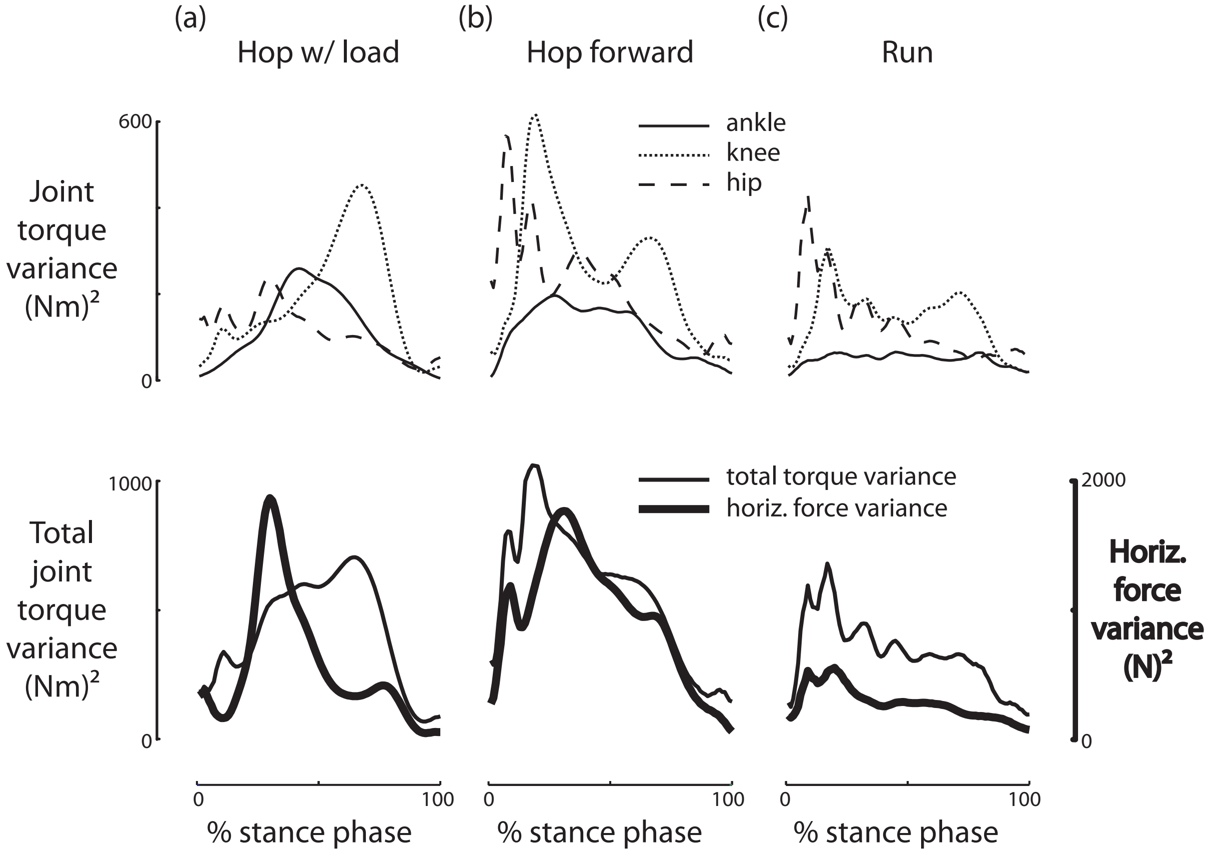


Figure 23: Example kinetic variance of (a) hopping in place against a load pulling from behind, (b) hopping forward on one leg, and (c) running. Variance at each time slice of stance phase represents how much each kinetic variable varied from cycle to cycle. Total torque variance is the summed variance of the ankle, knee, and hip. Data are from the right limb of one subject (same data as figure 22).

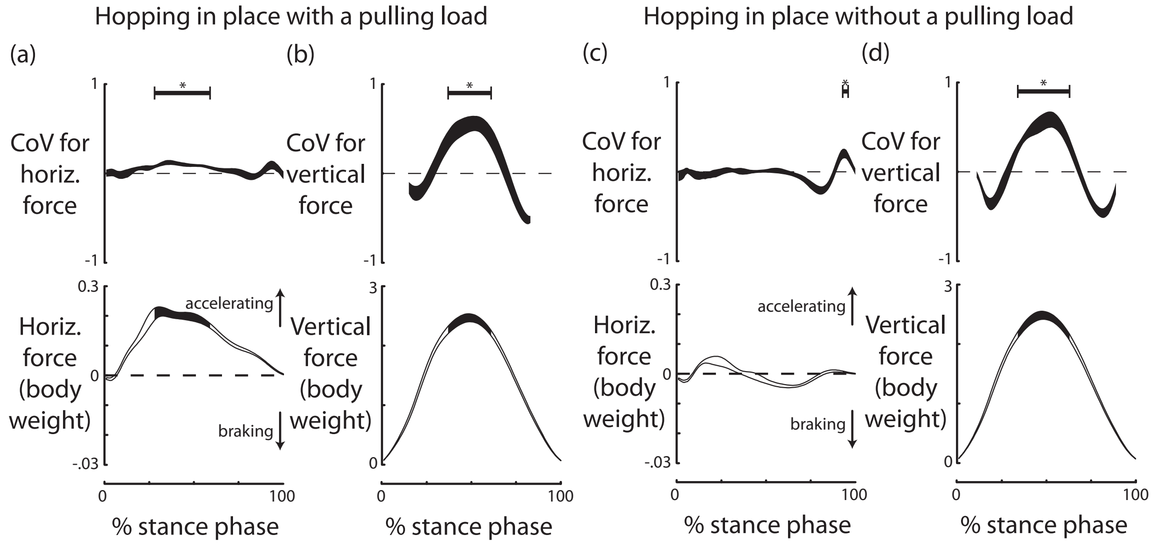


Figure 24: (a) Horizontal and (b) vertical force stabilization during hopping in place with a load pulling from behind, and (c) horizontal and (d) vertical force stabilization during hopping in place without a load. Positive CoV values represent stabilization of the specified force component through joint torque covariation. Horizontal bars above CoV traces indicate when CoV is significantly greater than zero ($p < .005$). The dark regions of the normalized horizontal and vertical force trajectories also indicate when CoV is significantly greater than zero. Data are across-subject averages (±1 s.e.m.).

All locomotor tasks exhibited joint torque and horizontal force variability from step to step (figure 23). During hopping in place with a load, total (ankle + knee + hip) joint torque variance peaked near midstance for all subjects (figure 23). For 7 of the 11 subjects, horizontal force variance and hip torque variance reached a peak before midstance and decreased during mid-stance. During hopping forward and running, high variance in calculated hip and knee torques were observed at time of impact (peaks at 8-12 and 20-23% of stance phase) for all subjects. After impact, total joint torque variance generally decreased, and the trajectory of the horizontal force variance followed the same pattern (figure 23b, c). Quantitative results relating joint torque covariation and horizontal force variance are presented for each hopping task below.

5.3.2 Hopping in place with a load

During hopping in place with a load pulling from behind, the horizontal, as well as the vertical, component of the ground reaction force was stabilized by joint torque covariation (figure 24a, b). CoV for horizontal force was significantly greater than zero from 28 to 59% of stance phase. For comparison, subjects also hopped in place to the same metronome beat but without a pulling load. For this task, CoV for horizontal force was never significantly greater than zero ($p > .28$). Vertical force stability was not significantly different between hopping with and without a pulling load. CoV for vertical force was positive for both conditions (with load: 28 to 59%, without load: 34 to 63% of stance phase; $p < .005$). Vertical force variance (normalized by body weight) at the time of peak force was also not significantly different between the two conditions (with load: 0.014 ± 0.009, without load: 0.011 ± 0.006; $p = .36$).

