



Society for Experimental Biology Annual Main Meeting 28th June – 1st July 2009, Glasgow, UK

A6 – GENERAL BIOMECHANICS

A6.1

09:00 Sunday 28th June 2009

What makes a great footballer? Trade-offs between athleticism and skill in human performance

Robbie S. Wilson (The University of Queensland)

Animal performance during critical behaviours such as predator-escape, prey-capture and fighting ability is determined by a complex assortment of underlying traits. Maximal physical capacity is widely appreciated to be an important determinant of performance during these complex behaviours. However, the role of individual skill in determining performance is virtually unknown and its role in the evolution of physical function has been surprisingly dismissed. Skill is likely to be a key determinant of performance for many complex behavioural traits. For example, male fighting capacity is likely to be determined by more than just strength alone, but also fighting technique, coordination, and decision-making. Given the difficulties associated with assessing skill in non-human organisms, we used analyses of human performance to investigate the possible interactions and trade-offs between skill and athletic ability. Performance of individuals during staged one-on-one football games was used as our model complex performance trait. Footballing ability was assessed for 30 subjects (aged 17–31 years) and their performance in 16 different athletic and skills tasks was also quantified. We compared ten different models that evaluated the relationships between individual morphology, athleticism and skill to overall footballing performance. We found that most maximal athletic tasks were positively correlated, as were many skill component tasks. However, there was no evidence of any positive or negative correlations between maximal athletic performance and skill, suggesting that these traits may be completely independent and under different selective pressures or even under separate genetic control. Implications of this work for the evolution of vertebrate physical performance will be discussed.

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A6.2

09:20 Sunday 28th June 2009

Functional and behavioral limits on human hammering performance

Duncan J. Irschick (University of Massachusetts at Amherst), Suellen Almeida (University of Massachusetts at Amherst)

One of the most fundamental trade-offs in any biomechanical system concerns that between force and velocity during a challenging motor task. How organisms cope with these seemingly conflicting functional demands is poorly understood. We study human hammering as a simple yet challenging motor skill that requires both high force and high accuracy. In particular, we have been studying which factors influence force–velocity relationships during hammering, including the degree of light (light versus dark), gender (male versus female), target size, and degree of learning. Our results indicate that all of these factors affect force–velocity relationships but in a complex manner, with significant individual variability that may be a signature of human performance.

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A6.3

09:40 Sunday 28th June 2009

How the snipe makes its drumming sound

Roland Ennos (University of Manchester), Adam Van Casteren (University of Manchester), Jonathan Codd (University of Manchester), James Gardiner (University of Manchester), Henry McGhie (Manchester Museum)

Male common snipe (*Capella gallinago gallinago*) produce a “drumming” sound with their outer tail feathers during their mating dives, but little is known about how this is achieved. We investigated the movements and sound producing capabilities of the outer tail feathers. Using a wind tunnel, we compared observations of the frequencies of sound produced with the predictions from aerodynamic theory. The

feathers were also filmed in an air-flow with a high speed video camera, and subjected to morphological examination and biomechanical testing. Video and audio analysis of the feather demonstrated that a fluttering of the trailing vane generated the sound. The flutter of the vane is facilitated by the rearward curvature of the feather shaft, reduced branching angles of the barbs in the trailing vane and the lack of hooks on the barbs, all of which increase the flexural compliance of the trailing vane, especially in a hinge region. Sound production occurred at the same frequency as the vane movements, at frequencies consistent with it being produced by a fluttering flag mechanism but too high to be caused by an Aeolian whistle mechanism.

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A6.4

10:00 Sunday 28th June 2009

Spring or strut? Biomechanical specialisations in elephant limbs

Charlotte E. Miller (Royal Veterinary College), Dimitrios Tsaopoulos (Royal Veterinary College), John R. Hutchinson (Royal Veterinary College)

The fore- and hindlimbs of elephants contain several specialised muscle–tendon units and fasciae. Differences in fore- and hindfoot form and function, with a spring-like ankle and strut-like wrist, appear to be balanced by differences in more proximal limb anatomy, consistent with measurements of similar overall mechanical functions in both limbs.

Here we present qualitative and quantitative anatomical data on the limb specialisations of elephants, with particular reference to the changes in morphology seen across a wide ontogenetic size range (~100–4000 kg). These are then integrated with available biomechanical data to infer possible locomotor function.

Elastic structures are more developed in the proximal fore- than hindlimb and become more extreme during growth. Pronounced flexion of the forelimb appears to be the default position when the muscles are inactive, as indicated by the normal orientation observed post-mortem. This flexed limb configuration is maintained, at least in part, by tension in the thick fascial layers covering the muscles, and is much more pronounced than in the hindlimb.

The elephant forelimb also contains two muscles which have become remarkably specialised when compared with the ancestral mammalian condition. The pronator teres forms a thick, fibrous band in larger elephants, fixing and stabilising the wrist joint in pronation. The flexor carpi radialis muscle is strongly compartmentalised by yellow elastic tissue, creating a long, springy connection between the radius and the carpus. This unusual structure may aid in damping the “heelstrike” impulse at the carpus, making wrist and ankle function more similar in the living elephant than seen in *in vitro* experiments.

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A6.5

10:40 Sunday 28th June 2009

Geometry and parallelism in the long bones of rodents and ungulates

Adrià Casinos (University of Barcelona), Oscar Rocha-Barbosa (Universidade do Estado do Rio de Janeiro), Eloy Gálvez-López (University of Barcelona)

Morphological parallelism between South American hystricomorph rodents and small ungulates from the Old World has been postulated for a long time. This research deals with this question from the point of view of biomechanical characteristics of the long bones. For that, cross-sectional area, second moment of area, polar moment, athletic ability indicators and strength were calculated for the long bones (humerus, radius, femur and tibia) of 5 species of Caviodea and 2 species of Artiodactyla. Regressions of each of these variables to body mass were carried out. Regarding the cross-sectional area, the confidence intervals show that the exponents calculated are always higher than the value predicted by geometrical similarity, except in the case of the femur, while exponents obtained for the second moment of area or the polar moment are not significantly different from the predicted values, except for humerus and tibia. The two indicators of athletic ability scaled as expected, except the humerus and tibia axial indicators. The exponent calculated for femur strength is not different from 0, while in the case of the humerus, strength decreases slightly with body mass. Additional statistical tests show no difference between the values of these parameters calculated for the studied samples of artiodactyls and rodents. The present results are consistent with the hypothesis that the parallelism between hystricomorph rodents and small ungulates is very important.

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A6.6

11:00 Sunday 28th June 2009

Allometric scaling of trabecular bone

Michael Doube (Imperial College London), Sandra J. Shefelbine (Imperial College London), John R. Hutchinson (The Royal Veterinary College), Alexis M. Wiktorowicz Conroy (Imperial College London), Michal M. Kłowski (Imperial College London)

The scaling of gross bone shape with size is well-studied. However, the mechanically important interior micro-architecture of bones has been more neglected. We measured trabecular scaling in a broad range of taxa, spanning the 6 orders of magnitude size range from Etruscan shrews (*Suncus etruscus*) to Asian elephants (*Elephas maximus*). We acquired 3D microtomographic scans (Metris X-Tek) of entire femoral heads (femoral head radius, $R < 7.5$ mm) or of 10 mm cubes cut from the centre of the femoral head ($R > 7.5$ mm). We cropped images to contain only trabecular bone and then binarised them. Trabeculae tend to increase in thickness as R increases, with greatest maximum thickness (T_{\max}) attained in elephant trabeculae ($T_{\max} \propto R^{2.6}$). For perspective, the radius of a mouse's (*Mus musculus*) femoral head is similar to the thickest elephant trabecula (both 0.77 mm). For small animals with $R < 10$ mm, mean trabecular thickness (T_{av}) scales strongly with R ($T_{\text{av}} \propto R^{2.4}$). Greatest mean trabecular thickness (0.197 mm) was found in relatively small animals – the mountain hare (*Lepus timidus*) and greater mouse deer (*Tragulus napu*) – possibly related to high acceleration propulsion by the hindlimbs. Trabecular thickness is not associated with volume fraction. Bone volume fraction and anisotropy did not scale with animal size, remaining within a similar range independent of animal size. Measurement of trabecular network parameters such as branch length, connectivity and rod/plate distribution may explain why the largest animals do not have relatively the most trabecular bone.

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A6.7**11:20 Sunday 28th June 2009****Post natal development of articular cartilage mechanics**

Mark C. Van Turnhout (Experimental Zoology Group Wageningen University), Sander Kranenbarg (Experimental Zoology Group Wageningen University), Johan L. Van Leeuwen (Experimental Zoology Group Wageningen University)

Articular cartilage (AC) is the thin layer of soft tissue that covers the surfaces of bones in diarthrodial joints. Tissue composition and structure plays an important role in the mechanical functioning of AC. AC composition and structure, and therefore its mechanical properties, need to develop before puberty. Mechanical loads that AC needs to support in adult animals, are also the loads that govern (early) AC remodelling.

We used sheep with ages between 0 and 78 weeks to assess the early development of AC, its influence on AC mechanics, vice versa. We measured collagen fibre orientation, collagen amounts, proteoglycan amounts and mechanical properties. AC mechanical properties are height dependent: they differ between articular surface and interface with the bone. A finite element model was used to predict tissue mechanics as a function of its (local) composition and structure.

During development, AC thickness decreases. Collagen fibre orientation develops from a layered structure to an arcade structure. Collagen amounts increase, and increase most near the bone. Proteoglycan content also increases, and also most near the bone. Tissue stiffness increases, and the height dependent gradient in mechanical properties is amplified between birth and maturity.

With the finite element model, we can predict height dependent mechanical properties that cannot be assessed experimentally. We use the model to investigate correlations between local AC mechanics and tissue remodelling.

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A6.8**11:40 Sunday 28th June 2009****Arborescent monocots as role models for biomimetic fibre-reinforced composites with gradient structure**

Thomas Speck (University of Freiburg, Competence Networks BIONIK and Biomimetics), Markus Milwich (Institute of Textile Technology and Process Engineering (ITV) Denkendorf), Sebastian Busch (University of Freiburg), Olga Speck (University of Freiburg, Competence Networks BIONIK and Biomimetics), Ingo Burgert (Max-Planck-Institute of Colloids and Interfaces), Markus Rüggeberg (Max-Planck-Institute of Colloids and Interfaces)

Fibre-reinforced composites represent products with increasing economic importance. Demands are low weight, excellent mechanical performance in stiffness, strength and energy damping, benign fracture behaviour and low production costs. Other requirements include a good eco-balance as to the materials used and to the production chain and a good biodegradability.

Arborescent monocots proved to be especially suitable as concept generators for the development of high performance fibre-reinforced composites. Their stems are composed of isolated highly lignified fibres and fibre bundles which are sometimes arranged in a complex three dimensional pattern, and show additionally stiffness gradients between the very stiff fibres/fibre bundles and the less stiff surrounding parenchyma. This structure is crucial for their excellent

mechanical properties of the stems often coupled with a light-weight construction. On the other hand this biological structure is very similar to fibrous technical structures that can be produced in complex 3D-arrangements by new production techniques.

We present an overview on recent structural and (micro-) mechanical analyses of stems of the palm *Washingtonia robusta*, the giant reed *Arundo donax* and several bamboo species. Additionally to the data of the biological role models new results for the 'Technical Plant Stem', a biomimetic fibrous compound material, are presented. Our data prove that this narrow fabric can compete with aluminium, titanium alloy and steel as well as to its specific modulus of elasticity and to its vibration damping, and excels these materials in regard to the specific impact resistance and specific absorbed impact energy.

