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Commentary ___

Unsteady locomotion: integrating muscle function with whole body dynamics and neuromuscular control

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Summary

By integrating studies of muscle function with analysis of whole body and limb dynamics, broader appreciation of neuromuscular function can be achieved. Ultimately, such studies need to address non-steady locomotor behaviors relevant to animals in their natural environments. When animals move slowly they likely rely on voluntary coordination of movement involving higher brain centers. However, when moving fast, their movements depend more strongly on responses controlled at more local levels. Our focus here is on control of fast-running locomotion. A key observation emerging from studies of steady level locomotion is that simple spring-mass dynamics, which help to economize energy expenditure, also apply to stabilization of unsteady running. Spring-mass dynamics apply to conditions that involve lateral impulsive perturbations, sudden changes in terrain height, and sudden changes in substrate stiffness or damping. Experimental investigation of unsteady locomotion is challenging, however, due to the variability inherent in such behaviors. Another emerging principle is that initial conditions associated with postural changes following a perturbation define different context-dependent stabilization responses. Distinct stabilization modes following a perturbation likely result from proximo-distal differences in limb muscle architecture, function and control strategy. Proximal muscles may be less sensitive to sudden perturbations and appear to operate, in such circumstances, under feed-forward control. In contrast, multiarticular distal muscles operate, *via* their tendons, to distribute energy among limb joints in a manner that also depends on the initial conditions of limb contact with the ground. Intrinsic properties of these distal muscle–tendon elements, in combination with limb and body dynamics, appear to provide rapid initial stabilizing mechanisms that are often consistent with spring-mass dynamics. These intrinsic mechanisms likely help to simplify the neural control task, in addition to compensating for delays inherent to subsequent force- and length-dependent neural feedback. Future work will benefit from integrative biomechanical approaches that employ a combination of modeling and experimental techniques to understand how the elegant interplay of intrinsic muscle properties, body dynamics and neural control allows animals to achieve stability and agility over a variety of conditions.

Key words: EMG, force, muscle strain, spring-mass, work.

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Introduction

Prior studies of terrestrial locomotor biomechanics have revealed common principles that underlie muscle function and mechanisms for reducing the metabolic cost of steady movement. Only recently has research of locomotor biomechanics expanded to include non-steady behaviors in more complex environments. Yet animals regularly move over uneven and graded terrain, changing orientation, speed and gait as they maneuver within their natural environment, necessitating the study of locomotion under these conditions. The variable and context-dependent nature of these non-steady behaviors, however, makes rigorous biomechanical analysis a formidable challenge. When animals move slowly through complex environments, voluntary control of movements through both higher brain centers and neural reflexes are likely of key importance. However, when moving fast, animals must rely on the interaction of local spinal sensorimotor circuits with intrinsic biomechanical properties of their musculoskeletal structures. This results from the slow response time of higher level neural control due to transmission delays relative to the fast response times required for running stability. Consequently, walking and running likely differ in stabilization behavior and neural and mechanical coordination mechanisms. Our commentary focuses on running; however, future work on

slower, voluntary coordinated movement through complex environments is needed and deserves attention.

Here we highlight the potential for an integrative biomechanical approach to uncover basic principles of running stability and maneuverability in non-steady behaviors that involve a response to sudden perturbations. A fundamental emerging principle is that understanding the integration across organizational levels (e.g. muscle fiber – muscle–tendon unit – neuromuscular circuit – joint and limb – body mechanics) is a critical component of the neuromuscular and mechanical control of locomotion. Direct measures of muscle function must be interpreted in the context of whole body, limb and joint dynamics. Conversely, body, limb and joint dynamics alone cannot predict or explain the mechanical role played by individual muscles. This is because multiple muscles often operate agonistically at a joint and biarticular muscles may transfer energy between joints, so that mechanical work performed by muscles at one joint appears as energy at a different joint (Bobbert et al., 1986; Prilutsky et al., 1996). Muscle–tendon architecture and choice of synergist muscle activation for a task can dramatically influence how an animal's neuro-musculoskeletal system responds to perturbations (e.g. Brown and Loeb, 2000). Consequently, elucidating the integration that occurs across organizational levels through a biomechanical approach will be critical for understanding the mechanics and neuromuscular control of terrestrial locomotion in complex environments.

To illustrate the critical insights that arise from an integrative biomechanics perspective, we summarize a number of key findings from steady locomotion, highlight recent advances in the mechanics and neuromuscular control of running stability in non-steady conditions, and suggest directions for future work. We focus on three areas: (1) the relationship between whole body mechanical energy changes and muscle work modulation during locomotion; (2) proximo-distal regional differences in muscle–tendon architecture and links between architecture and mechanical performance in steady and non-steady tasks; and (3) the interplay between intrinsic properties of the musculoskeletal system, reflex feedback and feed-forward control in stabilization of running following sudden perturbations.

These examples reveal that many principles emerging from studies of steady, level running also play important roles in the dynamics of non-steady movement. Nonetheless, important gaps in knowledge exist that require innovative approaches incorporating integrative biomechanical analysis, controlled neural and mechanical perturbation experiments, and advanced computational modeling tools.

Muscle function in relation to changes in whole body and limb work

Steady versus non-steady locomotion

Most studies of terrestrial locomotion have focused on steady level locomotion. For running, trotting and hopping gaits, a simple spring-mass model (Blickhan, 1989; McMahon and Cheng, 1990; Farley et al., 1993) explains surprisingly well the observed dynamics and energy fluctuations of the body's center of mass (CoM; Fig. 1A,B). The model represents the body's CoM supported on a mass-less 'limb' spring. The model simplifies single and multi-legged support phases of various
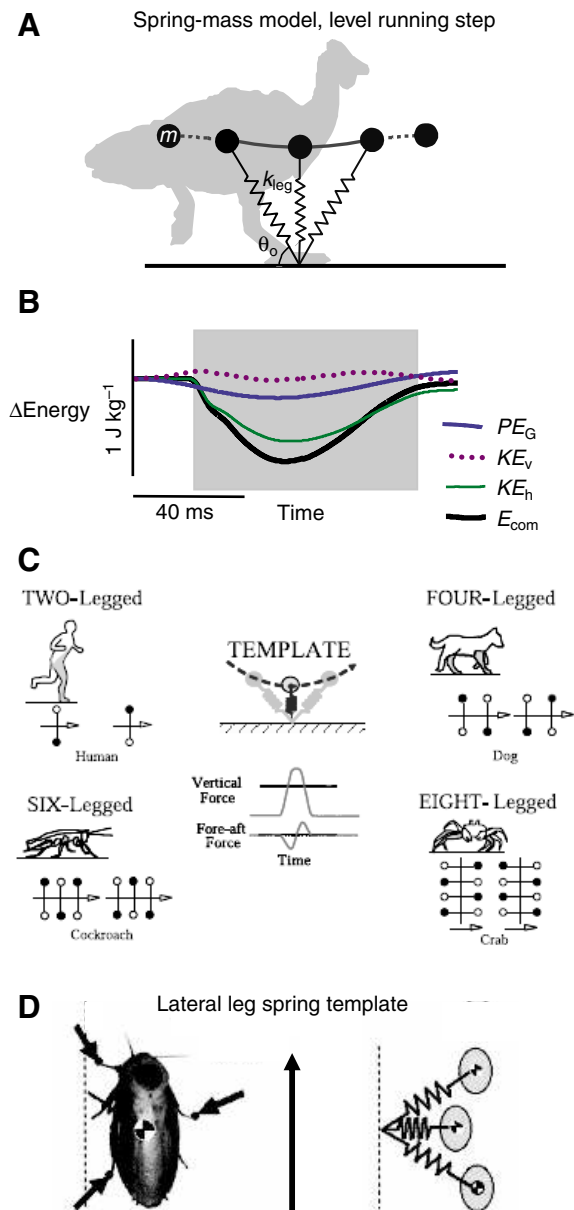