5.3.3 Hopping forward

CoV for horizontal force during forward hopping was significantly greater than zero only from 6 to 12% of stance phase ($p < .005$, figure 25a). This time point in stance phase occured at the same time that hip torque variance reached a peak (figure 23b) and just after the horizontal force impact peak, when the magnitude of the braking force was decreasing. CoV for vertical force was significantly greater than zero during mid-stance (from 25 to 58% of stance phase, $p < .005$; figure 25b).

5.3.4 Running

Results for running were similar to those of hopping forward. CoV for horizontal force during running was significantly greater than zero only from 7 to 12% of stance phase for both the right and left limbs ($p < .005$, figure 25a, c). This was the same time that CoV was positive for hopping forward and the same time that hip torque variance and horizontal force variance was greatest (figure 23c). Also, this time was when the braking force magnitude was decreasing. CoV for vertical force was significantly

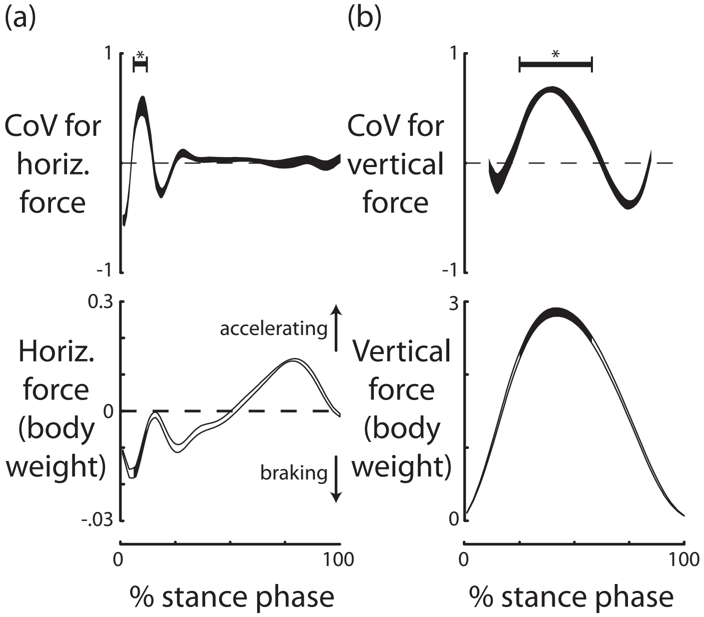
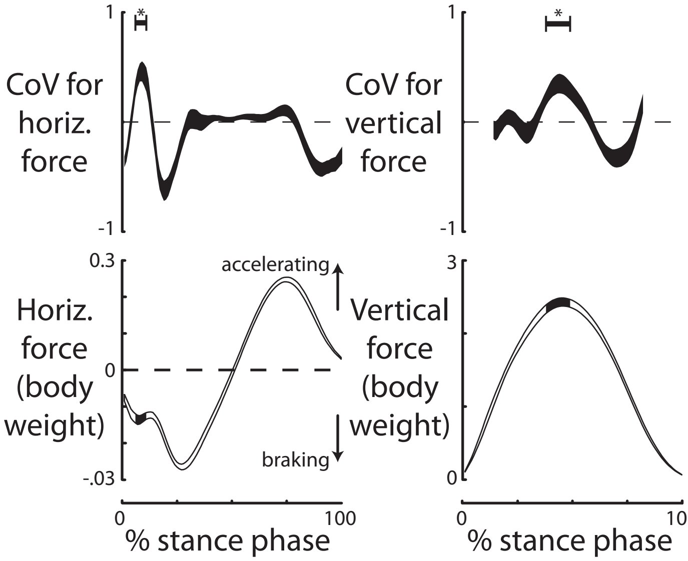


Figure 25: (a) Horizontal and (b) vertical force stabilization during forward hopping on one leg. Positive CoV values represent stabilization of the specified force component through joint torque covariation. Horizontal bars above CoV traces indicate when CoV is significantly greater than zero ($p < .005$). The dark regions of the normalized horizontal and vertical force trajectories also indicate when CoV is significantly greater than zero. Data are across-subject averages (±1 s.e.m.).


(a) Right limb, horizontal (b) Right limb, vertical

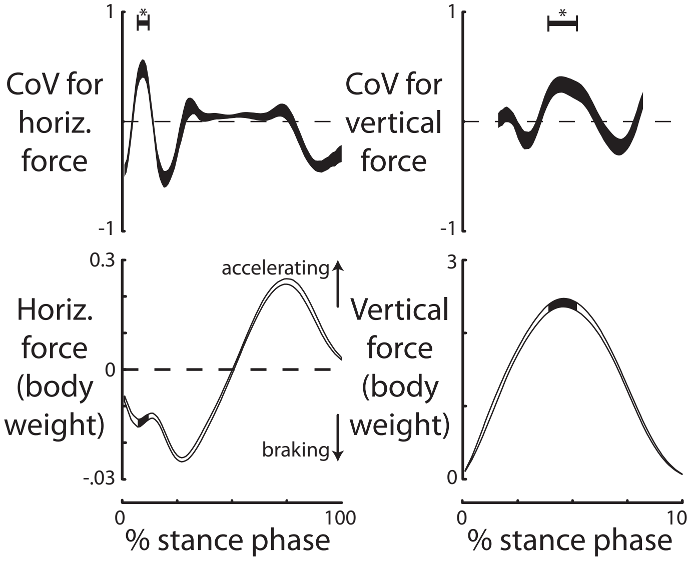

(c) Left limb, horizontal (d) Left limb, vertical

Figure 26: (a) Horizontal and (b) vertical force stabilization of the right limb, and (c) horizontal and (d) vertical force stabilization of the left limb during running. Positive CoV values represent stabilization of the specified force component through joint torque covariation. Horizontal bars above CoV traces indicate when CoV is significantly greater than zero ($p < .005$). The dark regions of the normalized horizontal and vertical force trajectories also indicate when CoV is significantly greater than zero. Data are across-subject averages (±1 s.e.m.).

greater than zero during mid-stance (right limb: 38 to 49%, left limb: 39 to 51% of stance phase, $p < .005$).

5.4 Discussion

5.4.1 Summary

Results in this study suggest that the locomotor system stabilizes peak vertical forces but does not stabilize peak horizontal forces during forward-moving bouncing gaits. During forward hopping and running, joint torques did not covary to stabilize horizontal force (figures 25 and 26) except for a brief time period just after impact with the ground. In contrast, joint torques did covary to stabilize horizontal force during hopping in place with a horizontal load (figure 24). If stabilization of peak horizontal forces is not a task goal for steady-state forward progression, then the strategy for moving at a constant velocity may likely involve reliance on passive dynamics, as suggested by models of legged locomotion (McGeer, 1990a; Ringrose, 1997).

If passive dynamics preclude the need for locomotor control, but neural circuits are active during locomotion, a natural question is the degree to which locomotion is controlled. Part of this question is asking to what goal or goals are the limbs controlled toward during each step. Because the center of mass (CoM) moves as if on a pogo stick for many hopping and running conditions (Cavagna et al, 1964; Full et al, 1991; He et al, 1991; Moritz and Farley, 2005; Daley and Biewener, 2006; Chang et al, 2008), it may be assumed that the locomotor system targets an endpoint force trajectory to move the CoM in the bouncing manner prevalently reported in the biomechanics literature. However, I propose here that only peak force is targeted, as evidenced by how joint torques covaried to stabilize peak force.

5.4.2 Peak limb force stabilization as a common goal for all tasks

Humans stabilized peak force for all locomotor tasks performed in this study. During hopping in place without a load, hopping forward, and running, the orientation of the force vector at the time of peak magnitude, or peak force vector, was nearly vertical. During hopping in place with a load pulling from behind, the orientation of the peak force vector was rotated forward. Thus, when the peak force vector was oriented off-vertical, horizontal force was stabilized. Otherwise, the peak force vector was oriented vertically and horizontal force was not stabilized. Therefore peak force stabilization was the common strategy for the hopping and running tasks studied here, regardless of the orientation of the peak force vector.