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A6.9**12:00 Sunday 28th June 2009****Branching in nature and technics: Plants as role models for bio-inspired branched fibre-reinforced composites**

Tom Masselter (University of Freiburg), Thomas Speck (University of Freiburg)

In many areas of fibre-reinforced composite technology there is a great need for a solution of how to manufacture nodal elements and/or ramifications with an optimised force flow. Examples are hubs of wind-power plants, branch points in framework constructions in building industry, aerospace, ramified vein prostheses in medical technology or the connecting nodes of bicycle frames. From this motivation, investigations were carried out in order to assess the potential of hierarchically structured plant ramifications as concept generators for innovative, biomimetic branched fibre-reinforced composites. Ramified plant species with pronounced fibre matrix structure served as biological models, amongst others monocotyledons of the genera *Dracaena* and *Freyinetia*. These plants possess a special hierarchical stem organization, which markedly differs from that of other woody plants by consisting of isolated fibres and/or wood strands running in a partially lignified basic tissue matrix. The plants exhibit Y- and T-shaped ramifications, which in their angles resemble those of the branched technical structures. Our preliminary investigations confirm that the ramifications possess mechanical characteristics interesting for a transfer into technical applications, such as a benign breaking behaviour, a good oscillation damping caused by high energy absorption and a high potential for lightweight construction. The results demonstrate the high potential for a successful technical transfer and lead to the development of concepts for producing demonstrators in lab scale that already incorporate "solutions inspired by nature".

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A6.10**Poster Session - Tuesday 30th June****Passive oscillation damping in plant stems**

Tobias Seidl (European Space Agency), Amelie Barth (Universitaet Freiburg, European Space Agency), Thomas Speck (Universitaet Freiburg)

Spacecraft design calls for careful reduction of technical complexity to reduce the risk of failure and hence, any reduction of parts and active control systems used is desired. In the present study we investigate on the potential of technological inspiration of plant stems for the implementation of passive oscillation damping mechanisms in satellite booms, which could one day remove active oscillation damping systems. In a pilot study we chose four available plant models with the following common features: 1) straight unbranched stems with high aspect ratio, 2) absence or easy removability of leaves, 3) non-lignified tissues, and 4) loads concentrated on the apex. The damping properties of *Allium tuberosum*, *Cyperus alternifolius*, *Equisetum hyemale*, and *Papaver somniferum* were determined in a deflection experiment. In a second experiment, the tissue distributions were characterized via FCA-stained cross-sections of the stems and polar and axial moments of inertia were calculated. First results show that *Papaver* and *Equisetum* exhibit strongest damping properties among the analyzed but employ different mechanisms: *Papaver* has a damping ratio of 0.041 and achieving its decay constant of 2.26 (1/s) through high angular frequencies (55.2 rad/s). *Equisetum* oscillates at lower angular frequencies (17.86 rad/s) but employs high damping per cycle (damping ratio: 0.066) reaching a similar decay constant of 1.17 (1/s). Their performance is comparable to high-performance booms made of carbon-fiber composites and hence, future work addresses both the influence of the structural arrangement of sclerenchyme tissue as well as potential biomimetic transfer to technical booms.

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A6.11

13:30 Sunday 28th June 2009

The impact of branch flexibility on orangutan locomotion

Susannah K. Thorpe (University of Birmingham)

Orangutans are nature's largest habitually arboreal mammal. For them, as for all arboreal mammals, access to the abundant fruits and narrowest gaps on the thin peripheral branches of tree crowns, poses considerable energetic demands and safety risks. Predictions suggest that the flexibility (compliance) of branches, and their long elastic recoil time compared to the cycle time of most quadrupedal gaits, means that arboreal mammals will lose energy to branches during locomotion. Locomotion on peripheral branches that are particularly small in diameter compared to the mass of an animal will therefore be particularly expensive. To assess the effect of support compliance on locomotion in a diverse locomotor habitat, we conducted a year long field study of orangutan locomotion and associated ecological variables, in particular the diameter of the supports used for locomotion. Most arboreal primates use flexed-limb postures to deal with problems caused by branch compliance and instability. But, we will show that Sumatran orangutans exhibit unique strategies to control support compliance and facilitate access to the terminal branch niche for feeding and gap-crossing.

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A6.12

13:50 Sunday 28th June 2009

Brachiation kinematics: The effects of support variation

Fana Michilsens (University of Antwerp), Kristiaan D'Avoult (University of Antwerp), Peter Aerts (University of Antwerp)

Gibbons live in a complex, three-dimensional environment and motions of the limbs and the centre of mass oscillations must thus be ready to adapt to the changing support opportunities. Yet, until now, all studies on brachiation mechanics in gibbons have been done in a predictable environment with fixed handholds, horizontally placed at fixed intervals. We will provide and compare kinematic data of siamang brachiation on three different setups. Setup 1 gives the animals the opportunity to choose their step length within a fixed range (handholds of 30 cm long are placed 50 cm apart, parallel with the direction of movement), while setup 2 restricts this freedom by placing the handholds perpendicular to the direction of movement (80 cm apart). Setup 3 is similar but has the handholds placed at different heights. Preliminary results show a small trend of decreasing energy recovery (ER) with increasing stride length (SL) and forward velocity, regardless whether the SL was induced or freely chosen. Interestingly, the animals mostly preferred SL's between 1m60 and 1m80, where the ER varies considerably (30% to 70%). This might indicate that SL is not a restricting factor concerning ER. Average ER seems low (50%), but 3D analyses show smooth trajectories of the centre of mass, indicating minimal collisional loss (Usherwood and Bertram 2003). We will proceed to use different setups to assess which variables impact energy recovery and collisional losses most and how robust (or not) gibbon locomotion is with respect to support variation.

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A6.13

14:10 Sunday 28th June 2009

Turning performance of horses

Huiling Tan (Royal Veterinary College), Alan Wilson (Royal Veterinary College)

Sprinting around a bend increases effective body weight as body mass experience both gravity and centripetal acceleration equal to v^2/r . Human maximum running speed has been shown to be limited by the ground reaction force legs can withstand and the maximum speed of human sprinters is lower on a bend with a speed reduction that is concomitant with a leg force limit. Greyhounds and mice do not have to run slower on a curve partly due to the decoupling between muscles for weight support and propulsion in quadrupeds. Here we explore the limits of turning performance in horses and dogs trained to perform maximum rate turns.

We collected horizontal speed and heading from polo horses undertaking maximum rate turns under field conditions during training ($n = 5$, 5 turns) and during a real competitive polo game at a range of speeds ($n = 16$; 200 turns) using mobile data collection techniques based on GPS and inertial sensors. The maximum angular velocity observed was 5 rad/s achieved at a horizontal speed below 2 m s^{-1} . The data fitted a model of a limiting centripetal acceleration, which was 8 m s^{-2} during the training for sharp turns on sand surface and surprisingly only 5.5 m s^{-2} during the polo game on grass surface. This may represent a safe grip limit in generating horizontal force or mechanical factors involving limb interference. We are therefore repeating these experiments on dogs and horses under different grip conditions and exploring methods of adding mass to turning dogs.

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A6.14**14:30 Sunday 28th June 2009****The roll plane: Body lean angle and ground reaction forces in turning goats**

Carlos Moreno (Harvard University), Andrew Biewener (Harvard University)

The mechanics of high-speed turning in terrestrial animals are not fully understood. Studies in terrestrial animals with a variety of body configurations have addressed the roles of limbs in deflecting the COM and producing yaw moments in the horizontal plane, but few have measured body lean in humans and other upright-postured bipeds and quadrupeds, perhaps due to the experimental challenges involved with a continually changing local coordinate system.

We measured a variety of kinematic and kinetic parameters in goats executing trotting and galloping turns. We first sought to describe the role of each limb during turning, and then to describe the relationship between the body lean angle and the lateral ground reaction force (GRF) generated to oppose the centrifugal force that occurs as a consequence of traveling along a curve. We developed a simple geometric model based on average angles and forces exerted by diagonal pair couplets in trotting and by all four limbs in galloping.

We also developed animations to visualize the alignment of the individual and summed limb forces with the estimated center of mass (COM) position and proximal limb joints. We found that the resultant GRF aligned more closely with the COM in trotting, whereas, in galloping, the GRF frequently caused net positive roll moments into the turn. This may be related to reduced traction on the surface of the runway. Combining experimental data with theoretical models can help us better understand complex non-steady behaviors.

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A6.15**14:50 Sunday 28th June 2009****Development of equine locomotion with age is linked to tendon stiffness**

Pauline Addis (Newcastle University), Sian Lawson (Newcastle University)

The equine distal limb can be represented as a passive mass-spring model, with age-related changes in locomotion expected due to increasing body mass. Normalisation to mass allows independent investigation of the influence of age on locomotion. The stiffness of the tendon "spring" has been found to increase during maturation and decrease after the onset of degeneration. The equine superficial digital flexor tendon (SDFT) and deep digital flexor tendon (DDFT) support the metacarpo-phalangeal (MCP) and distal interphalangeal (DIP) joints, thus age-related kinematic changes could be expected in these joints.

Kinematics of 39 horses were investigated with the hypothesis that maximum MCP and DIP angles decrease during tendon maturation and increase during tendon degeneration. Horses were divided into three age groups: 5.5 to 36 months, 36 to 100 months and 100 to 212 months. Videos of the distal forelimb of horses led in walk at self-selected speed were digitised with an automated marker-free tracking technique to obtain maximum MCP and DIP joints angles. After normalisation to mass, the Pearson correlation coeffi-

cient of joint angle with age in young horses was -0.85 ($p=0.000$) and -0.74 ($p=0.001$), for the MCP and DIP respectively. In mature horses, the correlations were only 0.06 in the MCP and 0.07 in the DIP. In older horses, the correlations were 0.67 ($p=0.048$) and 0.89 ($p=0.001$) for the MCP and DIP, respectively. These results indicate an effect of age, above that of mass, in young and older horses, suggesting that the changes to mechanical properties of tendon during maturation and degeneration affect locomotion.

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A6.16**15:40 Sunday 28th June 2009****Chickens on the cheap: Broiler chicken walking mechanics**

Heather Paxton (Royal Veterinary College), John R. Hutchinson (Royal Veterinary College), Sandra A. Corr (Royal Veterinary College), Monica A. Daley (Royal Veterinary College)

Artificial selection plays a major role in the intensive rearing of broilers, producing birds with rapid growth rates and large pectoral muscle mass to boost economic gain and meet the demands of the consumer. Unfortunately, their obvious change in body conformation has been linked to gait alteration, which may affect bone development and therefore be the underlying cause for some skeletal disorders as well as other pathologies. Here we investigate whether this alteration in basic morphology has indeed altered the way these birds walk, and whether their noticeable postural change means these birds experience increased mediolateral forces requiring excessive work. We collected force plate data and kinematic data from 22 birds, (including two breeding lines) over a range of walking speeds, to quantify the 3D movements of the centre of mass and determine the capacity of these birds to recover mechanical energy through pendulum-like energy exchange. Peak craniocaudal and mediolateral forces were similar, and represented approximately 10% of the peak vertical force, as seen in other erect species. However, the mediolateral impulse was in some cases two times larger than the craniocaudal impulse, which could be linked with their seemingly awkward plodding gait, with short sharp steps or increased roll at the hip. Energy recovery was unexceptional (~50%) and increased with speed, characteristic of human walking at comparably slow speeds. Similar to penguin waddling, 3D consideration of broiler chicken pendular mechanics led to improved estimates of recovery.

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A6.17**16:00 Sunday 28th June 2009****External, internal and total work during locomotion in Asian elephants**

Joakim Genin (Université Catholique de Louvain), Norman Heglund (Unité de physiologie et biomécanique de la locomotion Université Catholique de Louvain), Patrick Willems (Unité de physiologie et biomécanique de la locomotion Université Catholique de Louvain)

The exceptional size and unique shape of the elephant result in the lowest mass-specific metabolic cost of walking ever measured, but their effect on the mechanical work of elephant locomotion is poorly

understood. Therefore we measured the work (W_{ext}) required to move the centre of mass (CoM) in 34 Asian elephants (872–4000 kg) with a force platform. We also measured the work (W_{int}) required to move the limbs relative to the CoM from high-speed video. The total mechanical work (W_{tot}) was calculated as $W_{\text{ext}} + W_{\text{int}}$.