Fig. 1. (A) Spring-mass model (or 'spring-loaded inverted pendulum', SLIP) for the dynamics of legged terrestrial locomotion. The body is represented by a point mass m, located at the body center of mass (CoM; black circle), and the leg by a linear compression spring with leg stiffness k_{leg} and contact angle θ_o. (B) Despite its simplicity, the spring-mass model accurately describes the fluctuations in mechanical energy of the body during running (PE_g, gravitational potential energy; KE_v and KE_h, vertical and horizontal kinetic energy, respectively; E_{com}, center of mass energy) (Daley and Biewener, 2006; Daley et al., 2006). (C) Furthermore, all terrestrial animals appear to exhibit spring-mass dynamics, whether they run on two, four, six or eight legs. Multiple legs act in concert to produce the effective 'leg-spring' dynamics (Holmes et al., 2006). (D) Similarly, a lateral spring-mass model describes well the medio-lateral dynamics of cockroach locomotion, in which three legs operate as a single effective 'leg-spring' in the medio-lateral plane (Full et al., 2002).

running gaits as a single linear 'effective limb spring'. Despite a diversity of complex limb designs with varying

musculoskeletal organization and body size (Fig. 1C), the model emphasizes the fundamental role of spring elements to store and return elastic energy to reduce muscle work (Alexander, 1988). Despite its simplicity, the model's accuracy indicates that the combined action of muscles within the limb(s) is to store and return energy (in the form of elastic spring energy from tendons, ligaments and aponeuroses), reducing the demand for muscle work.

When used to describe forward locomotion, this spring-mass model is also called a 'spring-loaded inverted pendulum', emphasizing that the spring-mass sweeps through an arc during stance, like an inverted pendulum (Cavagna et al., 1977; McMahon and Cheng, 1990; Blickhan and Full, 1993). Recent modeling analysis has shown that this model also applies well to walking (Geyer et al., 2006). Rather than modeling walking as a simple inverted pendulum with no spring compliance, Geyer et al. (Geyer et al., 2006) show that the ground reaction force and mechanical energy patterns of walking are best described by a spring-loaded inverted pendulum model (Fig. 1A). Thus, use of limbs as a spring-mass inverted pendulum reduces the mechanical work muscles must do to move an animal's CoM during both walking and running (Fig. 1B,C), helping to lower its metabolic energy expenditure. As a consequence, the magnitude and rate of force generation by muscles, not mechanical work *per se* (Heglund et al., 1982), determines a large fraction of the metabolic cost of locomotion across animal size and running speed (Kram and Taylor, 1990), with differences in locomotor cost depending strongly on limb length (Pontzer, 2007).

Consistent with these observations, studies of *in vivo* muscle function have shown that distal muscles often generate force economically by contracting isometrically or with low shortening velocity (Roberts et al., 1997; Biewener et al., 1998; Daley and Biewener, 2003; Fukunaga et al., 2001; Lichtwark and Wilson, 2006; Lichtwark et al., 2007). In the gastrocnemius, the most accessible and commonly studied muscle, similar activation and strain patterns are observed for running in all of the animals studied (e.g. compare human and guinea fowl; Fig. 2). This suggests that active strain patterns observed within functionally similar, homologous muscle groups may not differ dramatically among species. By contracting with low shortening velocity or with an initial pre-stretch, muscles do little mechanical work and produce force using less ATP, reducing the amount of metabolic energy required to move (Biewener and Roberts, 2000). This also favors elastic energy storage and recovery in the muscle's tendon and aponeurosis, in addition to distal limb ligaments.

Yet, even when animals move at steady speed over level ground, some muscles produce or absorb mechanical energy, rather than contracting economically with little length change. In general, proximal limb muscle fascicles undergo larger strains during the stance phase of locomotion, in stretch–shorten cycles that suggest work absorption (through active lengthening) followed by production (through active shortening) (Fig. 3). Intriguingly, however, their strain patterns are often biased toward lengthening during the first half of stance (Figs 3 and 6 show examples for the rat, wallaby, dog and goat vastus lateralis and biceps femoris, as well as the horse triceps) (Carrier et al., 1998; Gillis and Biewener, 2002;
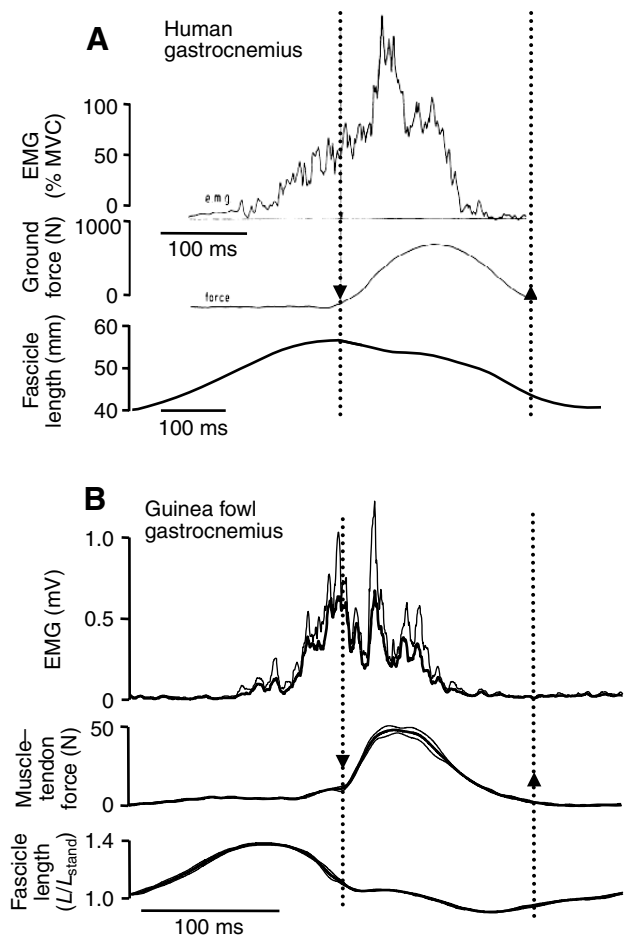

Fig. 2. Gastrocnemius muscle performance in a human (A) and guinea fowl (B) during running. Traces are scaled to align the stance periods of the running stride (broken lines). EMG traces in A and B are rectified and averaged over many stride cycles. (A) Average human gastrocnemius activity (EMG) relative to ground reaction force (Dietz et al., 1979), along with gastrocnemius fascicle length measured from ultrasound recordings [traced from fig. 3 in Lichtwark and Wilson (Lichtwark and Wilson, 2006)]. (B) Average guinea fowl gastrocnemius activity (EMG), muscle–tendon force and fascicle length [thin lines indicate s.e.m. (Daley, 2006)]. Note that the muscle is activated with similar timing and undergoes a similar strain pattern during stance in both the human and guinea fowl (as well as other animals). The muscle is activated in anticipation of stance, with increases in activity during stance suggestive of reflex feedback (e.g. Dietz et al., 1979).

