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A7 — INTEGRATION OF ACTIVE AND PASSIVE CONTROL MECHANISMS IN LOCOMOTION

A7.1
13:30 Tuesday 30th June 2009
Hierarchy in the motor system simplifies the task of motor coordination: Neural and architectural mechanisms of force distribution

Richard Nichols (Georgia Institute of Technology)

By virtue of the hierarchical design of the motor system, the control of coordination is distributed to the brain, spinal cord and the architectural features of the musculoskeletal system. Force feedback forms one such coordinating network in the spinal cord. Positive force feedback is mainly autogenic and increases muscular and limb stiffness and promote propulsion during locomotion. In contrast, intermuscular, inhibitory force feedback in principle increases limb compliance and promotes interjoint coordination. Experiments in cats suggest that during walking uphill, positive force feedback is more broadly distributed than in level walking. During walking downhill, where muscles serve a braking function and the interaction with the ground can be destabilizing, inhibitory force feedback predominates and controls the interaction between the body and the ground. Therefore, force feedback is subject to neural modulation according to the context of motor control. Deep fascia provides an architectural mechanism to promote coordination. Fascia distributes muscular forces outside of tendons and aponeuroses and provides an additional route for mechanical feedback. Force transmission through fascia depends on the state of activation of the muscles to which it is attached. Acute disruption of the crural fascia in the stepping premammillary cat results in a loss of stability, particularly in the mediolateral direction. The affected limb tends to wander more widely during treadmill stepping. Given the problem of controlling endpoint forces with muscles that cross different axes of rotation and joints, fascia appears to constrain these degrees of freedom and therefore simplifies motor coordination.

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A7.2
14:30 Tuesday 30th June 2009
What does a motor spike mean? Interpreting the causal efficacy of neural feedback during locomotor control tasks

Simon Sponberg (University of Washington)

Perturbation studies during extremes of locomotion have established the efficacy of neural and mechanical strategies for control. Yet for the vast majority of locomotor behaviors both neural feedback and mechanics will significantly impact stability and maneuverability. Therefore, a central challenge in neuromechanics is revealing how mechanics conditions the translation of neural feedback to dynamic output. Using a novel method for real-time re-writing of muscle activation patterns, we can repeatedly enforce simulated neural feedback to individual motor units in freely behaving animals. In conjunction with high speed videography and animal-mounted inertial sensors, we can reveal the control potential specific patterns of neural feedback have on body dynamics. Using the cockroach, *Blaberus discoidalis*, a model terrestrial insect runner, we show that comparable patterns of neural feedback to a single muscle can have highly variable control effects when the mechanical context is changed. Muscle work loop experiments illustrate how these variable control potentials arise from changes in muscle function. In this case, a positive mechanical feedback loop between muscle strain and force development enables a transition in muscle function from primarily absorbing energy to having a significant period of positive work. To complement the above approach, we consider the use of information measures between neuromuscular signals and dynamic output variables. We use this approach to test which output variables are most precisely determined by specific patterns of neural feedback. Integrating the *in vivo* control potential of neural feedback with an *in situ* mechanistic understanding of muscle function is critical for interpreting neuromechanical control strategies.

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A7.3

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Translating neural control to behavioral output: insights from insects and humans

Anna Ahn (Harvey Mudd College California)

The musculo-skeletal design of insects and humans can be used as model systems for studying the neuro-mechanics of locomotion. The cockroach leg, in particular, provides an elegant natural experiment, because a single motor neuron innervates two extensor muscles operating at the same joint. *In situ* measurements under *in vivo* running conditions showed muscle 178 neither produced nor absorbed net mechanical energy per cycle, while muscle 179 absorbed 19 W kg^{-1} per cycle. The insect provides a model system where the same neural control results in variable mechanical output. Humans, in contrast, have been shown to use variable motor recruitment during walking. In a sedentary group of subjects, the variability in neural control of the calf muscles was correlated with walking kinematics and limb morphometrics. Half of the sedentary group walked while activating their medial gastrocnemius (MG) muscles more strongly than their lateral gastrocnemius (LG) muscles during the majority of walking speeds (MG-biased). The other half of the subjects walked while activating their MG and LG muscles nearly equally (unbiased). The MG-biased walkers also exhibited larger MG muscles and shorter heels, or shorter MG moment arms about the ankle compared to that of the unbiased walkers. Walking kinematics, height, weight, lower leg length, and foot size did not differ between the two groups. The relatively less plastic skeletal system seems to drive the motor recruitment patterns of walking as well as calf muscle size in humans where variable neural control results in the same mechanical output.

