

### A9 - Function and control of elastic systems

#### A9.1

##### Function and control of biological elastic mechanisms: An introduction

Thomas J Roberts (Brown University), Alan Wilson (Royal Veterinary College)

Most biological tissues exhibit some degree of elastic behavior, that is, they store strain energy when deformed and release a portion of that energy while returning to their resting state. In some cases this pattern of deformation and energy cycling has important functional significance. The pogo stick like function of the limbs of running animals, and power-amplifying catapult mechanisms of specialised jumpers are familiar examples. Recent work expands this functional repertoire to important roles for springs in a range of cyclic and ballistic locomotor modes (e.g., swimming and flying, jumping and striking). The force length properties of springs also are important in locomotor control and mechanofeedback, sensory mechanisms, power attenuation and mechanical buffering. Compliance has an effect on the frequency response on a system and will provide an inherent stability where control of movement and response to perturbations may become easier or made more difficult. Also advancing is our understanding of the arrangement and interaction of the biomaterials that act as springs. The hierarchical structure of tissues such as skeletal muscle reveals springs nested within springs, with elastic functions that interact across multiple levels of organisation, from molecules to the whole organs. Interspersed within this are contractile elements which can act to modulate tissue external properties like stiffness and energy return. In this session we will explore some of the diversity of elastic structures and mechanisms in nature, highlight robotic designs inspired by biological systems, and discuss the mechanisms that allow control of tissues that act as springs.

Email Address for correspondence: roberts@brown.edu  
13:30 Friday 2nd July 2010

#### A9.2

##### Muscle springs: comparing the crossbridge, filament and tendon elasticity

Roger C Woledge (Imperial College London)

The rate at which muscle crossbridges can transduce chemical energy into work is limited to by the rate of crossbridge turnover. The rate at which work done on a lengthening active muscle can be transduced into heat, although much higher, is similarly limited. A muscle tendon unit can have rates of work output and input beyond these limits because the crossbridges are "buffered" by elastic energy stores. A muscle-tendon unit contains a hierarchy of compliant elements connected in a complex series/parallel manner: the muscle crossbridges themselves, the filaments, and the aponeuroses /tendons. The characterisation of each of these elements, and assessment of its potential to act as a useful energy store requires knowledge of its stress strain relationship, which can be expected to be non-linear. The time dependent properties of the element as seen in such observations as stress relaxation, creep and hysteresis show that the elastic elements can potentially dissipate energy as heat as well as store it. So an understanding of these visco-elastic properties is also required to understand the efficiency of energy storage. On a fast time scale (100us) crossbridge compliance is 0.3 % Lo/Po, but is ~1% Lo/Po on a slower time scale (10ms). Filament compliance is also time scale dependent and similar in magnitude. The short tendons on isolated dogfish muscle fibre were found to have compliance of 0.2 % Lo/Po on a the fast (100 us) time scale but 2% Lo/Po on the time scale of force development (100ms).

Email Address for correspondence: r.woledge@imperial.ac.uk  
13:50 Friday 2nd July 2010

#### A9.3

##### Influence of elasticity on muscle operating lengths

Manny Azizi (Brown University), Thomas J Roberts (Brown University)

A fundamental feature of vertebrate muscle is that maximal force can only be generated over a limited range of lengths. During ballistic movements like jumping, the effective use of series elasticity to amplify power output requires muscles to shorten substantially while producing high forces. We examined how specialized jumpers like

frogs overcome the constraints of the force-length curve to generate the substantial mechanical work to power jumps. We used direct measurements of muscle length in vivo and muscle force-length relationship in vitro to determine the operating lengths of the plantaris muscle in bullfrogs (*Rana catesbeiana*) during jumping. The plantaris muscle operates primarily on the descending limb of the force-length curve, resting at long initial lengths ( $1.3 \pm 0.06 L_o$ ) before shortening to muscle's optimal length ( $1.03 \pm 0.05 L_o$ ). Operating at long lengths allows for higher peak forces despite significant muscle shortening. We find that the surprisingly compliant muscles of the frog hindlimb facilitate the observed operating lengths. The relatively compliant elastic properties of frog muscles may be a critical feature of the system, as they allow muscles to operate at long lengths and improve the capacity for force production during a ballistic task. Supported by NSF grant 0642428 to TJR and NIH grant AR054246 to EA.