McGowan et al., 2007; Wickler et al., 2005) or shortening during the second half of stance [rat, wallaby and goat biceps femoris and dog semimembranosus (Gregersen et al., 1998)]. This suggests that energy is mainly absorbed by the vastus during the first half of stance and produced by the biceps during the second half of stance. Thus, whereas distal muscles tend to act as force transmission links, facilitating elastic energy storage in tendons, proximal muscles are recruited in more complex patterns to yield spring-like behavior at the level of the joint and whole limb. Nonetheless, spring-like performance of the limb and body is accomplished through the collective action of the limb muscles, although some muscles absorb energy and others produce energy.
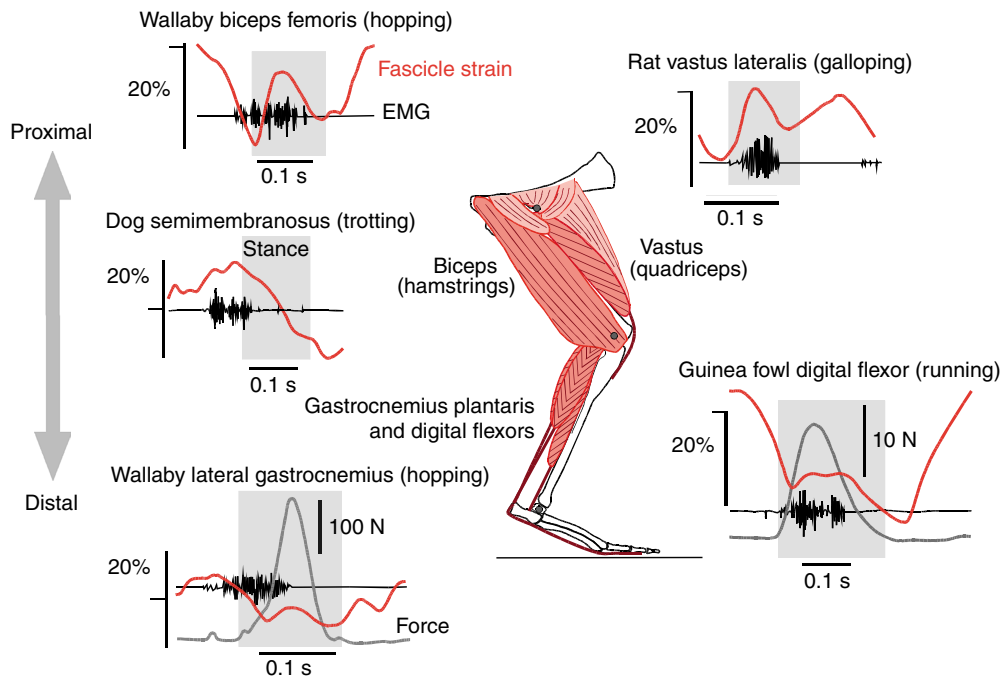
Fig. 3. Proximo-distal differences in muscle architecture within the hindlimb of a cursorial animal (similar patterns occur in the forelimb and in the limbs of other running birds and mammals). Representative fascicle strain (red) and myoelectric (EMG) patterns (black) recorded *in vivo* from muscles of various animals are shown in relation to proximo-distal differences in muscle–tendon architecture. For fascicle strain traces, the tick on the scale bar indicates zero strain (the estimated resting length of the fascicles, based on the average length during quiet standing). *In vivo* forces (gray) are also shown for the two distal muscles. Fascicle strain and time scales are the same for all muscle recordings shown. Duration of stance phase is shaded gray.

Differences in force–length performance among limb muscles appear to relate to the proximo-distal gradient in muscle–tendon architecture that is apparent within the limbs of terrestrial vertebrate animals (Fig. 3). Proximal muscles tend to have long-parallel fascicles with little in-series tendon elasticity, and distal muscles tend to have short, pinnate fascicles with long compliant tendons. Mechanical work output of muscles might be expected to be independent of differences in architecture because muscle tissue has constant work per volume capacity (Alexander, 1992). Nonetheless, in-series tendon elasticity decouples muscle fiber shortening and joint excursion, favoring elastic energy cycling, force control and force economy over direct control of joint position and work (Biewener and Roberts, 2000; Alexander, 2002; Roberts, 2002). In circumstances requiring short, high power bursts, such as during acceleration and jumping, tendon elasticity can enhance maximum power output by allowing the muscle to shorten against the tendon at relatively constant velocity, storing elastic energy in the tendon that is suddenly released as force declines and the tendon recoils (Roberts, 2002). Yet, proximal muscle architecture is better suited for precise control of joint position and steady work output. Natural selection also favors muscle mass to be concentrated proximally in the limbs to reduce inertial costs, particularly in larger animals. It is likely, therefore, that the majority of limb work is performed by larger proximal muscles. Thus, regional distribution of muscle–tendon architecture in the limb favors force economy and elastic savings in distal muscles, and position control and work modulation by proximal muscles.

Regional patterns of muscle work in relation to joint work and muscle architecture

One current research focus is investigation of regional patterns of muscle work within the limb during both steady and non-steady behaviors, to test hypotheses about the relationship between muscle architecture and function. This requires integrated studies of *in vivo* muscle function in concert with measurements of joint work and whole body mechanical energy changes. An integrative approach is necessary because (1) calculations of muscle work are more meaningful in the context of the whole body energy demand; (2) muscle work cannot be directly measured in most muscles, and must instead be estimated through approaches that combine *in vivo* measures with inverse dynamics analysis; and (3) energy is often transferred among joints of the limb *via* biarticular muscles.

Relatively little is still known about regional patterns of muscle work performance because most studies have focused on distal muscle function. Calculation of muscle work output requires direct measures of both muscle force and muscle fascicle strain. Muscle forces are most feasibly measured using tendon transducers, which can be placed only on distal muscles with sufficiently long tendons (Gregor et al., 1988; Herzog et al., 1993; Biewener and Baudinette, 1995). Recent studies have also investigated muscle strain and EMG patterns in proximal muscles during locomotion, although calculation of muscle work is not possible. Instead, inverse dynamics analysis, which combines ground reaction force and kinematic data to calculate joint torques and joint work, is used to evaluate how joint torque and work requirements change for different tasks. Nonetheless, inverse dynamics analysis must be interpreted with caution, as regional patterns of muscle work within the limb do not necessarily match patterns of joint work. This is because biarticular muscles often transfer energy between joints, so that muscle work performed at one joint may appear at a more proximal or distal joint (Fig. 4). Transfer of energy *via* biarticular muscles has been demonstrated during jumping or sprinting actions (Bobbert et al., 1986; van Ingen Schenau et al., 1994; Jacobs et al., 1996). However, it also occurs during steady locomotion in cats (Prilutsky et al., 1996) and wallabies (McGowan et al., 2007), and likely other animals. In cats and wallabies considerable net work appears at the ankle joint during
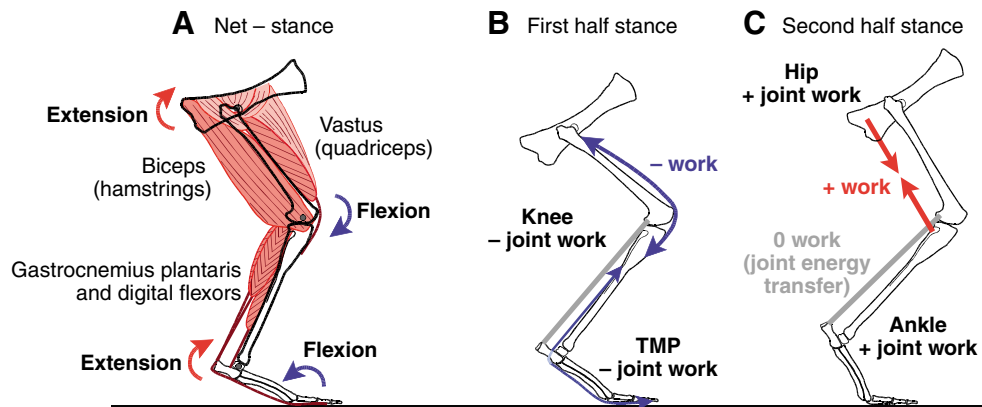
Fig. 4. (A) Schematic representation of regional patterns of joint work over the course of stance summarizing patterns observed for muscle groups of various animals during running. Curved arrows indicate the rotational motion of the distal segment of each joint (clockwise *versus* counterclockwise). Arrow color shows whether net energy is produced (red) or absorbed (blue) or zero (gray) at that joint during stance. These joint patterns are shown in relation to muscle work patterns in B and C. Muscle path arrows indicate hypothesized contraction of muscle groups, undergoing net shortening and positive work (red), lengthening and negative work (blue), or no net length change (gray). In this example, the hip extends, doing positive work mainly during the second half of stance (C); the knee flexes, doing negative work (energy absorption) mainly during the first half of stance (B); the ankle initially flexes during the first half of stance (B) and then extends during the second half of stance (C), doing net positive work; and the TMP (tarsometatarsal–phalangeal) joint dorsiflexes doing negative work throughout stance, though shown in B only (overall limb work is zero, characteristic of steady level locomotion assuming no work is done by other pelvic and trunk muscles). In comparison, the hamstrings (biceps) shorten while active, performing positive work (second half of stance, C); the quadriceps (vastus) undergo net lengthening while active doing negative work (first half of stance, B); the triceps surae [gastrocnemius (soleus, not shown) and plantaris] contract isometrically doing zero net work throughout stance, whereas the digital flexors are stretched and absorb energy initially (B) and then remain isometric during the second half of stance (not shown). As a result of their biarticular organization, the gastrocnemius, plantaris and digital flexor act as force links and, although they do no significant net work as a group, act to transfer energy from the hip and knee joints (*via* the hamstrings and/or quadriceps) to the ankle joint. This pattern is observed during steady level locomotion as well as during jumping in several species. See text for additional details.

