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A7–GENERAL BIOMECHANICS

Organised by Peter Aerts (University of Antwerp), Ulrike K. Müller and Johan L. van Leeuwen (Wageningen University)

A7.1
Altering energy use by specific muscle groups in running guinea fowl: Carrying loads and running uphill

R.L. Marsh, D.J. Ellerby, J. Rubenson and H.T. Henry, (Northeastern University, USA, r.marsh@neu.edu)

The cost of running in animals can be increased by running them uphill, or by loading either their center of mass or limb segments. Past investigators have used these manipulations to infer the costs of specific components of the stride and to investigate alterations in the function of individual muscles. However, these studies have been conducted without knowledge of the energy use by individual muscles. Our measurements were intended to fill this gap in our knowledge. We combined measurements of organismal energetics during running in guinea fowl *Numida meleagris*, with estimates of energy use by all the individual muscles based on measurements of blood flow. When the mass of the animals was increased by backpack loading, most of the increased energy use by the muscles was due to just four stance phase muscles. Loading the distal limb segments increased energy use by most of the swing phase muscles, and by one muscle group previously thought to be only used during stance phase. Running the birds uphill increased energy use by almost all the stance phase muscles, and, somewhat surprisingly, by some swing phase muscles. The increases were very non-uniform across the stance phase muscles. Overall, our data indicate that uphill running and weighting cause very specific alterations in the partitioning of energy use among the muscles. This information provides the basis for more targeted studies of muscle function under conditions of altered energetic demand.
Keywords: Running, Muscle, Energetics, Uphill, Load carrying

A7.2
Integrating the mechanics and energetics of the swing-phase during walking and running in guinea fowl

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We examined whether the metabolic cost of swinging the leg is determined by mechanical energetics in walking and running guinea fowl. Metabolic rates of swing-phase muscles (calculated from oxygen consumption and bloodflow measurements[1,2]) were used in combination with joint mechanical work from inverse dynamic modelling to compute limb-swing efficiencies. The positive mechanical efficiency of swinging the limb during walking is low (~5%), whereas efficiencies during running are greater (~12–17%). We were also able to calculate the mechanical efficiency for a single muscle, with the assumption that this muscle does all of the work during ankle flexion. Interestingly, this single muscle has similar efficiencies as those calculated for the entire limb. Given that the maximum positive efficiency of skeletal muscle is ~25%, our results indicate that, for running speeds, muscular work may determine a major portion of the metabolic cost of swinging the limb. The situation is, however, complicated due to possible transfer of energy via bi-articular muscles, co-contraction and passive joint moments, which are not accounted for in the present study. These factors may help to explain the discrepancy between efficiencies during walking and running.
Keywords: Swing phase, Mechanics, Energetics, Guinea fowl
1. R.L. Marsh, D.J. Ellerby, H.T. Henry, J.A. Carr, C.I. Buchanan. (2004) *Science*, 303, 80–83.
2. D.J. Ellerby, H.T. Henry, J.A. Carr, C.I. Buchanan, and R.L. Marsh (2005). J. Physiol. (in press).

A7.3
A functional analysis of muscle-fibre rearrangement during development in the zebrafish (*Danio rerio*)

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The muscle fibres in the trunk of teleosts are arranged in complex 3D patterns that are thought to allow uniform strain distributions. At two days of development, the angle between longitudinal direction of the muscle fibres and the longitudinal axis is still relatively small. At eight weeks, higher angles with the longitudinal axis occur and a well-developed pseudo-helical pattern is observed that resembles the patterns described for adult teleosts. We designed a quantitative biomechanical model that predicts the strain distribution from measured local muscle-fibre orientations and prescribed body curvature and muscle deformations. For the

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fast muscle-fibre mass, we demonstrate that at day two a fairly uniform muscle-fibre strain is possible during bending of the body due to the relatively limited variation in the muscle-fibre distance from the mid-sagittal plane. The computed variation in the strain increases sharply from day 2 to 3, but decreases steadily towards 8 weeks. The most uniform strain fields were computed for 8 weeks (the latest stage that was considered). The uniformity at 8 weeks results from the pseudo-helical fibre arrangement and an appropriate shear deformation of the trunk muscles. The developmental changes in muscle-fibre arrangement and associated strain distribution can be explained if the local mechanical conditions of the muscle fibres drive the fibre reorientation.

Keywords: Fish, Muscle, Model, Development, Biomechanics

A7.4
Validation of a freehand 3D ultrasound system for determining muscle tendon unitarchitecture

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Muscle architecture is usually determined by dissection of cadaver material and direct measurement of fibre length, pennation angle and muscle weight / volume. This is however not always practical or ethical and data can only be obtained for one muscle length which may be non physiological. 2D ultrasound imaging has been used to determine fibre length and angle in both static and dynamic studies but this is limited to predetermined planes. Here we use a combination of a 2D ultrasound imaging system and a 6 degree of freedom position sensor to build up a 3D image of an entire muscle in a single continuous sweep. The 3D image can then be rotated and sampled for measurement of muscle architecture. Our data show that the system is extremely accurate ($<$1% difference in phantom measurements) and precise (repeatability coefficient ranging from under 1% to 4.1% of mean muscle volume) for measurement of muscle volume. However, the interpolation technique used to combine the individual slices makes the identification of individual muscle fibres through a stack of images and hence the measurement fibre length and angle difficult. This can be circumvented by altering the orientation of the ultrasound transducer so that entire fibres are visible on individual slices but at the cost of not scanning the whole muscle in a single longitudinal sweep. In conclusion 3D ultrasound is valuable for determining muscle volume and shape but 2D images are better for measuring fibre length and fibre angle.

Keywords: Muscle architecture, Muscle volume, 3D ultrasonography

A7.5
Superfast muscular control of sound production in birds

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Many birdsongs contain sound elements that require extremely fast control. The trill of the ring dove (*Streptopelia risoria*) is a sequence of short sound elements that may be as short as 10 ms. If their generation is under active control, fast muscle contractions are required that approach the performance limits of vertebrate muscles. We showed that the vocal muscles of ring doves are superfast muscles. Simultaneous *in vivo* recordings of muscle activity and sound show that the syringeal muscles gate and frequency-modulate individual sound elements of the trill. Co-contraction of these antagonistic syringeal muscle pairs affords the bird rapid and accurate control of the sound generators' vibratory behaviour. *In vitro* force measurements confirm the superfast twitch characteristics of the syringeal muscles. The twitch half-times of the *musculus tracheolateralis* and *musculus sternotrachealis* were 9.2 ± 0.8 and 10.3 ± 1.7 ms, respectively (mean ± S.D., $n = 7$). Superfast muscle can no longer be considered a rare adaptation of a few highly derived acoustic organs such as in the toadfish and rattlesnake, but is probably the main muscle type controlling birdsong.

A7.6
Patterns of motor unit recruitment affect the forces generated by whole muscles

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During locomotion the different types of motor unit within each muscle can be recruited for specific locomotor tasks. Recently we have shown that the kinematic demands placed the muscle influence the motor recruitment with the faster fibres being preferentially recruited for higher velocity contractions. The different types of motor unit have different contractile properties and it should therefore be expected that the mechanical force and power outputs from a whole muscle depend on the recruitment pattern for each specific task. Here we have used a simulation of the tibialis anterior muscle to predict the force output during walking and running when the different types of motor unit can be recruited independently. The muscle tendon unit length was estimated from the segmental kinematics, the muscle activation and fibre recruitment was determined using wavelet decomposition of the electromyographic signals. The model showed that the force generated by the muscle was greater when using the *in vivo* recruitment patterns than when making the assumption that the muscle fibres had homogeneous properties (either fast, intermediate or slow properties). Varying and selective recruitment of the different types of motor unit as found *in vivo* can thus enhance the force output to levels greater than would be typically predicted. These results have important implications to clinical applications where the simulations of whole muscle outputs are used as part of larger biomechanical models.

Keywords: Motor unit, Recruitment, Force, Locomotion

A7.7
Muscle–tendon unit interaction during human gait; Power vs. efficiency

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The interaction of a muscle and associated tendon during dynamic activities such as locomotion is critical for both force production and economical movement. It is generally assumed that, under sub-maximal conditions, muscle activation patterns are optimised to achieve maximum efficiency of work. However, if we change the power output required by a muscle, are activation conditions adopted that achieve a near optimum efficiency or is the increased

requirement for power detrimental to the efficiency of that muscle? The interaction between the contractile component (CC) and the series elastic element (SEC) is key in understanding the relationship between a muscle's power output and efficiency. Here we have used synchronous ultrasound, motion analysis and electromyography (EMG) to distinguish between the length changes of the CC and the SEC during locomotion under the following conditions: walking (5 km/h) at −10, 0 and 10% grades and running (10 km/h) at 0 and 10% grades. It was apparent that with the increased power requirement associated with increased grade of inclination, the SEE was strained further but recoiled over the same time period, thereby increasing the positive power output of the muscle tendon complex (MTC). The elastic recoil of the SEC allowed the CC to act at speeds more concomitant with optimum power output and efficiency (maximum active shortening speed ~0.8 lengths/sec), whilst the MTC could shorten at speeds of up to 5 lengths/sec. Muscle activation timing varied little with change in grade, however activation amplitude increased with grade. This allowed the muscle to act at a more constant efficiency regardless of grade/power output.
Keywords: Biomechanics, Muscle, Elasticity, Locomotion, Efficiency

A7.8
Architectural changes of spastic muscle during human gait

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Cerebral palsy (CP) is a non-progressive upper motor neurone palsy resulting from infantile cerebral damage. Particular characteristics of CP are that muscle tone is high and range of movement of joints is reduced.
With CP, muscle force development plays a central role to the condition and many studies have focused on muscle activation patterns and the motor control deficits. Muscle however, is a labile tissue that responds to mechanical influences. The progression of the condition and the outcome of treatment is dependant on these responses. The response of muscle to changes in its mechanical environment is well characterised in normal muscle. The equivalent data for spastic muscle is sparse. Spastic muscle presents an interesting system to evaluate the effect of heightened tone on muscle architecture.
Here we examine the relationship between contractile element length and overall muscle length in spastic and non-spastic muscle to test the hypothesis that the increased muscle stiffness is the result of shortening of muscle fibres with a concomitant increase in the length of the series elastic element during walking.
Muscle fibre length was determined using ultrasound imaging during standing, walking and full passive range of motion for the medial gastrocnemius muscle. Segment length was taken to represent muscle tendon unit length. Data collection is ongoing and we aim to have evaluated twelve subjects in each group by the time of the conference.
Keywords: Cerebral palsy, Spasticity, Gait, Muscle