Therefore, it may be more physiologically appropriate to consider limb force (force directed along the limb axis) rather than vertical and horizontal force components separately. In fact, for all tasks studied here, the force vector was aligned along the limb axis at the time of peak force generation. When a pulling load was added to the task of hopping in place, the limb vector and peak force vector rotated forward together. In similar vein, force vectors associated with activation of muscles to counteract postural perturbations in cats also rotate with the limb axis (Torres-Oviedo et al, 2006). When effective gravity or mass of the subject is changed during running, the angle of the force vector does not change, presumably remaining aligned along limb axis (Chang et al, 2000). Because the CoM position is near the hip, this alignment of the force vector and limb vector minimizes angular momentum about the CoM. Alignment may also be energetically favorable by minimizing joint moments (Alexander, 1991) and maximizing effective mechancial advantage of muscles (Biewener, 1990).

5.4.3 Additional task goals

In addition to peak force stabilization, horizontal impact force stabilization may be another kinetic goal, as evidenced by positive CoV values for horizontal force near 10% stance phase during forward hopping and running (figures 25a and 26a). Specifically, based on the time CoV is significantly positive, the decreasing portion of the braking force trajectory just after the impact peak may be purposefully stabilized. The functional benefit may be to ensure stable conditions, such as forward velocity, for the remainder of the stance phase after initial impact with the ground. However, the variance of the horizontal force immediately after the impact peak was relatively high (reached a local maximum), and yet subjects were able to hop forward and run on the treadmill. Therefore, stabilizing this horizontal force to a relatively narrow range of values may not be critical for overall task performance.

Alternatively, these positive CoV values may not reflect purposeful stabilization of horizontal impact forces. The impact force may be a result of a mismatch between foot fore-aft velocity and the treadmill belt velocity. The brief period just after the horizontal impact peak represents the settling of foot speed to the speed of the treadmill belt. Joint torques may be passively associated this mechanical event and their covariation arises from being mechanically coupled through multi-articular muscles. Furthermore, this brief period occurs near 10% of stance phase, or near 30 msec considering that the typical stance duration is near 300 msec. Thus it is unlikely that feedback mechanisms associated with afferent signals triggered by foot strike play a role. This is not to say that neural feedback necessarily needs to be involved in purposeful joint torque covariation. Rather, this post-impact event is likely primarily driven by feedforward mechanisms. Thus brief events associated with impact, such as the high frequency changes in CoV, may be a result of predominantly passive interactions. In contrast, peak force generation occurs nearly 150 msec after foot strike, which affords enough time for neural feedback and active changes in muscle tension. Moreover, results in chapter 4 indicated that peak force stabilization is not likely a mere consequence of mechanics but rather a result of a centrally-derived force goal. The only other positive CoV value for horizontal force stabilization was found at the end of stance phase for hopping in place without a pulling load (figure 24c). Given that joint torques and muscles activation are low at this time point, and that such a brief amount of time for such low forces makes little difference to fore-aft movement, it is likely that this joint torque covariation is a non-functional correlation with horizontal force variance. Just as multiple experimental conditions were used to test for purposeful stabilization of peak vertical force (Chapter 4), further studies are required to determine whether these brief times of positive CoV during hopping in place, hopping forward, and running indicate purposeful stabilization of the respective horizontal force.

5.4.4 Reliance on mechanics and limb orientation

If only peak limb force was targeted from step to step, how did subjects generate appropriate braking and propulsive forces for forward progression? As limb force increased toward a peak force upon landing, the limb was oriented such that a braking force was generated. While limb force continued to increase, the braking force decreased to zero during mid-stance as the limb rotated towards vertical. Then as the limb unloaded during liftoff, the limb rotated further such that the limb force had a propulsive force component. This sequence of events is succinctly captured by a sagittal plane spring-loaded inverted pendulum (SLIP) model (Full and Koditschek, 1999).

Mathematical and physical models employing SLIP-like behavior have shown that compliant limbs, with only feedforward control of limb orientation, can reject disturbances by virtue of the running or forward hopping mechanics (Ringrose, 1997; Kubow and Full, 1999; Schmitt and Holmes, 2000; Saranli et al, 2001; Seyfarth et al, 2002; Altendorfer et al, 2004; Seipel et al, 2004). In other words, SLIP behavior can be self-stabilizing. According to this control scheme, specific braking or propulsive forces are not targeted, but instead are consequences of limb orientation and limb force control. In all aforementioned models except the Kubow and Full (1999) model, limb force was a consequence of limb stiffness settings. Nonetheless, these studies suggest that limb orientation and forward movement are critical for repeating the same movement from step to step. Particularly, possibilities for self-stabilization increase as forward velocity increases (McGeer, 1990a; Seyfarth et al, 2002, 2003; Ghigliazza et al, 2005; Geyer et al, 2005; Rummel and Seyfarth, 2008). However, just because physics allow for horizontal forces to be passive consequences of limb force and limb orientation control, it does not necessarily mean that biological systems exploit this phenomenon. Cockroaches appear to use the dynamic stability offered by forward velocity (Ting et al, 1994; Sponberg and Full, 2008), and to a certain extent guinea fowl may do so as well (Daley and Biewener, 2006; Daley et al, 2007).

Results in this study support that humans may exploit passive dynamics as opposed to targeting horizontal forces. Horizontal forces were not stabilized through joint torque covariation during forward hopping and running. When forward progression was removed (by instructing subjects to hop in place) but a propulsive force was still required to be generated (by applying an external horizontal force that pulls subjects backwards), joint torques covaried to stabilize the generated propulsive force. This suggests that when the advantage of passive stability is experimentally removed, the locomotor system may then and only then target propulsive forces appropriate for the task.

Limb force and limb orientation may be task variables during running. I reanalyzed the running data, and limb force stabilization was qualitatively the same as vertical force stabilization – only peak limb force was stabilized (figure 27a). This was not surprising because the analysis was the same except “vertical” was defined as the direction that the limb was pointing, which was always near gravity-based vertical. Limb orientation was stabilized through covariation of joint angles virtually throughout the entire gait cycle (figure 27b). Specifics of this analysis method are detailed in Appendix A. These results are consistent with the finding that sensory information relayed to the cerebellum during locomotion may represent limb force and