stance, even though the ankle extensors, which span both the knee and ankle, contract under nearly isometric conditions (Fig. 3). In these animals, the biarticular ankle extensors have been observed to function as isometric links to transfer energy from proximal muscles acting at the hip and knee (Fig. 4). This occurs during different phases of limb support, with energy absorbed through negative muscle and joint work during the first half of stance (Fig. 4B) and produced during the second half of stance (Fig. 4C). Similarly, the hamstrings and rectus femoris may transfer energy between the hip and knee joints, or to the trunk, as observed during vertical jumping (Bobbert et al., 1986). As a result, measurements of joint torque and work are most informative when accompanied by *in vivo* measurements of muscle strain, EMG and muscle tendon forces, where possible.

One way to examine the regional distribution of work performance within the limb is to study muscle and joint net mechanical energy changes during locomotion on a steady grade. Energy must be produced with every step to move uphill, and absorbed to run down hill. In these tasks, the total net work demand is easily quantified by the change in the gravitational potential energy (PE_g) of the body with each step. This provides an opportunity to compare the net work output of muscles to the total body net work demand. Certain distal muscles of turkeys and guinea fowl, the lateral gastrocnemius and peroneus longus, modulate their net work output with changes in grade (Roberts et al., 1997; Daley and Biewener, 2003; Gabaldón et al., 2004) (Fig. 5). Changes in muscle work are achieved through multiple mechanisms, including shifts in the amount of muscle shortening *versus* lengthening (Fig. 5C) and shifts in the timing

of force relative to the strain pattern (Daley and Biewener, 2003; Gabaldón et al., 2004). Although these distal muscles increase their net work output during locomotion on a grade (Fig. 5A), the change in work is less than expected for their mass, and relatively small compared to the total body work demand (Fig. 5B) (Daley and Biewener, 2003; Gabaldón et al., 2004). Furthermore, in wallabies and humans, distal muscles remain nearly isometric during incline locomotion, with little or no change in net work output (Biewener et al., 2004b; Lichtwark and Wilson, 2006).

The importance of proximal muscles for modulating mechanical work output on graded surfaces is consistent with muscle strain and EMG patterns recorded in the proximal muscles of rats, wallabies and horses when running, hopping or galloping up a grade. A variety of proximal muscles show shifts toward net shortening on an incline, or in the case of the rat and wallaby vastus lateralis, significantly decreased net lengthening (Gillis and Biewener, 2002; Wickler et al., 2005; McGowan et al., 2007) (Fig. 6). For decline locomotion (not shown in Fig. 6), Gillis and Biewener (Gillis and Biewener, 2002) found decreases in biceps and vastus shortening (resulting in greater vastus net lengthening). Although direct measurements of muscle force and work are not possible for proximal muscles, inverse dynamics analysis of joint work patterns also suggests that proximal muscle work is modulated (Roberts and Belliveau, 2005; McGowan et al., 2007). Inverse dynamics analysis in humans reveals that nearly all the net work output for incline running occurs at the hip (Roberts and Belliveau, 2005), with the ankle and knee joints retaining the same function as during steady level running.
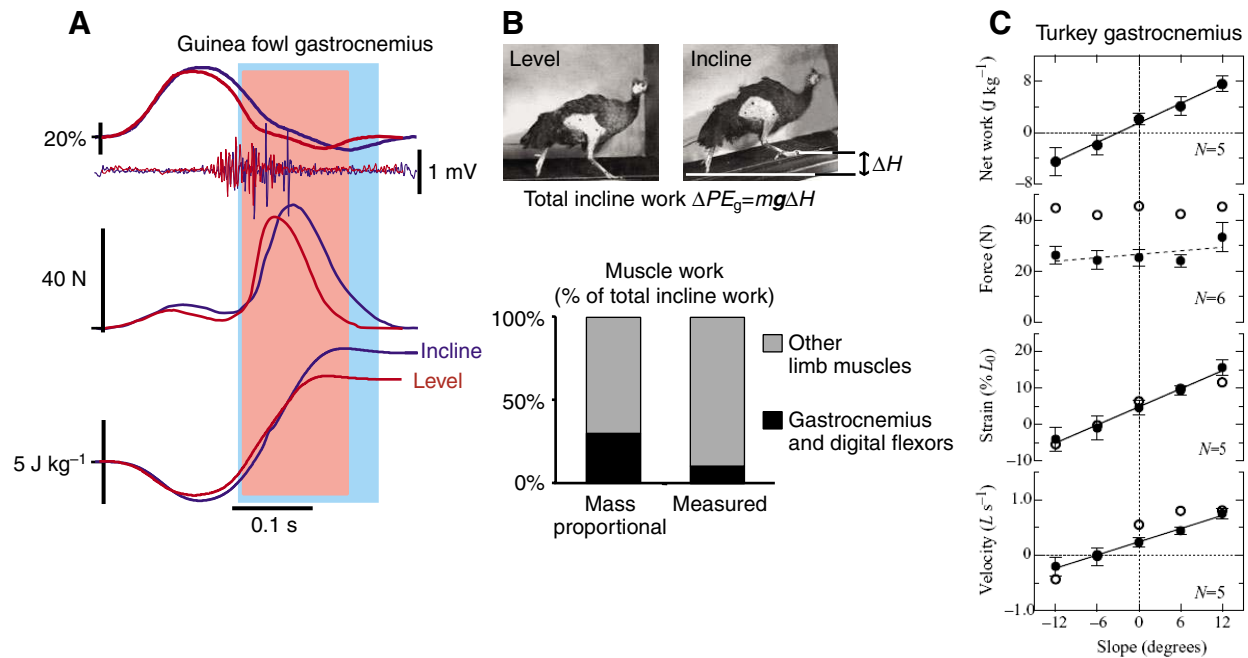
Fig. 5. Distal-limb muscle performance during running on a slope in guinea fowl (A,B) and turkeys (C). (A) Fascicle strain (*via* sonomicrometry), EMG and muscle–tendon force in the lateral gastrocnemius (LG) of guinea fowl during running on the level *versus* the incline. Although LG work output increases by increased fascicle shortening and force development on an incline, (B) total and mass-specific work performance of the LG (and digital flexors) is less than if each hindlimb muscle contributed work in proportion to its mass, and small compared to the whole-body work demand (see Daley and Biewener, 2003). (C) Patterns of fascicle strain, force and muscle work for the LG and peroneus longus (PL) of turkeys running on the level, incline and decline show that these muscles also modulate their mechanical work output largely by changes in lengthening *versus* shortening strain [part C was originally published in Gabaldón et al. (Gabaldón et al., 2004)]. In C, negative strain and velocity indicate lengthening, filled circles are averages over stance, and open circles are averages over the period of force production within stance.

How do muscle, limb and body dynamics change during non-steady locomotion?