A7.9
Histo-morphological attributes of bone adaptation to mechanical loading mode in birds

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We studied the occurrence of torsion-resisting morphological and histological features (thin bone walls, circular shaft cross-section, oblique collagen fibers and laminar tissue arrangement) in a sample of 168 long bones from wings and legs of 22 bird species. These structural parameters were measured in mid-diaphyseal under-mineralized cross-sections, and analysed using uni-, bi- and multivariate (Principal Components Analysis) data analysis techniques. We found that the four variables are significantly, positively correlated, and that covariation between variables accounts for as much as 58% of the total variation. These results suggest that torsion is a main determinant of the macro- and micro-structural design of long bones in birds. Humerus, ulna and femur generally possess torsion-resisting features, while other bones (radius, carpometacarpus, tibiotarsus, tarsometatarsus and foot phalanx) rather show bending/axial loads-resisting structural properties. These results are congruent with in vivo strain data from the literature, which reported high torsional loading in humerus and ulna during flapping flight, but also in the sub-horizontal avian femur during terrestrial locomotion. Some species (*Procellariiformes* and *Alcidae*) showed a discrepant pattern, with poor torsion-resisting optimisation in humeri and ulnae. These patterns can be discussed, with regards to flight modes and associated morphologies (e.g. wing aspect ratio). The precise biomechanical outcomes of the laminar tissue 3D spatial arrangement are another point of discussion. In conclusion, we argue that the balance between torsion and bending/axial loads appears as a new, advantageous biomechanical framework for elucidating structure–function relationships in extant and fossil bone.
Keywords: Laminar bone tissue, Torsion, Bending, Flapping flight

A7.10
Bone growth and tissue microstructure in relation to in vivo bone strains in the goat radius during ontogeny

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Hypotheses concerning a link between form and function in vertebrate limb bones have sought to explain how the architecture and geometry of trabecular and cortical bone reflect habitual loading within the limb skeleton. The goal of this study is to examine how ontogenetic changes in limb bone geometry and microstructure within the cortex of the goat radius relate to ontogenetic changes in the measured strain environment. Bone strain data were collected from the cranial, caudal, and medial midshaft surfaces of the goat radius in animals of three age/size groups. Prior to strain data collection, fluorescent bone labels were given to the animals to be incorporated in to the growing/remodeling bone. After the strain data were collected, histological thin-sections were prepared from each radius and imaged using plain, fluorescent, and circularly polarized light microscopy to quantify bone porosity, secondary osteon density, periosteal growth rates, and the orientation of the collagen fibers. Using cross-sectional strain distributions and the anatomical bone axes, each cross-section was divided into eight sub-divisions and the above histological variables measured in each. Preliminary results show there are no distinguishing microstructural (porosity and collagen fiber orientation) differences between regions of the bone loaded in tension or compression. High periosteal growth rates laterally and low growth rates cranially do not correspond to differences in the underlying strain environment, but are consistent with the growing radius maintaining a higher second moment of area in the medio-lateral, than in the cranio-caudal direction, which has been argued to increase loading predictability.

Keywords: Bone, Ontogeny, Histology, Growth, Strain

A7.11
Gliding performance in fruit bats

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Of the three classes of flying vertebrate, bats exhibit unique morphological and aerodynamic characteristics. Bats fly at Reynolds numbers (*Re*) of the order of 50 000, where transition from laminar to turbulent flow occurs. However, their wing morphology is comparable to that of the Pterosaurs, which operated at *Re* above 100 000, in the turbulent flow regime. Bats have membranous wings, with the arm bones and finger bones of the third digit forming a spanwise spar. Deflection of the thumb downwards creates a leading edge flap of varying angle. The remaining digits form chordwise struts, helping to control and maintain wing shape and membrane tension. In Pterosaurs, the wing bones were thought to lie beneath the wing membrane. However in bats, they protrude a significant amount above the wing surface suggesting an effect upon aerodynamic performance. Aerodynamic force measurements were taken at *Re* 50 000 from 2D membranous wing profiles based upon two species of fruit bat, *Rousettus aegyptiacus* and *Pteropus rodricensis*. High lift and drag coefficients are consistent with those produced from a similar model based upon Pterosaur wing morphology and operating at *Re* 120 000 (Wilkinson, 2002). Smoke flow visualisation studies suggest that interplay between leading edge flap angle (and therefore entry angle to the airflow), and leading edge spar position and depth, may be important in regulating flow separation and force production during gliding flight in such a difficult flow regime.

Wilkinson, M.T., 2002. Flight of the Ornithocheirid Pterosaurs. *Unpublished PhD thesis, University of Cambridge*.

A7.12
Arm and hand wing flow on bird wings

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The flow around a brass model of a swift wing with variable sweep back angles was visualised and analysed using digital particle image velocimetry in a re-circulating water tunnel. The water was seeded with neutrally buoyant PVC particles of 50 μm diameter. The flow velocity was either 0.3 or 0.45 m s^{-1} (equivalent airspeeds would be 4.2 and 6.3 m s^{-1} respectively). Measurements were conducted at three positions along the wing: beyond the end of the arm wing, half way down the hand wing and close to the wing tip. The displacement of particles in time in a plane formed by a 2 cm thick laser light sheet perpendicular to the leading edge was filmed using a video frame rate of 125 or 250 Hz. The hand wing had a sharp leading edge. Hand wing sweep angles of 0°, 30°, 45° and 60° were tested at geometric angles of attack of 0°, 5°, 10° and 15° with respect to the horizontal free flow. A large number of flow fields of the 96 different experimental situations were analysed for the distribution of velocity and vorticity and for the presence of vortex cores. Depending on the conditions and the position on the wing model, the flow pattern showed either an unsteady von Karman vortex street or attached flow. The latter was either conventional attached flow or a stable leading edge vortex on top of the wing. Leading edge vortex flow is associated with increased sweep angles and with larger angles of attack.

Keywords: (Un)attached, LEV, DPIV, Sweep angle, Angles of attack

A7.13
Wake dynamics of hummingbirds flying over a wide range of speeds

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Hummingbirds fly with their wings almost fully extended during their entire wingbeat. This pattern is associated with having proportionally short humeral bones and long distal wing elements, and it leads to predictions that hummingbirds hover more like insects than other birds, and that they should produce negative thrust during forward flight, thereby presenting a functional limit to maximum speed. To test these predictions, we flew rufous hummingbirds (*Selasphorus rufus*, 3.3 g, $n=4$) in a variable-speed wind tunnel (0–12 ms^{-1}). We measured wake structure and dynamics using digital particle image velocimetry (DPIV). During hovering, hummingbirds produced 75% of their weight support during downstroke and only 25% during upstroke. This asymmetry is due to inversion of their cambered wings during upstroke. Thus, hummingbird hovering approaches that of insects, yet remains distinct due to effects resulting from an inherently dissimilar avian body plan. During forward flight, circulation during downstroke was sufficient to support body weight. Upstrokes produced positive, rather than negative, thrust as evinced by doublet shed into the wake of all upstrokes (4–12 m s^{-1}). Our results provide new insight into the aerodynamic function of the hummingbird wing. NSF IBN-0327380.

Keywords: Particle image velocimetry, Kinematics, Flight

A7.14
Integrated modeling and simulation of free flight in realistic insect

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To provide an overall understanding of aerodynamic and dynamic mechanisms in insect free flight we have succeed in establishing a biology-inspired dynamic flight simulator, which is capable to mimic free flights in realistic insects, involving hovering, forward flight and quick-turn on a basis of modeling of realistic geometry and wing kinematics, and modeling of wing-body flight dynamics. By routinizing the imaging, the segmentation, the surface fitting, and the gridding in morphological modeling, we have developed a feasible and efficient computer-aided method that is capable to unify the geometric- and kinematics modeling associated with an arbitrary, three-dimensional flying animal. Coupling of an in-house CFD solver and a newly developed flapping flight dynamic solver enables the free flight simulation with consideration of both the wing–wing interaction and the wing–body interaction, and hence a systematic and quantitative evaluation of aerodynamics and flight stability in realistic insect. We carried out a systematic computational study on the hovering- and forward-flight of a wing–body moth model and validated the numerical results through comparing with the force- and moment-measurements based on our moth robot. Our results quantified the influence of the wing–body interactions and how much the aerodynamic force and inertial force contribute in lift generation and power requirement, in particular in flight maneuverability.

Keywords: Free flight, CFD, Flight dynamics, Moth

A7.15
A directional escape response in *Drosophila melanogaster*

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The escape response of *Drosophila melanogaster* is comprised of a stereotyped sequence of leg extension and wing elevation (1). Muscle recordings show that leg and wing muscle contractions occur with consistent latencies from activation of the descending giant fiber, which has been shown to be visually triggered (2). Previous studies of the escape response or giant fiber activity, however, have primarily used non-directional stimuli (e.g. lights-on/off). It thus remains unclear whether the fly's escape strategy is to use a dedicated neural pathway, enabling rapid take-off without regard for direction, or whether the fly is able to process the direction of a threat so as to jump away from it during escape. We used high-speed video to capture the 3D behavior of escaping flies. Individual stationary flies were confronted with a falling black disc on a collision course with their location. The azimuth of the falling stimulus relative to the fly's position was varied so that the full 360-degree range of possible stimulus directions was tested. Analysis of take-off trajectories showed that initial take-off azimuth was a compromise between the fly jumping directly away from the stimulus and the fly jumping directly forward. Further experiments confirmed that this directional escape behavior is mediated primarily by the visual stimulation of the falling disc and that a directional jump can be produced by leg extension alone, without the aid of the wings.

Keywords: *Drosophila*, Flight, Takeoff, Escape, Giant fiber

1. Trimarchi and Schneiderman (1995) J Zool Lond 235: 211–222.
2. Trimarchi and Schneiderman (1995) J Exp Biol 198: 1099–104.