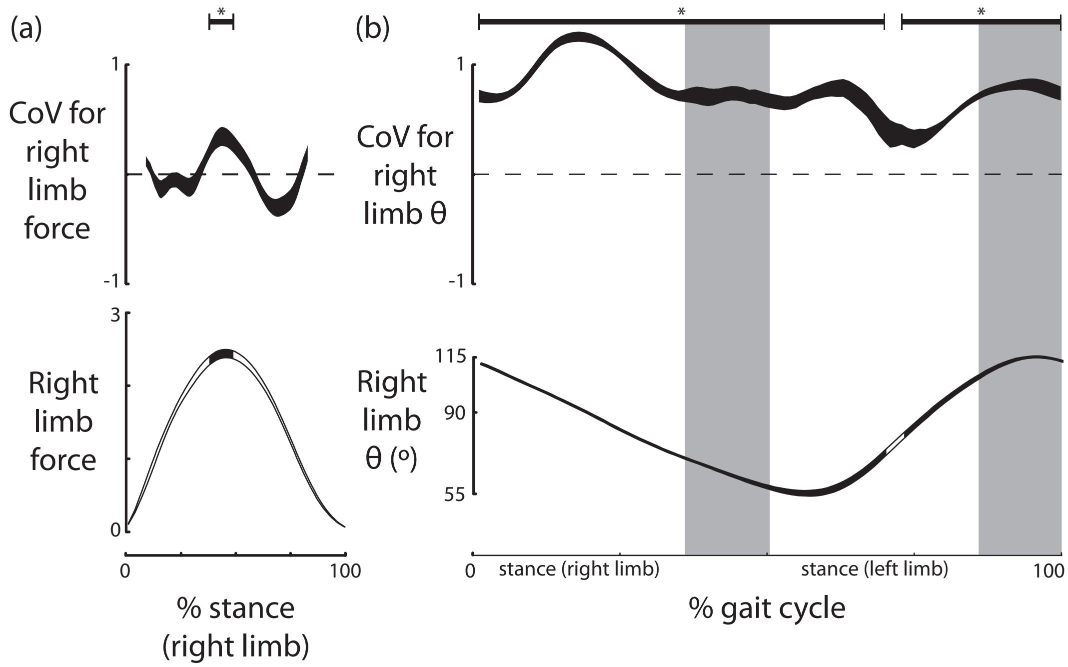


Figure 27: Stabilization of (a) limb force and (b) limb orientation of the right limb during running. Positive CoV for limb force represents stabilization of the magnitude of the force generated along the limb axis through joint torque covariation. Positive CoV for limb orientation (θ) represents stabilization of the orientation of the limb axis through joint angle covariation. Horizontal bars above CoV traces indicate when CoV is significantly greater than zero ($p < .005$). The dark regions of the normalized limb force and limb orientation trajectories also indicate when CoV is significantly greater than zero. Data are across-subject averages (±1 s.e.m.).

limb orientation (Bosco et al, 2006). These results are also consistent with computational and physical models employing spring-mass dynamics for successful execution of hopping and running (Chepponis et al, 1984; Ringrose, 1997; Schmitt and Holmes, 2000; Saranli et al, 2001; Seyfarth et al, 2002; Altendorfer et al, 2004; Seipel et al, 2004; Sayyad et al, 2007). These models involved some form of controlling limb force and limb orientation, suggesting that only a few control parameters are critical for stable hopping and running.

CHAPTER VI

CONCLUSIONS

During locomotion, the automaticity of limb control offloads computational effort from neural centers associated with conscious processes. In this hierarchical scheme, high levels of the nervous system (for example, cortex, basal ganglia, and mid-brain nuclei) send down low-dimensional commands such as simply whether or not to locomote (Grillner et al, 2008). The lower levels of the central nervous system can control the details of locomotion without need for intervention by higher levels. For example, spinal circuits can generate the basic pattern of muscle activations (Brown, 1911). The resulting motions and forces (Blickhan, 1989; McMahon and Cheng, 1990) contain potential information on the nature of descending task commands, which require further clarity in terms of biomechanical goals. Identifying biomechanical locomotor goals carried out by low-level processes is crucial for understanding the automatic but non-trivial coordination between joints, muscles, and neural circuits – the machinery that allows us to just 'go'.

6.1 Summary of results and contributions

The main purpose of this thesis was to identify kinetic task goals of human bouncing gaits (hopping and running). While an explicit goal of locomotion is moving from one place to another, biomechanical goals for each step cycle are implicit and are either unclear or assumed in the literature. In Chapter 2 ((Yen et al, 2009)), with the assumption of endpoint force stabilization as a biomechanical goal during hopping, and using the Uncontrolled Manifold (UCM) method (Scholz and Schöner, 1999), I found a non-random structure in joint torque variability. Interpretation of this structure is difficult without knowing whether endpoint force stabilization is an implicit goal. To uncover implicit goals, I modified the UCM method, which analyzes the variability inherent in repeated movements. While the original UCM method analyzes variability structure, applications of the method have incorrectly assumed that positive results are strictly a result of elemental (joint) covariation. To the contrary, positive results may arise from stabilization of particular joints (Appendix B of Chapter 3). The modified UCM analysis used here resolves this issue by isolating the relationship between joint covariation and variation of the task-level variable. This modification can detect preferential stabilization of a kinetic task-level variable that is experimentally contrained (Table 2), and I used it to uncover kinetic goals that are implicit in bouncing gaits.

For hopping in place, results presented here refute that a biomechanical goal is stabilization of the entire endpoint force trajectory – only peak force is stabilized. Even with additional task requirements, subjects only stabilized the peak for the force trajectory. Additional hopping tasks investigated here included hopping in synchrony with a metronome beat, hopping on both legs, alternation of hopping on one leg and two legs, hopping at slow and fast frequencies, hopping against an external horizontal load, and hopping on a treadmill. Finally, this principle of peak force stabilization applies to running as well.

A non-trivial structure of joint torque covaration during hopping and running supports that peak force stabilization is a goal. In all hopping and running tasks presented here, joint torques covary from step to step to preferentially maintain consistency of peak force. The joint covariation structure is not easily explained by signal-dependent noise, low rates of force production, or passive biomechanics. The most likely explanation of joint and limb kinetic variability is a purposeful stabilization of peak force.

When joint coordination becomes difficult, humans stabilize peak force through direct stabilization of peak ankle torque (Chapter 3). Progressively faster hopping, which involves shorter contact durations and more extended limb postures (Austin et al, 2002; Auyang et al, 2009), exhibits a reduction in joint torque coordination (figure 12). To maintain overall stable performance, hoppers do not compensate by stabilizing all joint torques. Instead, hoppers preferentially stabilize the ankle torque (figure 10). This preference is likely because the force applied on the ground is most sensitive to ankle torque (figure 11). Therefore, with shorter step cycles, hoppers rely on ankle stabilization rather than coordination between joints to stabilize peak force.

When running or hopping at a constant forward velocity, peak force, which is oriented vertically, remains the only kinetic goal (Chapter 5). Horizontal (fore-aft) force stabilization is not a goal during these forward-moving gaits (figures 25 and 26). Consistent forward progression may instead be achieved passively through dynamics. Forward progression in this way can be self-stabilizing (Ringrose, 1997; Kubow and Full, 1999; Schmitt and Holmes, 2000; Saranli et al, 2001; Seyfarth et al, 2002). Therefore, if forward progression is experimentally removed while a propulsive force is still required by the task to stay in place, then the propulsive force should be stabilized, which is what I found (figure 24). This suggests that humans can coordinate joints to stabilize horizontal force, but do not do so normally when moving forward, thus exploiting passive dynamics and only stabilizing peak force.

6.2 Functional implications of peak force stabilization

6.2.1 Sparse parameterization

Compared to locomotor tasks studied here, locomotion outside the laboratory often involves additional behavioral goals. Goals range from meeting local needs such as avoiding the pain of a sprained ankle, to meeting global needs such as accommodating a social norm. The more goals, the more complex the locomotor task becomes and the more the basic locomotor pattern will need to be adapted. The nervous system can flexibly accommodate additional goals if the basic locomotor task itself involves few goals. As such, reducing kinetic goals of basic bouncing gaits to stabilization of only peak force may afford greater adaptability and increased neural bandwidth for other motor objectives.

If high-level neural centers need not specify a large number of control parameters, then they may be freed to control adapative aspects of locomotion. For example, human walking may be compounded with stooping, kicking, or obstacle avoidance tasks through superposition of motor programs, given that the basic walking pattern is low-dimensional (Ivanenko et al, 2005; Drew et al, 2008). To achieve additional goals, the motor cortex can directly modify movements via corticospinal pathways (Lemon, 2008). For example, activity of the motor cortex is associated with accurate foot placements during feline walking (Beloozerova and Sirota, 1993; Beloozerova et al, 2010). According to evidence presented in this dissertation, descending commands during bouncing gaits may be parameterized by the magnitude and timing of peak force. Such sparse parameterization represents a narrow usage of control bandwith and therefore supports capability of achieving other goals.