Principles emerging from studies of steady level locomotion, such as simple spring-mass mechanics that explain body and leg dynamics of trotting, running and hopping gaits (McMahon and Cheng, 1990; Blickhan and Full, 1993; Farley et al., 1993), also appear to apply to the dynamics of stabilization. When animals encounter an unexpected force (Full et al., 2002; Jindrich and Full, 2002), a change in substrate compliance or damping (Fig. 7A,B) (Ferris et al., 1999; Moritz and Farley, 2003; Moritz and Farley, 2004), or a sudden change in terrain height (Fig. 7C,D) (Daley and Biewener, 2006), they use spring-mass dynamics to help passively stabilize their locomotor trajectory. These observations support the view that simple spring-mass dynamics serve as a template (Full and Koditschek, 1999) for understanding the mechanics and neuromuscular control of legged terrestrial locomotion. These principles of spring-mass function and common CoM mechanical energy patterns, which apply to all terrestrial gaits (Blickhan and Full, 1993; Cavagna et al., 1977; Farley et al., 1993; Geyer et al., 2006), also suggest that diverse running animals employ similar stabilizing mechanisms when perturbed. Nevertheless, animals that use a greater number of limbs will likely have increased running stability.

When impulsively perturbed, running cockroaches rapidly stabilize CoM roll, pitch and yaw moments, often within the period of support of the perturbed step (Jindrich and Full, 2002). This rapid adjustment suggests intrinsic stabilization *via* muscle–tendon and limb compliance and damping properties.

These intrinsic stabilizing properties, which reflect the inverse force–velocity property of muscle, have been termed 'preflexes' (Brown and Loeb, 2000). Although these occur prior to neural feedback *via* reflexes, they also apply throughout a neuromuscular response to a perturbation. The lateral stabilization of running cockroaches also exhibits spring-mass dynamics characteristic of a virtual lateral leg spring (Fig. 1D) (Full et al., 2002; Schmitt and Holmes, 2000). In addition to the vertical direction, running animals exhibit stable periodic motion of their CoM in the lateral direction when running. An impulsive perturbation that disrupts a cockroach's periodic lateral motion also disrupts its lateral (yaw) rotational velocity, body orientation and heading direction. Dynamical systems analysis reveals that the animal's lateral rotational velocity and body orientation are stabilized independent of neural reflexes, enabling the animal (and lateral leg spring-mass model) to establish a new stable heading direction (Schmitt and Holmes, 2000). This work shows the importance of simple spring-mass dynamics as an underlying principle of the control and stabilization mechanics of legged locomotion in both the lateral and vertical plane during running.

How are these body dynamics related to underlying limb, joint and muscle function? Recent analysis of the passive viscoelastic properties of the legs of cockroaches (Dudek and Full, 2006), based on a hysteretic model, reveal that the limbs exhibit both elastic and damping properties in the vertical direction, consistent with the vertical spring behavior observed during running. This behavior arises from the orientation of arthropod limb joints that
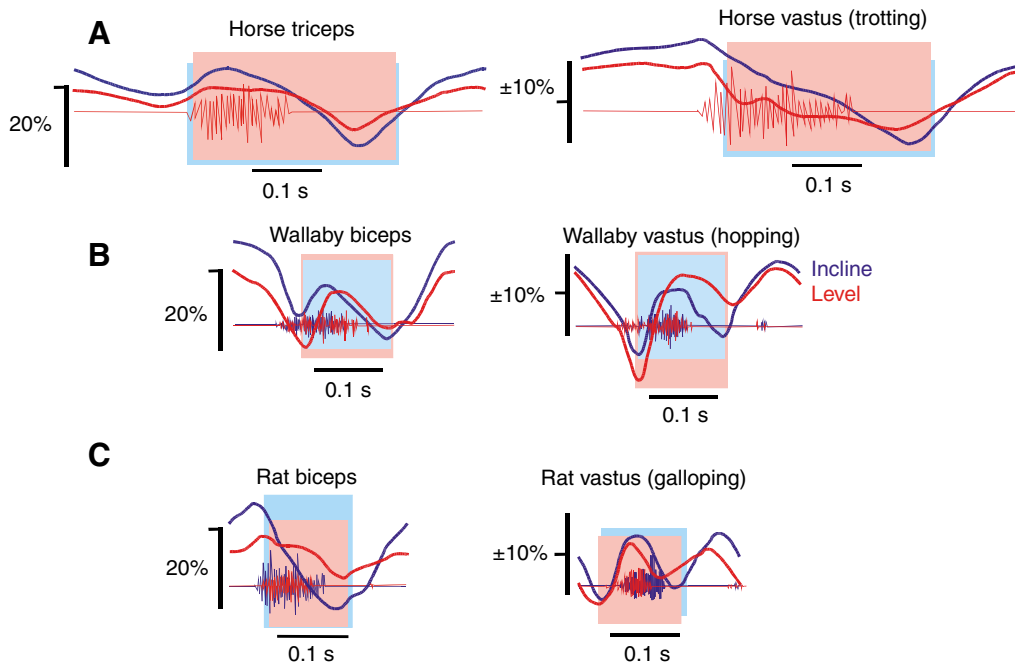
Fig. 6. Proximal muscle strain (bold lines) and EMG patterns (thin lines) recorded *in vivo* during level (red traces) *versus* incline (blue traces) locomotion for muscles of various animals (gait indicated in parentheses on right). Example patterns show increased shortening of the horse triceps and vastus (Wickler et al., 2005), the rat biceps (Gillis and Biewener, 2002) and wallaby biceps femoris (McGowan et al., 2007), as well as reduced net lengthening of the wallaby vastus, when moving on an incline. Stance duration is shown by the light red (level) and light blue (incline) shading. All muscles are displayed with the same fascicle strain and temporal scales. For fascicle strain traces, the tick on the scale bar indicates zero strain.

allow motion primarily in the vertical plane. However, studies to date do not show how underlying joint moments and muscle forces developed during running in arthropods act in response to perturbations and help to stabilize the animal.

To examine how underlying muscle forces and joint moments influence stabilization dynamics in bipeds, we (Daley and Biewener, 2006; Daley et al., 2006; Daley et al., 2007) have recently investigated the response of running guinea fowl to a sudden unexpected drop in substrate height, camouflaged by tissue paper to remove visual cues. This perturbation, equal to ~40% of the bird's hip height, results in a sudden loss of PE_g as the animal falls and extends its limb to make contract with the ground (force platform) below. These studies show that guinea fowl adjust limb mechanical function to stabilize their CoM dynamics in a posture-dependent manner (Fig. 7C,D, Fig. 8B,C). Depending on the initial contact angle of the limb on the ground (θ_o) and relative limb extension (L_o/L_T, ratio of initial stance limb length to maximally extended length), guinea fowl adjust the distribution and amount of net joint work that the limb performs. The knee joint plays a large role in determining the overall limb posture, but contributes little to the total energy production during stance (Fig. 9) (Daley et al., 2007). With a more extended knee, lower θ_o and greater L_o/L_T, the distal joints (ankle and tarsometatarsal, TMP, joints) absorb net energy, resulting in a net loss of total mechanical energy of the body during stance (Fig. 7D, Fig. 9B). However, if limb motion following tissue breakthrough results in a more flexed knee, more vertical θ_o and lower L_o/L_T, these distal joints act more as springs and net work during stance is positive (Fig. 7D, the hip joint produces positive work under all breakthrough conditions; Fig. 9B) (Daley et al., 2007). As a result, the decrease in body PE_g is converted into forward kinetic energy (KE), helping to stabilize the animal's motion.

Thus, we observed two modes for stabilizing the perturbed vertical motion of the body in running guinea fowl (Fig. 7D) (Daley et al., 2006). When the limb contacts the ground with a more vertical angle and the distal joints behaving as springs, PE_g is converted to KE, and the animal stabilizes by speeding up during the perturbed step (E_{KE} mode). This stability mode was observed most frequently (63% of trials). When the limb contacts the ground with a more extended knee and at a shallower limb angle, however, net energy absorption by distal joints results in net decrease in total body mechanical energy (E_{com} mode, 37% of trials), and the animal avoids speeding up. Interestingly, when the substrate drop was visible, guinea fowl had difficulty negotiating it, often stumbling and slowing down more to avoid falling. These results show that an animal's stabilization strategy is variable and context-dependent. Nonetheless, when confronted with an unexpected drop perturbation guinea fowl running performance was remarkably robust, with only one fall observed in total of 72 trials.