Email Address for correspondence: manny\_azizi@brown.edu  
14:30 Friday 2nd July 2010

#### A9.4

##### Probing strain dependent crossbridge kinetics in $Ca^{2+}$ -activated insect flight muscle fibers via white-noise length perturbations

Bertrand C.W. Tanner (University of Vermont), Bradley M Palmer (University of Vermont), David W Maughan (University of Vermont)

We developed a technique to examine cross-bridge kinetics by applying random changes in muscle length (small amplitude white-noise length stimuli). This technique samples muscle responses in a fraction of the time required for sinusoidal length perturbation analysis, a complementary technique used widely for describing viscoelastic muscle behavior. These reduced temporal constraints and the benefit of simultaneously sampling the muscle response over a specified frequency range facilitate combining noise stimuli with additional length transients. This allowed us to investigate cross-bridge behavior during periods of varied load by combining noise with linear shortening and lengthening transients. Measurements from demembrated *Drosophila melanogaster* dorsal longitudinal muscle fibers show longer cross-bridge attachment time ( $t_{on}$ ) during shortening and reduced  $t_{on}$  during lengthening, implying slower kinetics during shortening and faster kinetics during lengthening. Computational simulations exploring strain-dependent cross-bridge kinetics suggest that these shifts in  $t_{on}$  increase with strain rate. Preliminary experiments combining noise stimuli with small amplitude workloops (0.125-0.5% muscle length) show greater oscillatory work production and increased non-linearity as strain amplitude increases. Concurrent

noise analyses show that muscle responses lose their classical signature of enzymatic cross-bridge cycling with increasing strain amplitude, behaving more like a passive or rigor muscle. These initial applications of noise analysis show promise for future studies focused on the underlying molecular processes associated with more complicated length transients that occur during normal muscle contraction.

Email Address for correspondence: btanner@uvm.edu  
15:00 Friday 2nd July 2010

#### A9.5

##### Is titin an exponential spring in active muscle?

Kiisa Nishikawa (Northern Arizona University), Jenna A Monroy (Northern Arizona University), Theodore A Uyeno (Northern Arizona University), Leslie A Gilmore (Northern Arizona University), Krysta L Powers (Northern Arizona University)

Before the advent of the sliding filament theory, physiologists believed that muscle functions as a tunable spring, with elastic elements that become shorter and stiffer upon activation. The contribution of titin to muscle passive tension gives new relevance to this idea, but a role for titin in active muscle is needed. We test the hypothesis that  $Ca^{2+}$ -activation shortens and stiffens titin in active vs. resting muscle via  $Ca^{2+}$ -dependent binding of titin to thin filaments. We studied mdm mice, which carry a 779-bp deletion in the N2A region of TTN. Passive stiffness is greater in mdm homozygotes than in wild-type mice, and intermediate in heterozygotes. In contrast, active stiffness is lower in mdm homozygotes than in wild-type mice. We compared elastic recoil in active vs. passively stretched soleus muscles at the same initial force. In wild-type mice, spring elements were shorter (12.7%) and stiffer (25-fold) in active vs. passively stretched muscles. In mdm homozygotes, there was no change in length or stiffness upon activation. Results suggest that an epitope in titin's N2A region binds to thin filaments upon  $Ca^{2+}$ -activation, and that this epitope is absent in mdm mutants. Binding of titin to thin filaments in active muscle would prevent low-force straightening of Ig domains that occurs upon passive stretch. We suggest that muscle functions as a tunable spring, in which  $Ca^{2+}$ -activation shortens and stiffens titin. The hypothesis provides an elastic mechanism for force enhancement with stretch, force depression with shortening, and intrinsic stability to perturbations in load.