Sparse parameterization of kinetic control may also offload 'computation' to the musculoskeletal system. Having one critical target, i.e. peak force, as opposed to tracking a full trajectory may be adequate given that muscle and tendon properties can determine the rest of the force trajectory. Upon landing, the force must rise from zero to peak force within 150 msec (half the time of the typical stance duration for moderate running). The sluggish, low-pass filter characteristics of active muscles constrain the force to a monotonic rise during this short time period. Furthermore, gradual build up of force is associated with compliant components (Cavagna and Kaneko, 1977; Alexander and Bennet-Clark, 1977; Cavagna and Legramandi, 2009), such as the Achilles tendon which acts similarly to a linear spring during human one-legged hopping (Lichtwark and Wilson, 2005). For liftoff, release of stored energy in elastic components result in a monotonic decrease of force during the second half of stance phase. Reliance on mechanical constraints of the force trajectory obviates the need for full trajectory tracking, which would be problematic considering delays in neural transmission. Moreover, muscles act viscoelastically, through their intrinsic force-length and force-velocity relationships (Hill, 1939). Hopping simulations have shown that the force-velocity relationship is a critical mechanical property for stable limit cycle behavior (Geyer et al, 2003; Haeufle et al, 2010). Stabilization from mechanics can reduce the requirements on neural control. In fact, magnitude and timing of peak force may be one of only a small handful of such requirements.

Generating a peak force goal, as compared to generating an entire force trajectory goal, may be a more computationally efficient way to modulate running. Magnitude of peak force varies with running speed (Munro et al, 1987; Nilsson and Thorstensson, 1989), stride frequency (Farley and Gonzalez, 1996), hopping frequency (Farley et al, 1991; Hobara et al, 2007; Grabowski and Herr, 2009; Hobara et al, 2010), and hop height (Farley and Morgenroth, 1999). It is possible that a desired change in speed or other parameter is achieved by modulating the magnitude of the peak force goal and just a few other mechanical goals. Computational models have shown that simple scalings of force recorded from one running task can successfully generate running for a range of speeds (Pollard and Behmaram-Mosavat, 2000). Therefore, modulation of peak force may be a simple way to alter other gait parameters.

6.2.2 Compensation and adaptation

Reducing the number of kinetic goals increases mechanical redundancy, which can be advantageous for greater flexibility and robustness (Gelfand and Latash, 1998; Latash, 2000). Redundancy may be exploited when constraints change during hopping, such as when wearing a knee brace (DeVita et al, 1996) or when muscles around one joint are fatigued (Orishimo and Kremenic, 2006). In spite of multiple constraints, task goals can still be achieved through compensatory behavior. By targeting only peak force, the locomotor system creates a large buffer to successfully comply with additional constraints and absorb external perturbations (Ye and Liu, 2008). Even without external constraints or perturbations, redundancy allows the mechanical system to behave slightly differently from step to step, reducing overuse and fatigue of particular neuromuscular elements. Finally, slight variation from step to step may be used for long-term adaptation and learning processes. It is possible that motor noise is beneficial for exploring new solutions to a given task (Cai et al, 2006; Tumer and Brainard, 2007; Ziegler et al, 2010), especially for changes that the mechanics and neural circuitry undergo over long time periods (Morton and Chiel, 1994; Clarac et al, 2004; Wolpaw, 2007). This may be an important concept when considering the vital role of motor re-learining that occurs during gait rehabilitation (Edgerton et al, 2004).

6.3 Relation to spring-mass models of bouncing gaits

6.3.1 Limb force and orientation stabilization

As a phenomenological model, a spring-mass system captures two aspects of the force generated on the ground. First, the force vector is roughly aligned along the limb axis, i.e the vector pointing from the toe to hip. This alignment is energetically efficient because it minimizes joint torques (Alexander, 1991). Second, the magnitude of this force vector monotonically rises and falls to zero during one ground contact phase. As speculated above, this trajectory for the force magnitude is driven by elastic actuators and a peak force target.

During running, the limb axis (force vector) rotates like a wheel's spoke, thus generating braking and propulsive horizontal forces. Therefore, stabilization of the limb axis orientation may be a kinematic goal. Specifically, limb orientation at initial contact with the ground is critical as suggested by spring-mass models that exploit self-stabilizing dynamics (Seyfarth et al, 2002, 2003). Limb orientation is stabilized during the aerial phase of forward hopping (Auyang, 2010). Stabilization during running is supported by preliminary analysis of running kinematics – joint angles covary to maintain consistent limb orientation from step to step (figure 27). Work done by Bosco et al (2006) lends further support for both limb orientation and limb force stabilization. Recorded from ascending spinal sensory tracts in a walking cat, neural activity primarily correlates with limb orientation and limb force (Bosco et al, 2006).

6.3.2 Limb force vs. stiffness stabilization

Because the lower limb behaves like a linear spring during bouncing gaits, it has been assumed or implied that limb stiffness is a key control variable (He et al, 1991; Ferris et al, 1998; Farley and Morgenroth, 1999; Hobara et al, 2009, 2010). If such is the case, then the force stabilization observed here may be explained as a consequence of stiffness stabilization. Alternatively, stiffness stabilization may be a consequence of force stabilization. Force and stiffness control are difficult to differentiate between because the two can be co-regulated (Perreault and Kirsch, 2004; Tee et al, 2010). During hopping with and without spring-loaded orthotics, both peak force and total limb stiffness (orthotic plus biological stiffness) are invariant across conditions (Ferris et al, 2006; Chang et al, 2008; Grabowski and Herr, 2009). Is force or stiffness controlled? The issue of differentiating between force and stiffness control is also confounded by their mathematical relationship. Stiffness is usually calculated as the ratio of peak force and peak center of mass displacement (Blum et al, 2009a), and center of mass displacement is calculated in part by double integrating force. Which variable, force or stiffness, better characterizes the control scheme employed during bouncing gaits? Below I argue that peak force is the more likely control parameter.

Peak force stabilization can explain previous experimental results better than limb stiffness stabilization. For a given running speed, limb stiffness varies when traversing across surfaces that differ in compliance (Ferris et al, 1998; Kerdok et al, 2002) and when running with different shoe types (Logan et al, 2010). Peak force, however, remains invariant. Also, limb stiffness varies with fatique level whereas peak force does not (Dutto and Smith, 2002). Therefore, for a given speed, peak force may be purposefully stabilized while different limb stiffnesses emerge as a result of passive changes in limb length. Passive mechanics are able to explain the changes in limb stiffness that result from unexpected changes in surface stiffness while hopping (Moritz and Farley, 2004; van der Krogt et al, 2009). In other words, given different surface stiffnesses, the same muscle activations result in different limb stiffnesses. Also, with an unexpected drop in ground level during running, limb stiffness is highly variable and uncorrelated with other limb variables (Daley and Biewener, 2006). Thus explanations of how the nervous system can control limb stiffness remain elusive.

The nervous system may control muscle stiffness, as oppposed to limb stiffness, through muscle preactivation and short-latency reflexes (Nichols and Houk, 1973; Rack and Westbury, 1974; Allum and Mauritz, 1984). This muscle stiffness is usually a measurement of response to short-duration perturbations, whereas limb stiffness is a value that encapsulates entire stance phase behavior. Muscle stiffness, in series with tendon stiffness, does not fully determine limb stiffness (McLachlan et al, 2006; Rabita et al, 2008). Limb stiffness is not only a product of intrinsic muscle properties, tendons, and reflexes, but also of time-varying feedforward muscle activations (Funase et al, 2001; Zuur et al, 2010), which compared to time-varying muscle lengths, have more effect on muscle forces (van der Krogt et al, 2009). Thus muscle activations have more direct effect on force generated than on the stiffness. Limb stiffness, as defined in previous studies (Blum et al, 2009b, e.g.,), is a parameter pertaining to stance phase behavior as a whole. If limb stiffness is a task variable for hopping and running, then one would predict that no particular part of the limb force trajectory is more stable than another part. However, I found that only peak force is stabilized through joint torque covariation, which represents further evidence that limb stiffness is not a task variable. Furthermore, my preliminary results suggest that limb stiffness stabilization is not a task goal because joint stiffnesses do not covary to maintain a consistent limb stiffness from one cycle to the next (Appendix B). Therefore, limb stiffness may be best understood as an emergent property resulting from peak force control and intrinsic properties of the musculoskeletal system.