The ability of guinea fowl to stabilize their running by converting PE_g into KE, and speeding up, is consistent with the passive dynamics of a simple spring-mass system (Fig. 7C) (Daley and Biewener, 2006; Daley et al., 2006), which requires no net change in CoM energy over a full stride. However, the posture-dependent work performance of the distal joints suggests that variation in intrinsic mechanical factors and neural control sometimes results in altered work performance of the distal muscles.

Integrating mechanics and neural control for stability of non-steady locomotion

Up to this point we have focused primarily on mechanical aspects of locomotion in steady and non-steady tasks. However, accomplishing context-appropriate locomotor behavior in a complex environment requires integration of body, limb and muscle dynamics with reflex feedback and feed-forward neural control.

As we have noted, the body and limb of terrestrial animals are tuned to operate around a spring-mass template, which allows passive–dynamic mechanisms to facilitate a return to a
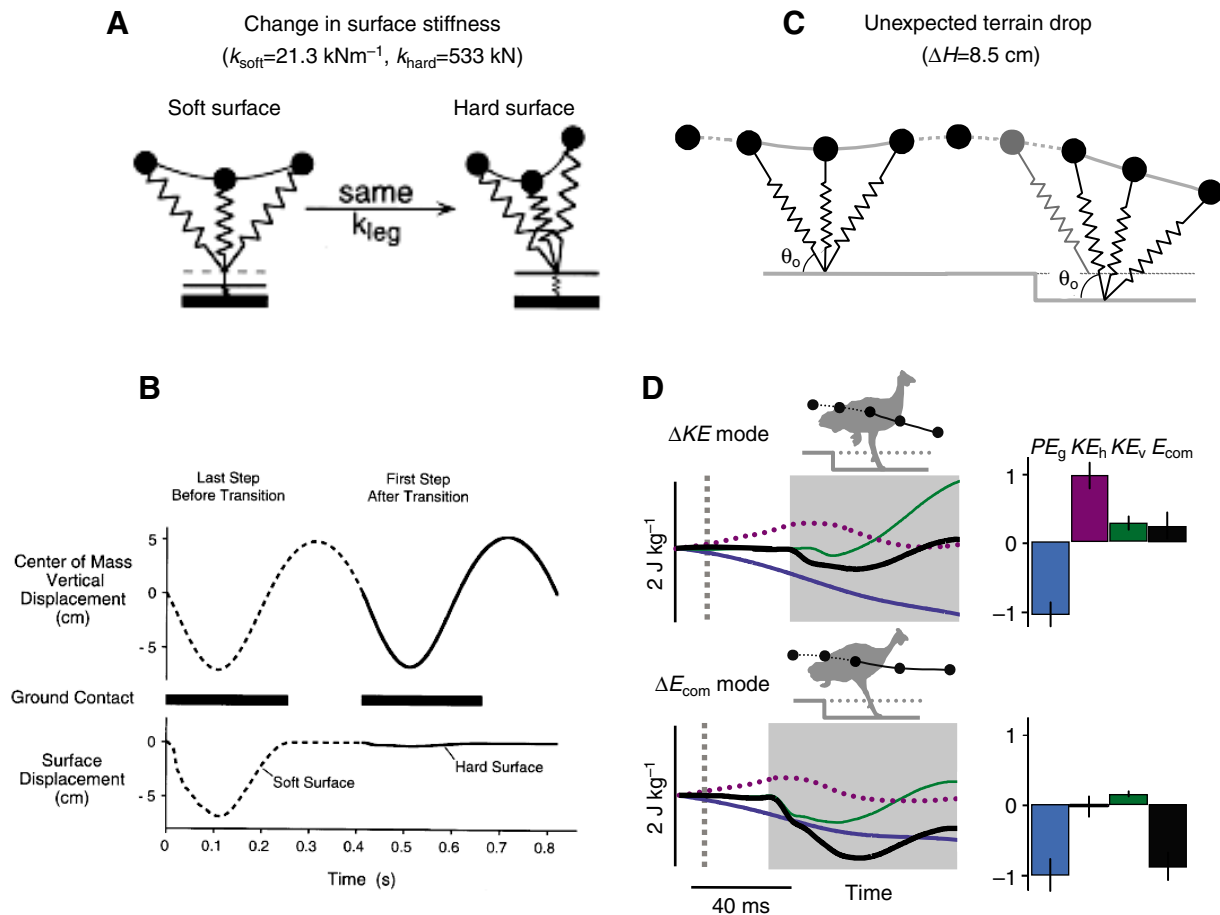
Fig. 7. Body CoM dynamics following perturbations in relation to spring-mass model dynamics. (A) Computer simulation of the spring-mass trajectory following a change from a soft to hard surface, with no change in leg stiffness (k_{leg}), resulting in an asymmetrical CoM path and a steep trajectory during take-off at the end of support. (B) Actual CoM vertical displacement of a human runner encountering an abrupt but expected change from a soft to hard substrate. The runner maintains similar (symmetrical) CoM motion by anticipating the change and adjusting k_{leg} within the first step (Ferris et al., 1999). (C) Computer simulation of the spring-mass trajectory following a sudden, unexpected drop in substrate height (40% of leg length). In the perturbed step, the only model value that differs from the level step is the limb contact angle (θ_o), which is steeper due to the backward motion of the limb before it contacts the ground (see also Fig. 8B). The angle used in the simulation was that measured experimentally from guinea fowl. (D) Actual CoM trajectory and energy changes of running guinea fowl following an unexpected drop in substrate height equal to 40% of leg length (PE_g, solid blue line; KE_v and KE_h, solid green and broken purple lines; E_{com}, total center of mass energy, solid black line). The broken vertical gray line indicates when the foot contacted the tissue paper 'false floor', and the gray box indicates the duration of stance. The bar graph (right) shows the net energy changes during the step (between the start and end of the traces on the left). Two response modes were observed: in most cases the body dynamics of the bird match the conservative spring-mass model (as shown in C), converting lost PE_g to forward KE (D, top graphs). In some cases, however, the limb muscles absorb net energy, decreasing the total body mechanical energy (E_{com}; D, bottom graphs). The different response modes are associated with different limb postures when the foot contacts the ground (Daley and Biewener, 2006; Daley et al., 2006).

steady locomotor trajectory following a perturbation (Ferris et al., 1999; Schmitt and Holmes, 2000; Full et al., 2002; Jindrich and Full, 2002; Daley and Biewener, 2006). Passive–dynamic control mechanisms (also called preflexive, intrinsic mechanical, or just intrinsic), can simplify control of locomotion. Intrinsic control mechanisms rely on the natural dynamics of the mechanical system as it moves through the environment, without the need for any explicit modification of muscle activity through neural pathways. Nonetheless, maintaining a spring-mass trajectory in the face of a changing environment often requires tuning of limb properties, including k_{leg} (Fig. 7A,B, Fig. 8A) (Ferris et al., 1999) and θ_o (Fig. 7C,D, Fig. 8B) (Daley and Biewener, 2006; Seyfarth et al., 2003).

Furthermore, muscles can produce or absorb energy to change E_{com}, allowing the animal to change velocity or body height. These adjustments in limb performance can occur both through intrinsic dynamics and through active neural control, including feedback and feed-forward modification of muscle activity. Furthermore, intrinsic mechanical and neural aspects of control are inherently linked because mechanical changes elicit proprioceptive feedback. Little is known about how these effects are integrated during natural locomotor behaviors to help stabilize and maneuver in complex environments.