A7.16
Structure, stability and strength of leading edge vortices in insect flight

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Leading Edge Vortices (LEVs) form the secret of insect flight as they suck insect wings with an extraordinary force through the air, affording insects a remarkable agility and performance in flight. This study focuses on the importance of rotational accelerations (e.g. the centrifugal and Coriolis acceleration) on the structure, stability and strength of LEVs. The significance of these rotational accelerations is expressed by the dimensionless Rossby number ($Ro = U/\omega L$) of the flapping wing. The maximum Rossby number in hovering flight reduces to the aspect ratio of the wing semi-span ($r/2L$), linking it directly to the wing geometry. Force measurements and flow visualizations were obtained with a hovering robotic flapper in a tank filled with mineral oil and water. The wing shape was based on a fruit fly wing (*Drosophila melanogaster*). The experiments were carried out over a Reynolds number range of 110 to 14 000 using three types of kinematics; propeller kinematics, synthetic flapping kinematics and fruit fly kinematics. The Rossby number at the base of the wing was varied from zero (true flapping) to infinite (translational flapping) by changing the distance between the axis of rotation and the base of the wing. The maximum angle of attack was varied between 0 and 90 degrees. We found that the characteristics of LEVs in insect flight strongly depend on the Rossby number, which measures the strength of rotational accelerations. The results are also relevant for other animals that flap their wings, fins or paddles in nature and in technology for propellers and windmills.

Keywords: Insect, Aerodynamics, LEV, Centrifugal, Coriolis

A7.17
Analysis of aerodynamic force acting on the flapping wing of mechanical flapping robot MOTH-1

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Mechanical flapping robot (MOTH-1) was developed to investigate the aerodynamic and inertia phenomena on the flapping wing. MOTH-1 was elaborated to realize the various flapping motion having any time series of three angular components of wing (sweep, elevation, and rotation angle). Motion input of MOTH-1 was derived from natural hawkmoth flapping motion in hovering. Its motion was periodic and then could be decomposed into basic harmonic component and its higher order series. We measured aerodynamic force acting on the robot wing moving in the basic harmonic mode with or without higher order series, and compared their aerodynamic characteristics. Consequently, it was found that aerodynamic force generated by basic harmonic component with higher order series was larger than that by only basic component, indicating that the higher order components of wing motion adjust the relative angle of wing appropriately to the surrounding air flow to enlarge the lift, thus performing actively to support insect body.

Keywords: Aerodynamic force, Wing, Flapping robot, MOTH-1

A7.18
The biological implications of self-generated airflow in flying insects

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A natural consequence of flapping flight is an induced velocity gradient along the body of flying insects. Although much recent work has focused on the near-field mechanisms of aerodynamic force generation by flapping wings, the measurement and biological implications of self-generated airflow have received comparatively little attention. Because the pattern of airflow on an insect's body determines how sensory stimuli are delivered to its mechanosensory and chemosensory organs, it is important to understand how flapping activity itself modulates these signals. For

example, the flightless silkworm moth *Bombyx mori* actively fans its wings to increase the air flux over its body thereby enhancing the rate at which its antennae encounter odor molecules (Loudon and Koehl, 2000). In flying locusts, wind sensory hairs located on the head are activated by motion of the head and self-generated air flow and provide phasic input that entrains its flight motor output (Horsmann et al., 1983). Self-generated airflow also enhances convective heat loss in many endothermic insects and influences odor tracking activity of many flying insects. In this paper, I will outline a theoretical method to estimate the induced flow resulting from circulatory changes on flapping wings. To test the predictions of this theory, I have carried out hot-wire anemometry on tethered *Manduca sexta* to measure the magnitude of self-generated airflow. Using the theoretical and experimental results, I will broadly discuss the influence of self-generated airflow in flying insects on the physiology and sensory biology of flying insects.
Keywords: Aerodynamics, Circulation, Induced flow, Odor tracking, Heat convection

A7.19
Study on longitudinal flight control system of bumblebees using transfer functions

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Longitudinal flight control system of bumblebees is studied. We aim to represent the system as a simple mathematical model, and to investigate how the bumblebees behave when the system is varied. The experiments are performed in a tethered flight condition under optical stimuli. Vertical forces and flapping motions are simultaneously recorded by using a load cell and a high-speed video camera. Both open-loop and closed-loop measurements are tried. The open-loop means that the optical stimuli are set in advance. In the closed-loop, the optical stimuli are controlled by the measured forces. To evaluate the performance of the system, transfer functions are introduced. A transfer function is a mathematical representation of the relation between the input and output of a linear time-invariant system. We compare the responses of open-loop and closed-loop measurements, and estimate the flight control model by using the transfer functions. We also try to vary the feedback conditions of the closed-loop measurements. We compare the measured flight control system with a human-aircraft system, and discuss the difference between the two.
Keywords: Bumblebee, Flight control, Transfer function, Optical stimuli
1. Franklin G. F., Powell J. D. and Emami-Naeini A., “Feedback Control of Dynamic Systems”, Prentice Hall, 4th Ed., (2002).
2. McRuer D. T. and Jex H. R., “A Review of Quasi-linear pilot models”, IEEE Trans. HFE-8, (1967), 231–249.
3. Sherman A. and Dickinson M. H., “A comparison of visual and haltere-mediated equilibrium reflexes in the fruit fly Drosophila melanogaster”, J. Exp. Biol., (2003), 295–302.

A7.20
Abdominal motions in maneuvering insect flight: Does the abdomen generate or stabilize body rotations?

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Flying insects perform rapid maneuvers to track moving targets, avoid obstacles and escape from predators. A variety of wing kinematic changes are used to alter forces and moments acting on the body, but the role of the abdomen during maneuvering flight has received less attention. Several studies have suggested that lateral deflections of the abdomen and legs are used to initiate rapid turns away from predators or obstacles. In other cases, abdominal flexion appears to be used to correct unintentional course changes. However, nearly all of these experiments have been performed on insects tethered in an oncoming airstream and presented with artificial stimuli. To investigate the role of abdominal flexion in free flight, we collected high speed kinematic data on hawkmoths (*Manduca sexta*) tracking oscillating robotic flowers, over sequences of 50–100 wingbeats. We find that maneuvering hawkmoths display significant abdominal flexion in concert with changes in body pitch or yaw. In both the dorso-ventral and lateral directions, the rate of abdominal flexion is correlated with the rate of body rotation, but abdominal flexion consistently occurs after the moth has begun pitching or yawing, and in the direction that would oppose the observed rotation. Thus, in slow maneuvering flight, hawkmoths appear to use their abdomen primarily as a brake to slow body rotations initiated by changes in wing kinematics. Our results suggest that abdominal flexion may serve several different roles in flight, depending on whether insects are engaged in voluntary tracking behavior or responding to sudden, unexpected threats.
Keywords: Insect flight, Maneuvering, Abdominal flexion, *Manduca sexta*

A7.21
A computational fluid dynamic study of free swimming in larval fish

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Aiming at providing a quantitative evaluation of hydrodynamics and energetics in larval fish when performing free swimming we have developed a computational biomechanical simulator, which combined an in-house CFD solver and a newly developed undulating locomotion dynamic simulator and hence is capable to simulate free swimming of an undulating swimmer with an arbitrary geometry.
A 3D CFD model was made based on a realistic larval fish with a body-length of 4 mm (0–5 days), which can mimic a coasting mode, a cyclic swimming mode and a prescribed fast-start mode. Results of a benchmark study show good agreement with the observations in terms of the flow patterns (2D PIV). We then performed a systematic study on the wake structure, hydrodynamic forces, mechanical power, and propelor efficiency of the larval fish model. Our results quantified the relationship between the 3D wake structure and the hydrodynamics as well as the energy budget, pointing to the discrepancy and hence the importance of the free swimming hydrodynamic modeling compared with the conventional modeling of a ‘tethered’ swimming model.
Keywords: Free swimming, CFD, Wake structure, Energetic, Larval fish

A7.22
Cyclic swimming in larval fish: From body wave to wake

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Zebrafish larvae (*Danio rerio*) perform strong escape responses, during which they can reach swimming speeds in excess of 50 body lengths per second and swim further than 50 body lengths. As a first step towards quantifying locomotory forces and the demands on larval musculature, we studied swimming larvae (body length BL 3.9 mm) using motion analysis and two-dimensional flow visualisation. Zebrafish larvae assume a C-shape within 5 to 6 ms, 7 ms later they reach maximum accelerations of up to 40 000 BL s^{-2}. The initial C-bend generates a strong suction flow backwards and towards the concave side of the body, imparting considerable kinetic energy to the water while the larva's centre of mass still travels relatively little. Early larvae (age 2 to 4 dpf) reach their peak swimming speed usually within the second or third half tail beat. The wake generated during the following cyclic swimming episode contains mainly lateral flow. The swimming larva develops a thick boundary layer around its anterior body. Along the posterior body, vorticity peaks locally at several points along the body wave. This chain of vorticity peaks is shed at the tail and forms a wake of laterally moving vortex pairs. Vertical slices through the flow field suggest that the wake of one complete tail beat contains two vortex rings, one shed to each side of the fish. The observed swimming kinematics served as input to model the flow field of swimming zebrafish larvae using computational fluid dynamics (CFD).
Keywords: Hydrodynamics, Kinematics, Wake dynamics

A7.23
Hydrodynamic function of dorsal and anal fins in teleost fishes

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Fish oscillate their dorsal and anal median fins during locomotion. The kinematics of these fins suggests that they produce rolling moments on the fish's body. How moments produced by dorsal and anal fins affect fish stability is not well understood. Previous flow visualization experiments have shown the dorsal fin produces large lateral jets above the fish's rolling axis possibly causing rolling instabilities during swimming. The location and structure of the anal fin suggests it may counteract the forces produced by the dorsal fin. To date, anal fin wake structure has not been described. In this study we use particle image velocimetry to visualize the wake structures of dorsal and anal fins of rainbow trout (*Onchorynchus mykiss*). Using two parallel light sheets with a high-speed digital camera (Photron Fastcam at 250 fps) filming each sheet, we simultaneously assess the timing, magnitude and direction of forces produced by dorsal and anal fins during swimming. We find the anal fin is synchronously producing large lateral jets of similar magnitude and direction compared with the dorsal fin. We hypothesize the timing, direction and magnitude of dorsal fin jets are balanced by anal fin jets to minimize rolling perturbations experienced by fish.
Keywords: Hydrodynamics, Median fins, Fish swimming, Stability

A7.24
Fast start performance and bending behaviour in gobies

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Little is known on the effect of postural curvature on fast-start performance and manoeuvring, since most past work has investigated escape responses in fish starting from a relatively straight posture. The black goby (*Gobius niger*) is bottom dwelling fish that can be found resting on the bottom with its body bent into a "C" shape. This posture can occur as the result of a peculiar bending behaviour as a response to weak stimulation. This behaviour does not imply any noticeable displacement and it corresponds to a postural curvature that can last for a relatively long time (i.e. minutes). However, when threatened by a strong mechanical stimulation, black gobies perform an escape manoeuvre. Our aim was to study the effect of postural curvature on the escape behaviour and locomotor performance of black gobies. To induce curvature, fish were first given a weak stimulus. This was followed by a strong stimulus which elicited an escape response. Swimming performance was analysed using high speed video (500 frames/second). Locomotor performance increased with the initial body curvature when the escape response was in the direction opposite to the postural curvature (i.e. bending on the convex side), while performance decreased with body curvature when fast starts implied further bending of the body. The possibility that performance differences may be related to differences in the initial posture and, consequently, in tail kinematics during the response will be discussed.
Keywords: Fast start, Locomotion, *Gobius niger*, Bending

A7.25
No Abstract received

A7.26
Remodelling in the acellular vertebrae of sea bass (*Dicentrarchus labrax* L.)