W_{ext} is $\sim 0.16 \text{ J kg}^{-1} \text{ m}^{-1}$ and varies little with speed, showing a minimum at 1.55 m s^{-1} and increasing slightly up to the maximum measured speed of 4.94 m s^{-1} . W_{int} is somewhat less than W_{ext} at low speed, increasing strongly with speed. The $W_{\text{int}}:W_{\text{ext}}$ ratio attains a value of 3:1 at top speed, a much higher ratio than seen in cursorial animals (even heavy-legged humans at much higher speeds only reach $\sim 2:1$). This high ratio could very well represent a speed limiting factor in elephants. The increase in W_{int} shows no discontinuity, indicating that elephants use one gait throughout their entire speed range.

Contrary to the current conception that mass specific mechanical work is independent of body size, this study shows that W_{tot} tends to decrease with body mass. Elephants only develop 25–55% of the mass-specific W_{tot} of other animals. At an optimal speed of 1.33 m s^{-1} their W_{tot} is $0.37 \text{ J kg}^{-1} \text{ m}^{-1}$ and their metabolic cost is $0.84 \text{ J kg}^{-1} \text{ m}^{-1}$, resulting in a maximum locomotion efficiency of 44%.

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A6.18

16:20 Sunday 28th June 2009

High speed locomotion: Insights from cheetahs and racing greyhounds

Penny E. Hudson (Royal Veterinary College), Sandra A. Corr (Royal Veterinary College), Rachel C. Payne (Royal Veterinary College), James R. Usherwood (Royal Veterinary College), Alan M. Wilson (Royal Veterinary College)

The ability to achieve high speed is essential for the survival of many species for both prey capture, and escape from predatory attacks. The cheetah (*Acinonyx jubatus*) is widely acknowledged as the fastest living land mammal capable of speeds up to 28.6 m s^{-1} . The racing greyhound has been selectively bred for high speed and aerobic capacity, but can only achieve 17 m s^{-1} during a race. We have recorded anatomical data on both species and are comparing the kinematics and kinetics of the cheetah and greyhound in order to investigate how cheetahs attain such high speeds.

We collected architecture and moment arms of the forelimb and hindlimb muscles of eight cheetahs and three greyhounds. We also obtained ground reaction force and kinematics during moderate speed galloping for several other cheetahs and greyhounds whilst they chased a mechanical lure along a 90 m runway containing six Kistler force plates and were filmed using four AOS high speed cameras (1000 Hz).

Preliminary data shows that at a sub maximal speed ($14\text{--}17 \text{ m s}^{-1}$) cheetahs have similar stride length, stride frequency and duty factors to greyhounds at their maximum speed (17 m s^{-1}). When scaled geometrically, increased limb bone diameters in cheetahs (with the exception of the fibula) may indicate stronger limbs as an adaptation for lower duty factors. Our current goal is to collect cheetah data at higher speeds to explore whether this is indeed the case; whether cheetahs at top speeds use exceptionally low duty factors and high relative limb forces.

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A6.19

16:40 Sunday 28th June 2009

Increased whole body inertia decreases maximum attainable running speed in humans

Mark V. Bowtell (Royal Veterinary College), Huiling Tan (Royal Veterinary College), Alan M. Wilson (Royal Veterinary College)

It has been shown that increased effective weight by bend running limits speed for humans, unlike greyhounds, due to the force that can be withstood by the legs whilst in contact with the ground. This has also been shown to account for differences in attainable speed across human individuals, and in a previous study we found that a 30% decrease in effective body weight allowed a 3.3% increase in attainable speed (s.e. 1.4%).

Here we measured the effect of increased inertia, independent of weight, on achievable speed by using a novel feedback-controlled treadmill and partial suspension system. Eight participants attempted maximum speed three times in each condition (normal, increased inertia only, increased weight and inertia, normal). Kinematic data and foot event timings were analysed.

We found that unchanged weight and 30% increased inertia caused a 6.8% decrease in attainable running speed (s.e. 1.7%); a much smaller effect than 30% increased weight and inertia (14.2% decrease, s.e. 2.1%). Preliminary analyses of kinematic data suggest that, with increased inertia, centre of mass vertical excursion is reduced and the leg is more flexed during stance. The increase in duty factor (6.8%) is proportional to the decrease in speed.

The decrease in speed suggests the existence of a limit to running speed that is not the direct result of effective gravity or leg swinging. We consider the presence of a power limit by gaining insight from downhill treadmill running (decreased power requirement) and overground running (increased power requirement).

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A6.20

17:00 Sunday 28th June 2009

Measurement of ground reaction forces in wood ants during straight locomotion on a level surface

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The biomechanics of running in small animals have remained poorly characterized due to the difficulty of recording three-dimensional ground reaction forces. Currently available techniques limit investigations to animals with a body mass above 1 g. Here we present for the first time single-leg ground reaction forces of Central European wood ants (foraging workers of *Formica polyctena*, body mass $\approx 10 \text{ mg}$), measured with a custom-built miniature force plate. These ants populate shrubs and meadows, i.e. highly structured habitats. Accordingly, the foragers typically have to climb. We investigated forces and high-speed kinematics for straight level runs (average speed: 8.4 cm s^{-1}). Both, the time course of ground reaction forces and the kinematics differed strongly from previous observations in larger insects. Maximum vertical force was reached during the first third of the tripod contact phase. During this period the body was decelerated predominantly by the front legs. Subsequently, the front legs pulled and accelerated the body. This "climbing" type of

stride may be useful on the bumpy and unstable substrates that the animals face in their natural habitats, and may therefore also occur on level ground. Propulsive forces were generated predominantly by the front and hind legs. Dragging of the gaster on the substrate resulted in a breaking momentum, which was compensated by the legs. Future investigations will reveal, whether the identified pattern is due to specialization.

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A6.21

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Leg parameter adaptation for stable running

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Human locomotion can be described as a series of alternating stance and swing phases. Due to its simplicity and explanatory power, the spring-mass model is an adequate and popular mechanical template to describe human gaits like walking and running: The complex structure of a human leg is simplified by a linear spring supporting a point mass, which represents the body's center of mass. In order to control a desired running pattern at a given system energy, we consider a linear adaptation of the leg parameters (angle of attack, leg stiffness and leg length) during late swing phase. The proposed swing-leg control is capable of generating or enlarging the predicted region of stable running, characterized by combinations of appropriate leg adjustment rates. The redundancy of these control policies provides versatility and flexibility to the system and can therefore be used to match additional requirements during locomotion, such as desired foot placement strategies (e.g. to achieve sufficient ground clearance or ground speed matching). Taking this into account, the control strategy can be considered as a trade-off between stable and comfortable (e.g. low impact) running. Surprisingly, it is found that minimizing impacts at touch-down has a negative side-effect on running stability. This is in agreement with experimental data, showing that subjects do not significantly reduce the landing impacts by the selected swing leg strategy, even when they are running barefoot.

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A6.22

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Swing-leg strategies for stable dog trotting

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The trotting gait of quadrupeds seems to be similar to bipedal running. In both, specific leg behavior has been observed for the swing-leg moving backwards just before touch down. This swing-leg retraction at the end of the swing phase allows for adaptation to ground speed.

In this study, the effect of swing-leg retraction was examined using an enhanced spring-mass model to identify the influence on locomotion of four-legged animals during trotting. The planar model consists of a rigid body and springs represent legs which are attached at anterior and posterior ends of the body. Model parameters are based on experimental data collected from experiments on dog trotting on an instrumented

treadmill (Kistler force sensors, Qualisys motion capture). Spatiotemporal and dynamic data show that trotting is closely related to human running with legs acting like springs. Simulations predict no self-stability with fixed angles of attack at a trotting speed of 2 m/s. The trotting gait can be stabilized by applying swing-leg retraction, however, the dog's retraction speed was higher than predicted. Introducing adaptation of leg stiffness (i.e. leg stiffening) during retraction largely increases trotting stability, diminishing disturbances after a few steps. These combined leg strategies (retraction and leg stiffening) for stabilizing gait further explain why legs retract and muscle activity increases before touch down.

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A6.23

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Kinematic variability for dynamic stability in human gait

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Greater kinematic variability in human gait is often considered as negative impact on dynamic stability. Interestingly, findings from studies on human walking suggest that gait stability may be improved at the cost of local variability.

To get more insight into kinematic and spatial-temporal variability in human gait, we looked at data previously collected of 21 human subjects walking and running on a treadmill.

Both gaits show periods of high and periods of low variability on the joint level within the gait cycle, but time lines are gait-specifically different. Highest variability is found in midstance of walking and during swing phase in running. In contrast, variability is reduced at midstance in running and during double-support in walking. Thus, gait stability seems not to rely on continuous kinematic invariability but allows periods of high variability which are tolerated by the locomotor system. These findings might indicate that the double-support phase in walking has a similar function as the single-support phase in running: both diminish kinematic variability during loading of the system and then accelerate the center of mass (CoM) upward. Conversely, the flight phase in running corresponds to single-support in walking with increased kinematic variability during unloading of the system and subsequent downward acceleration of the CoM. However, the stabilizing mechanisms during ground contact are inherently different for both gaits with two legs simultaneously accelerating (trailing leg) and breaking (leading leg) the CoM in walking and one single leg first decelerating and finally accelerating the CoM in running.

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A6.24

11:30 Monday 29th June 2009

Aerodynamic performance of flapping flexible wing in insect flight

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Insect wings are complex, deformable structures that change shape dynamically due to inertial and aerodynamic forces during flight. The large flexibility of insect wings often leads to complex fluid-structure interactions, while the kinematics of flapping and the

spectacular maneuvers result in highly coupled nonlinearities in fluid mechanics, aero-elasticity, and flight dynamics. Such effects of wing structure and dynamic shape changes on unsteady aerodynamic force production in flapping flight are important, intersecting with some of the richest problems in Micro Air Vehicles but still remain unknown yet.

We present here, for the first time, a comprehensive study of computational aerodynamics of three-dimensional, flapping and flexible insect wings by solving the nonlinear problem of fluid–structure interactions. An integrated and rigorous computational framework has been established by coupling an *in-house* CFD-based insect dynamic flight simulator (Liu, 2009) and a recently developed FEM-based structural dynamics solver. Our computational model is capable to integrate realistic wing–body morphology, realistic wing–body kinematics, aerodynamics including wing–wing and wing–body interactions, and their interactions with structural dynamics of flexible wings.

Computed results reveal that the flexibility of wings can delay burst and stall of the leading-edge vortices, and hence enhance aerodynamic performance of flapping wings. Our results not only offer an integrated interpretation on the similarity and discrepancy of the unsteady aerodynamics between rigid and flexible wings in insect flapping flight but also demonstrate that our methods can be an effective tool in the MAVs design.

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A6.25

11:50 Monday 29th June 2009

Passive unsteady aerodynamic force of a swallowtail butterfly

Hiroto Tanaka (The University of Tokyo)

In forward flight of a swallowtail butterfly, the body moves up and down due to the low-frequency flapping motion. By using a tailless ornithopter with the dimension of a swallowtail butterfly, we demonstrate that the up–down body motion is caused passively without active feedback control and produces unsteady large aerodynamic force. We evaluated aerodynamic force of the free-flying ornithopter by measuring the acceleration of the gravity center with a high-speed video camera. We also measured the lift and drag curves of the wing in steady flow with a load cell. As a result, lift coefficient at the beginning of the downstroke in free flight was much higher than that in steady flow. This lift enhancement was thought to be an unsteady aerodynamic effect so called “delayed stall” and caused by a large angle of attack due to the passive up–down body motion. Finally, we compared a forward flight of an actual swallowtail butterfly with that of the ornithopter. The body motion and oscillation of the angle of attack of the butterfly were similar to those of the ornithopter, and a large aerodynamic force at the beginning of downstroke was also seen. These results suggest that a swallowtail butterfly makes use of a passive body motion to enhance their aerodynamic force.

