Running birds, humans and robots:
Principles of leg control for robustly stable and agile bipedal locomotion

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Birds are diverse and agile vertebrates with exceptional ecological range, capable of many combinations of aerial, terrestrial, and aquatic locomotion. Although birds are most noted for flight, birds are among the most agile terrestrial bipeds, with a 230-million-year evolutionary legacy from theropod dinosaurs. Consequently, ground birds such as guinea fowl serve as useful animal models to study the integration of mechanics and neuromuscular control for bipedal locomotion [1]. In this talk, I will review my lab's research using terrain perturbations, in vivo recordings of muscle dynamics and integrative biomechanical analysis to reveal neuromechanical control strategies for robust, stable and agile locomotion (Fig. 1). We focus on revealing fundamental principles that can be applied in the design and control of bio-inspired robotics and human-assistive devices.

Bipedal animals must precisely control limb-substrate interactions to move effectively over varied terrain while avoiding falls, collisions and injury. A key challenge for animal movement is sensorimotor delay that inherently limits feedback response time. Delays have likely shaped the evolution of animal sensorimotor control mechanisms, leading to strategies that exploit inherently stable intrinsic mechanics and simple control heuristics. Biomechanics studies of perturbation recovery and transient maneuvers can help reveal these control mechanisms. We are particularly interested in revealing how birds integrate intrinsic mechanics with predictive (feedforward) and reactive (feedback) control to achieve agile bipedal locomotion.

Previous studies of steady level and incline locomotion highlighted a division of neuromechanical function among limb muscles, with large, parallel fibered muscles in the proximal limb enabling power and large joint excursions, and short-fibered pennate muscles in the distal limb facilitating economic weight support and tendon elastic energy cycling (Fig. 2) [2-3]. Differences in function arise from the proximo-distal gradient in muscle–tendon architecture that is apparent within the limbs of terrestrial vertebrate animals (Fig 2). However, little is known about how these differences in muscle-tendon architecture influence neuromechanical function for non-steady locomotor tasks, such as perturbation recovery and navigating uneven terrain.

Experiments in guinea fowl running over an unexpected 'pothole' (a sudden drop in terrain height) revealed rapid intrinsic mechanical responses that facilitate disturbance rejection and stable recovery [4-5]. Inverse dynamic analysis of joint mechanics (Fig. 3) and *in vivo* measures of muscle-tendon dynamics, revealed that distal limb muscles rapidly change force-length dynamics and work output in response to altered leg posture and loading, which stabilizes gait [6-7]. We have compared *in vivo* force-length dynamics of distal leg muscles during locomotion over: 1) steady level terrain, 2) constant incline 3) unexpected drops in terrain, and 4) periodically repeating obstacles [2,6-8]. These studies revealed that distal leg muscles are inherently sensitive to changes in leg posture and loading, due to intrinsic mechanical effects and rapid proprioceptive feedback. The findings suggest that the pennate architecture and compliant tendons of distal muscles facilitate rapid stabilization.

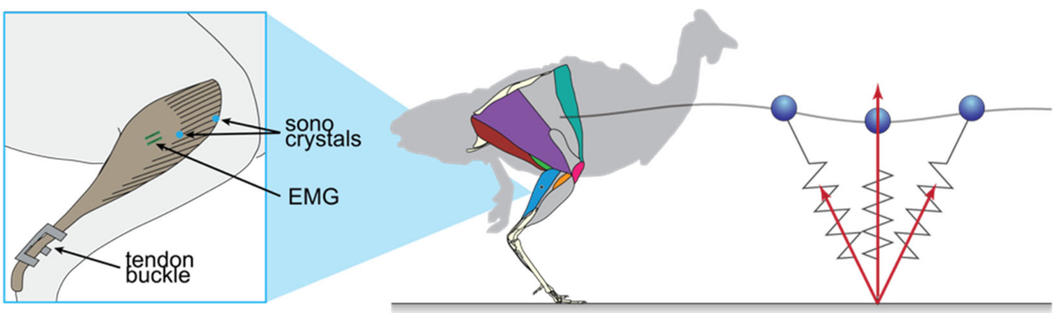

Figure 1. Experimental measures of in vivo neuromuscular function, limb biomechanics and whole-body gait dynamics help reveal principles for effective integration and coordination of mechanics and control for agile locomotion.