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Musculo-skeletal deformities occur frequently in the aquaculture of many teleost species. Lordosis is an example of such a deformity and is characterized by a ventrad curvature of the vertebral column, and the affected vertebrae show an increased bone formation. We investigated the effects of lordosis on the strain distribution in sea bass (*Dicentrarchus labrax* L.) vertebrae under compression. The response of the local tissue is analyzed spatially and temporally in terms of bone volume. Lordotic vertebrae show a significantly increased strain energy compared with normal vertebrae. This increase is partially compensated for by a change in architecture due to the increased bone formation. The increased bone formation is seen mainly at the articular surfaces of the vertebrae, while high strain regions are largely confined to the vertebral centrum. This conflicts with the general belief that in mammals localized high strains mediate an adaptive modelling response of bone tissue to mechanical loading, with osteocytes acting as strain gauges. The acellular sea bass bone lacks osteocytes, however, which possibly prevents a fully compensatory adaptive response in the centre of

lordotic vertebrae. Histological analysis showed chondroidal ossification at the articular surfaces where it mediates a rapid adaptive response, attenuating high stresses on the dorsal zygapophyses.
Keywords: *Dicentrarchus labrax* L., Vertebrae, Adaptive modelling, Lordosis

A7.27
Mechanics of cancellous bone in dolphins

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De Buffrénil at al. (1988) showed that flipper periosteal bone in common dolphin becomes cancellous. In the present research, the mechanics of this process was investigated by means of microhardness and nanohardness tests, according to Currey and Bear (1990) and Rho et al. (1999), respectively. Radii from 51 specimens (27 females and 24 males) of striped dolphin (*Stenella coeruleoalba*), ranging from fetuses to adults, were used. On plates obtained from cross sections, indentation was carried out on three different positions, called conventionally centre (cancellous bone), east, and west (cortex). When the whole section (cortex + cancellous) was considered, Vickers hardness increased until the maturity age, and decreased from this age to the eldest one. The variation of elastic modulus was parallel. Vickers hardness and elastic modulus corresponding to cancellous core displayed a less clear pattern. No significant variation in nanohardness was found between the different indented zones, either for females or males. It can bee concluded that the mineral content had a clear effect on the matrix density, but it did not affect the modulus and hardness in the way it has been shown in osteoporotic femoral heads, for example.
Keywords: Microhardness, Nanohardness, Bone, Dolphins
De Buffrenil, V., D. Schoevaert 1988. On how the periosteal bone of the delphinid humerus becomes cancellous: Ontogeny of a histological specialization. J. Morphol. 198:149–164.
Currey, J.D., Brear, K. 1990. Hardness, Young's modulus and yield stress in mammalian mineralized tissues. J.Mat. Sci. Mat.Med.1:14–20.
Rho, J., Zioupos, P. et al. 1999. Variations in the Individual Thick Lamellar Properties Within Osteons by Nanoindentation. Bone 25:295–300.

A7.28
Optimisation of orientation of the semicircular ducts (*scd*) in the vertebrate head

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In virtually all vertebrates, the vertical semicircular ducts (*vsd*) are positioned under equal angles with the medial plane (the pitch plane). The horizontal ducts (*hsd*) are mostly in the plane of yaw, irrespectively of the average posture of the animal's head (an exception is found in man where the *hsd*'s are transversally tilted about 30° with the plane of yaw). The question arises whether these orientations can be considered as an optimisation for e.g. a maximum sensitivity or response speed. Muller and Verhagen (1988, 2002) developed a physical theory in which the *scd*'s are mutually coupled thus providing a hydrodynamical interaction between them. Substitution of measured values of duct dimensions in these equations reveals that for yaw, pitch and roll the ducts behave almost as uncoupled sensors. Optimisation can be achieved only by a *neural* coupling of ducts which explains the natural position of the *vsd*'s. The *hsd* does in yaw hydrodynamically interact with the anterior *vsd*. An optimisation has not been found here. Finally, the hydrodynamical coupling of ducts is important for functions which are not directly connected with the sensing of rotation i.e. a proper division of neural signals of all three ampullae, robustness against damage, equalisation of physical properties and pressure of endolymph and evolutionary simplicity.

A7.29
Scaling of the feeding system in the African catfish (*Clarias gariepinus*)

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Effects of animal size are pervasive and affect nearly all aspects the biology of animals and plants. Theoretical scaling models have been developed to predict the effects of size on the functioning of musculo-skeletal systems. Although numerous experimental studies have investigated the effects of size on the movements of skeletal elements, relatively little is known about the scaling of the muscles and bones. Here we examine the scaling of external morphology, skeletal elements of the feeding system, and a number of cranial muscles to understand how this may affect the movements observed during feeding in the African catfish *Clarias gariepinus*. The results show that neither the head, nor the cranial elements scale according to geometric similarity models. Relative to head size, distinct changes in the mass and configuration of the feeding structures takes place. Unexpectedly, different cranial muscles show different scaling patterns resulting in a positive allometry of muscle cross sectional area relative to head size. This suggests that the scaling of the cranial elements cannot be predicted based on the scaling of external head dimensions. An analysis of the consequences of the observed scaling patterns on performance traits (bite force and jaw closing speed) suggests a close link between the scaling of the feeding system and the diet of these fish. Whereas for smaller size classes the system is tuned towards high bite forces, for animals with cranial lengths greater than 65 mm the scaling of the feeding system appears dictated by the hydrodynamic constraints on suction feeding.
Keywords: Feeding, Fish, Scaling, Morphology

A7.30
Scaling of suction feeding kinematics and dynamics in the African catfish (*Clarias gariepinus*)

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Ontogenetic changes in the size of the cranial apparatus of suction feeders have important consequences on prey capture kinematics, dynamics and performance. Although scaling relationships on aquatic feeding kinematics have been studied previously, the size-related effects of kinematics on performance (displacing the prey towards the mouth) and the biomechanical causes of the observed changes in suction feeding kinematics (decreasing speed of cranial expansion with growth) remain unclear. In this study, we analyzed

prey capture kinematics in an ontogenetic series of African catfish (*Clarias gariepinus*) using high-speed video. By modelling the observed expanding head of *C. gariepinus* as a series of expanding hollow elliptical cylinders, spatio-temporal patterns of water flow, buccal pressure and power requirement for the expansive phase of prey capture were calculated. The calculated flow of water generated by buccal expansion reaches further in front of the mouth, almost proportionally to head size, while peak and average flow velocities are roughly size-independent. Both maximal prey size and the maximal distance from which prey can be caught successfully by suction, are estimated to increase significantly with increasing head size. Although a decreasing (angular) speed of buccal expansion with increasing size could be predicted (based on calculations of power requirement and the expected mass-proportional scaling of available muscular power in *C. gariepinus*), the observed drop in (angular) speed during growth exceeds these predictions. The calculated muscle-mass-specific power output decreases significantly with size, suggesting a relatively lower suction effort in the larger catfish compared to the smaller catfish.
Keywords: Prey capture, modelling, Flow velocity, Power requirement

A7.31
Self-repairing membranes for pneumatic structures: Transferring nature's solutions into technical applications

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Over the last few years, plants have proved to be a real treasure trove as models for the construction of biomimetic technical structures and materials. One on-going project deals with the construction of technical membranes with rapid self-repair mechanisms inspired by plant structures. For analytically describing the (fast) self-repair characteristics of the parenchyma, lianas (e.g. *Aristolochia*) and herbaceous plants (e.g. *Phaseolus*, *Ricinus*) are used as model organisms. These plants react to fissures in their peripheral tissues with repair mechanisms on at least three hierarchical levels, which seal the lesion very effectively and secure the functional integrity of the plant structure. The mechanism on one level is based on fast strain-triggered deformation processes of pressurized parenchyma cells sealing the fissure. In cooperation with the Swiss company 'prospective concepts ag', biomimetically inspired self-repair functions are transferred into technical membranes of ultra-light pressurized beams based on the Tensairity® concept.
Keywords: Biomimetics, Self-repair mechanism, Strain-triggered, Cell deformation, Tensairity®

A7.32
Structure, chemical composition and mechanical properties of epicuticular waxes in the pitchers of the carnivorous plant *Nepenthes alata*

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The zone situated below the peristome inside the pitchers of the most carnivorous plants from the genus *Nepenthes* (waxy zone) is covered with a thick layer of epicuticular wax and is reported to play a crucial role in animal trapping and retention. In *N. alata*, two layers of waxes were distinguished. These layers differ in their structure, chemical composition and mechanical properties, and they decrease the attachment of insects in different ways. The lower level resembles a foam composed of interconnected membraneous platelets, whereas the upper layer consists of densely placed separate irregular platelets bearing a pedicel-like "foot". These morphological distinctions are caused primarily by differences in chemical composition of waxes. Waxes of the upper and lower layers exhibited different mechanical properties: wax of the lower layer is harder and stiffer than that of the upper layer. Moreover, crystals of the upper layer are very brittle and may be easily exfoliated or broken to tiny pieces. The laboratory experiments showed that both wax layers reduce the attachment force of insects. Both layers lead to the reduction of the contact area of insects' feet with the plant surface. Additionally, crystals of the upper layer contaminate insects' adhesive organs.
Keywords: Wax crystals, Hardness, Elasticity, Insect attachment