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A6.26

12:10 Monday 29th June 2009

Vortex flow visualization of a flapping butterfly wing performing a fixed flight

Masaki Fuchiwaki (Kyushu Institute of Technology)

The authors have conducted a flight observation experiment of *Cynthia cardui* and clarified behaviors of its wing in its flight. By spacial evaluation of the wing in a flapping flight, the authors have clarified that flapping angles of the butterfly have periodic triangular waveforms and the ratio of the time needed for flap-up and flap-down is approximately 1:1.25. Moreover, we have clarified that the wing deforms elastically not only in the wing chord direction but also in the wing span direction. Furthermore, we evaluate dynamic behaviors of a wing observed from the butterfly's viewpoint in its flight. The butterfly realizes its flapping motions by changing not only flapping angles but also lead-lag angles in free and fixed flights. In particular, in a free flight, a butterfly performs flapping by greatly changing feathering angles in the wing span direction and furthermore, it has been found that its vein at the wing tip twists in opposite phase around the body and wing tip. In this study, we evaluate the detailed vortex flow structure on a flapping butterfly wing. In particular, the authors conduct a PIV measurement around a flow field of the flapping butterfly wing, *C. cardui*, performing a fixed flight. We clarify the vortex flow structure developed in the wing chord direction on a flapping butterfly wing and we aim at clarifying the relation between the vortex flow structure on the wing and the dynamic behaviors of the wing.

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A6.27

13:30 Monday 29th June 2009

Bat flight – Comparison of kinematics and aerodynamics between two nectar feeding species

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Kinematics, the movements of the wings in the air, and aerodynamics, the aerial footprint of the wing movements, together provide a basis for understanding the mechanisms of animal flapping flight. The wing movements generate vortices that reflect the forces to overcome weight and drag. We can now measure both the wing movements and the vortices with high time resolution, using high speed stereo filming and digital particle image velocimetry (DPIV) for flow visualization.

Here we present data on the kinematics and aerodynamics of two nectar-feeding bat species (*Leptoncycteris yerbabuena* and *Glossophaga soricina*). These two tropical Glossophaginae have similar morphology but differ in size (with 25 g and 10 g body mass respectively), which allows for an optimal comparison of the effects of body size. The experiments were performed in a low-turbulence wind tunnel over the entire speed range at which the animals would fly, using the same experimental setup for both kinematics and flow visualization for both bat species.

We found surprisingly few differences in flight style between the two differently sized bat species. Although we examined many

different parameters, such as angle of attack, downstroke ratio, stroke plane angle and span ratio, the only significant difference was the wing beat frequency, which was clearly size dependent. Also the aerodynamic properties were very similar, with features typical of bat flight present in both species, including separate vortices shed from the wing root as well as during the transition of up- and downstroke associated with a small amount of negative lift.

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A6.28

13:50 Monday 29th June 2009

Aerodynamic costs of flying with holey wings

Melissa S. Bowlin (Lund University), Florian Muijres (Lund University), Christoffer Johansson (Lund University), Rhea Von Busse (Lund University), Anders Hedenström (Lund University)

Molt, or feather replacement, is a significant event in the avian annual cycle. It has important consequences for migration performance and, ultimately, fitness. However, molting strategies, which include the timing of molt in the annual cycle, the rate of molt, and the number of feathers dropped at a time, vary widely among avian species for reasons we do not yet understand. One cause of this uncertainty is that we have not yet measured the aerodynamic costs of molt. Here we present data on the kinematic and aerodynamic consequences of experimentally-induced molt gaps in the pied flycatcher (*Ficedula hypoleuca*). Using PIV analysis, we show that the total circulation per wingbeat, and therefore induced drag, increases dramatically following experimentally-induced molt. This appears to be due to the fact that molting wings generate two tip vortices, one from the actual tip of the wing and one from the feathers just proximal to the molt gap. We discuss the implications of these results for the scheduling of molt in the annual cycle and for scientists collecting wing feathers for stable isotope analysis.

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A6.29

14:10 Monday 29th June 2009

Aerofoil sections from a Steppe eagle *Aquila nipalensis* in free flight: Wind tunnel and computational testing

Anna C. Carruthers (Oxford University), Adrian L. Thomas (Oxford University), Simon M. Walker (Oxford University), Graham K. Taylor (Oxford University)

Birds naturally occupy the Reynolds number regimes, $10^3 < Re < 10^5$, in which unmanned and micro air vehicles are now being developed to fly. The mechanisms that birds use to control their flight are of interest for adaptation to these aircraft for improved control and manoeuvrability in highly unsteady air flows. High speed (500 Hz) and onboard (50 Hz) video analysis of a Steppe eagle *Aquila nipalensis*, has revealed a leading edge flap comprised of lower surface coverts on the arm wing. The feathers passively deflect during unsteady manoeuvres when the angle of attack rapidly increases and possible functions of this device are discussed.

The wing of an eagle in free flight during a gliding perching sequence, when the leading edge flap is deflected, has been reconstructed and modelled. The software has been written and developed in Matlab, within the Department of Zoology. Multiple

camera photogrammetry is used to identify natural markers on the bird's wing to reconstruct 3D point data. The arm wing surface is modelled using regression techniques and the optimised model, with a confidence interval of 92%, has constant aerofoil shape but allows for variation in chord, twist, and bending. A manufactured 2D aerofoil section based on this model is tested in the wind tunnel and the results, both with and without leading edge flap, are presented. Comparisons are made with preliminary results from CFD (Fluent) modelling of the 2D aerofoil section.

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A6.30

14:30 Monday 29th June 2009

Effects of flight speed upon muscle activity and metabolic rate in hummingbirds

Bret W. Tobalske (University of Montana), Tyson L. Hedrick (University of North Carolina), Andrew A. Biewener (Harvard University), Douglas R. Warrick (Oregon State University), Donald R. Powers (George Fox University)

Hummingbirds are hypothesized to represent an extreme among birds for their morphological and physiological adaptations for powered flight. We tested whether rufous hummingbirds (*Selasphorus rufus*, 3.5 g) vary muscle activity and metabolic power differently from other birds by flying them over a wide range of speeds in a wind tunnel. We measured electromyographic (EMG) activity in the pectoralis and supracoracoideus ($n=4$) and rates of oxygen consumption ($n=6$). Previous research indicated that hummingbirds used unique single-spike "twitch" contractions in their pectoralis during hovering and that spike number and spike amplitude increase during forward flight. Our EMG measurements likewise showed the amplitude of EMG increasing with flight speed; however, multiple spikes (3–5) per EMG were exhibited at all speeds including hovering, and speed did not have an effect upon spike number or EMG duration. Variation in EMG amplitude was comparable to that in larger species, so we conclude that flexibility in motor-unit recruitment is not correlated with body size. Previous research also suggested that metabolic power in hummingbirds varies with flight speed according to a "J" shaped curve – a surprising result given that the mechanical power required for flight is predicted to be greater at low speeds. Our measures of oxygen consumption revealed a "reverse-J" curve with significantly higher metabolic rate during hovering. Our EMG and metabolic data reveal that muscle use in hummingbirds is not particularly optimized for hovering. This helps explain why they are adept at forward flight and use long-distance migration. NSF IOB-0615648.

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A6.31

14:50 Monday 29th June 2009

Mechanisms of takeoff and landing flight in columbids

Angela M. Berg (Harvard University), Andrew A. Biewener (Harvard University)

When taking off, a bird accelerates in the forward direction; when landing, it accelerates in the rearward direction. We sought to understand how the kinematics of the wings and tail result in the

forces required for a bird to accelerate during takeoff or landing. Using high-speed video, we obtained kinematics of pigeons (*Columba livia*) taking off from and landing on a perch. Birds took off with horizontal body angles and landed with their bodies pitched upward, occasionally beyond the vertical. Dramatic differences were also found in the downstroke plane angle, which was up to +45° during takeoff and as low as –20° during the final wingbeats of landing. During takeoff, the geometric angle of attack during mid-downstroke was as shallow as 0°; during landing, it increased to above 45°. In both flight modes, the tail was broadly flared.

We hypothesized that during takeoff these kinematic features each decreased drag or increased forward force, while during landing, these features increased drag and produced rearward force. Digital particle image velocimetry (DPIV) data collected from pigeons (*C. livia*) and ringneck doves (*Streptopelia risoria*) support these hypotheses. DPIV data have also revealed a strong downwash during landing that frequently has a forward component. In addition, despite the low flight velocities and high geometric angles of attack during landing, DPIV data have not shown strong flow separation over the wings.

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A6.32

15:40 Monday 29th June 2009

Evidence for self-cleaning in fluid-based smooth and hairy adhesive systems of insects

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Insects possess versatile adhesive organs for attachment to a range of surfaces. They are able to recycle this adhesion throughout their lifetime even when they are exposed to contamination. Many insects groom, but an additional self-cleaning property of adhesive organs may be an extremely important adaptation to remove contamination. To investigate a self-cleaning property of insect pads, we measured adhesion forces on glass when contaminated with microspheres. We show that both smooth pads of the Indian stick insect (*Carausius morosus*) and hairy pads of dock beetles (*Gastrophysa viridula*) are self-cleaning adhesives. Insects with contaminated feet recovered high levels of adhesion after only eight steps: this was correlated with the deposition of spheres. However, recovery required a proximal sliding movement while in contact. Particle size had a significant effect on the rate of recovery in the hairy adhesive system of the beetle, but not in the smooth system of the stick insect. Our results suggest that hairy pads possess an increased efficiency of self-cleaning over smooth pads.

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A6.33

16:00 Monday 29th June 2009

Structural correlates of adhesion and friction in tree frog toe pads

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Knowledge of both surface structure and physical properties is essential to understanding any adhesive system. In this study of the

tree frog, *Litoria caerulea*, we combine techniques that investigate the microstructure and properties of the toe pad epithelium with methods that examine the thickness of the fluid layer beneath the pad. Under the microscope, the toe pads can be shown to consist of a hexagonal array of flat-topped epithelial cells, separated by mucus-filled channels. Atomic force microscopy shows this 'flat' surface to be highly structured at the nano-scale, consisting of a tightly packed array of columnar nanopillars, 326 ± 84 nm (mean \pm SD) in diameter. In fixed tissue (transmission electron microscopy), the nanopillars are approximately as tall as they are broad. Although the whole toe pad is extremely soft and easily deformable, the epithelium itself is slightly stiffer, having an Effective Elastic Modulus equivalent to that of silicone rubber (median = 5.7 MPa), as measured by nano-indentation. Interference reflection microscopy of living adhering frogs indicates that the fluid layer beneath hexagonal cells in close contact is extremely thin (median thickness = 6 nm), and the areas in close contact may become even larger when frogs are tilted and thus need to adhere. These findings are discussed in terms of maximising capillary adhesion and boundary friction by conforming closely to surface irregularities at different length scales.

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A6.34

16:20 Monday 29th June 2009

Attachment forces of single tarantula adhesive setae

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Spiders and geckos have convergently evolved dry fibrillar adhesives on their feet that allow them to climb smooth vertical surfaces. These two types of adhesives are materially and morphologically distinct. Gecko adhesive fibrils ("setae") branch dendritically, into small flattened tips (called "spatulae"). Spider setae are paddle-shaped, with a planar array of spatulae at a constant (ca. 5 μ m) height from the stalk. In this study I present the first attachment force measurements for single setae from both the claw tufts and tarsal pads of a spider, the theraphosid *Grammostola rosea*. Claw tuft setae, like claws, are oriented to engage with the substrate during a pulling motion of the foot. *G. rosea* additionally bear setae on the ventral surface of the tarsus, which are oriented to engage during pushing motions. I measured the frictional and adhesive forces generated when individual setae attached to a glass substrate and detached at various angles, corresponding to different motions of the feet. These preliminary data suggest that claw tuft setae detach at lower angles with respect to the substrate than tarsal setae, but that they otherwise function similarly. Future studies will integrate single seta function with the kinematics and ground reaction forces of individual legs during climbing.