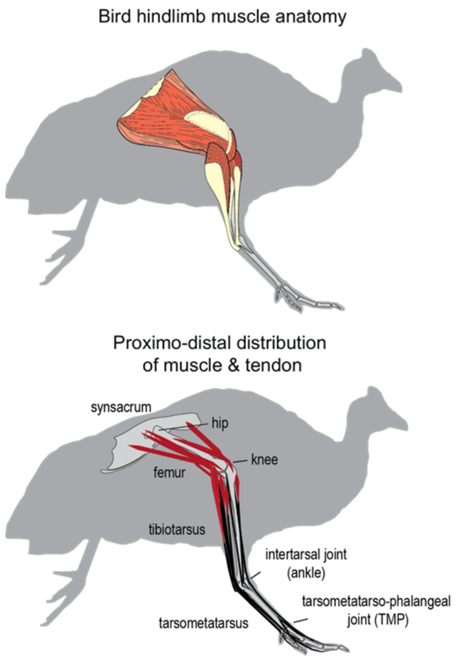

Figure 2: Guinea fowl hindlimb muscle anatomy, highlighting the proximo-distal gradient in musculoskeletal structure. Powerful muscles are located proximally at the hip and knee, with the distal joints controlled by a network of compliant tendons.

Biomechanical analysis and simulations of simple theoretical models has further revealed that intrinsically stable running dynamics of ground birds can be approximated by a point mass-model with a 1) an intrinsically damped and compliant leg, 2) clock-like feedforward leg angular cycling at the hip, and 3) rapid adjustment of leg-length actuation in late stance to rapidly adjust stance-push off, stabilizing body mechanical energy. This simple model can achieve robust stability over uneven terrain with a 2-3 step recovery from large perturbations. The recovery dynamics of this simple model match well with experimentally measured running dynamics [9-11].

Further experiments and model analysis have confirmed the role of the hip-driven feedforward control of leg angular cycling for regulating gait timing and leg loading in uneven terrain [9-10]. Following in initial 'unexpected pothole' terrain perturbation experiments, we investigated how birds optimize leg control depending on the type of perturbation (pothole, step, obstacle), visibility of terrain, and with ample practice negotiating terrain features [8,10].

We discovered several control strategies used by birds consistently across terrain contexts: (1) independent control of leg angular cycling and leg length actuation, achieved through the proximo-distal gradient in limb function, which facilitates dynamic stability through simple control mechanisms, (2) feedforward regulation hip-driven leg cycling rate, which tunes the foot-contact dynamics to maintain consistent leg loading in uneven terrain, minimizing fall and injury risks, (3) load-dependent muscle actuation at the distal limb joints, which rapidly adjusts stance push-off and stabilizes body mechanical energy, and (4) multi-step recovery strategies that allow body dynamics to transiently vary while tightly regulating leg loading to minimize risks of fall and injury.

Finally, I will discuss some similarities and differences between human and avian bipeds, which highlight different solutions to the problems of locomotor stability and sensorimotor delay. In on-going work, we are investigating how sensorimotor mechanisms are integrated and adapted across multiple time-scales to achieve balance during transient maneuverers. The principles revealed from studies of bipedal neuromechanics can directly inform control policies for to bio-inspired robots and human-assistive devices to enable robustly stable and agile locomotor dynamics.

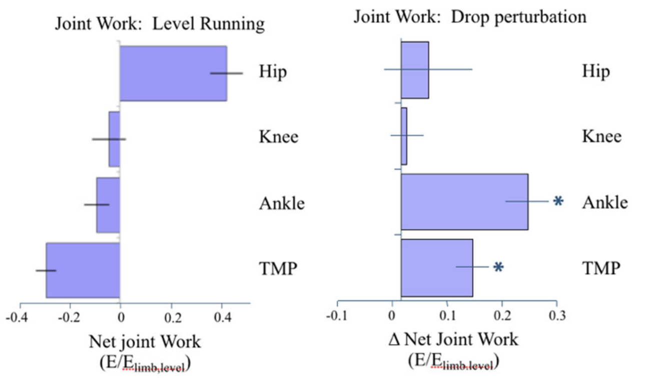

Figure 3. *Left*: Joint work contributions to whole limb mechanical work during level running reveal a proximo-distal distribution with positive work produced at the hip, and energy absorbed by the distal joints. *Right*: Changes in joint work in response to a sudden terrain drop are relatively greater at the distal ankle and TMP joints, reflecting greater sensitivity and responsiveness to foot-substrate interactions.

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