Email Address for correspondence: Kiisa.Nishikawa@nau.edu  
15:40 Friday 2nd July 2010

#### A9.6

## Is virtual leg stiffness a task variable for running that generalizes across posture and leg number?

Andrew J Spence (Royal Veterinary College), Caragh N Kelleher (Royal Veterinary College), Greg Byrnes (University of Cincinnati)

Hierarchical hypotheses of motor control posit that animals overcome the curse of dimensionality by controlling, planning, or stabilizing their motion around a reduced dimension model of the body. Spring mass models in which one or multiple legs behave as a virtual leg spring have been proposed as one such control target. Human runners increase their virtual leg stiffness as surface stiffness decreases, allowing them to maintain similar dynamics of the centre of mass (COM). In contrast, a six-legged, sprawled posture runner, the cockroach *Blaberus discoidalis*, has recently been found to exhibit altered COM dynamics on a compliant surface, in a manner that is consistent with constant virtual leg stiffness. We tested the hypothesis that upright posture, trotting quadrupeds compensate for compliant surfaces using the mechanism of a stiffened virtual leg. Dogs (virtual leg stiffness 5 kN/m) were trotted over four different surfaces: rigid, 4, 8, and 21 kN/m. Dog virtual leg stiffness *decreased* significantly as surface stiffness decreased (linear mixed-model regression,  $n=6$ ,  $p<0.001$ ). Vertical stiffness was lower on the most compliant surface, but showed no significant difference across the other three surfaces ( $32.87 \pm 1.41$  body-weights (BW)/trunk-height (TH), 4 kN/m surface, vs.  $39.46 \pm 1.10$  BW/TH, rigid surface; mean  $\pm$  s.e.m., mixed-model ANOVA;  $p<0.001$ ). These findings suggest that although bipeds and polypeds exhibit similar spring mass behavior on rigid surfaces, the task level variables that are controlled during locomotion on soft surfaces may differ based on leg number.

Email Address for correspondence: [aspence@rvc.ac.uk](mailto:aspence@rvc.ac.uk)  
16:10 Friday 2nd July 2010

### A9.7

#### Leg swing powered by the ankle joint in human walking

Susanne Lipfert (Lauflabor Locomotion Lab Friedrich-Schiller-Universität Jena Germany), Michael Günther (Eberhard-Karls-Universität Tübingen Germany), Sten Grimmer (Lauflabor Locomotion Lab Friedrich-Schiller-Universität Jena Germany), Andre Seyfarth (Lauflabor Locomotion Lab Friedrich-Schiller-Universität Jena Germany)

In horses, it has been shown that high power output required for rapid limb protraction is achieved by a catapult action of the biceps muscle (Wilson 2003).

Thanks to this mechanism and the elastic muscle property, a horse can swing its leg forward much faster than the mass of the non-elastic muscle could do. A comparable action may be observed in human walking. Leg swing is typically shorter than ground contact indicating the need for fast leg protraction similar to a galloping horse. Elastic property and catapult action of the human gastrocnemius muscle is reported (Ishikawa 2005). In our study, we investigated kinematics and kinetics during human walking to find out whether the human leg provides a sufficient catch-release system for catapult-like action. Similar to findings in horses, we found that the forward movement of the center of mass and the orientation of the ground reaction force (GRF) stretch the gastrocnemius muscle during single stance. This stretch is further intensified by the knee joint extending. At about 75% of stance, the GRF vector has rotated backwards and intersects the knee joint axis, no longer balancing the flexing torque exerted by the gastrocnemius muscle. The knee then buckles forwards, destabilizing the leg (Seyfarth 2001). Other than observed in the horse's catapult muscle (biceps), the recoil of the human's gastrocnemius does not directly accelerate the leg forwards, but extends the ankle joint. This powerful ankle extension against the ground accelerates the shank upward, folding the leg, and results in fast leg swing.