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A6.35

16:40 Monday 29th June 2009

The frictional properties of human finger pads

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It is generally assumed that fingerprints improve the grip of primates, but the efficiency of their ridging will depend on the type of frictional behaviour the skin exhibits. Ridges would be effective at increasing friction for hard materials, but in a rubbery material they would reduce friction because they would reduce contact area. In this study we investigated the frictional performance of human fingertips on dry acrylic glass using a modified universal mechanical testing machine, measuring friction at a range of normal loads while also measuring the contact area. Tests were carried out on different fingers, fingers at different angles and against different widths of acrylic sheet to separate the effects of normal force and contact area. The results showed that fingertips behaved more like rubbers than hard solids; their coefficients of friction fell at higher normal forces and friction was higher when fingers were held flatter against wider sheets and hence when contact area was greater. The shear stress was greater at higher pressures, suggesting the presence of a biofilm between the skin and the surface. Fingerprints reduced contact area by a factor of one third compared with flat skin, however, which would have reduced the friction and casts severe doubt on their supposed frictional function.

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A6.36

08:20 Tuesday 30th June 2009

Patterns of motor unit recruitment in feline ankle extensor muscles during different motor tasks

Emma F. Hodson-Tole (Manchester Metropolitan University), Robert J. Gregor (Georgia Institute of Technology), Huub Maas (VU University), Brad J. Farrell (Georgia Institute of Technology), Boris I. Prilutsky (Georgia Institute of Technology)

Investigation of the time-varying recruitment of different motor unit (MU) populations is now possible as a result of advances in signal processing techniques of myoelectric signals. In the cat, interplay between the ankle extensor muscles [Gregor et al., 2006] and between regions of known fibre type populations within these muscles [English, 1984] varies in response to different motor demands. Specific details of the recruitment of MU populations within these muscles have, however, only been reported in two previous studies [Hodson-Tole et al., 2008; Wakeling et al., 2002]. We present wavelet and principal component analysis of myoelectric signals from the plantaris (PL), soleus (SO), medial and lateral gastrocnemius (MG, LG) muscles of four cats, collected during walking on different inclines (0%, $\pm 50\%$) and the paw shake response (PSR). Analysis of whole stride and PSR revealed significant differences in principal component loading scores (PCLS) between conditions in three of the muscles (LG $p = 0.046$; MG $p = 0.03$; PL $p < 0.001$). During locomotion, recruitment of faster MUs occurred when greater force output was required (up-slope versus down-slope walking). When strides were partitioned into 10 equal time-windows, significant differences in PCLS occurred between conditions (SO $p = 0.034$; PL $p = 0.012$) and time windows (LG $p = 0.016$; MG $p < 0.001$; PL $p = 0.05$; SO $p < 0.001$). Results of PSR data revealed varied PCLS in LG and MG, which were influenced by the position of the individual shake within the whole PSR episode i.e. first, middle or last shake. The co-ordination of different MU populations therefore varies within and between muscles to facilitate force production during different motor tasks.

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A6.37

08:40 Tuesday 30th June 2009

Mechanisms underlying the sprint-endurance trade-off in rat lateral gastrocnemius muscle mechanics

Rob S. James (Coventry University), Isabel Walter (University of Sydney), Frank Seebacher (University of Sydney)

An important constraint on locomotor performance is the trade-off between sprint and endurance performance. One intuitive explanation for this trade-off is that muscles cannot be simultaneously optimised for both sprint and endurance performance. However, the mechanisms responsible for inter-individual variation in muscle performance are little known. The aim of this study was to test the hypotheses that inter-individual variation in muscle mechanics is associated with differences in: a) tissue metabolic capacities; b) expression of calcium handling proteins. Lateral gastrocnemius was dissected from 20 rats and subjected to isometric studies at 30 °C to determine muscle kinetics during both maximal and sustained activities. Metabolic capacities were estimated from lactate dehydrogenase, citrate synthase, and cytochrome c oxidase activities. Additionally, we determined SERCA1 protein concentrations, along with mRNA concentrations of isoforms of SERCA, troponin I and ryanodine receptors. There was a trade-off in muscle mechanics as higher fatigue resistance was associated with lower tetanic stress ($r = -0.536$, $P = 0.015$) and slower tetanus force relaxation rate ($r = -0.526$, $P = 0.017$). Higher tetanus stress was correlated with lower lactate dehydrogenase activity ($r = -0.473$, $P = 0.035$). Shorter time to half peak tetanus was correlated with increased ratio of fast to slow isoform expression of both troponin I ($r = 0.486$, $P = 0.030$) and SERCA ($r = -0.466$, $P = 0.038$). Pharmacological blockade of the ryanodine receptor significantly decreased peak tetanus force and muscle activation rates ($P < 0.001$), although blocking SERCA activity had no effect on muscle biomechanics. Overall these data indicate that muscle function is constrained by Ca^{2+} release.

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A6.38

09:00 Tuesday 30th June 2009

Muscle properties of the tibia-metatarsus joint flexors in the labidognath spider *Cupiennius salei*

Tom Weihmann (Friedrich-Schiller-University Jena), Tobias Siebert (Friedrich-Schiller-University Jena), Reinhard Blickhan (Friedrich-Schiller-University Jena)

Hydraulic leg extension in spiders seems to have contributed to their long-lasting success story. This hydraulic mechanism, amongst others, enables the increase of the flexor muscles cross-sectional area. In this study, for the first time, spider muscle dynamics were measured. We focused on the force-length and force-velocity relations of the flexors in the tibia-metatarsus joint of the second leg pair.

Five spiders were fixed permitting the flexion of the tibia-metatarsus joint exclusively. The distal end of the metatarsus was connected with a muscle lever system (Aurora Scientific 300B-LR). The flexors were stimulated supra-maximally via needle electrodes inserted into the ventral patella. We calculated muscle length changes and forces from the measured joint angles and moments using a geometric model.

We determined the force-length relationship by a series of isometric contractions at joint angles from 85° to 200° and the force-velocity

relation by a series of isotonic contractions. The maximum tension was 25 N/cm^2 at joint angles of $159.3^\circ \pm 6.9^\circ$, but even at 200° the muscles could still generate $71.5 \pm 13.0\%$ of the maximum moment. The force–velocity relation showed the typical hyperbolic characteristic ($v_{\max} = 5.7 L_{\text{opt}}/s$; $curv = a/F_{\max} = 0.34 \pm 0.07$).

At preferred locomotion speed spider muscles produce maximum power output. The characteristics of the force–velocity relation are similar to those of cockroach muscles (Ahn and Full, 2002). In spiders the effective mechanical advantage is comparatively small with regard to its prey. In turn, this enables relatively higher maximum running speeds.

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A6.39

09:20 Tuesday 30th June 2009

Modelling hydrodynamics and swimming efficiency of fish

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Fish vary greatly in body shape and swimming style. However, little is known about how these factors affect swimming efficiency. Although experimental data are available from case studies, such as on a mullet (*Chelon labrosus*) and an eel (*Anguilla anguilla*), these data are few, because experimental analysis of swimming fish is both difficult and time-consuming. Therefore questions remain. Here, we use a computer model of hydrodynamics to systematically study different swimming styles. The model is a recently developed mesoscale method, called Multi-Particle Collision Dynamics. We tune it to fit the experimental results of the mullet and the eel. We measure the resulting swimming efficiency and wake structure for different swimming styles as regards tailbeat frequency, wavelength and amplitude. From this, we generate new hypotheses to be tested with real animals.

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A6.40

09:40 Tuesday 30th June 2009

Managing fluid and wave resistances by whirligig beetles swimming on water surface

Jonathan Voise (IRBI CNRS UMR 6035), Jérôme Casas (IRBI CNRS UMR 6035)

Whirligig beetles (Coleoptera: Gyrinidae) are semi-aquatic insects with a very well adapted morphology and propulsion system to their life at the interface between air and water. When swimming on the water surface, beetles are submitted to both fluid resistance and wave resistance. The purpose of this study was to analyze the swimming speed, legs kinematics and capillarity waves produced by whirligig beetles on water surface in a simple environment. Whirligig beetles of the species *Gyrinus substriatus* were filmed in a large container with a high speed camera. Resistance forces were also

derived. We found that these beetles use three types of leg kinematics, differentiated by their sequence of leg strokes, two types at low speed and one type at high speed. Four main speed patterns were produced with different combinations of these types of leg kinematics, and the minimum speed for production of surface waves (23 cm s^{-1}) appeared to be an upper limit when beetles used low speed leg kinematics. Each type of leg kinematics produced characteristic capillarity waves, even if beetles moved slower than 23 cm s^{-1} . Our results indicate that whirligig beetles use low and high speed leg kinematics to avoid maximum wave drag and swim at speed corresponding to low resistances.

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A6.41

10:20 Tuesday 30th June 2009

Three-dimensional structure and hydrodynamics of the nasal passageway of a hagfish

Jonathan Cox (Bath University), Gavin Tabor (University of Exeter), Matthew Baker (University of Exeter), Philippe Young (Simpleware Ltd), Ross Cotton (Simpleware Ltd), Viet Bui Xuan (Simpleware Ltd), William Holmes (University of Glasgow)

Using magnetic resonance imaging, we have generated a three-dimensional data set of the nasal passageway of an *Eptatretus* species of hagfish, and converted this data set into real and virtual models. With these models we have been able to investigate the fluid dynamics of flow within the nasal passageway of the hagfish, and in particular in the olfactory region. We have found that the nasal passageway of this particular species of hagfish contains several physical devices that ensure that the surfaces on which the olfactory receptors are mounted are thoroughly ventilated, thereby optimising the chances of odorant capture. All in all, the olfactory organ of this hagfish species represents a sophisticated piece of natural engineering, and one which might conceivably be mimicked to create an artificial sensing device.

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A6.42

10:40 Tuesday 30th June 2009

Pivot feeding performance in pipefish and seahorses analysed by forward dynamic modelling

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Syngnathid fishes capture prey by rotating their head quickly towards prey, and subsequently sucking it into their snout. Previous studies showed that head pivoting is driven by elastic recoil of the epaxial muscle tendons. However, not only the head moves during pivot feeding in syngnathids: the head pushes off against the anterior part of the trunk, which is displaced in the opposite direction. Since the position of the trunk relative to the head is unique (for a fish) in some species of syngnathids (e.g. seahorses, seadragons), this could have consequences (or even be an adaptation) for pivot feeding. To

study the effects of several mechanical characteristics of the head and trunk during pivot feeding, a forward dynamic model of a pipefish and a seahorse was developed using Matlab-Simulink. In all simulations, an equal amount of elastic energy is released to actuate the joint between head and trunk. Increasing the pipefish's head-to-trunk orientation from parallel to perpendicular changes the path traveled by the mouth to become more distant from the initial location of the eyes, which may be favorable to avoid prey escape during the approach. However, in the latter case, the eyes must withstand considerably higher accelerations (+30%, >70 g) and the epaxial tendon system must be able to generate higher torques (+35%) to obtain a similar velocity of the mouth approaching the prey. The effects of stiffness and inertia of the trunk and the presence of a curved, neck-like morphology on prey-capture performance will also be discussed.

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A6.43

11:00 Tuesday 30th June 2009

Feeding performance in two chelonian frontier-runners: *Manouria emys* and *Sternotherus odoratus*

Egon Heiss (University of Vienna), Josef Weisgram (University of Vienna), Nikolay Natchey (University of Vienna)

Feeding performance in turtles is highly influenced by the surrounding medium: water or air. Due to the huge differences in viscosity of both media, getting food items into the mouth most effectively is highly contingent on anatomical and sub-anatomical adaptations. To date, many chelonians are known to be fully terrestrial, fully aquatic, or both terrestrial and aquatic. Such environmental shifts apparently occurred independently in different chelonian taxa. Both *Manouria emys*, the Asian forest tortoise, and *Sternotherus odoratus*, the American common musk turtle, show amphibious lifestyles. Both species try to feed in both media, but while *M. emys* is able to feed only on land, *S. odoratus* completes the feeding process only underwater, as shown by behavioral studies and the analysis of digital high-speed videos. Morphological studies on the oropharynx of both species involving computed tomography, light- and electron microscopy reveal the anatomical constraints that limit their food uptake to air or water, respectively. *M. emys* has a cartilaginous hyoid apparatus with a large, beefy tongue studded with tall, slender and mostly keratinized papillae along with giant mucus gland entities throughout the oral cavity. *S. odoratus*, in contrast, has a well-developed and largely ossified hyoid apparatus with a small and weak tongue bearing few lobe-like papillae that are never keratinized.