A7.33
Adhesion of echinoderm tube feet to rough surfaces

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Echinoderms attach strongly and temporarily to the substratum by means of specialized organs, the podia or tube feet. They consist of a basal extensible cylinder, the stem, which bears an apical flattened disc that attaches and detaches repeatedly to the substratum through adhesive and de-adhesive secretions. In their activities, echinoderms have to cope with substrata of various roughnesses, as well as, with changing hydrodynamic conditions, and therefore their tube feet must adapt their attachment strength to these environmental constraints. This study is the first attempt to evaluate the influence of substratum roughness on the temporary adhesion of echinoderm tube feet and to investigate the material properties of their contact surface. It was demonstrated that tube foot discs have viscoelastic properties (E-modulus of 6.0 and 16.4 kPa for sea stars and sea urchins, respectively), adapt their surface to the substratum profile, and show increased tenacity (i.e. adhesive force per unit area) on rough substratum in comparison to its smooth counterpart (e.g. 0.17 and 0.34 MPa on smooth PMMA, 0.20 and 0.47 MPa on rough PMMA for sea stars and sea urchins, respectively). Under slow self-imposed forces disc material behaves viscously to adapt to substrate macro-roughness while the adhesive fills out only very little surface irregularities (micro-roughness), being deposited as a low thickness film ideal for generation of strong adhesion. Under short pulses of wave-generated forces, attached discs behave elastically, distributing the stress along the entire contact area, in order to avoid crack generation or disc peeling and thus precluding tube foot detachment.
Keywords: Sea star, Sea urchin, Tube foot disc, Tenacity, Viscoelastic material

A7.34
Critical roughness for insect attachment: Experimental evidences for the beetle *Gastrophysa viridula*

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The leaf beetle *Gastrophysa viridula* (Coleoptera, Chrysomelidae) has adhesive setae on legs, serving for attachment to various surfaces. To understand the functional mechanism of the attachment system, the effect of surface roughness on the traction force, generated by the beetle, was studied. The epidermal cells on both adaxial and abaxial leaf surfaces of beetle's host plant, *Rumex obtusifolius*, are larger than the terminal elements of setae. However, the traction force on the abaxial epidermis was lower than that on the abaxial one. This may be caused by the higher surface roughness of the abaxial surface due to the presence of stomata. The effect of surface shape and roughness (from >1 nm to 600 nm (RMS)) on traction force were also observed. The results demonstrated that the traction force was corresponded to an adhesion parameter of setae on a fine structured surface. The critical roughness for traction force was 100 nm (RMS) and it was depended on a height and a wavelength of a surface fine structure.
Keywords: Insect, Attachment device, Adhesion, Friction, Surface roughness

A7.35
Slippery ant–plants and skillful climbers

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Biomechanical factors play an important role in many insect–plant interactions. Analogous to the ability to sequester or detoxify defensive plant compounds, some specialist insects are capable of circumventing biomechanical barriers set up by plants. Ant–plant interactions in the genera *Macaranga* and *Nepenthes* provide two fascinating examples of biomechanical specializations to slippery plant surfaces. In the mutualism between ants and *Macaranga* trees, ant partners of the genera *Camponotus* and *Crematogaster* are capable of running on slippery waxy stems that effectively keep other ant species away from the host plant. The carnivorous pitcher plant *Nepenthes bicalcarata* is inhabited by the specialized ant *Camponotus schmitzi* that can easily run across the slippery pitcher peristome and never gets trapped by the pitchers. In both insect–plant interactions, slipperiness for insects is based on different surface properties. On the stems of *Macaranga* trees, epicuticular wax crystals detach and contaminate the tarsi of climbing insects, whereas in *Nepenthes*, the microstructured peristome surface is completely wettable so that insect legs skid on thin water films. We measured attachment forces of insects on natural and artificial model substrates. Our findings indicate that in both ant–plant systems, the ants' capacity to cope with the slippery surfaces is less the result of superior adhesion than of behavioral and/or locomotory adaptations.
Keywords: Adhesion, Myrmecophytes, Locomotion, *Macaranga*, *Nepenthes*

A7.36
Adhesion and friction in stick insect tarsal pads

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To investigate the mechanisms of adhesion and friction in smooth adhesive pads of insects, we measured single pad forces in stick insects (*Carausius morosus*) using a 2D force transducer and a computer controlled translation stage. By simultaneously recording contact area using reflected light, we obtained shear stress. Friction forces were maximal in the direction toward the body. This anisotropy appeared largely due to variation of contact area but not of shear stress. Several lines of evidence indicate that adhesive pads can generate static friction: The transition from rest to sliding was associated with a force peak that increased with contact time before the movement. As this classic concept of 'static' friction appeared inappropriate because peak forces were velocity dependent, we measured the remaining force 2 minutes after a sliding movement; shear stress still averaged 20–200 kPa. The considerable static friction is inconsistent with the assumption of a continuous fluid film between pad and surface. Moreover, the sliding shear stress exceeded predictions derived from viscosity estimates obtained using interference reflection microscopy. Both findings indicate that the pad cuticle directly interacts with the substrate. To elucidate the function of the 'adhesive' fluid we performed long distance slides and multiple consecutive pull-offs to deplete adhesive secretion. Surprisingly, adhesion and friction strongly *increased* with decreasing amount of fluid. However, the fluid may be important for increasing the contact area on rough substrates, reducing wear and removing contamination. Our study shows that a consistent model of insect adhesion still needs to be established.
Keywords: Insect adhesion, Shear stress, Adhesive fluid, Friction, *Carausius morosus*

A7.37
Arthropod exoskeleton mechanical properties gradients visualized by phase imaging AFM

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The arthropod cuticle provides a highly efficient exoskeleton that is adaptable to a wide spectrum of functions. These range from lightweight aeronautical applications to flexible devices for energy storage and attachment as well as rigid protective structures. The great variance in material composition that forms one of the underlying principles for this adaptability has been studied to quite an extent using diverse methods. In this context nanoindentation measurements have provided information on cuticle hardness. Especially the mouthparts responsible for chewing are prone to aberration and as such are reinforced. Harder regions are thereby often located at the cutting edges with the softer regions situated at non-incisive regions. This gradient is proposed to ensure a self-sharpening of mandibles as the softer material preferentially wears away, leaving angled edges at the harder regions.
Atomic Force Microscopy provides an effective tool for measuring material characteristics. Force mapping in AFM contact mode was performed on the mandibles of several arthropods in order to supply information on indentation hardness. Furthermore phase

imaging in intermittent contact mode was performed. As the interaction between AFM probe and sample in intermittent contact mode can be seen as a mass spring oscillator system, where the sample's elasticity (or lack thereof) is regarded as the damping parameter on spring (AFM probe) oscillation, proposed gradients in arthropod mandibles could be pointed out.

A7.38
No Abstract received

A7.39
Mechanical properties of the toe pads of the tree frog, *Litoria caerulea*

W.J.P. Barnes, P. Perez-Goodwyn and S.N. Gorb, (Glasgow University, UK; Max Planck Institute for Metals Research, Germany, J.Barnes@bio.gla.ac.uk)

Mechanical properties of surfaces and, in biological systems, underlying structures make important contributions to friction and adhesion, but have all too often been neglected. Here, we use white light interferometry and micro-indentation to analyse three-dimensional surface topography and mechanical properties of toe pads in living adult and juvenile White's tree frogs, *Litoria caerulea*. White light interferometry reveals toe pads to be dome shaped, broader than long, with radii of curvature of ca 1.5×0.75 mm (juveniles) and ca 7×3 mm (adults). Indentation of the surface of individual toe pads was carried out using glass or sapphire spheres of different diameters (64 μm, 264 μm and 1.5 mm) at a constant velocity of 16 μm s^{-1}. Force/indentation-depth plots allowed estimates of reduced Young's Modulus and Work of Adhesion using Hertz and JKR equations. Results showed that indentation depth was inversely related to Young's Modulus; that values of Young's Modulus were higher for juvenile than adult frogs (ca 20,000 Pa compared to ca 7,000 Pa); and higher when smaller rather than larger spheres were used. From these data, we can conclude that tree frog toe pads are amongst the softest of biological materials (comparable to jellyfish mesogloea) and that the surface layer is harder than the material beneath. The softness of the material will aid conformation of the pad to the substrate, conducive to higher adhesion. That values are lower for adults than juveniles may partly explain the increased efficiency of adult toe pads in many species. Results are related to pad ultrastructure as determined by scanning and transmission electron microscopy.
Keywords: Adhesion, Tree frog, Young's Modulus, Work of Adhesion, Micro-indentation

A7.40
Toe pad cell structure and function in tree frogs adhering to smooth surfaces

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Many species of tree frog are noted for their ability to adhere to smooth vertical surfaces. This is conferred by specialised disc-like digital pads, the morphology of which is remarkably similar across the many groups in which they appear. However, relatively few studies have attempted to investigate adhesion as it relates specifically to pad structure, mostly due to limitations in methodology. Consensus is that frogs are chiefly dependent on a wet adhesive mechanism facilitated by mucosal glands scattered across the pad surface. Whilst it is likely that this is the main mechanism involved in the tree frogs' abilities to scale smooth substrates, a recently developed technique, interference reflection microscopy (IRM), has allowed us to observe toe pad cells in live frogs. It shows that in many places cells are in much closer contact than would be expected for such a system. IRM images further suggest that peg-like nanostructural features, previously considered residual artefacts, may be of key importance to adhesive function. A tilting microscope, developed for use in the field, has also illuminated hitherto hidden elements of the adhesive system, allowing observation of responses during tilts from the horizontal to angles beyond the vertical. Particularly in larger frogs, there is a dynamic element. At increasing angles, higher proportions of the cells come into close contact with the surface, creating greater friction by increasing points of contact and facilitating a larger contribution for viscosity (Stefan adhesion). Images also show cells are deformable enough to mould closely around small diameter surface asperities.
Keywords: Adhesion, Tree frog, Toe pad, Cells, Interference reflection microscopy

A7.41
Vertical jumping in bonobo (Pan paniscus)

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This study investigated how morphological differences between humans and bonobo relate to differences in vertical jumping performance and jump execution. The bonobo jump was analyzed in terms of jump height, kinetics and kinematics and compared to human jumping. Jump height, defined as the vertical displacement of the body center of mass in the airborne phase, was nearly twice as high in bonobo (0.75 m) as in humans (0.35 m–0.45 m). Morphological traits that have been related to successful jumping, such as long legs and massive hind limb musculature are more readily associated with humans than with bonobos. Nevertheless, the bonobo manages to produce relatively more work during the push-off than humans. Most work and power is generated at the hips while the mechanical output at the knees is negligible. This distribution is attributed to the bonobos relatively short legs in combination with the biarticular hamstrings. The bonobos superior performance is explained by (a) the low starting position that the bonobo assumes by virtue of its long muscles, (b) the more forceful arm swing and (c) the active extension of the trunk.