Email Address for correspondence: [s.lipf@uni-jena.de](mailto:s.lipf@uni-jena.de)  
16:30 Friday 2nd July 2010

### A9.9

#### Undulatory swimming: Can models reproduce fish like kinematics exclusively passive?

René S Sonntag (Bionic-Innovation-Centre Bremen University of Applied Sciences), Antonia B Kesel (Bionic-Innovation-Centre Bremen University of Applied Sciences)

DPIV is an established method for assessing drag and thrust in the analysis of fish swimming. Yet detailed reproducible flow patterns are often difficult to attain, as individual reactions and unsteady locomotion of test animals may induce changes in wake structures. Even in the most sophisticated fish-like robots active mechanical movements may override reaction forces of the fluid and thus may not reflect in vivo conditions. Fish-like models whose movements are predetermined only by driving frequency and anterior deflection angle therefore may seem more promising. In fish swimming, kinematics and propulsive forces are modulated by different tissues, e.g. tendons, skin and bones. As body stiffness plays an important role in swimming it should be possible to create fish like kinematics passively, in models with an appropriate gradient of flexural stiffness along the body axis. Flexible rectangular plates with the same height to length ratio as rainbow trout (*Oncorhynchus mykiss*) and with different gradients of flexural stiffness were

fabricated from carbon fibre/epoxy resin composite and tested in a flow tank. Models were powered by an oscillating rod while keeping driving frequency, angle and swimming speed constant. Resulting kinematics were analyzed with high speed video equipment. Wake structures in the horizontal mid plane were visualized with DPIV. Both model kinematics and wake structure were compared with that occurring in *O. mykiss*. Experiments showed; fish like swimming kinematics can be reproduced with models exclusively passive by adding an appropriate gradient of stiffness.

Email Address for correspondence: Rene.Sonntag@hs-bremen.de  
11:40 Saturday 3rd July 2010

## A9.10

### Muscle tendon interaction in locomotion

Alan M Wilson (The Royal Veterinary College), Glen A Lichtwark (University Queensland)

Limb muscle tendons provide a temporary elastic energy store that can contribute to energy cycling and economical locomotion. The tendons and associated anatomical structures are particularly well adapted for this role in large cursorial herbivores like horses and antelope which need to stand for long periods and move economically. These animals' limbs are stable in compression and can function with minimal muscle activation reducing limb muscle mass and activation costs. Such highly elastic systems can however be susceptible to high temperatures due to hysteretic damping and secondary modes of oscillation or vibration during locomotion.

Muscles are usually arranged in series with tendons and whilst the force in both muscle and tendon will be similar the timing of length change can be very different. For instance in human running the medial gastrocnemius muscle fibres will shorten at about three lengths per second whilst the shortening velocity of the muscle tendon unit can be several times that.

The interaction between muscle and tendon becomes more sophisticated in pennate muscles where there is a complex interaction between the elastic aponeurosis and the muscle fibres such that the elastic properties of the muscle tendon unit will vary with timing and level of muscle activation. This provides a means of modulating the properties of the tendon spring and hence the dynamics of movement.

Email Address for correspondence: awilson@rvc.ac.uk  
10:30 Saturday 3rd July 2010

## A9.11

### The utilisation of a compliant environment by Grey Squirrels

Rebecca A Snarey (The Royal Veterinary College), Andrew Spence (The Royal Veterinary College), Alan M Wilson (The Royal Veterinary College)

Grey squirrels (*Sciurus carolinensis*) live in a complex, heterogeneous, compliant environment. They provide an ideal model system in which to investigate the anatomical and locomotor specialisations required to function in an arboreal habitat. Squirrels rely on jumping to move between sparse, compliant branches. The force and impulse they can apply is determined by limb and muscle dynamics, coupled to the stiffness and inertia of the branch. Among the ways they can modulate this is by 1) preloading the branch, 2) taking off at a different position along the branch, or 3) changing take off angle. We used a simple one-dimensional model of a 600g jumping squirrel, consisting of a point mass falling onto a sprung surface, into which it extends a length actuator in 100ms. We varied surface stiffness and timing of limb extension after contact. The maximum impulse was 0.62Ns which corresponded to a surface stiffness of 600Nm<sup>-1</sup> with a phase delay of 0.005s.

