A7.3
15:40 Tuesday 30th June 2009
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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Neuromechanical interaction during locomotion : Bipedal gait transition as a paradigm

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

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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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Biomechanical imperatives in the neural control of locomotion

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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

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

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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

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From neuromechanics to robot controllers: Bio-inspired design

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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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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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