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A7.4

16:10 Tuesday 30th June 2009

Neuromechanical interaction during locomotion : Bipedal gait transition as a paradigm

Veerle Segers (Ghent University)

The study of the transitions between terrestrial gaits (walk, run/trot, gallop) when increasing the speed of locomotion is paradigmatic in the context of the control of voluntary movements. For a long time it was believed that the control of voluntary movements was regulated by the nervous system planning future actions by sending appropriate motor programs to the muscular system activating the appropriate motor program (e.g. walking or running). In this so-called 'central programming approach' gait transitions reflect switches between different neural programs. Over the last decades, however, biomechanical research results in the finding that the intrinsic characteristics of the locomotor system and the physical environment also determine how coordinated movement patterns emerge, the *neuromechanical interaction*. The passive mechanical features of the musculo-skeletal and environmental components (e.g. inertial properties and dimensions of body segments, visco-elastic material properties, etc…), the instantaneous dynamical status of the multi-segmented body in its environment (speed and acceleration), and the intrinsic dynamics of the physiological processes at the neuro-muscular level transform simple neural commands into complex, coordinated, stable locomotor patterns. Translated to the context of gait transitions, this view implies that the biomechanical properties and the dynamics of the multi-segmented body (in interaction with the environment) automatically generate (abrupt) transitions when the gradually changing locomotor speed (i.e. the control variable) exceeds specific threshold values. This is the viewpoint of the 'dynamic system approach' on gait transitions.

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A7.5

16:40 Tuesday 30th June 2009

Modelling the interplay of central pattern generation and sensory feedback in the neuromuscular control of running

Monica A. Daley (Royal Veterinary College), Ludovic Righetti (EPFL Swiss Federal Institute of Technology), Auke Jan Ijspeert (EPFL Swiss Federal Institute of Technology)

The balance of feedforward (clock-like) versus feedback (sensory reflex mediated) control may have important impact on running stability in animal locomotion: a completely feedforward strategy might not adapt properly to altered terrain, but a completely feedback strategy might be unstable due to system delays. This study investigates how animals integrate feedforward central pattern generation (CPG) with sensory feedback in the neuromuscular control of running. To approach this problem, we use neuromechanical models to predict muscle activity during running, and test predictions against in vivo measurements of muscle activity. The goal is to determine the simplest neural model that is consistent with experimental observations across a range of running conditions. Initial models consist of a single neural oscillator (with independent swing and stance frequencies) coupled to reflex feedback (muscle-tendon force, fascicle length, fascicle velocity). The CPG-reflex coupling rules (gain, polarity) can differ in stance and swing. The models have been trained on *in vivo* muscle data on guinea fowl hindlimb muscles, using a parameter search and optimization algorithms to determine the relative contribution of feedforward and feedback and the CPG-reflex coupling rules that best predict stride-to-stride variability in muscle activity. This approach has resulted in several competing models that predict level running EMG patterns well (cross-correlation >0.80, with a time-lag $<5\%$ of stance period). Each of these models makes different predictions for how EMG patterns should change with altered feedback. In continuing work we will test each of these models against experimental data over a range of speeds and uneven terrain conditions.