According to this model, when jumping from a branch of average environmental stiffness (200Nm<sup>-1</sup>), using an average observed leg extension time of 0.1s, squirrels maximise impulse with a phase delay of 0.063s whilst still only attaining a horizontal distance of 0.95m.

We are training Grey squirrels to jump from a variable stiffness take-off platform with an integrated Kistler forceplate and high speed video camera. Kinetics and kinematics, combined with anatomical data will provide an insight into whether and how squirrels alter their jump mechanics to cope with, or utilise, surface compliance.

Email Address for correspondence: rsnaey@rvc.ac.uk  
11:00 Saturday 3rd July 2010

## A9.12

### Differential strain of the human Achilles free tendon and aponeurosis *in-vivo*

Dominic J Farris (UNC-Chapel Hill NC State University), Glen A Lichtwark (The University of Queensland), Grant Trewartha (University of Bath), Miranda P McGuigan (University of Bath)

The storage and return of elastic energy in the Achilles tendon (AT) enhances muscle power output and efficiency of human locomotion. Often, the AT is considered to act as a single spring of uniform stiffness. However, the AT consists of a 'sheet-like' intramuscular aponeurosis and cylindrical free tendon and their elastic properties may be different. The aim of this study was to measure *in-vivo* if strain differed between the aponeurosis and free tendon during muscular contraction of the triceps-surae. It was hypothesised that strain would be greater in the free tendon.

Three-dimensional images of the AT were obtained at rest and during isometric contraction of the triceps-surae of eleven subjects, using novel ultrasound imaging techniques. Ultrasound images were recorded (50 Hz) as the transducer was swept over the gastrocnemius and AT. The position of the transducer was tracked using motion analysis (200 Hz) and these data were used to compile the ultrasound images and reconstruct the AT in three dimensions. Longitudinal strain of aponeurosis (the AT proximal to the insertion of Soleus) and free tendon were calculated for the contracted state. Orthogonal strain was calculated for the aponeurosis. Longitudinal strain was greater in the free tendon than in the aponeurosis ( $5.2 \pm 1.7\%$  vs.  $2.6 \pm 2.0\%$ ,  $P < 0.05$ ). Orthogonal strain of the aponeurosis was  $6.0 \pm 4.0\%$ . Differences in the elastic behaviour of the free AT and aponeurosis may be due to biaxial strain in the aponeurosis and could represent different functional roles of the two parts of the tendon.

Email Address for correspondence: djfarris@ncsu.edu  
9:40 Saturday 3rd July 2010

### A9.13

#### Limb muscle-tendon unit function in power-attenuation during rapid energy absorption

Nicolai Konow (Brown University EEB), Emanuel Azizi (Brown University EEB), Thomas J Roberts (Brown University EEB)

Energy absorption via active muscle lengthening is important during deceleration in animal locomotion. Our mechanistic understanding could benefit from in vivo studies of how tendon influences active fascicle behavior. We measured knee and ankle joint kinematics, fascicle lengths and EMG, and used strain gauges on the calcified tendon of turkey lateral gastrocnemius to calculate muscle-tendon unit force during drop-landings. The aim was to determine how energy is absorbed during high-powered deceleration, and if power is attenuated during its transmission through tendon to the muscle fascicles. Landings generated  $200 \pm 89\text{N}$  or fourfold the muscle forces measured at intermediate running speed, and involved a striking decoupling of joint flexion and fascicle length-change. Three-quarters of the impact absorbing joint-flexion occurred during the initial phase when muscle-tendon unit force was rising. During this initial phase of impact, muscle fascicles shortened and produced power as the tendon was stretched. During the subsequent period of force-decay, the fascicles lengthened ( $\sim 25\% L_0$ ) and absorbed energy ( $\sim 20\text{J/kg}$ ), as the tendon recoiled. Peak power input to the tendon (during force-rise) significantly exceeded peak power input to fascicles (during force-decay). Our data suggest that during initial impact, energy is stored rapidly in tendon, and then released more slowly to do work on the muscle fascicles during force-decay. This series elastic shock-