Perturbation experiments help elucidate the interplay between intrinsic and neural control. Experiments that perturb terrain stiffness, viscosity or surface height have provided

Postural effects on intrinsic limb dynamics

A Unexpected change in surface stiffness

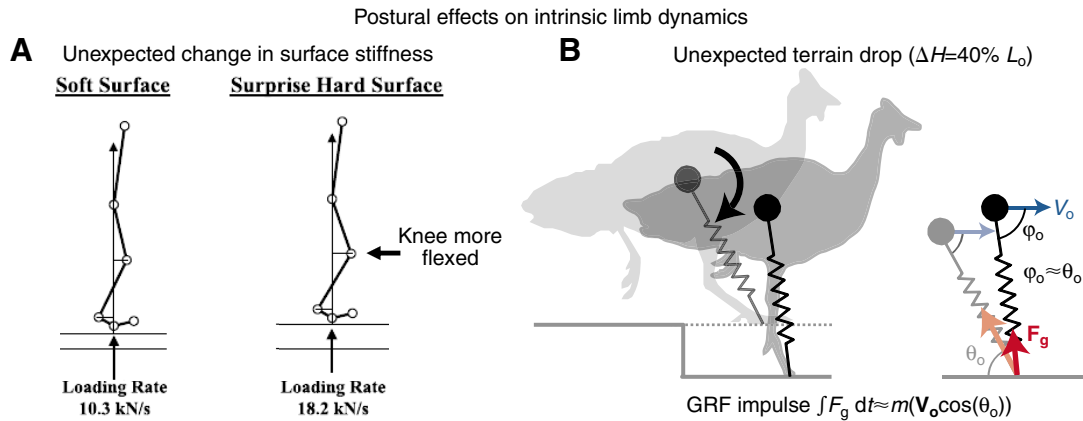**B** Unexpected terrain drop (ΔH=40% L_o)

Fig. 8. Postural influences on intrinsic limb dynamics following a perturbation. Intrinsic mechanical changes can simplify control and stabilization of running dynamics, because these mechanisms rely on the natural dynamics of the body and limb interacting with the environment, without the need for altered muscle activation through central or reflex neural pathways. (A) Following an unexpected change in substrate properties during hopping in place, humans exhibit an intrinsic decrease in limb stiffness (k_{leg}) due to increased flexion of the knee in response to rapid limb loading (Moritz and Farley, 2004). (B) Upon encountering an unexpected drop in terrain height, guinea fowl exhibit an intrinsic increase in limb contact angle (θ_o) due to the normal backward motion of the limb during late swing phase just prior to ground contact (to match foot and ground speed). If the limb acts as a simple compression spring, limb loading (and ground reaction force) depends on the angle between the limb and the bird's velocity (φ_o). The backward motion of the limb in the drop step results in altered geometry as shown, which is associated with an intrinsic decrease in the ground reaction force impulse over stance (the time integral of force, $\mathbf{F_g}$), due to decreased peak force and shorter contact duration. These dynamics are consistent with the spring-mass model (Daley and Biewener, 2006).

insight into how intrinsic mechanical and neural mechanisms are coordinated. Limb posture plays a crucial role in stabilization through the intrinsic mechanical response to a perturbation. Adjustment of limb posture to a more crouched (flexed joint) or upright (extended joint) stance changes the effective mechanical advantage, or gearing, of limb muscles (Biewener, 1989; Carrier et al., 1994; Biewener et al., 2004a) and intrinsic limb stiffness (Fig. 8A) (Moritz and Farley, 2004). The normal backward motion of the limb during late swing phase just before foot contact, to match foot and ground speed, also leads to automatic adjustment of θ_o in variable terrain (Fig. 8B,C) (Daley and Biewener, 2006; Seyfarth et al., 2003). This simple mechanism alters leg-spring loading (Fig. 8B) (Daley and Biewener, 2006), facilitating rapid stabilization following a sudden change in substrate height.

Changes in limb posture are mediated through a combination of feed-forward and intrinsic mechanical mechanisms. Muscles are activated in a feed-forward manner in anticipation of the stance phase of locomotion (Figs 2, 3 and 9). When the interaction with the ground suddenly changes, feed-forward muscle activation and intersegmental dynamics lead to altered joint angles (Fig. 8A and Fig. 9) (Daley et al., 2007; Patla and Prentice, 1995; Moritz and Farley, 2004). The resulting change in limb posture leads to altered limb stiffness, limb loading and whole body dynamics (Moritz and Farley, 2004; Daley and Biewener, 2006).

Additional intrinsic mechanical effects result from the nonlinear and time-varying mechanical properties of muscle tissue. Muscle force production depends on a number of mechanical factors, including instantaneous length and velocity, as well as recent work history (reviewed by Josephson, 1999). These intrinsic properties of muscle tissue can provide inherent stabilization following a perturbation (Brown and Loeb, 2000).

Muscle–tendon architecture is also likely to influence a muscle's intrinsic mechanical response to a perturbation. Because in-series tendon elasticity decouples muscle fiber shortening and joint excursion, muscles with long, compliant tendons facilitate elastic energy cycling and economic force production at the expense of direct control of joint position and work (Biewener and Roberts, 2000; Alexander, 2002; Roberts, 2002). Additionally, tendon elasticity could either amplify or buffer a perturbation's effect on muscle fascicle strain, depending on whether the disturbance occurs when the muscle fascicles are passive or actively contracting at high stress. If a perturbation occurs when the muscle is passive or at low force (for example an obstacle encountered at the initiation of stance), most of the angular excursion at a joint will likely occur in the muscle fascicles (fascicles being less stiff than the tendon). This could dramatically alter the subsequent active force–length dynamics of the muscle. In contrast, if a perturbation occurs when the muscle is already actively developing high force (such as a sudden drop in terrain in the middle of stance), much of the angular excursion at a joint could occur through tendon stretch or recoil (fascicles being more stiff than the tendon, so length change occurs mainly in the tendon). If a perturbation leads to large changes in muscle fascicle length or velocity, it will likely result in dramatic changes in the force and energy output of the muscle, due to its intrinsic tissue properties. Consequently, changes in limb posture near the onset of force production, when muscle force is low, will likely have a larger effect on the length and contractile dynamics of the muscle fascicles.

Because muscle–tendon architecture likely influences a muscle's sensitivity to external perturbations, as discussed above, muscles with substantial in-series elasticity are likely to exhibit high sensitivity to perturbations that occur at low muscle force and low sensitivity to perturbations at high muscle force. Muscles with little in-series elasticity, however, will exhibit relatively constant sensitivity to perturbations. The proximo-
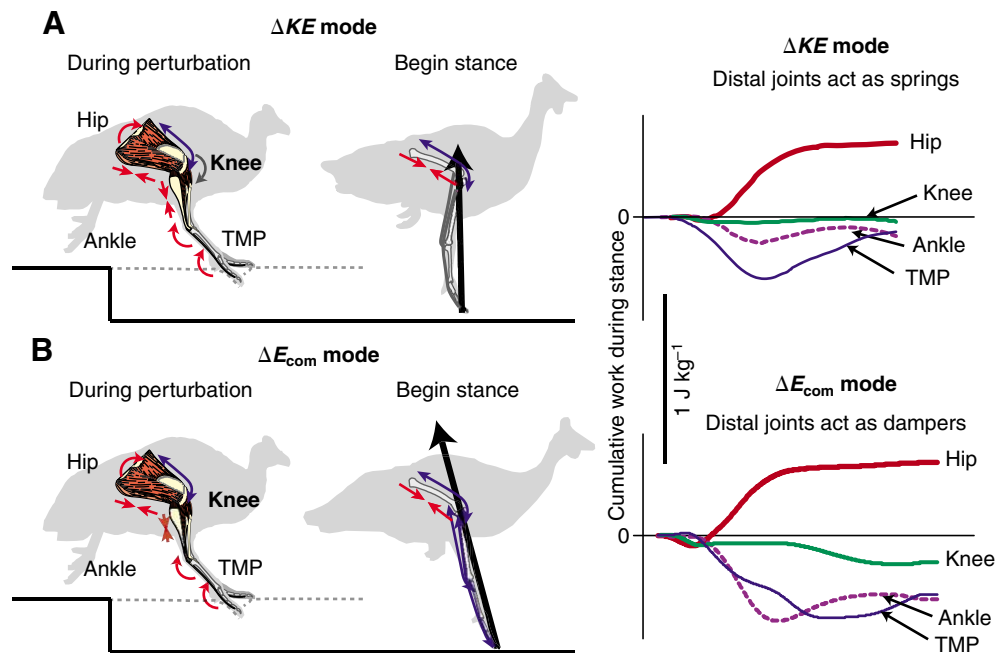
Fig. 9. The left panel schematically illustrates the hypothesized interplay between feed-forward muscle activation and intrinsic mechanical effects during running over a terrain drop (solid line) perturbation. Arrow color and direction conventions are the same as in Fig. 4. (A) Activation of muscles in anticipation of stance results in extension of the hip, ankle and TMP joints upon tissue paper (dotted line) contact. Depending on the balance among multiarticular muscles at the knee joint, the knee either flexes (A) or remains relatively extended (B). This alters limb posture and limb loading at ground contact. When the knee is flexed and θ_o close to vertical (A), limb loading is low, and the distal joints act as springs (purple and blue cumulative work curves for the ankle and TMP joints absorb with low net work output). When the knee is relatively extended and θ_o is lower (B), limb loading is greater, and the distal muscles undergo stretch, resulting in net energy absorption (blue arrows for distal muscles, and negative cumulative work for the ankle and TMP joints). In contrast the hip behaves uniformly, producing energy, as if the hip extensors are under feed-forward control and insensitive to perturbations. The knee does little net work under either condition. We hypothesize that variation in the breaking force of the tissue paper results in altered distal muscle contraction dynamics during the perturbation (on left, greater and lower distal muscle work production in A and B, respectively), leading to altered stance phase limb posture and dynamics