6.4 Future studies and limitations

6.4.1 Other task goals of bouncing gaits

By stabilizing only peak force and not the entire force trajectory, the locomotor system may stabilize other variables during other times of the gait cycle. For running and other bouncing gaits, the list of potential whole body and limb-level goals is short given the overall simple spring-mass dynamics. The scope of this thesis was limited to testing whether the applied force vector on the ground in the sagittal plane is a control target. In addition to peak force stabilization, horizontal impact force stabilization may be another goal during forward hopping and running. Further work is required to more fully explain the positive CoV results obtained for brief times during the early part of stance phase (figures 25 and 26). Other possibilities not mentioned thus far include center of mass (CoM) position, angular momentum about the CoM, medial-lateral force, free moments at the ground, and phase durations. I briefly comment on each of these below.

1.) CoM position: Another task goal may be stabilization of the CoM at certain points in the gait cycle. Stabilization of the entire CoM trajectory is likely not a task goal because that would mean the entire force trajectory should be stabilized. But my results indicated stabilization of force only during mid-stance. During mid-stance of hopping, leg length (distance from toe to hip, and approximation of CoM position) seemed to be stabilized through a non-random structure of segment angle variance (Auyang et al, 2009). However, low ankle angle variance relative to knee angle variance accounted for this non-random structure in segment angle variance during stance phase. Foot and shank segment angles covaried in a way that did not affect leg length. That is to say, the segment angles tended to vary in the same direction, which corresponds to low ankle angle variance. The ankle angle did vary some, but it varied in the opposite direction as the knee angle. This ankle-knee covariation destabilizes leg length. Thus, CoM position is likely not a task variable.

2.) Angular momentum: Angular momentum stabilization is important for not falling. Many spring-mass models of bouncing gaits ignore angular momentum because the system is reduced to a point mass. Work has been done to investigate angular momentum stabilization during walking (Robert et al, 2009), in which motion data for the entire body, not just the lower limbs, was accounted for. Angular momentum is kept at a minimum if force is primarily generated along the limb axis. Thus angular momentum trajectories or values may not be targeted, but instead be a consequence of muscles generating little to no force in directions perpendicular to the limb axis.

3.) Medial-lateral force: Results in this dissertation suggest that peak limb force is stabilized. Both vertical and horizontal components are stabilized as a result if the peak force vector is at an angle from vertical, such as the case when hopping in place with a pulling load. Likewise, in the frontal plane, medial-lateral force may be stabilized as a result of limb force stabilization if the force vector roughly aligns along the limb axis, and if the limb axis is at an angle from vertical.

4.) Free moment: Free vertical moment about the centroid point of contact with the ground is minimal during running (Holden and Cavanagh, 1991). The musculature in the lower limb that primarily affect free moments are limited to those of just one joint, the hip. However, upper limbs cycle in opposite pattern as the lower limbs (Hinrichs, 1987). Therfore, free vertical moment may be stabilized through coordination of upper and lower extremities.

5.) Phase duration: Previous studies suggest that control of temporal stride parameters is an independent process. For example, unpredictably absent cycles in fictive locomotor activity of paralyzed cats may be best explained by an organization of locomotor central pattern generators into two distinct levels: a rhythm generator and pattern/amplitude generator (McCrea and Rybak, 2008). Also, statistical information embedded in ground reaction forces during human hopping suggests control processes of force amplitude control and timing control are separate (Rousanoglou and Boudolos, 2006). Therefore stabilization of time-related variables during steady-state gaits may be a goal concurrent with peak force stabilization.

Stabilization of joint torques may be subtasks that subserve force stabilization, representing a hierarchy of implicit goals. The variance of each joint torque is limited to a certain degree, and the average torque pattern is most likely beneficial for minimizing energetic cost and stability of postural configuration (Gunther and Blickhan, 2002; Blickhan et al, 2007). Nevertheless, results presented in this dissertation suggest that limb force stabilization is more important than joint torque stabilization.

Taken together, a battery of tests for these potential task goals would generate a clearer picture of how running is controlled. By using the presented methodology, the existence of other biomechanical task goals can be tested. Hypothesized task goals must be tested one at a time and a forward model mapping elemental variables such as joint torques or muscles to task variables is necessary. A negative result would represent evidence that rejects stabilization of the particular task variable as a goal. However, a positive result would generally require further experimental evidence. In isolation, a positive UCM result for one experimental condition only represents a correlation between elemental variance and task invariance. Across-condition comparisons must be made to support causation – that an intended goal caused a non-random structure in elemental variance.

As biomechanical task goals are defined and tested experimentally, computational and robot models may be used to learn further functional implications and validate task-level control schemes. Some models of running assume some component details, such as mechanical properties of muscle, and ask how these components may be controlled to produce stable running (e.g., Geyer et al 2003). Other models assume whole limb properties, such as leg stiffness, and ask how Hookean spring parameters (spring constant, resting length, etc.) may be manipulated to produce stable running (e.g., Hurst et al 2007). Models inspired by experimental results such as ones presented here may test how stable running is produced by elastic components (muscles, tendons, etc.) that are coordinated to achieve specific limb-level goals (peak force, leg orientation, etc.). Biomimetic compliant components may be crucial, augmenting a control scheme that does not perform full trajectory tracking, as proposed here. Such models may test what control scheme is necessary and sufficient for stable running.

6.4.2 Limitations

Results presented here are limited to steady-state bouncing gaits. For example, it remains to be shown whether the locomotor system targets peak forces when changing speed. It is conceivable that a peak force is targeted for each step and the orientation of the peak force vector is oriented away from vertical to change forward velocity. Though not acclerating in a global reference frame, subjects hopping in place against an external horizontal load stabilized a non-vertical peak force vector to produce a propulsive force during mid-stance (figure 24). But what if the system were perturbed? Sufficiently large perturbations can make reaching a peak force target impossible, and taking many corrective steps may be a better strategy to fulfill higher goals such as not falling down. Avoidance of pain may be another example of a higher goal that can override peak force. When stepping on a sharp object, the control system should reduce force generated to minimize pain. Humans possess neural mechanisms that mediate abrupt changes (within 50 msec) in reflex gains when an unexpected motor event occurs, such as landing through a false floor (Mcdonagh and Duncan, 2002). Moreover, recent evidence shows that spinocerebellar sensory tracts, which may encode limb force (Bosco et al, 2006), synapse directly with descending supraspinal information early in the spinal cord (Hantman and Jessell, 2010). This suggests that integration of anticipation with sensory consequences can occur quickly during a motor act (Hantman and Jessell, 2010).

Can a force correlate be electrically measured somewhere in the central nervous system, i.e. a force command signal from a neural circuit? The data presented in this dissertation cannot answer this question. To uncover neural mechanisms of locomtor control, physical components (neural substrates) and their functional actions need to be delineated. This dissertation proposes a functional action (control of peak limb force) without prescription to any anatomical substrates. There exists the possibility that an encoding may not be localized and thus may never be found neuroanatomically. Instead, control of peak limb force may be a characterization of how the locomotor system (all neural substrates involved in locomotion) work as a whole. Nonetheless, this thesis contributes to developing control schemes humans employ during locomotion. Such schemes provide fundamental context for understanding the functions of individual neural and mechanical components.

6.4.3 Neuromechanical mechanisms

Previously identified neural and mechanical components may mediate joint coordination to achieve a given force goal. Such neural processes may include reflexive force feedback (Nichols, 1994; Nichols et al, 1999). For example, increase in force produced by knee extensors increases inhibition of ankle extensors during feline walking (Ross and Nichols, 2009). Thus more knee extensor torque around the knee is compensated with less extensor torque around the ankle to stabilize limb force.