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A6.44

11:20 Tuesday 30th June 2009

Vertical posturing, defensive strikes, and leaping in African elapid snakes

Bruce Young (University of Massachusetts Lowell), Donald Schultz (Herp Recon)

Several African elapids, most notably the cobras (*Naja*) hold the forefront of their body vertically while defending themselves. This behavior is typically interpreted as a visual display intended to make the animal appear larger or more dangerous. This display comes at the cost of postural stability; as more of the body is held vertically, the torque exerted on the remainder of the body increases, which limits the snake's mobility. We used a combination of biomechanical analyses and high-speed video kinematics to examine this vertical posture. We then quantified the kinematics of defensive strikes which are launched from this vertical posture. These snakes typically use a kinetic chain style strike in which the pivot point with the ground accelerates first, and the head is the last part of the snake's body to move toward the target. Lastly we explored how some African elapids can exploit the vertical posture, and their momentum, to propel their entire body into the air and "leap" at a potential predator.

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A6.45

11:40 Tuesday 30th June 2009

GPS-INS integration: A valuable tool for measurement of kinematics in the field

Kyle Roskilly (The Royal Veterinary College), Huiling Tan (The Royal Veterinary College), John C. Lowe (The Royal Veterinary College), Alan M. Wilson (The Royal Veterinary College)

Global Navigation Satellite System (GNSS) technologies, such as GPS, offer a convenient method for obtaining kinematic measurements in challenging field environments. Unlike routinely used laboratory methods, such as optical motion capture, GPS offers the advantage of near worldwide operation without requiring extensive local infrastructure. High grade differential receivers can provide position and velocity estimates at a rate of 20 Hz with accuracies around 2 cm and 0.03 m/s respectively, but are expensive (>£5000) and heavy (>1 kg). Additionally GPS receivers suffer increased noise or even loss of lock during the high dynamics of animal locomotion. The compromise required between receiver size, cost, accuracy and dynamic performance currently prohibits prolific GPS use in many biomechanics applications.

An Inertial Navigation System (INS) provides high rate position, velocity and orientation. Errors accumulate unbounded with time however, so that even tactical grade sensors can drift by metres of position within 1 min. Here we use data fusion techniques (Kalman filtering) to integrate the complimentary properties of GPS and MEMS inertial sensors. The core principles of these integration algorithms are explained and the development and validation of a credit card sized, low-cost, lightweight GPS-INS sensor platform are described.

System validation in realistic scenarios, such as human running, shows significantly increased accuracy in position and speed estimation over the use of GPS alone, and can additionally provide orientation information. Kinematic measurements can also be produced at much higher rate, making characterisation of higher frequency biomechanical motion feasible.

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A6.46**12:00 Tuesday 30th June 2009****Dynamical aspects of relationship between group-shape and mutual interaction in a collective motion of organisms**

Yoshinobu Inada (Japan Aerospace Exploration Agency (JAXA)), Hideaki Takanobu (Kogakuin University), Masanao Futakami (Kogakuin University)

Group-shape in a collective motion of organisms such as bird flock or fish school is not constant but varies from time to time like a water blob. Not only individuals on the group surface changes their positions but also individuals inside switch their positions with those of neighbors even when the surface shape is constant. In this sense, the group-shape is amorphous and differs distinctly from a rigid structure like a crystal. The possible factors to change the group-shape are mutual interaction among individuals, i.e. internal factor, and predator's attack or some kinds of fluid-dynamic effects that induce escaping deformation or a V-form of flying geese, respectively, i.e. external factors. In this study, the dynamical change of group-shape is simulated by using computer simulation focusing on the mutual interaction among individuals. When the range of mutual interaction varies depending on the local density of neighbors around the individual, the group-shape changes continuously showing repeated expansion and contraction like those observed in fish school or bird flock.

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A6.47**12:20 Tuesday 30th June 2009****Speed, strategy, drag and drafting in thoroughbred horse racing**

Andrew J. Spence (Royal Veterinary College), Andrew Thurman (Omnisense Limited, UK), Michael Maher (TurfTrax Course Services Ltd, UK), Alan M. Wilson (Royal Veterinary College)

The speed and position of individuals within a group of herding, flocking, or schooling animals have important biological consequences. The significance of physiological ability *versus* decision making during such collective motion is not well understood. We performed an observational study of these factors using a large, novel data set consisting of the 2D position and speed of 28,376 race horses competing in 2480 races at 10 different race courses in the UK. We found that horses won by maintaining higher average speed throughout the race (finish position positively correlated with average speed, 73 of 82 course/distance groups, Spearman correlation, $P < 0.05$, N between 20 and 1411 horses/group), and not by taking a shorter route (distance run not negatively correlated with finish position, 74 of 82 groups, $P > 0.05$). We observed that winning horses spent a smaller percentage of the race in first place as race distance increased ($r_s = -0.26$, $P < 0.001$, $N = 2462$), and hypothesized that reduction of aerodynamic drag by drafting becomes important in long races. We tested this prediction by using the position data to compute the potential energetic benefit of drafting, and found that winning horses do more work overcoming drag in short races but not in long races (multiple regression, $P < 0.05$). We conclude that horses win short races through physiological performance, but in long races winners maintain higher average speed at no additional aerodynamic drag cost through better strategy, in the form of differential time spent drafting behind competitors.

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A6.48**08:20 Wednesday 1st July 2009****Scaling of sensorimotor control in terrestrial mammals**

Heather L. More (Simon Fraser University), Max Donelan (Simon Fraser University), Douglas J. Weber (University of Pittsburgh), John R. Hutchinson (Royal Veterinary College), Steven K. Aung (University of Alberta), David F. Collins (University of Alberta)

In this study we investigated the relationship between the size of an animal and the conduction velocity, diameter and number of its axons. We hypothesized that there is a size-dependent tradeoff between the time it takes to sense and respond to stimuli (*responsiveness*) and the ability to distinguish between sensory stimuli and generate graded muscle forces (*resolution*). Responsiveness depends on axon diameter, due to its relationship with conduction velocity, while resolution is proportional to the number of axons per unit volume. Nerve cross-sectional area is a combination of these two factors – increasing animal size forces a tradeoff between responsiveness and resolution in order to keep the nerve within reasonable size limits. To test our hypothesis, we used electrophysiological techniques to measure conduction velocity in least shrew (*Cryptotis parva*) and Asian elephant (*Elephas maximus*) sciatic nerves. To find axon number and diameter, we used histological techniques and scanning electron microscopy to acquire and analyze images of shrew and elephant nerves. This analysis demonstrated that shrew conduction velocity was 38 ± 5 m/s, with the largest shrew axons being about 9 μm in diameter, and elephant conduction velocity was 70 m/s, with the largest axons approximately 15 μm in diameter. Combining our measured data with that available from literature demonstrates that conduction velocity (CV) is nearly independent of body mass (M), with CV proportional to $M^{0.045 \pm 0.017}$ ($p = 0.016$). Conduction velocity only doubles over the 100-fold increase in leg lengths between shrews and elephants, resulting in large conduction delays and poor sensorimotor responsiveness in larger animals.

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A6.49**08:40 Wednesday 1st July 2009****Tendons as power attenuators**

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

The spring-like behavior of tendons can act to conserve mechanical power for cyclical activities like running, or amplify it for high-power activities like jumping or acceleration. The function of tendon springs during dissipative activities such as deceleration or landing from a jump has received relatively little attention. We used an in situ preparation (turkey lateral gastrocnemius) to test the hypothesis that tendons can act to attenuate power input to muscles during energy absorbing contractions. We implanted sonomicrometer crystals to measure muscle fascicle length, and used a muscle servomotor to measure muscle force and to control muscle-tendon length. A series of constant-velocity ramp stretches was applied to the muscle-tendon coincident with a 50 ms stimulation pulse. In all contractions, most of the work done during muscle-tendon lengthening was initially stored in the tendon. Stored elastic strain energy was then released to do work on the muscle contractile element. The rapid storage of energy in tendon followed by the relatively slow flow of

mechanical energy from the tendon to the muscle allowed for significant attenuation of power input to the muscle. The highest power input to muscle fascicles was approximately 600 W kg^{-1} , while the muscle–tendon unit absorbed energy at a maximum rate of more than 2000 W kg^{-1} . The power attenuating mechanism of tendons may enhance muscle's capacity for energy absorption, and may play a role in limiting eccentric muscle damage. Supported by NIH grants F32AR 054246 to EA and AR055295 to TJR.

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A6.50

09:00 Wednesday 1st July 2009

Biaxial strain and variable stiffness in aponeuroses

Emanuel Azizi (Brown University), Thomas J. Roberts (Brown University)

The role of tendinous structures in the storage and recovery elastic energy is well established in various modes of locomotion. In many muscles these elastic structures include both an extramuscular free tendon as well as a sheet-like aponeurosis. Unlike the free tendon, aponeuroses function as the insertion and attachment site of muscle fascicles and therefore cover a substantial portion of the muscle belly. As a result, aponeuroses are more likely to strain along multiple axes when contracting muscles bulge to maintain a constant volume. We used biplanar high-speed fluoroscopy to track the strain patterns of the turkey lateral gastrocnemius aponeurosis during active and passive force production in situ. During active force production the aponeurosis was stretched both parallel (longitudinal) as well as perpendicular (transverse) to the muscle's line of action. In contrast, passive loading of the muscle–tendon unit stretched the aponeurosis only in the longitudinal direction. Differences in loading patterns under passive and active conditions significantly altered aponeurosis stiffness along the muscle's line of action. These results suggest that consideration of strain measured only in the longitudinal direction may underestimate aponeuroses' capacity for elastic energy storage. We conclude that biaxial strain during active force production distinguishes aponeuroses from free tendons and may function to dynamically modulate stiffness. Supported by NIH grants F32AR 054246 to EA and AR055295 to TJR.

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A6.51

09:20 Wednesday 1st July 2009

Mechanical power amplification in a compliant muscle–tendon working on an inertial load in gravity

Gregory S. Sawicki (Brown University), Peter Sheppard (Brown University), Thomas J. Roberts (Brown University)

During explosive movements (e.g. jumping, accelerating) animals can deliver peak mechanical power that exceeds the power limits of their muscles alone. One possible explanation for this power amplification is storage and release of energy in tissues that are in series with the muscles (such as tendon). Series elastic elements can

act to redistribute the delivery of muscle mechanical work with timing that augments the peak power output of the muscle–tendon unit. Theoretical studies predict that muscle–tendon peak mechanical power output can reach two times the peak power of the muscle alone when working on an inertial load in gravity.

We studied the limits of muscle–tendon power amplification in vitro using bullfrog plantaris muscle–tendon and a servomotor. We developed an admittance controller that took muscle–tendon force input from the servomotor load sensor and then computed and applied servomotor position consistent with the dynamics of a mass on a fulcrum (lever arm in/out ratio = 1) in gravity. This apparatus allowed us to measure peak muscle–tendon power during contractions against a variety of simulated loads (weight ~ 0 to $1.0 \times F_{\text{max}}$ muscle). To compute a peak power ratio we divided peak muscle–tendon power during loaded contractions by peak muscle power from the isotonic force–velocity curve. Preliminary results from two preparations indicate a maximum peak power ratio of 1.82 at weight $\sim 0.23 \times F_{\text{max}}$ muscle. Peak power ratio was lower for loads above and below the optimal load.