A7.42
A biomechanical analysis of jumping performance in the frog, *Rana pipiens*

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In a previous study, we found that maximal or near maximal jumping performance in the frog is achieved with a catch mechanism of the plantaris longus (PL), one of the major contributors to frog jumping performance. For the catch mechanism to work, the muscle fibres need to shorten early in the

propulsive phase of the jump while the muscle tendon unit remains at a constant length, thereby stretching series elastic elements of the muscle. In the latter part of the propulsive phase, the muscle tendon unit then shortens and the shortening speed is enhanced by the release of energy from the series elastic elements. We speculated that for the catch mechanism to work effectively, large forces are required early in the propulsive phase, and therefore that the catch mechanism would be more pronounced for near maximal jumps and would be less important for sub maximal jumps. In order to test this speculation we measured jumping performance in six frogs (36 jumps ranging from 13 to 67 cm), while simultaneously measuring PL force, fibre length and muscle tendon unit length. The magnitude of the catch mechanism was defined as the maximum difference between fibre and muscle tendon unit length. Linear regression analysis between jump distance and catch magnitude indicated that increasing jump performance was associated with an increase in the catch mechanism. We conclude from these results that frogs evoke the catch mechanism in PL to enhance performance of the muscle.

A7.43
Negotiating obstacles: Running kinematics of the lizard *Sceloporus malachiticus*

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The ability to climb obstacles is an ecological advantage for small vertebrates because it allows expansion of their spatial niche across distinct structural microhabitats. However, locomotion over obstacles involving abrupt changes in substrate incline may be constrained in lizards by their sprawled posture and fused girdle elements. In this study, individuals of *Sceloporus malachiticus* were videotaped at 500 fps during steady level locomotion and when moving over rectangular obstacles of different heights. Animals traversed the low barrier with little change in their general pattern of running compared with level locomotion, but paused more frequently when negotiating medium and high barriers. The lizards most commonly climbed or jumped to negotiate the highest barrier. The occurrence of bipedal running also increased with barrier height. During obstacle climbing, the forelimb acted as a lever to pull the animal's body over the obstacle, while the hind limbs pushed against the ground to propel the pelvis upward and forward. Body speeds decreased 20% from low to high obstacles and trunk was more elevated for negotiating high barriers. 3-D reconstruction of fore and hind limb motion showed that vertical limb displacement increased with barrier height while horizontal motion decreased. Hand and foot positions on the barrier varied among obstacles and slipping incidence increased at highest barriers. Limb duty factors increased with barrier height, and fore limb step frequency decreased at the highest obstacle.
Keywords: Lizard, Obstacles, Kinematics, Behavior

A7.44
Three-dimensional joint kinematics and kinetics during bipedal running: Effect of limb posture

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Birds and humans provide a useful comparison for understanding the effect of limb orientation on joint mechanics. We examined and compared joint mechanics during running in humans and ostriches – the largest avian biped – thus minimizing the confounding effect of body mass. 3-D-kinematic models of the ostrich and human lower limbs were used in conjunction with high-speed video and force-plate data to compute 3-D joint angles, moments and powers using inverse-dynamics. The greatest joint motion in both species occurs in flexion/extension. However, non-flexion/extension joint motion is considerable, primarily during the swing-phase. Interestingly, the joint axes alignment of the ostrich knee and ankle result in substantial non-sagittal segment motion that is coupled to flexion/extension at these joints. Despite differences in limb design and orientation, many features of ostrich and human joint kinetics exhibit similar behaviour. Overall patterns of the net joint moments and powers indicate that general rules governing bipedal locomotion may exist at lower levels of organization than simple centre of mass movement. Nevertheless, several characteristics of joint kinetics in the ostrich are distinct from humans. Notable is the distribution of energy amongst distal joints; the metatarso-phalangeal joint of the ostrich, rather than the ankle, provides power during stance. Ostriches exhibit considerably larger frontal and transverse plane moments and powers, in particular at the knee. The extent to which these moments and powers are generated passively (e.g. ligaments) or actively via muscle may provide insight into the mechanisms for joint control and stabilization during bipedal locomotion.
Keywords: Joint, 3-D, Kinematics, Kinetics, Bipedal

A7.45
Segment orientation and direction of locomotion

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In locomotion, the leg is retracting during stance and protracting during swing. In stance phase, the leg needs to build up leg force to support body mass. Larger animals prefer to use almost straight leg configurations to cope with their increased ratio between body mass and muscle force. Here, we ask to what extend the leg's segmental orientation could further influence its mechanical advantage (ratio leg force to muscle force). To address this issue we build a two-segmented robotic leg with a servo motor at the hip and an elastic leg joint between the segments. We asked for periodic movement patterns of such a one-legged hopping robot for a given sinusoidal pattern of the hip joint angle with respect to the vertical axis. We found that stable hopping can occur in both movement directions: (1) with the leg joint pointing forward (similar to the human knee) when a high frequency was applied to the hip joint motor and (2) with the leg joint pointing backward (similar to the ankle joint of birds) for lower frequencies. We suggest that depending on segmental orientation with respect to the movement direction legs can (1) increase their mechanical advantage if the leg joint is pointing forward reducing the muscular effort to support body weight or (2) increase the elastic capacity of the leg if the leg joint is pointing backward enhancing the amount of leg flexion and elastic energy recoil.
Keywords: Leg design, Mechanical advantage, Elastic joints, Stable running

A7.46
The spring–mass model for walking

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The inverted pendulum for walking and the spring–mass model for running are frequently used as basic gait paradigms in animal and human locomotion. However, both models rank differently when assessing their value as gait templates that parsimoniously encode the whole body dynamics distinguishing both gaits. In this respect, only the spring–mass model prevails and the inverted pendulum model must be refuted. Correspondingly, experiments revealed that instead of vaulting over rigid legs, in walking, significant stance limb compressions are observed, which at high speeds are even comparable to those in running. Motivated by these experimental findings, we asked whether the characteristic walking pattern can be explained by compliant, rather than stiff, leg behaviour. Hereto, we extended the spring–mass model by a second idealized leg spring, and found that the bipedal model can display self-stable locomotion with whole body dynamics similar to that observed in walking; suggesting leg compliance to be essential not only in walking, but in legged locomotion in general. In comparison to the inverted pendulum model, the bipedal spring–mass model establishes two new qualities: it emphasizes the importance of the double support, and incorporates the experimentally observed motion along the leg axis as an additional degree of freedom. Moreover, as a direct derivative of the simple spring–mass system, the bipedal model combines the two fundamental gaits of walking and running within a single mechanical framework, contradicting the general belief that both represent two distinct phenomena of legged locomotion.
Keywords: Leg compliance, Self-stable walking, Gait template

A7.47
Galloping: The long and the short of a mechanically ambiguous gait

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The gallop is a high speed asymmetric quadrupedal gait. Although a consistent footfall pattern is used by both large and small mammals, the mechanics of the gait and the functional significance for the footfall sequence is unclear. There is some potential for elastic energy storage in flexion and extension of the spine, but axial movements are limited in larger galloping forms. We present an alternative evaluation of the gallop and suggest that the sequence of footfalls, centre of mass motions and velocity changes within a stride can all be explained in terms of minimizing energy loss resulting from collisional contacts between the animal and the substrate over which it moves. Collisional contacts cannot be entirely avoided for an animal moving rapidly over a solid surface by means of a finite number of legs, but the losses associated can be reduced to manageable levels if 1) the angle of incidence of the initial contact is small and 2) the entire contact is divided into multiple ‘sub-collisions’. This strategy is particularly effective for large, fast running quadrupeds, such as ungulates. It does not, however, match the movement observed in the gallop of small animals, even though the footfall pattern is similar. Thus, small and large mammals may not be performing the same mechanical function with their highest speed gait, even though these have traditionally been defined as a gallop.
Keywords: Gallop, Collision, Locomotion, Scaling

A7.48
Walking mechanics in bipeds and quadrupeds

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Bipedal walking following inverted pendulum mechanics is constrained by two requirements: sufficient kinetic energy for the vault over midstance; and the sufficiency of gravity to provide the centripetal acceleration required for the arc of the body about the stance foot. While the acceleration condition identifies a maximum walking speed at a Froude number of 1, empirical observation indicates favoured walk–run transition speeds at a Froude number around 0.5 for birds, humans and humans under manipulated gravity conditions. In this study, we demonstrate that the risk of ‘take-off’ is greatest at the extremes of stance. This is because before and after kinetic energy is converted to potential, velocities (and so required centripetal accelerations) are highest, while concurrently the component of gravity acting in line with the leg is lower. Limitations to the range of walking velocity and stride angle are explored. At walking speeds approaching a Froude number of 1, take-off is only avoidable with very small steps. With realistic limitations on swing-leg frequency, a novel explanation for the walk–run transition at a Froude number of 0.5 is shown. Quadrupedal walking can be considered mechanically as a pair of linked inverted pendulums. Kinematics of quadrupedal walking are compared with those calculated for simple unlinked inverted pendulums. Deviation from passive dynamics are considered within a collisional context: slowing of the shoulders or hips prior to foot-strike of the fore- or hindlimbs, and leg extension at the same instant, reduce collisional losses.
Keywords: Inverted pendulum, Collision, Froude number

A7.49
Walk–trot transition speeds in quadrupeds

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The mechanisms underlying the gait transition from walk to a ‘bouncing gait’ (run, trot or pace) have been widely investigated in humans. The Froude number – a dimensionless speed taking into account leg length and gravity – of transition for bipeds, is generally documented as 0.5. There are few equivalent values for quadrupeds. Studies have observed a Froude number of 0.35 at transition in horses (Griffin et al, 2004), and a Froude number of 0.5 in dogs (Jayes and Alexander, 1978). Both of these speeds fall well below the theoretical limit of walking speed for an inverted pendulum of 1. Here we examine whether the preferred dimensionless transition speed in two morphologically distinct breeds of dog is the same as the previously observed value of 0.5, or closer to that recorded in horses. Six Greyhounds and six Labradors of similar weights were trained to locomote on a re-geared equine treadmill at a self-selected gait. Kinematic data were collected across a range of speeds and used to determine the walk–trot transition speed using both kinematic and mechanical gait definitions. Preliminary results

suggest that dogs have a preferred dimensionless transition speed of nearer 0.5, although this is remarkably variable (from 0.3 to 0.5). There may also be an inter-breed difference in transition speed, with Greyhounds making the transition at a lower Froude number than Labradors.