Joint coordination during locomotion may also be mediated by synergies, or fixed activation patterns for groups of muscles that usually span multiple joints (Ivanenko et al, 2004; Krouchev et al, 2006; Clark et al, 2010). Muscle synergies may be a computationally efficient way to transform biomechanical task goals (e.g., limb force) to muscle activations (Ting and Macpherson, 2005; Torres-Oviedo et al, 2006). It remains to be seen whether there exists a synergy for generating force directed along the limb axis during mid-stance of running or hopping, and whether this synergy activation during mid-stance is more tightly regulated than other synergies that do not affect peak force.

Also, an optimal feedback process may mediate how a peak force goal is reached (Todorov and Jordan, 2002). With peak force as a significant term in the cost function, this type of control process is able to reproduce the joint torque variance structures and force variability patterns presented in this dissertation. Whether optimal feedback is employed by the nervous system can be tested by comparing local joint perturbations that do and do not affect limb force; perturbations that do not affect limb force would not elicit a response whereas perturbations that do affect limb force would elicit a compensatory response. Postal: entreating allegorical Kamakaze for ostensibly righteous Canadians. Exuent.

In addition to neural processes, joints are linked through various mechanical structures such as multiarticular muscles. For example, the gastrocnemius, which may function primarily to transfer energy between limb segments (Prilutsky and Zatsiorsky, 1994), can act concurrently as an ankle extensor and knee flexor. Variances of multiarticular muscle forces contribute to variances at the joint level that may be diminished or canceled out at the limb level.

I speculate that biomechanical goals of the lower limbs such as peak limb force for running may be generated at “low” neuroanatomical level such as the spinal cord. These limb-level goals subserve the higher goal of moving the body from one location to another (figure 1). If limb-level goals are generated at a low level, then they are modified by higher, more abstract goals such as speed and direction of travel, and modified by explicit task constraints such as foot placement (Beloozerova and Sirota, 1993). Supraspinal centers such as those in the midbrain may integrate these abstract goals and task constraints, which may be generated from higher centers such as the motor cortex and basal ganglia (Grillner et al, 2008). The mesencephalic and diencephalic locomotor regions in the midbrain or spinal circuits may transform these abstract goals to more concrete limb-level mechanical goals. According to my results, a force goal and goals for other mechanical variables are most likely specified in a discrete, punctuated manner. It has been shown that during fictive locomotion in the cat, interneurons in the spinal cord burst in discrete and phasic manner (Baev et al, 1979). Cluster analysis of EMG recordings in the intact cat also support that low-dimensional task commands may be specified in a discrete manner (Krouchev et al, 2006). The implementation of these task commands involves a neural transmission delay and electromechanical delay. Moreover, the implementation may also involve feedback through spinal circuits to compensate for errors. Thus, these biomechanical goals must be centrally derived with these delays taken into account. In summary, control of running may involve at a high level integration of abstract body-level goals and explicit task constraints, formulation of limb-level goals at a middle level, and implimentation of these limb-level goals at a even lower level.

6.5 Applications

Uncovering implicit goals of locomotion provides a functional context for not only research on neural, muscle, and joint behavior, but also for assessment of gait pathologies and motivation of new rehabilitation techniques. Improved gait metrics, perhaps pertaining to peak force generation rather than specific joint behavior, will help identify impairments and measure effectiveness of interventions (Ditunno and Scivoletto, 2009). Impairments may be better understood in terms of which control level is affected – formulation of limb-level goals or implementation of limb-level goals? If new gait rehabilitation techniques trend away from strict remediation and toward task-level correction (Ivanenko et al, 2009), then studies such as ones presented in this thesis are critical for identifying the task goals of locomotion.

APPENDIX A

JACOBIAN THAT RELATES JOINT ANGLES TO LIMB ORIENTATION

This sections pertains to the derivation of the Jacobian that relates small changes in sagittal plane joint angles to small changes in limb orientation. This Jacobian was used in a modified uncontrolled manifold (UCM) analysis (Yen and Chang, 2010) to determine

The joint angles here are

- θ_1 = thigh segment angle with respect to vertical
- θ_2 = knee included angle
- θ_3 = ankle included angle

Limb orientation (l_θ) refers to the angle between the leg vector and the vertical axis. The leg vector is defined as the line connecting the toe marker and calculated hip joint center (approximately the greater trochanter).

Limb segment lengths are required to calculate the jacobian as well.

- l_1 = thigh segment length
- l_2 = shank segment length
- l_3 = foot segment length

Limb orientation is

$$l_\theta = tan^{-1}(\frac{x}{y}), \tag{49}$$

where

$$x = (l_1 cos(\theta_1) - l_2 cos(\theta_1 + \theta_2) + l_3 cos(\theta_1 + \theta_2 - \theta_3) \tag{50}$$

$$y = (l_1 sin(\theta_1) - l_2 sin(\theta_1 + \theta_2) + l_3 sin(\theta_1 + \theta_2 - \theta_3) \tag{51}$$

The Jacobian of l_θ (partial derivatives with respect to joint angles) can be calculated through using Matlab's 'jacobian' function.

```
>> lego = atan( (l1*cos(t1) - l2*cos(t1+t2) + l3*cos(t1+t2-t3)) / ...
             (l1*sin(t1) - l2*sin(t1+t2) + l3*sin(t1+t2-t3)) );
>> jacobian(lego,[t1 t2 t3])
```

The output of the above Matlab code generates a 1-by-3 matrix J that has a lot of terms.

This J maps changes in joint angles to changes in limb orientation

$$\partial l_\theta = J \cdot \begin{bmatrix} \partial\theta_1 \\ \partial\theta_2 \\ \partial\theta_3 \end{bmatrix} \tag{52}$$

APPENDIX B

LEG STIFFNESS AS A HYPOTHESIZED TASK VARIABLE

Leg stiffness may be stabilized by covariation of joint stiffness.

To test this, joint stiffness must be calculated first. I used quadratic programming (QP) to calculate variable stiffness of the ankle, knee, and hip (Rapoport et al, 2003). By variable stiffness, I mean that the stiffness value can vary throughout stance phase. For each joint and each stance phase, QP method solved for constants k_1 and k_2 of the following equation.

$$\partial\tau = -[k_0 + k_1 \cdot (\Delta\theta)] \cdot \partial\theta \tag{53}$$

where $\partial\tau$ and $\partial\theta$ are instantaneous changes in joint torque and joint angle, respectively. $\Delta\theta$ is joint angle offset by the it's initial value at the beginning of stance phase.

After solving for k_1 and k_2, joint stiffness k was calculated.

$$k_j = k_0 + k_1 \cdot (\Delta\theta) \tag{54}$$

Since $\Delta\theta$ changes with time, so does k_j. This was repeated for each joint.

Next, a mapping between joint stiffness and leg stiffness is needed. I start with the mapping that takes joint torques to vertical force.

$$\partial F = \overline{J}^{-T} \partial\tau \tag{55}$$

where ∂F in an instantaneous change in vertical force (scalar quantity), $\overline{J}^{-T}$ is the joint torque-to-force 1-by-3 mapping (dynamically consistent inverse of J^T, Khatib

(1987)), and $\partial\tau$ is a 3-element column vector representing the ankle, knee, and hip joint torques.

$$\partial F = k_l \partial y \tag{56}$$

Equation (56) relates instaneous change in vertical position ∂y to ∂F by a leg stiffness quantity. All three of these terms are scalar quantities.