distal distribution of muscle–tendon architecture discussed above (Figs 4 and 9) also suggests a similar gradient in the perturbation response of the limb muscles. In particular, we predict that the perturbation sensitivity of proximal muscles will be relatively low and less variant with muscle contractile state, whereas the perturbation sensitivity of distal muscles will be especially high at low force (such as at the initiation of stance) due to amplified intrinsic mechanical effects. The high perturbation sensitivity of distal joint mechanics of guinea fowl during the unexpected drop experiments are suggestive of this architectural principle (Daley et al., 2007). However, these ideas remain to be directly tested in more controlled experimental settings.

Multiarticular muscles likely play a key role in integrating neural and intrinsic control mechanisms, yet the details of how this plays out remain largely speculative and should be addressed by future research (Figs 4 and 9). Because the force and displacement of multiarticular muscles relate to the torques and angular excursions of multiple joints, their performance is likely to be especially sensitive to the configuration and loading of the limb. Most of the distal limb muscles are multiarticular; thus, the high sensitivity of distal joint mechanics to limb posture supports this idea (Daley et al., 2007). Multiarticular muscles also transfer energy between joints (Bobbert et al., 1986; Prilutsky et al., 1996; McGowan et al., 2007).

Consequently, their altered force–length behavior in response to changing mechanical environment could influence the distribution of energy among the joints, even if they exhibit relatively little change in total muscle energy output. Thus, we believe that further research will show that multiarticular muscles play a key role in redistributing force and energy among the joints and muscles of the limb in response to perturbations.

Intrinsic mechanical effects must be tightly integrated with reflex feedback. Due to neural transmission and electromechanical delays, the immediate response of the musculoskeletal system depends entirely on intrinsic mechanical properties, including force–length, force–velocity and history-dependent properties of muscles, and postural effects on joint dynamics. Nonetheless, reflex feedback follows with a short delay and can contribute to further stabilization within a single stance phase (Hiebert and Pearson, 1999; Nichols and Houk, 1973). Both stretch (from muscle spindles), and force (from Golgi tendon organs) feedback contribute to locomotor control (reviewed by Pearson, 1995). However, the relative effects of intrinsic mechanics, stretch feedback and force feedback likely depends on the speed of locomotion. Due to shorter mechanical delays, force feedback might improve locomotor stability over stretch reflex feedback, especially at higher speeds. Evidence suggests that positive force feedback

plays a key role in the control of stable locomotion (Geyer et al., 2003; Pearson, 1995). At high locomotor speeds, intrinsic mechanical effects are likely to play a predominant role in control, because feedback delays could be destabilizing. Indeed, reflex gains tends to be reduced with increasing speed of locomotion (Capaday and Stein, 1987). Thus, the intrinsic mechanical stabilization mechanisms we have highlighted likely play a predominant role in fast locomotion, such as running and galloping. However, sensorimotor reflexes and higher brain centers likely play a substantial role in stabilizing slower gaits, such as walking (e.g. Marigold and Patla, 2005; Marigold and Patla, 2007).

Future work

The work examined here points to the need for further studies of terrestrial locomotion that integrate whole body and limb dynamics with the contractile function of individual muscles. *In vivo* studies of individual muscles are valuable for testing hypotheses about design and function of muscle–tendon elements in the limbs of animals. However, because many muscles are activated to execute locomotor movements and muscles often span two or more joints, an understanding of their functional integration within the limb as a whole will benefit from being linked to studies of joint, limb and whole body dynamics. Much of the work to date has focused on muscle synergists that function to support and move the animal during limb support. Nevertheless, the role of antagonist muscles for joint and limb stabilization also needs to be considered in relation to muscle synergists that are active during limb support. The interaction of antagonist muscles for controlling joint motion and overall body dynamics is likely to be particularly critical when animals negotiate obstacles more slowly or are perturbed from steady movement. To date this issue has received scant attention, beyond studies of EMG and limb kinematics.

A theme emerging from studies of steady level terrestrial locomotion and more recent studies involving various sudden perturbations is that a simple spring-mass template can explain much of the behavior of the limb and body as a whole. Not only does this model help to explain how terrestrial animals economize their movement during steady locomotion, it also serves as a framework for understanding how animals simplify the control problem of stabilization. Intrinsic force–length and force–velocity muscle properties also help to simplify the problem of control, yet both are clearly linked to subsequent neural reflex mechanisms.

Given the complexity of reflex effects on locomotion, and the nonlinear nature of limb and muscle contractile dynamics, there is a substantial need for further research to investigate how intrinsic mechanical effects and reflex feedback are integrated during natural movements.

It is well known that reflex contributions to the control of movement are highly context-dependent (Pearson, 1995; Zehr and Stein, 1999). Each muscle also receives a unique combination of reflex inputs depending on its unique set of actions and muscle synergies (Nichols, 1994). Given the complexities of the neuromuscular system, an integrative biomechanics approach is required to understand its design and control features in relation to movement; one that combines analysis of behavior, whole body dynamics, inverse dynamics analysis of joint mechanics, and *in vivo* measures of muscle performance. Computational modeling approaches will likely become increasingly important for formulating and testing hypotheses about control strategies for stable and agile locomotion.

A challenge for studying non-steady locomotion and the neuro-musculoskeletal principles that guide its control is the inherent variability of these behaviors. Again, understanding how animals contend with the more variable conditions of non-steady movement depends on recognizing that the biomechanics and neural control of such movements is context-dependent. Different responses for achieving stability will apply, depending on the initial conditions of the animal's physical interaction with its environment. Studies conducted to date suggest that postural effects are key to establishing the initial conditions that govern an animal's stability response. It is interesting that simple kinematic features of limb movement and changes in posture appear to govern the distribution of work within the limb and the contractile function of muscles underlying this, influencing the manner in which they are activated and controlled.

List of symbols

CoM	body center of mass
θ_o	initial contact angle of the limb on the ground
L	limb length
L_o/L_T	relative limb extension
PE_g	gravitational potential energy
KE_v	vertical kinetic energy
KE_h	horizontal kinetic energy
E_{KE}	mode
E_{com}	center of mass energy
m	point mass
k_{leg}	leg stiffness
H	height
$\mathbf{V_o}$	bird's velocity
$\mathbf{F_g}$	ground force

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