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A6.52

09:40 Wednesday 1st July 2009

Decoupling of muscle shortening and joint kinematics during frog jumping

Henry C. Astley (Brown University), Thomas J. Roberts (Brown University)

Elastic tendons can decouple changes in muscle length from changes in joint angle, allowing the muscle to function at closer to optimal conditions for force production and allowing elastic energy storage in the tendon. While elastic tendons have been well-studied in steady-speed locomotion, their role in acceleration is not well understood. The remarkable jumping ability of anurans is an excellent system for addressing this issue due to well-characterized muscle physiology, extensive prior work, static pre-jump posture, and recent data suggesting that elastic energy storage in tendons may occur. In order to test the hypothesis that elastic tendons decouple muscle contraction from joint movement during accelerations, I quantified simultaneous joint movement and muscle contraction in the ankle of *Rana pipiens*. The ankle is extended almost exclusively by the plantaris, a large muscle of the frog hindlimb with sufficient tendon to generate noticeable decoupling. Jumps were studied using X-ray Reconstruction Of Moving Morphology (XRMM), a high-speed biplanar X-ray cinefluoroscopy system, with radiopaque markers implanted into the muscle and bones to simultaneously track muscle strain and joint movement. Preliminary data from 7 jumps shows 7.7% ($\pm 0.8\%$) shortening strain of the muscle fascicle preceding any substantial joint movement, followed by a 38.7° ($\pm 3.4^\circ$) joint extension without muscle fascicle length change, indicating a decoupling of muscle strain from joint angle as well as the storage of strain energy in the tendon. Funded by NSF Grant 064242.

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A6.53**Poster Session – Tuesday 30th June 2009****Function and strategies of a primate hand (*Microcebus murinus*) in climbing: Evolutionary implications**

Elodie Reghem (HandiBio USTV), Emmanuelle Pouydebat (HandiBio USTV), Vincent Bels (USM 301 MNHN), Philippe Gorce (HandiBio USTV)

Grasping branches in primates implies a power grip to secure the adhesion. Primates evolve in an arboreal environment with branches oriented at all possible angles. However, researches which are currently carrying out to understand locomotor behaviour of grasping hand in primates with variation of substrate direction are poor. In this paper, functional aspect of the hand of a small primate (*Microcebus murinus*) is studied during grasping branches in horizontal walking and vertical climbing. Results showed two strategies that result from the various wrist heights: a hand in supination during climbing and in pronation during walking. Furthermore, *M. murinus* exhibits different climbing finger grips with a dominant use of schizaxonic axis. These results are discussed in the field of primate locomotion evolution.

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A6.54**Poster Session – Tuesday 30th June 2009****Asymmetric contraction cycles in skeletal muscle: A trade off between power and efficiency?**

Natalie C. Holt (University of Leeds), Graham N. Askew (University of Leeds)

Muscle performance is a major determinant of an animal's fitness. Important components of performance are the mechanical power output and the efficiency of conversion of metabolic to mechanical energy. Often strategies to enhance one of these aspects are detrimental to the other. Muscle power output increases with the proportion of the contraction cycle spent shortening (Askew, G.N. and Marsh, R.L. 1997. *J. Exp. Biol.* 200, 3119–3131). Here the effects of the proportion of the cycle spent shortening on initial mechanical efficiency were examined. Muscles were subjected to sawtooth shaped contraction cycles at 5 Hz, using the workloop technique *in vitro* at 37 °C. Cycles with 25, 50 and 75% of the cycle spent shortening were used (saw25, saw50 and saw75 respectively). Work and heat output were measured and efficiency calculated [Efficiency = work / (work + heat)]. Mechanical power output increased with the proportion of the cycle spent shortening, as previously reported. Efficiency increased ($p < 0.01$) between saw25 and saw50 cycles, but was not significantly different between saw50 and saw75 cycles. These effects may be due to changing activation costs and, potentially, force enhancement. The similarity of efficiency between saw50 and saw75 is interesting as asymmetric cycles with more than half of the cycle spent shortening are seen in several high power output systems such as bird take-off flight and frog vocalization. The similarity in efficiencies demonstrated here indicates that these cycles may represent a way in which animals can increase the power output of muscle without compromising the efficiency of contraction.

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A6.55**Poster Session – Tuesday 30th June 2009****Nonlinear passive dynamic stability of hawkmoth hovering: A computational study by coupling equations of 6DOF motion with Navier–Stokes equations**

Na Gao (Chiba University), Hao Liu (Chiba University)

Dynamic stability in flapping-wing flight can be affected not only by active motion in wing flapping and body orientation but also by passive movements and/or deformation due to inertial and aerodynamic forces acting on the wings and body. In this study we perform a computational study on passive dynamic stability and try to answer a question: how an insect responds to a sudden disturbance about a steadily hovering state. To tackle this high nonlinear problem we have developed an integrated computational model, which couples equations of 6DOF (Degree Of Freedom) motion and Navier–Stokes equations. An *in-house* dynamic flight simulator (Liu, 2009) is employed with realistic morphological and kinematic models of a hovering hawkmoth, *Manduca*. We first computed unsteady flows around the hovering flyer and calculated time-varying forces and moments generated by the prescribed wing-body kinematics under both equilibrium and disturbance conditions. The calculated periodic forces and moments in a complete beat cycle are then decomposed into Fourier series, and added as external forces into the equations of 6DOF motion to construct a nonlinear dynamic model, which is resolved by a Fourth-order Runge–Kutta method. With this model, features of 6DOF motion in a hovering insect can be predicted in terms of flight trajectory and body attitude under either steady state or disturbances. Application to the passive dynamic stability of hawkmoth hovering shows very reasonable results, which indicate that a hovering hawkmoth shows high sensitivity with respect to translational disturbances but much lower to rotational disturbances of pitch, roll and yaw.

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A6.56**Poster Session – Tuesday 30th June 2009****Balancing acrobats: Grass-carrying ants avoid falling over by controlled head movements**

Karin Moll (University of Cambridge Department of Zoology), Walter Federle (University of Cambridge Department of Zoology)

Leaf-cutting ants of the species *Atta vollenweideri* harvest grass and individual workers carry fragments many times longer than their body over considerable distances to their nest. Considering the significant shift of the centre of gravity when carrying such long fragments, the position of the fragment has to be controlled to avoid falling over. To investigate how grass-cutting ants transport grass fragments, head and fragment positions were measured from high-speed video recordings of carrying ants. Workers walking on a horizontal trail carried long fragments at a significantly steeper angle than short fragments of the same weight. In doing so, the angle between the head and fragment remained constant, whereas the angle of the head relative to the surface changed significantly. Thus, workers did not hold fragments in a different way between their mandibles, but they altered their head position to maintain stability. By forcing ants to transport fragments across inclined paths we further examined whether this head reaction is plastic during load carriage. When walking uphill, workers carried fragments at a

significantly steeper angle and downhill at a significantly shallower angle than ants walking horizontally. However, similar head movements were also performed by unloaded workers walking uphill and downhill, suggesting that this is a generalized reaction to slopes which may have other functions in addition to maintaining stability. Our results illustrate the importance of proximate, biomechanical factors in the foraging process of leaf-cutter ants.

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A6.57

Poster Session – Tuesday 30th June 2009 Picometre scale mechanics in the cicada ear

James Windmill (University of Strathclyde), Daniel Robert (University of Bristol), Jérôme Sueur (Muséum National d'Histoire Naturelle)

Female cicadas use sound to select their mate from a chorus of singing males. Cicadas have tympanal ears, with both the ear's tympanal membrane, and constituent tympanal ridge, acting as acousto-mechanical transducers and frequency filters. Within the ear the tympanal ridge is mechanically connected to a large number of mechanosensory neurons via a cuticular extension known as the tympanal apodeme. Using microscanning laser Doppler vibrometry, the *in vivo* vibrations of the tympanal apodeme of female *Cicadatra atra* have been measured for the first time as they respond to the motion of the tympanal membrane driven by sound. These precise measurements reveal that the tympanal membrane's nanometre motion is over a magnitude greater than that of the tympanal apodeme at the point where the neurons attach. Further, the tympanal apodeme acts as an additional mechanical frequency filter, enhancing the frequency filtering of the tympanal ridge, to narrow the frequency band of vibration at the mechanoreceptor neurons solely to that of the male calling song. This study thus enhances our understanding of the mechanical links between the external ear of the cicada and its sensory cells.

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A6.58

Poster Session – Tuesday 30th June 2009 Why have more than one pad per leg? Determining the mechanical and adhesive properties of hairy attachment pads in beetles

James Bullock (Cambridge University), Walter Federle (Cambridge University)

Many beetles employ arrays of adhesive hairs (setae) to control attachment during locomotion. Here we investigate whether and how variation in seta structure, both between sexes and between tarsal pads on the same leg, determines the mechanical properties and adhesive performance of fibrillar arrays. We vertically compressed individual adhesive pads to determine their effective elastic modulus. Distal adhesive arrays were significantly softer than middle and proximal ones. Variation in stiffness was mainly due to different seta diameters, while calculated elastic moduli of seta cuticle were relatively constant at 5–16 GPa. Consistent with their greater compliance, distal pads generated higher adhesion and friction on rough substrates. However, the greater stiffness of proximal pads conveys a superior ability to push. Proximal pads of

males were less direction-dependent than distal pads and generated larger pushing forces in the distal and lateral directions. In females, proximal pads also produced higher friction forces than distal pads, but only in the lateral direction. Video recordings of vertically climbing beetles confirmed that each pad was used differently. When legs above the body centre of gravity (COG) were pulling, beetles mainly engaged the distal pads, whereas legs below the COG mainly pushed with the proximal pads. Attachment performance was additionally compared between sexes on different substrates. Our findings demonstrate the presence of sex-specific specialisations of the fibrillar system as well as a division of labour between different adhesive pads on the same tarsus.

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A6.59

Poster Session – Tuesday 30th June 2009 The kinematics and kinetics of grey squirrel jumping

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

Squirrels cope with a discontinuous 3-D arboreal environment, yet they have a quadrupedal body plan similar to terrestrial animals of similar size. This makes them an ideal system for comparative study into how locomotor behaviour and anatomy is specialised for arboreal environments. Here, we examine whether and how external mechanical compliance influences the locomotion of squirrels.

Free living wild Eastern Grey squirrels (*Sciurus carolinensis*) are trained to jump from a take-off platform with an integrated Kistler (T9286AA) forceplate and observed with a high speed video camera (Casio EX-F1, 300 fps). The squirrels have the choice of using rigid or compliant take-off platforms (similar in design to a diving board) to jump to a landing platform with a nut dispenser. Data collection and nut dispensing are triggered by a movement sensitive security camera (Axis 211W). Segment lengths and muscle architecture have been characterised on road casualty wild squirrels.

We will determine whether squirrels prefer compliant or rigid substrates. Kinematics and kinetics will be compared between jumps from the rigid and compliant platforms, to determine whether they alter their jump mechanics in a manner appropriate to utilise the compliant surface as an energy store.

Preliminary data, on rigid surfaces, show that squirrels use a countermovement prior to take-off, increasing the distance over which acceleration can occur and achieving an average take-off velocity of $2.9 \pm 0.03 \text{ m s}^{-1}$ (mean \pm SE). Estimates of extensor muscle power were on the order of 414 W/kg, which is comparable to the maximum power of skeletal muscle.

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A6.60

Poster Session – Tuesday 30th June 2009 A hard coat, a tough choice? The effects of host seed morphology and mechanics on the egg laying behaviour of the bruchid beetle (*Callosobruchus maculatus*)

Adrian M. Goodman (University of Lincoln), Giddings J. Joseph (University of Lincoln)

This study investigated whether the egg laying behaviour of *Callosobruchus maculatus*, an important storage pest of leguminous seed crops, was related to the mechanical properties of the host seed. The hypothesis was that females avoid laying eggs on seeds with particularly tough seed coats and hard cotyledons to reduce the resistance their larvae are subjected to when they bore into the seed to complete their development.

Females were presented with seeds from three leguminous species: *Vigna unguiculata*, *V. angularis* and *V. radiata*. The distribution of oviposition sites on the seed's surface was related to the morphology and mechanical properties of the seed. Vickers micro-hardness and fracture tests were used to investigate regional variation and compare the properties of seeds with and without eggs adhered to their surface.