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A7.6

10:30 Wednesday 1st July 2009

Biomechanical imperatives in the neural control of locomotion

Arthur Prochazka (University of Alberta), Craig Sorensen (University of Alberta)

The neural control of locomotion involves an interplay between a central pattern generator (CPG) and sensory input. Recent work suggests that the CPG oscillator is pre-set to produce the long extensor and short flexor phase durations of the step cycle characteristic of normal locomotion. Neuromechanical modeling indicates that these durations are predicated by the biomechanics

(Prochazka and Yakovenko 2007). We posit that descending input from higher centers continually adjusts the drive to the CPG oscillator according to the anticipated biomechanical outcomes. When the predictions are good, CPG-generated phase durations closely match those of the evolving kinetics and kinematics, and little or no sensory adjustment occurs. When the predictions are less satisfactory, sensory input triggers phase-switching according to identifiable rules, adjusting the duration of each phase and thereby maintaining biomechanical stability. Sensory input also modulates motoneuronal activation through stretch reflexes, which contributes to stability. One puzzling feature of the modeling so far has been the tendency for the velocity of locomotion of a particular modeled "animal" to stabilize to a given value. Recently we found that by using velocity as the command signal to modulate muscle activation as well as the timing elements of the CPG oscillator, a large range of locomotor velocities and cadences could be achieved, matching the range seen in real animals. We suggest that velocity is the elusive "controlled variable" underlying the neural control of mammalian locomotion.. Predictive and reactive tuning of the locomotor CPG. Integrative and Comparative Biology 47: 474-481, 2007.

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A7.7

11:30 Wednesday 1st July 2009

Mechanical motives to gallop at higher speeds (Supported by DARPA Biodynotics)

Ivo G. Ros (Harvard University), Andrew A. Biewener (Harvard University), David V. Lee (University of Nevada Las Vegas), Jennifer Anttonen (Harvard University), Trevor E. Higgins (Harvard University)

During steady locomotion, energy that is lost during each stride needs to be regenerated. Walking quadrupeds conserve mechanical energy by exchanging center of mass (CM) gravitational potential and kinetic energy (KE). In trots, energy losses are reduced by elastic strain energy storage and consequent release. It is generally believed that galloping is energetically advantageous to trotting at higher running speeds. To enhance our understanding of the underlying mechanics for this change in gait, we contrasted the interactions of the whole body ground reaction force (GRF) and CM between trotting and galloping. Dogs steadily galloped and trotted over four adjacent force platforms while we simultaneously recorded 3D body and limb kinematics. In trot symmetrical placement of the diagonal leg couplets leads to increasing horizontal KE fluctuations with speed. In contrast, during gallop GRFs of the fore legs act in front of the CM, while the hind legs act behind the CM. This configuration produces torques about the CM that add rotational KE to the body. The resulting oscillating pitch rotations allow for CM mechanical energy to be directed more vertically. As a consequence, galloping dogs travel with more vertically oriented GRFs and more uniform horizontal speeds than would be expected for trots at similar speeds. Our results support the hypothesis that galloping utilizes the energy saving mechanisms found during both walking and trotting. Surprisingly, however, the rotational KE fluctuations are responsible for allowing these energy saving mechanisms to occur in concert during the fastest quadrupedal running gait.

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A7.8

11:50 Wednesday 1st July 2009

From neuromechanics to robot controllers: Bio-inspired design

Shai Revzen (University of California at Berkeley), Robert J. Full (University of California at Berkeley)

Despite vast differences in posture and morphology, legged animals can be modelled by a neural clock coupled to a mechanical oscillator comprising a mass atop a single, virtual leg-spring. These controllers restrict animal dynamics to behaviour-specific, low-dimensional manifolds we term templates, thereby simplifying control. Neuromechanical control architectures can be classified based on whether or not there is an independent neural clock state, whether stability is governed by neural or mechanical feedback, and whether the clock is affected by feedback. An assay of perturbation experiments can decide among the competing architectural hypotheses by examining kinematic phase — an estimate of phase obtained from the kinematic state of the body. Sprawl postured running insects are ideal subjects for this study, as they provide considerable kinematic information from multiple legs oscillating in a plane. By using a suite of controlled perturbations applied to running insects that include hurdles, lateral impulses, substrate stiffness changes, and added mass and moment of inertia, existing neuromechanical control hypotheses can be identified, new architectures proposed and quantitative model predictions tested. These methods open a new frontier of biomechanical research by allowing meaningful control hypotheses to be tested by simple kinematic data collection. Drawing on dynamical systems and developing novel tools for data analysis provides a new paradigm for mutualistic interchange between biology and robotics and the interplay of mechanical and neural control.