A7.50
Gait patterns and hoof impact in a captive giraffid, the Okapi (Okapia johnstoni)

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Okapis are endangered giraffids endemic to Central African rain forest. In captivity, they often develop highly problematic hoof malformations, whose etiology is multifactorial. Substrate type may be one of the major factors. We collected data for nine individuals of the Antwerp Zoo (six healthy, three with minor to serious hoof malformations), walking on hard (concrete) and soft (sand) substrates. Kinematic analysis (50 fps unilateral video) yielded basic gait variables for 331 sequences (e.g. velocity, stride frequency, duty factor) and segment and joint angles for 35 selected sequences. Additionally, we collected accelerometry data (5000 Hz) for selected individuals and preliminary pedobarographic data (300 Hz) and morphometric data for two subjects. We found significant differences in most kinematic gait variables between healthy and malformed subjects, and between the two substrate types. The most striking difference is in the fetlock joint, which is much more extended in malformed subjects than in healthy subjects, possibly leading to overstressing of the digital flexors and of the suspensory ligament. Unsurprisingly, peak accelerations for walking on concrete are higher than those on sand. Additionally, wavelet analysis of the vertical component revealed high impact frequencies (up to 500 Hz) when walking on concrete. Our analyses show that substrate type influences gait in both healthy and malformed okapis, and that malformed okapis walk differently from healthy ones on either substrate. Future research, combining kinematic, kinetic and morphometric data should allow to compare quantitatively the load on the musculoskeletal system in healthy and malformed okapis walking on various substrates.
Keywords: Okapi, Gait, Hoof problems, Kinematics, Accelerometry

A7.51
Detailed kinematical analysis of terrestrial locomotion in gibbons

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In captivity, gibbons frequently travel terrestrially, using a bipedal, tripedal or quadrupedal gait, at a wide range of speeds. We question how the kinematics of the bipedal locomotion of gibbons (*Hylobates lar*), having a distinct morphology and lacking any bipedal specializations, compares to the bipedal locomotion of bonobos and humans. In addition we also briefly discuss the atypical tripedal and quadrupedal gaits of gibbons. The data were collected in the Animal Park of Planckendael, Belgium using four fixed S-VHS cameras (50 Hz). These were positioned laterally and frontally to a walkway to record the terrestrial locomotion of four non-trained gibbons. The different views of each sequence ($N = \pm 50$) we digitised and synchronised using Kwon3D 3.1 software. In each sequence we selected one hindlimb stride for which we calculated the spatio-temporal parameters, the 3D joint angles and some additional parameters. Gibbons have a rather fast bipedal gait with a bent-hip, bent-knee position and a slightly inclined trunk. The hip and ankle excursions are large compared to bonobos and humans and increase with increasing speed. Speed has also an important influence on foot clearance, on some 3D joint angles and on most spatio-temporal parameters. The ankle is plantar flexed at initial contact and there is a secondary knee flexion during the stance phase, similar to the knee pattern seen in humans. Despite the lack of bipedal or terrestrial adaptations gibbons appear to be adept in terrestrial locomotion. However, their specialized body proportions do influence the gait characteristics.
Keywords: Gait analysis, Biomechanics, Primate, Bipedalism

A7.52
The effect of size on the kinetics and kinematics of ostrich locomotion

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Most studies of the relationship between size and locomotion compare different species rather than different sized individuals of a single species. The ostrich (*Struthio camelus*) is the fastest living cursorial biped and demonstrates a rapid growth rate, increasing in mass by 100 times and hip height by seven times in six months. Here we studied the effect of size on the mechanics of locomotion in fifteen ostrich chicks over a period of six months from hatching. The chicks were trained to run over a force plate, enabling measurement of ground reaction forces. Synchronous kinematic data were collected using an infra-red motion analysis system. From the age of three months the birds were also trained to run on a treadmill, enabling the collection of kinematic data at varying and pre-determined speeds (1.8 ms^{-1} to 9.5 ms^{-1}). During each testing period bird weight and hip height were recorded. We found that growth rates varied slightly between individuals, but that a consistent scaling relationship existed between hip height and mass (M) during the first 6 months of growth, such that hip height and long bone segment length were all proportional to $M^{0.4}$. This is somewhat higher than geometric similarity ($l \propto M^{0.33}$), and published values for scaling of length with mass between species. The relationship between speed and body-weight-corrected peak ground reaction force was independent of body mass. Evaluation of stride frequency, duty factor and leg stiffness parameters is ongoing.

A7.53
The locomotor kinematics of Asian and African elephants: Changes with size and speed

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We collected kinematic data from 52 elephants (46 Asian, 6 African) across a range of speeds (539 steady-speed trials across 10m), as a first step toward characterizing their locomotor dynamics. Video framing rates differed (e.g., 60–240 Hz) between sessions but gave similar results. The fastest observed speeds were 6.8 m/s for Asian but only 4.2 m/s for African elephants; however we explain why the former speed is probably near-maximal for both species. Interestingly, similarly sized individuals of the two species had strongly similar kinematics across speed. Hence other elephantids such as mammoths probably also moved similarly. Smaller elephants used relatively longer but absolutely shorter strides. In absolute terms small and large elephants could reach similar near-maximal speeds although smaller elephants were capable of relatively higher performance, matching that of even some galloping larger mammals. These trends lead us to infer that very large elephantids are limited in their maximal performance (i.e., duty factors >0.5, Froude numbers <1.0). We discuss whether a gait change can be deduced from kinematic variables. Like many animals, elephants increased speed with a combination of larger stride lengths and higher stride frequencies up to moderate speeds, then almost exclusively via larger stride lengths. Similarly, proximal limb joints contributed most to stride length, and patterns of joint flexion/extension matched those of many other mammals. Humans and elephants share striking similarities in limb protraction/retraction angles and other kinematic patterns, illuminating a common locomotor mechanism related to their similar limb anatomies and habitually more extended limb joints.

Keywords: Elephants, Biomechanics, Locomotion, Scaling

A7.54
Mechanical energy fluctuations of symmetric and asymmetric gaits in Icelandic ponies

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Preferred gait at a particular speed is probably driven by a combination of mechanical cost, stability, manoeuvrability and performance requirements. Here we investigated the mechanical cost and stride parameters for different gaits and speeds in eight Icelandic horses at walk, trot, canter, tolt and pace. Speed was measured using GPS. Foot-on and foot-off times for each leg were from an accelerometer attached to the dorsal hoof wall. Trunk motion was determined using a 6 degree of freedom inertial sensor attached over the approximate centre of mass. Gaits were classified using: the ratio between midstance time for left and right forelimbs, the ratio between front and hind midstance timing and the ratio of the difference in time between the fore and hind timings for both left and right sides of the horse were examined. The relationship between stance time and speed was similar for the different gaits. There were significant differences between gaits in linear and rotational trunk motion as a function of speed. We calculated external work (potential energy and linear kinetic energy changes) through each stride. We modelled the horse trunk as a cylinder to estimate the rotational inertia in each plane and calculated the components of internal work represented rotation of the trunk around the centre of mass. There were significant differences between vertical displacement and pitch and roll amplitude for the different gaits. Cranio-caudal kinetic energy fluctuations were the greatest component of total energy fluctuations for all gaits at all speeds.

A7.55
Effect of surface on mechanics of horse locomotion

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The aim of this study was to determine the effect of different surfaces on the mechanics of horse locomotion at walk and trot. Surfaces act in series with the runner's leg and may influence overall limb compliance. Humans adjust leg stiffness in response to changing surface stiffness so that the leg plus surface combination remains constant. It is unclear if horses respond in a similar manner. If a horse can compensate by increasing leg stiffness it should maintain similar stance times, duty factors and fluctuations in centre of mass motion (and external work) on different surfaces. Alternatively if the horse cannot adjust leg stiffness it should increase stance time and duty factor on soft surfaces. This would reduce peak limb force and possibly injury risk but may change the work performed on the centre of mass through the stride. Six thoroughbred horses were walked and trotted in hand on level concrete and sand runways. Stride parameters were obtained from foot mounted uniaxial accelerometers logged directly onto a hand held computer. Two inertial sensors were positioned over the thoracic vertebrae and pelvis to record vertical and horizontal trunk movements by double integration. Preliminary investigations indicate there was no difference in stance time or duty factor at walk and trot on the two surfaces. Protraction times of both fore and hind limbs appear to increase on soft ground.

A7.56
No Abstract received

A7.57
Stretch activation versus shortening deactivation in invertebrate muscle

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It may be illuminating to apply biomechanical analysis by quick stretch and release to muscular tissues which serve very different functions, such as cardiac muscle and body wall muscle. Such an analysis is here applied to molluscan cardiac muscle and holothurian body wall muscle, both of which have a history in Biomechanics dating back at least to the invention of the Levin–Wyman ergometer. The work to be reported here is restricted to experiments depending on the use of the Dual-Mode Lever Arm System (Cambridge Technology/Aurora Scientific). Shortening deactivation has been studied in ventricular trabeculae of *Spisula solidissima*. This is the flip side of heterometric autoregulation of molluscan hearts, as described by W. Straub (1901, 1904). That is, stretch induces increased force of contraction while release leads to diminished force (H. Nomura, 1963). In this study, quiescent trabeculae have been stimulated before a stretch/release cycle so that isometric force at a predetermined fixed length before a release may be compared to peak force during a quick release to a set length. An expression for shortening deactivation has been derived. Stretch activation and force redevelopment after release have been studied with isolated sections of longitudinal muscle of the body wall of *Thyonella gemmata*. Quiescent muscle may be activated by

stretch or with 56 mM KCL. After activation, active force was released in a cumulative series of lever movements. Measurements were taken of length of release and time constant of active force redevelopment, as an index of active state.