absorbing mechanism may reduce the risk of eccentric muscle damage both by reducing the lengthening rate and the mechanical power imposed directly on the muscle fascicles. Supported by NIH-AR055295 to TJR.

Email Address for correspondence: nkonow@brown.edu

11:20 Saturday 3rd July 2010

### A9.14

#### The importance of neuromechanical leg models in the design of powered prostheses

Herr M Herr (MIT)

A long standing goal in engineering is to exploit the robust designs of biological systems to guide the development of autonomous machines that exhibit agility, strength and speed in a variety of natural environments. Critical to this effort is the development of actuator technologies that behave like muscle-tendon, device architectures that resemble the body's own musculoskeletal design, and control methodologies that exploit principles of biological movement. In this lecture, I discuss how parallel and series-elastic actuation and neuromechanical, model-based control algorithms can result in economical, low-mass, and dynamically-realistic prostheses for walking. Control schemes for powered prostheses are typically based on fixed torque-state relationships derived from intact humans walking at specified speeds and across known terrain. These schemes work well in situations for which they are trained, but do not allow for robust adaptation to environmental disturbances. In the lecture insights from a neuromuscular walking model are used to posit a compliant actuator design and a reflex control strategy for a powered ankle-foot prosthesis. Kinematic and kinetic data are presented from a transtibial amputee walking on level ground at various speeds as well as across sloped ground surfaces. The powered prosthesis is shown to automatically adapt net ankle work and peak power for distinct ground slopes and walking speeds in a manner comparable to an intact human ankle, without the difficulties of explicit terrain and speed sensing. These results highlight the importance of compliant actuation and neuromechanical, model-based controllers in the design of highly functional powered prostheses.

Email Address for correspondence: hherr@media.mit.edu

09:00 Saturday 3rd July 2010

### A9.15

#### Viscoelastic properties of arthropod cuticle for the fine tuning of vibration and flow sensors

Friedrich G BARTH (University of Vienna)

Animals use composite materials for numerous functions, among them the uptake of information by their sensory organs. The outstanding properties of many animal sensors prompted numerous studies on the relation between structure and function which, however, can only be adequately understood if the organism's behavior in its natural habitat is taken into account. Corresponding studies of such integrative nature repeatedly demonstrated a surprisingly close match between the biologically relevant stimulus patterns and the sensor's finest structural details. This basic feature of sensory organs will be illustrated using two types of spider mechanoreceptors, where the clever application of visco-elastic material to a large extent explains the tuning to the biologically relevant frequency ranges and stimulus dynamics. Spiders use these sensors for prey localization, predator avoidance and communication during courtship.

Email Address for correspondence: friedrich.g.barth@univie.ac.at

**13:30 Saturday 3rd July 2010**

#### **A9.16**

##### **The power of piercing, pounding shrimp**

Sheila Patek (University of Massachusetts Amherst), Marco Mendoza Blanco (University of California Berkeley), Michael V Rosario (University of Massachusetts Amherst), Jennifer Taylor (University of California Berkeley)