There were no significant regional differences in the hardness of the cotyledon material along the longitudinal axis of the seed ($P > 0.05$). However, there were significant differences between the mechanical properties of the seed coat and the cotyledons; in *V. unguiculata* the seed coat was tougher, $1249 \pm 80.8 \text{ J m}^{-2}$, than the cotyledons, $402 \pm 30.0 \text{ J m}^{-2}$ ($P < 0.01$). There was no significant difference between the hardness or toughness of oviposited seeds compared to seeds left bare; oviposited *V. unguiculata* seeds had a mean hardness of $9.22 \pm 0.458 \text{ kg mm}^{-2}$ and non-oviposited seeds $9.11 \pm 0.425 \text{ kg mm}^{-2}$ ($P > 0.05$). Mechanical data are discussed in relation to the egg laying behaviour of *C. maculatus*.

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Poster Session – Tuesday 30th June 2009

Wet insect feet – Mechanisms of fluid secretion in adhesive pads

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For hundreds of years, scientists have been fascinated by the adhesive mechanisms of insects. Insect adhesion is mediated by a thin film of fluid secreted into the contact zone.

As both larger and smaller amounts of adhesive secretion can lead to a loss of adhesion and friction, a controlled secretion of the adhesive fluid seems likely. However, the detailed mechanism of fluid secretion is still unclear. Here we investigate for the first time the rate of secretion under different experimental conditions.

Adhesive pads of cockroaches (*Nauphoeta cinerea*) repeatedly pressed against smooth surfaces with a controlled normal force deposit small droplets of fluid. The droplets were imaged using Interference Reflexion Microscopy and the volume of single droplets was calculated from their diameter and contact angle. Measurements were performed for series of consecutive press-downs, performed at different frequencies. We found that the amount of fluid deposited decreased exponentially, indicating the presence of a significant storage volume. A storage volume of the appropriate size might be provided by the specialised, sponge-like inner cuticle structure of smooth adhesive pads.

After multiple contacts, the rate converged to a non-zero steady-state, representing the pad's fluid production rate. Preliminary results suggest that fluid production per unit contact area is independent of the "step" frequency. Thus, the secretion mechanism of wet adhesive systems appears to be based on simple physical principles.

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Poster Session – Tuesday 30th June 2009

Fast and furious: Prey capture in the Chinese Giant Salamander *Andrias davidianus*

Egon Heiss (University of Vienna), Nikolay Natchev (University of Vienna), Anton Weissenbacher (Zoo Vienna), Josef Weisgram (University of Vienna)

Andrias davidianus, the Chinese Giant Salamander, is the largest recent amphibian. It can reach a maximum length of 152 cm and a weight of over 40 kg. This giant amphibian is fully aquatic and generally nocturnal, relying mainly on smell and touch to locate its prey. It lives in muddy, dark rock crevices along riverbanks and can capture elusive prey such as fish and handle aggressive prey such as crayfish. The present study analyzes the feeding performance of *A. davidianus* using digital high-speed video and MatchX software. Our animals never showed sideways snaps to catch the offered prey as described from earlier studies on the North American Giant Salamander *Cryptobranchus alleganiensis*. *A. davidianus* very slowly approaches the prey, reducing the distance to a minimum, and ingests the food item by using "inertial suction". Peak gape is reached within 50 ms ($V_{\text{max}} = 294 \text{ cm/s}$) and the whole ingestion cycle lasts about 100 ms. Suction of the prey toward the mouth starts early in the jaw opening phase. The expansion of the pharyngeal cavity caused by hyoid depression does not begin until peak gape. Therefore, we propose that the suction forces acting on the prey are a result of the extremely fast jaw displacement rather than of pharyngeal expansion due to hyoid depression.

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Poster Session – Tuesday 30th June 2009

Do nearby obstacles modify escape response? A preliminary investigation in Pacific Staghorn Sculpin (*Leptocottus armatus*)

Giovanna Serena (University of Padova), Amanda I. Banet (University of California), Paolo Domenici (CNR-IAMC Torregrande-Oristano)

It has been known that prey may respond to a predator attack by a very fast escape but the environmental constraints may influence this performance too. Escape response in fishes, or "C-start", is generally mediated by large neurons called Mauthner cells and consists of a very fast contraction of the musculature during which the body bends in a C-shape within a few milliseconds (stage 1) and in a subsequent stage 2, a contralateral contraction, which causes the tail to bend in the opposite direction, propelling the fish forwards. In the last stage 3 the fish may swim or glide. The aim of this research was to build upon previous studies by observing the effect of walls on the escape response and characterize the relationship between other escape response variables and wall distance in Pacific Staghorn Sculpins (*Leptocottus armatus*). Traditionally the escape response has been studied by placing a fish in an open arena without obstacles and startling it. For species that live in structurally complex environments, it may be more ecologically relevant to understand the escape response in the presence of obstacles. We measured directionality, speed, stage 1 turning rate, and stage 2 trajectories of the escape response in fish placed at different distances from a wall. Sculpins alter their directionality and stage 2 trajectory when close to a wall. No effect was found either for speed or stage 1 turning rate, suggesting that this species has the ability to avoid

obstacles whilst leaving unchanged other aspects of the escape response.

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A6.64

Poster Session – Tuesday 30th June 2009 Does running downhill affect maximum speed?

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A number of interrelated factors limit maximum and submaximal running speed including limb force, muscle power and energy supply. Racing scenarios in a range of species which have been bred/trained for athletic performance provide a good experimental framework for studying limits. Here we aim to investigate force and power as potential limits to running speed using downhill locomotion as a perturbation in thoroughbred racehorses (*Equus caballus*), greyhounds (*Canis familiaris*) and human subjects.

We hypothesise that, if speed is limited by power, subjects' maximum speed will increase on a decline and decrease on an incline. The relationship between speed and potential energy power (speed x incline) relative to total work and cost of locomotion, should be informative. If other limits dominate, maximum running speed will remain constant on a decline (unlike in humans where peak sustainable limb force is raised by the change in muscle dynamics). If there is a power reserve then the animals should maintain their speed on a slight incline.

Horse data are taken from racehorse speed and position data recorded during racing on hilly courses. A GPS-IMU logging system will record data from dogs whilst they chase a mechanical lure on different inclines and declines. Human data are recorded using a modified treadmill, the speed of which is controlled by the position of the subject on the treadmill with a PD controller.

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A6.65

Poster Session – Tuesday 30th June 2009 Scaling relationships in avian moment arms

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It has been demonstrated that in terrestrial animals relative muscle moment arms increase with mass while relative ground reaction force moment arms decrease so that the effective mechanical advantage (EMA) of the muscle increases, which presumably prevents musculoskeletal damage. Do these two moment arms behave similarly in birds? This is what we set out to investigate.

Bird bone data collection was carried out at The Tring Natural History Museum in order to establish scaling relationships of various lengths with mass. Additionally, data were collected to determine moment arms of the pectoralis muscle and wings; specifically the site of the muscle attachment: the delto-pectoral (d-p) crest on the humerus.

Initial results indicate a similar positive allometric change in d-p distance from the proximal end of the humerus and humeral length

change with mass suggesting that the d-p crest stays at the same relative position on the bone. These results support out theory that in birds the muscle moment arm and the aerodynamic force moment arm tend to increase with the same allometric relationship which effectively keeps the EMA constant. This contrasts with the related relationship for the terrestrial animals in which EMA is seen to increase with size.

Further results show that muscle area and muscle volume measurements scaled with a slight negative allometry to mass. The distance between the delto-pectoral crest and the lowest part of the carina scaled with a slight negative allometry potentially suggesting a need to keep the frontal area exposed to air in an aerodynamic shape.

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Poster Session – Tuesday 30th June 2009 The comparative biomechanics of frog hopper-like and locust-like jumping insects

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What are the consequences of different leg design on the generation of targeted jumping behavior? We used high-speed video and kinetic modeling to determine the constraints and opportunities presented by two designs of jumping insect: locusts (*Schistocerca*) and frog hoppers (*Cercopis*). Locusts jump by applying torque across the femur-tibia joint, while frog hoppers jump by applying torque across the coxa-femur joint. The locust-like design can easily change the jump direction by rotation at the coxa-femur joint. It also minimizes the torques that each leg puts on the center of mass. This has the consequence that that asynchronous leg extension doesn't lead to great problems in jump control, because both legs push in the same direction, and place little torque on the centre of mass. Thus, asynchronous leg extension causes little problem with a locust jump, and one-legged locusts have little difficulty jumping. On the other hand, the frog hopper-like design causes leg extension to apply forces in different directions and apply large torques on the center of mass, requiring the legs to work together to balance the forces and torques. To achieve this balance, both legs must extend synchronously. If a frog hopper extends its legs asynchronously, it causes the jump direction to change as well as the body to rotate. The locust-like design allows the jump to be controlled at the coxa-femur joint and reduces the need for mechanisms of synchrony, while the frog hopper-like design requires the jump to be controlled with body positioning and requires mechanisms to ensure synchronous leg extension.

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A6.67

Poster Session – Tuesday 30th June 2009 The effect of formaldehyde cross-links on the mechanical properties of wallaby tail tendons

Rebecca Wilkinson (University of Leeds), Robert Ker (University of Leeds)

This investigation stems from an interest in the role of cross-links in determining the fatigue quality of tendons. Tail tendons were

tested (Instron 8500) before and after soaking in 4% formaldehyde solution, to increase cross-linking. For fatigue tests, tendons soaked in buffer were used as controls. Fatigue is of particular interest, because fatigue damage appears to be part of each tendon's normal life. In life, damage is kept non-symptomatic by ongoing repair. Without repair, time-dependent damage accumulates, leading ultimately to rupture.

Formaldehyde-treatment changed the stress–strain curve only slightly. It still has a toe region and the slope, at stress 10 MPa, was not significantly altered. In contrast, hysteresis loss was sharply reduced and an increased resistance to bending was qualitatively obvious. Fatigue tests ran for 24 h with formaldehyde-treated tendons, with no sign of tertiary creep or fatigue damage (37 °C, 2 Hz sinusoidal stress peak 20 MPa). Primary creep remained, and stiffness did not change with time. Controls showed a progressive reduction in stiffness and ruptured at a mean time of 1300 ± 440 s. The fracture mode produced by a rapidly-applied overload changed. Controls showed pull-out of thin interdigitating threads. Formaldehyde-treatment seems to produce a more localized rupture, though many breaks were near a clamp.

Tentative implications from this mix of results are: (i) formaldehyde cross-linking increases shear stiffness between fibrils and, perhaps, within collagen fibrils; (ii) hysteresis and fatigue in untreated tendons involve shear displacements; (iii) even in untreated tendons, (almost) the whole tensile load is carried by collagen chains.

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Dispersion of oil spills in aquatic environment is under the influence of natural phenomenon, such as physical transport (e. g. gravity or turbulence), dissolution or microbial degradation. Dispersion of the oil slick and its fragments can be sped up through the use of artificial methods based on mechanical and/or chemical dispersion (e.g. surfactants). Therefore, surface-dwelling organisms, such as marine mammals and birds, can be protected from oil-induced injuries. However, dispersion does not remove oil from the environment and can thereby adversely affect marine organisms present in the water column. The effects of a set of dispersion methods were investigated in golden grey mullet, *Liza aurata*. Chemical and mechanical methods were used to disperse oil spill characterized by sub-lethal concentrations. After acute exposure (48 h) to the resulting water mass, escape performance in juvenile *L. aurata* was measured. Escape responses were elicited by triggering the fall of a small cylindrical object on the experimental tank. A high speed camera ($500 \text{ frames s}^{-1}$) was used to record the escape responses. Locomotor variables, such as cumulative distance, speed and acceleration, were analysed. Responsiveness, latency and directionality were also measured as indicators of the fish neuro-sensorial performance. Results will be discussed considering that sublethal concentrations may indirectly induce an increasing probability of mortality through reduction in escape performance.

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Poster Session – Tuesday 30th June 2009

Fast start performance in golden grey mullet *Liza aurata* exposed to sub-lethal concentrations of dispersed oil

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