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A7.9

13:30 Wednesday 1st July 2009

Decoding the mechanisms of gait transition in the salamander using robots and mathematical models

Auke Ijspeert (Swiss Federal Institute of Technology EPFL)

Animal locomotion control is in a large part based on central pattern generators (CPGs), which are neural networks capable of producing complex rhythmic patterns while being activated and modulated by relatively simple control signals. These networks are located in the spinal cord for vertebrate animals. In this talk, I will present how we model CPGs of lower vertebrates (lamprey and salamander) using systems of coupled oscillators, and how we test the CPG models on board of amphibious robots, in particular a new salamander-like robot capable of swimming and walking. The goal of the project is to explore three important questions related to vertebrate locomotion: (i) the modifications undergone by the spinal locomotor circuits during the evolutionary transition from aquatic to terrestrial locomotion, (ii) the mechanisms necessary for coordination of limb and axial movements, and (iii) the mechanisms that underlie gait transitions.

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A7.10

14:30 Wednesday 1st July 2009

When mechanics matter: Utilizing passive dynamics to gain benefits in human locomotion

Steven H. Collins (Delft University of Technology)

Humans walk and run much more effectively than most legged machines, but we still expend significant energy in tasks that could require negligible energy input in principle. How do humans walk so well, and how can we help them do even better? By integrating passive and active mechanisms, of course. Anything but idle, passive dynamics allow fast, energy-effective motions crucial to high-performance gait. These motions can appear muscle-driven at first, but understanding the un-actuated system can help sort dynamics-dominated motions from neuro-centric ones. The relatively large scale, significant mass, and low friction of human limbs tend to yield a wide range of passive-dynamic motions, the most beneficial of which can be chosen and utilized. Passive dynamics can aid disturbance rejection, either through self-stability against small disturbances or by leaving significant muscle or motor capacity to deal with large ones. Passive motions tend to use less energy than active ones, and by clever use of elements such as springs even greater energy economy can be achieved. Understanding the passive dynamics at play during walking or running can give us the insights we need to push past barriers in human performance. Of course, we will need some active control along the way. A combination of simulations, robots, biomechanical devices, and human-subject experiments are useful in exploring the role of passive mechanisms in locomotion. We'll consider a machine that walks with humanlike energy expenditure, a foot that restores performance to amputees without big batteries, and the mysterious motion of the arms during walking.

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A7.11

15:40 Wednesday 1st July 2009

Insects running on elastic surfaces: The role of feedforward control

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In nature, multi-legged animals run rapidly over complex terrain. Cockroaches traversing leaf litter is one example. These substrates are rarely rigid, and are frequently very compliant. Movement over compliant surfaces may affect the speed, energetic cost, and viable control architectures of legged locomotor systems that encounter them. In past experimental research, we tested the hypothesis that a running insect can maintain average forward speed over an extremely compliant elastic surface (10 N/m) equal to 2/3 of its virtual leg stiffness (15 N/m). We found that cockroaches, *Blaberus discoidalis,* maintained forward speed on this elastic surface, exhibited unchanged step frequency, and showed smaller amplitude oscillations of the centre-of-mass (COM) in the vertical axis. Here, we use analytical and mathematical models to interpret the consequences of these experimental results for legged locomotor control. The observed change in COM acceleration over an elastic surface requires no change in effective leg stiffness when duty factor and ground stiffness are considered. Due to the lowering of the COM towards the elastic surface, the swing leg lands earlier and increases the period of double support. A simple feedforward control model with actuation at the hip (the clock-torqued spring loaded inverted pendulum, or CT-SLIP) explains the experimental result and provides one plausible mechanism.

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A7.12

16:00 Wednesday 1st July 2009

Conceptual models for jumping, running and walking: How leg compliance shapes the way we move

Andre Seyfarth (University of Jena)

Human and animal locomotion is characterised by clearly different discrete movement patterns, which are used depending on the species, the environmental conditions and on the speed of progression. In jumping, a quite specific movement goal may exist, e.g. to reach a certain height or distance. In steady state locomotion, however, the foot placement is less critical, which requires a more relaxed definition of an appropriate gait strategy.