A muscle, a spring and a weapon are the essential elements of powerful predatory strikes in animals. The opportunities and limitations posed by these structures have rarely been examined in a macro-evolutionary context. This study examined the function and evolutionary variation of the muscles (physiological cross-sectional area and sarcomere length), springs (mineralization patterns and elastic energy storage) and weaponry (strike kinematics) of mantis shrimp (Stomatopoda). Mantis shrimp have evolved diverse appendages that stab, spear or hammer prey at extremely high speeds and accelerations. We found that mantis shrimp use large extensor muscles with long-sarcomere fibers to compress an exoskeletal tape spring. While muscle physiological cross-sectional area increased with appendage size regardless of appendage type, sarcomere lengths were longer, in some cases 50% longer, in hammering species than in spearing ones. Across all taxa, spring force was positively correlated with appendage size, but spring constant was not. Thus, spring shape or material composition must change with size, perhaps to accommodate limitations in maximum muscle force with increased body size. Hammering appendages moved with greater speeds and shorter durations than spearing appendages. In conclusion, hammering shrimp used muscles with the greatest force

output to power springs that were mechanically similar across species. Consistent with generating more force to compress a spring, hammering shrimp produced faster movements. These results suggest both connections and constraints, ranging from conserved spring mechanics to highly variable sarcomeres and predatory kinematics, and offer new windows into the evolutionary dynamics of power amplification.

Email Address for correspondence: patek@bio.umass.edu

14:10 Saturday 3rd July 2010

#### **A9.17**

##### **Controlling energy release: two strategies insects use to direct jumping**

Gregory P Sutton (University of Cambridge), Malcolm Burrows (University of Cambridge)

To jump, insects generate large amounts of energy in short amounts of time, vastly exceeding the ability of muscle to generate power. Insects solve this problem by storing and releasing energy from cuticular 'springs'. Once the energy is stored, the insect must release the energy so that the jump is in a prescribed direction. The control mechanism depends on which physiological plane the hindmost legs are oriented in and on which leg joint the cuticular spring is placed. To show this, we will compare the control mechanisms of the locust and the frog hopper. Locusts have hindmost legs that are placed in the sagittal plane and cuticular springs that are placed at the femur/tibia ('knee') joint. This construction allows locusts to direct the jump in the sagittal plane by simply rotating the coxa/trochanter ('hip') joint. Moreover, this construction allows one-legged locusts to control a jump with no difficulty. In contrast, frog hoppers have hindmost legs that are oriented in the transverse plane and cuticular springs that are placed at the coxa/trochanter ('hip') joint. This construction allows frog hoppers to direct the jump in the transverse plane by simply rotating the femur/tibia ('knee') joint. Unlike the locust, however, a one-legged frog hopper cannot generate a controlled jump. Both mechanisms have a common principle: directing the jump in the plane of the leg is simply controlled by rotating one joint in that leg, making it easy for an insect to direct a jump.

Email Address for correspondence: RScealai@gmail.com

15:40 Saturday 3rd July 2010

#### **A9.18**

##### **Flower heliotropism: Elucidating mechanical principles of plant stem movement**

Markus Rüggeberg (Max Planck Institute of Colloids and Interfaces), Ingo Burgert (Max Planck Institute of Colloids and Interfaces), Peter Fratzl (Max Planck Institute of Colloids and Interfaces)

Plants are able to move their living organs such as branches, leaves and flowers in response to various stimuli, e.g. light or gravity. The actuation is mediated either by reversible changes of the turgor pressure, or by differential growth of cells.

Heliotropism is the daily movement of leaves and flowers in order to track the sun. This movement can be seen in a variety of plant species. Flower heliotropism is of particular interest from a biomechanical perspective. The stem represents an upright beam, which is fixed on one end, whereas the other end, the flower, tracks the sun over an angle of about 180°. Thus, torsion of the plant axis might be involved as well as differential growth and/or changes in turgor pressure, facilitating this particular movement.

In our study, we investigate the mechanism of floral heliotropism under laboratory conditions taking the alpine plant *Ranunculus alpestris* as model organism. We track the 3D-movement of the stem and the flower. In combination with a detailed analysis of the stem, especially regarding cell dimensions and orientation, we intend to distinguish between reversible and irreversible movements and to elucidate the underlying mechanism. The first results point to a discontinuous movement. Rather than following the sun in a continuous arch, a nodding movement can be seen.