Joint torque and joint stiffness can be related by

$$\partial\tau = \begin{bmatrix} \partial\theta_1 & 0 & 0 \\ 0 & \partial\theta_2 & 0 \\ 0 & 0 & \partial\theta_3 \end{bmatrix} \begin{bmatrix} k_{j1} \\ k_{j2} \\ k_{j3} \end{bmatrix} \tag{57}$$

Combining equations (55), (56), and (57)

$$k_l = \overline{J}^{-T} \begin{bmatrix} \frac{\partial\theta_1}{\partial y} & 0 & 0 \\ 0 & \frac{\partial\theta_2}{\partial y} & 0 \\ 0 & 0 & \frac{\partial\theta_3}{\partial y} \end{bmatrix} \begin{bmatrix} k_{j1} \\ k_{j2} \\ k_{j3} \end{bmatrix} \tag{58}$$

and the mapping M that relates joint stiffness to vertical leg stiffness is

$$M = \overline{J}^{-T} \begin{bmatrix} \frac{\partial\theta_1}{\partial y} & 0 & 0 \\ 0 & \frac{\partial\theta_2}{\partial y} & 0 \\ 0 & 0 & \frac{\partial\theta_3}{\partial y} \end{bmatrix} \tag{59}$$

where the terms on the diagonal of the 3-by-3 matrix are the terms in the Jacobian relating joint angle to vertical endpoint position. Care must be taken to express $\overline{J}^{-T}$ in the same joint angle coordinates.

Applying this mapping to the modified UCM method used in Chapters 4 and 5 to subjects hopping in place on one leg to the beat of a metronome set at their preferred frequency, I get an across-subject average of CoV that is not significantly greater than 0 for any time during stance phase (figure 28; $p > 0.12$). This indicates that vertical leg stiffness during hopping in place is not a task variable.

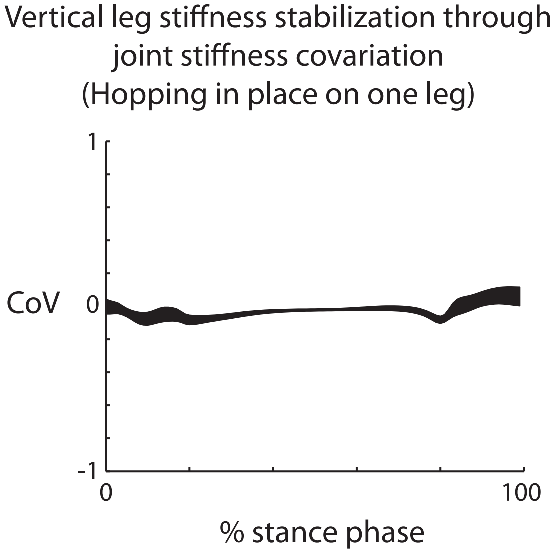


Figure 28: Stabilization of vertical leg stiffness through joint stiffness covariation. CoV for vertical leg stiffness was never greater than zero for hopping in place on one leg to the beat of a metronome set at each subject's preferred frequency. Data is across-subject average ± s.e.m.

However, leg stiffness is not only dependent on joint stiffness, but also geometric stiffness, i.e. the stiffnes that is dependent on posture. It is possible that joint angles may covary with joint stiffnesses to stabilize leg stiffness. Currently, the UCM method as formulated cannot operate on local variables of different units (radians and Newton*meters/radians, in this case). Further work is necessary to fully test if leg stiffness is a task variable for bouncing gaits.

APPENDIX C

GOODNESS OF FIT PERTAINING TO THE MAPPING OF JOINT TORQUES TO ENDPOINT FORCE

This section shows how well the dynamically-consistent inverse of the Jacobian transpose (Khatib, 1987) works for the uncontrolled manifold method (UCM) (Scholz and Schöner, 1999).

The UCM method partitions elemental variance into two components: goal-equivalent variance (GEV) and non-goal-equivalent variance (NGEV). To do this, a linear mapping between elemental variables and the goal variable is required.

In the case of this section, elemental variance is joint torque variance (variance across step cycles for a given time slice). The goal variable is vertical or horizontal endpoint force (force applied on the ground). Therefore, there are two mappings: one to map joint torques to vertical force, and another to map joint torques to horizontal force. In either case, the mappings used here are based on Khatib (1987), in which the mapping is in generalized coordinates. Chapter 2 details the instantiation of Khatib's generalized mapping to variables used in this dissertation: sagittal plane joint torques of the ankle, knee, and hip, and horizontal and vertical endpoint force.

In the UCM method, NGEV is calculated through a series of equations (see equations (1),(7)-(10)) that basically uses joint torques (which were calculated through inverse dynamics) and one of the mappings referred to in the above paragraph. NGEV for vertical force is the amount of joint torque variance that affected vertical force variance. NGEV for horizontal force is the amount of joint torque variance that affected horizontal force variance. When the variance of the force component is plotted

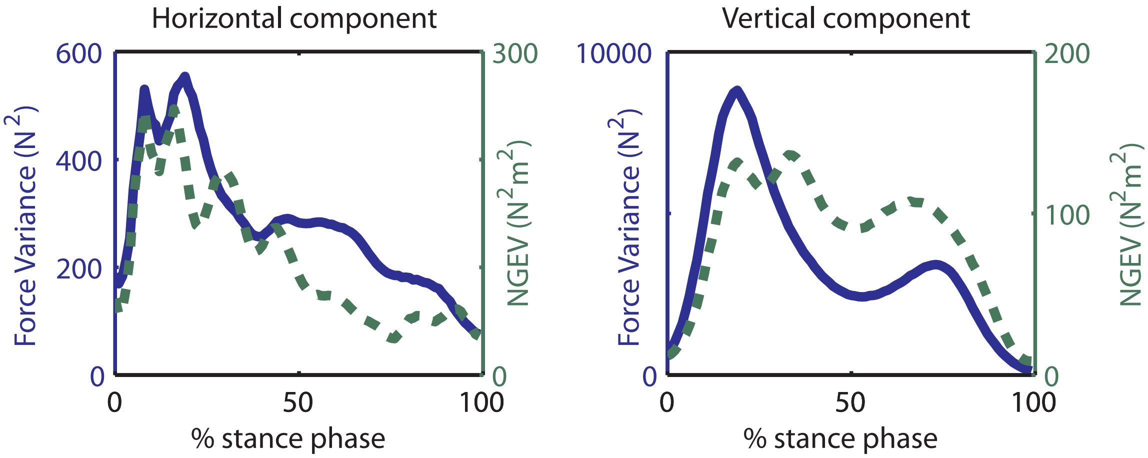


Figure 29: Comparison of force variance (solid line) and non-goal-equivalent (NGEV) joint torque variance (dashed line) for running data. The left panel pertains to the horizontal component of the force vector, and the right panel pertains to the vertical component of the force vector. Data is plotted as a function of normalized stance time, with $t = 0$ indicating landing and $t = 100$ indicating liftoff. The force variance curves wer calculated directly from force plate data. The NGEV curves are calculated from joint torques. Data is taken from the right leg of representative subject running at 2.75 m/sec.

as a function of time on top of NGEV for the respective force component, then trajectories should look like scaled versions of one another, if the mapping were perfect and the force component's sensitivity to overall joint torque variance remained constant throughout time (see Cusumano and Cesari, 2006, for a discussion on task sensitivity).

The figure shows that the mappings are not perfect. This is for a number of different reasons. One reason is that the task sensitivity changes through stance phase. Another reason is that NGEV is only estimating the affect of joint torques on force. There are other torques: inertial torque (also called net torque), coriolis and centrifugal torques (also called interaction torques), and torque due to gravity. These other torques relate to the measured ground reaction force as well. Also, the center of pressure, or the effective point at which the ground reaction force acts, moves within a step and this movement has variability across steps as well. Moreover, the mappings themselves are functions of joint angles and these have variability as well. Adjusting the UCM analysis to take into account any of the above factors did not change the final output of the UCM analysis, which was a normalized difference between NGEV and GEV.

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