Still, there are clear differences in gait types, e.g. at certain conditions (e.g. speed) a sudden change in a new gait may occur. So far, it is still not clear how different gait patterns are separated from each other. With the help of conceptual models of legged locomotion we therefore aim to gain a better understanding of the nature and the underlying mechanisms of human and animal gait.

The spring-like leg behaviour during locomotion could be a key in understanding the organisation of the observed movement patterns. It provides not only simple explanations for the different gait patterns but also helps to identify appropriate strategies to stabilise a desired movement. This includes the selection of a specific centre of mass trajectory as well as the vertical alignment in human walking and the control within the segmented leg. With this approach we hope to provide a framework for analysing and better understanding of both human and animal locomotion.

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A7.13

Poster Session - Tuesday 30th June 2009

Coping mechanisms for rough terrain running in Guinea fowl (*Numida meleagris*)

Aleksandra V. Birn-Jeffery (Royal Veterinary College), Monica A. Daley (Royal Veterinary College)

Locomotion in natural terrain is never perfectly uniform. Animals must regularly cope with obstacles and drops in terrain. Yet, little is understood about the kinetics and kinematics of rough terrain running. Strategies for maintaining stability and economy of locomotion may differ depending on terrain conditions. Revealing the mechanical and neural control strategies for coping with rough terrain will advance understanding of how bipeds move and inform legged robots designs.

Three types of responses can be used to negotiate a sudden change in floor height: 1) conversion between potential energy and kinetic energy, 2) adjustment of effective leg length and stiffness to avoid changes in energy and 3) absorption or production of muscular work to adjust for the step without a change in velocity. Here we ask two questions: 1) Which of these strategies are used to negotiate obstacles in terrain?, and 2) Does obstacle negotiation strategy depend on obstacle height?

We ran guinea fowl over a force plate runway with markers for Qualisys motion tracking. The runway was level in control trials, and had two obstacles of the same height placed 150cm apart (approximately 2 strides) in obstacle negotiation trials. The birds ran over obstacles ranging in height from 2 to 10 cm, corresponding to 9–54% of leg length. We found that as obstacle height increased, negative work done during stance increased corresponding to strategy 3 above. Responses in lower obstacles tended towards a mixture of strategies 1 and 2, revealing that control strategy does depend on obstacle height.

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A7.14

Poster Session - Tuesday 30th June 2009

Ants can't be knocked off: A ‘preflex’ as an extremely rapid attachment reaction

Thomas Endlein (Department of Zoology University of Cambridge),
Walter Federle (Department of Zoology University of Cambridge)

Many insects possess powerful adhesive organs that can produce extreme attachment forces of more than 100 times body weight. We studied in Weaver Ants (*Oecophylla smaragdina*) how such extreme adhesion is compatible with locomotion. These ants use only a fraction of their maximum adhesive contact area, even when walking upside-down on a smooth surface. While this might allow easier detachment during running, the ants should be more susceptible to sudden and unexpected detachment, e.g. by rain or wind gusts.

We investigated the reaction of the ants' adhesive pads to rapid horizontal displacements of the walking substrate. In untethered ants, the contact area of feet in contact with the underside of a glass plate was recorded using epi-illumination and high-speed video at 1000 fps. We found that the pad's contact area could more than double within less than a millisecond of the perturbation. This pad expansion is clearly faster than any neuronal reflex and therefore represents a passive 'preflex', resulting from the mechanical properties and geometrical arrangement of the pretarsus. This preflex reaction protects ants effectively against unexpected detachment, and allows them to use less contact area during locomotion.

The ants' preflex is direction-dependent. Pad contact area expanded most strongly when the displacement generated a pull along the tarsus axis. The preflex might be based on the ability of Hymenopteran adhesive pads to unfold in response to pulls toward the body. We therefore tested whether similar fast reactions also occur in other insects which possess pads that are not unfoldable.

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