Email Address for correspondence: markus.rueggeberg@mpikg.mpg.de  
16:00 Saturday 3rd July 2010

## A9.19

### Do dogs adjust their virtual leg stiffness on compliant surfaces?

Caragh N Kelleher (Royal Veterinary College), Andrew J Spence (Royal Veterinary College)

Humans compensate for elastic surfaces by increasing their virtual leg spring stiffness, which allows them to maintain the overall system (or vertical) stiffness, and displacement of the centre of mass. We tested the hypothesis that trotting quadrupeds compensate for compliant surfaces using the same mechanism. Six Labrador dogs (virtual leg stiffness ~5 kN/m) were trotted over four surfaces: rigid, 4 kN/m, 8 kN/m, and 21 kN/m, constructed from foam rubber. We calculated virtual leg stiffness, vertical stiffness, and COM displacement using optical motion capture and force plate measurements from hand-trotted subjects. Virtual leg stiffness (normalised by body weight (BW) and trunk height (TH)) was significantly lower on compliant surfaces ( $9.44 \pm 0.19$  BW/TH, 4 kN/m surface vs.  $13.26 \pm 0.19$  BW/TH,

rigid surface; mean  $\pm$  s.e.m., linear mixed-model,  $n=6$ ,  $p < 0.001$ ). Vertical stiffness was lower on the most compliant surface, but showed no significant difference across the other three surfaces ( $32.87 \pm 1.41$  BW/TH, 4 kN/m, vs.  $39.46 \pm 1.10$  BW/TH, rigid surface;  $p < 0.001$ ). Dogs sank into the softer surfaces (COM height above the surface  $0.97 \pm 0.0032$  m/TH, 4 kN/m surface, versus  $1.03 \pm 0.0013$  m/TH, rigid surface;  $p < 0.01$ ). These findings suggest that although bipeds and polypeds exhibit similar spring mass behaviour on rigid surfaces, the task level variables that are controlled to maintain stability on soft surfaces differ based on leg number.

Email Address for correspondence: ckelleher@rvc.ac.uk  
14:40 Saturday 3rd July 2010

## A9.20

### Undulatory swimming: gradients in body stiffness affect propulsive force output

René S Sonntag (Bionic-Innovation-Centre Bremen University of Applied Sciences), Antonia B Kesel (Bionic-Innovation-Centre Bremen University of Applied Sciences)

Body stiffness plays an important role in fish swimming as it affects propulsive force and swimming speed. Previous studies indicate that skin, connective tissues, tendons or even the skeleton passively increase the flexural stiffness of the body, whilst negative muscle work actively does. At high undulatory frequencies e.g. the stiffer a body is the faster its swimming speed becomes. However it remains unclear how changes in stiffness along the body may affect propulsion. In order to address this issue, abstract models with different gradients of flexural stiffness along the longitudinal axis were fabricated from a carbon fibre/epoxy resin composite. In all models the fish body was reduced to a flat rectangular plate with a beam attached to the "head region". Plate undulation was induced by oscillating the beam at driving frequencies between 0.5 - 6 Hz. Models were mounted in a flow tank and tested at different swimming speeds from 0-2 BL/s. Propulsion was measured using a force balance, plate undulation was recorded using high speed video equipment. The highest propulsive forces were found in models with a sharp decrease in longitudinal stiffness. Furthermore, although only purely passive elements were taken into account, these models showed kinematics similar to those observed in rainbow trout. Further studies should find an appropriate combination of stiffness gradients, driving frequencies and swimming speed resulting in maximal propulsive force and verify if actual fish show a similar decrease in flexural stiffness along the body axis.

Email Address for correspondence: Rene.Sonntag@hs-bremen.de  
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