Keywords: Invertebrate muscle, Isometric contractions, Stretches, Releases

A7.58
Dynamical analysis in the manoeuvrability of hovering insect

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A biology-inspired dynamic flight simulator was established based on a mathematical model of rigid multibody dynamics with one body and two wings firstly. And the contribution of inertial forces during the steering manoeuvres of a hovering *Drosophila* was analyzed systematically. Initially, to eliminate the contribution of aerodynamics and focus the analysis on inertial forces, the flying manoeuvres were simulated within vacuum ambience. Then, the inertial forces were compared with the aerodynamic forces published. The wings' kinematics schemes were idealized from the real wings' motion of hovering *Drosophila*, keeping the stroke plane invariant and the up- and downstroke symmetrical in one complete wingbeat. The morphological parameters, such as wings' size and aspect ratio, were in concordance with those of real *Drosophila*. The simulation results and the comparisons imply that inertial forces may play some roles in the steering manoeuvres of insect free flight accompanied with aerodynamic forces. For the symmetrical flapping motion of bilateral wings, only inertial pitch force moment exists, which conducts the rotation tendency of nose-up climbing or nose-down falling. And for the asymmetrical flapping cases, all force moments, including yaw-, pitch- and roll torque, can influence synthetically the attitude of whole insect and finally result in the corresponding steering manoeuvres.

Keywords: Insect, Flapping flight, Hovering, Multibody, Manoeuvrability

Dickinson, M. H., Lehman, F. O. and Sane, S. P. (1999). Wing rotation and the aerodynamic basis of insect flight. *Science* 284, 1954–1960.

Sun, M. and Tang, J. (2002). Lift and power requirements of hovering flight in Drosophila virilis. *J. Exp. Biol.* 205, 2413–2427.

A7.59
Ants running at different inclinations: Footfall patterns and tripod geometry

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A comparative kinematic study between the wood ant *Formica pratensis* and the desert ant *Cataglyphis fortis* aims at both clearing up the mechanisms underlying three dimensional path integration (monitoring distances and inclinations presumably by proprioceptive mechanisms) and a fundamental analysis of the locomotor system of two organisms that are morphologically similar and vary mainly in the relative lengths of their legs (Sommer and Wehner, unpublished). For this purpose animals of both species were trained to forage within a setup that allowed to take high speed recordings (250 Hz) at different inclinations (0, ±30, ±60 deg) from both lateral and dorsal views. The two species vary in running speed: Within channels wood ants run at speeds of 0.05–0.25 m/s. In general they slow down at steep inclinations, regardless in which direction they run. Desert ants run faster (0.1–0.4 m/s) and seem to speed up on downhill paths in contrast to slowing down during ascents. Increase in speed is accomplished by an increase in stepping frequency with a resulting lower duty factor (time of stance phase in relation to the whole step cycle). A first analysis indicates that in both species of ants speed and duty factor follow the same relationship at level ground, but show different relationships on inclined surfaces. As footfall patterns and tripod geometry vary with load, we shall also analyze whether a changing gravity vector shows a similar effect.

A7.60
Does hagfish slime thwart gill-breathing predators?

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Hagfish are capable of producing large amounts of slime when harassed, but the precise function of their slime is unclear. The list of common hagfish predators includes several air-breathing animals, but lacks fishes. This observation has lead to the hypothesis that hagfish slime functions as a defence against gill-breathing predators, whose gills may become clogged by the slime's mixture of mucins and fibres. We tested this hypothesis by measuring the effects of slime from a live hagfish on water flow rates through an artificial gill analogue and real gills in isolated rockfish heads. In a small aquarium, we used a "slime vacuum" apparatus consisting of artificial or real gills connected to a siphon system to measure water flow over a time period during which the hagfish slimed. The release of slime by the hagfish significantly reduced flow rates through both the gill analogue and rockfish gills, and increased gill resistance considerably. Our analysis shows that hagfish slime is capable of impairing water flow through the gills of fish predators. The effect may be fatal if the slime reduces gas exchange through a decrease in water flow, or an increase in diffusion distance across the gills. Respirometry of slimed fish predators should be studied in the future to test the predator-defence hypothesis further.

Keywords: Hagfish, *Eptatretus stouti*, Slime, Gill resistance, Predator defence

A7.61
Limits to the climbing ability of lobsters (*Homarus americanus*)

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American lobsters (*Homarus americanus*) are mobile benthic invertebrates which make long seasonal migrations. Obstacles on the highly varied ocean floor may present an impediment to their progress. Previous applied research has been conducted in our laboratory to evaluate the potential of submerged natural gas pipelines to obstruct lobster migration. From this research, the three main limits to the climbing ability of lobster were hypothesized to be: angle of the surface to be climbed, body size

of lobster, and surface texture of the incline. To test the limits proposed above, experiments were performed using a moveable flat platform that can be raised to various angles. Inclines of 0°, 20°, 30°, and 40° were examined. Lobsters were obtained locally and tested individually. At each angle, the lobster's movement was filmed from several different angles for behavioural observations. Sequences of still shots were also captured during climbing attempts and used to examine changes in body position used by the lobsters while climbing at different angles. To investigate the limitation imposed by surface texture, different surface textures were used on the climbing platform. Results from this work give a more detailed understanding of how lobsters climb over obstacles in their natural environment.

Keywords: Lobster, *Homarus americanus*, Locomotion, Climb, Walking

A7.62
Flow visualization and force measurements on a flapping wing model

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Flow visualization and direct force measurements on a bird model with flapping wings allow a new insight into the mechanisms of flapping flight. The bird model based on the body shape and the aerodynamic characteristics of a goose ($Re = Uc/v = 00{,}000$; $k = \pi fc/U = 0.04$; v—kinematic viscosity, U—flow velocity, c—chord of wing, f—frequency of wingbeat). Geese get over long distances during migration with a constant, low energy, flight mode and a typical wake structure. Because of the low reduced frequency bird flight usually is treated as quasi-steady state. The investigations show more about the accuracy of this assumption and the influence of the different flight parameters like frequency, amplitude and angle of attack. The model has been investigated in a large (2.2 m × 2.9 m), low-speed wind tunnel. Particle image velocimetry has been used for the visualization of the wake structure behind the wings and has been synchronised with the force measurements of an internal three-component balance. Planes perpendicular to the flow direction and parallel to the flow direction have been observed to show both the tip vortex and the traverse vortices shed from the wing trailing edge. The presence of traverse vortices indicates a change of the circulation which can be calculated by vorticity and Stokes theorem. In addition to the balance showing the whole forces produced by the model the visualization of different planes over the wingspan provide an insight into the distribution of the circulation over the wingspan.

Keywords: Bird flight, Flapping wing, Wake structure, Unsteady

A7.63
No Abstract received

A7.64
Stiffness of the attachment device in *Gastrophysa viridula* (Coleoptera, Chrysomelidae)

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The beetle *Gastrophysa viridula* has hairy attachment devices which enable the animal to walk on vertical plant surfaces or underside of leafs. The single hairs (setae) are located in a distinct area on the tarsi and taper off in thin endplates (spatulae). Intermolecular and probably adhesion forces between these spatulae and the substrate yield the necessary attachment ability. Geometry, density and material properties of these attachment hairs play an important role for proper functionality of the attachment device. To find out more about material properties we used ball microindentation to determine bending stiffness of setae for male and female beetles, in living and dried status, with two different methods. (1) Assuming that the setae pattern of the attachment device behaves as a layer of soft bulk material, an effective elastic modulus can be calculated by Hertz theory. With this and the average setae length and density, a calculation of seta bending stiffness is possible. (2) We consider the setae pattern as a pattern of compressible springs and compute bending stiffness of a single seta by using an analytical model. Both methods showed values of bending stiffness in the range of 0.4 N/m in the living status. When dried out, stiffness of setae can be up to 3 times higher. The results show that microindentation is an effective way to evaluate setae stiffness and can possibly be used to compare different hairy attachment devices in insects, spiders and geckos.

Keywords: Material properties, Setae, Microindentation, Beetle

A7.65
Are the intrinsic properties of muscles related to locomotor function?

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A large amount of data exist on the intrinsic properties of many different muscles. Quantitative analysis of such information can provide valuable insights into the basic principles of muscle design. The present study analysed data for 69 species taken from 118 sources. Muscles were categorised as flight, swim, terrestrial or non-locomotory. ANCOVA were used to compare group values for maximum shortening velocity (V_{max}), time to maximum twitch force, twitch half relax time and the curvature of the force–velocity relationship (a/σ_0). Experimental temperature was used as the covariate. Where appropriate Bonferroni *post hoc* analyses were carried out. Geometric mean regression was used to assess the relationship between V_{max} and time to maximum twitch force, half relaxation time and a/σ_0. The results indicated that a significant relationship exists between V_{max} and time to maximum twitch force and between V_{max} and twitch half relax time. The association in each case was however weak ($r^2 = 0.35$; $r^2 = 0.26$ respectively), with a large amount of scatter in the data. Non-locomotory and flight muscles in particular showed distinct variation from the regression line. A significant relationship was also found between V_{max} and a/σ_0, with the association again being weak ($r^2 = 0.19$). Flight and non-locomotory muscles were once more distinct from the regression line. These data indicate substantial inter-specific variation in the relationship between the intrinsic speed (V_{max}) and the activation rates, contrary to previous speculation. Such information has implications in the future development and validation of muscle models.

Keywords: Muscle, Mechanics, Shortening velocity, Force–velocity relationship

A7.66
AFM imaging of barnacle cement nanostructure in artificial seawater

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Barnacle larvae adhere to surfaces by producing a protein cement which is capable of curing underwater. Investigations on barnacles (Wiegemann and Watermann, 2003) showed, that barnacle cement seems to consist out of nanoscopic globular structures. Depending on the substrate's topography, elasticity and surface free-energy, these cement globuli form varying fibrillar network structures. This is interpreted as an adaptation process to enhance the adhesion strength on different types of natural (or artificial) substrata. Studies on barnacle cement nanostructure have mainly been performed with scanning electron microscopy (SEM). However, this method induces crucial changes in the spatial arrangement of cement globuli during sample drying, hence leading to artifacts in SEM pictures and interpretation. In contrast, the AFM is capable of imaging in liquid without sample fixing or drying. We present high resolution images of barnacle cement under physiological conditions in artificial seawater, using atomic force microscopy (AFM). Barnacles (*Balanus* sp.) were allowed to settle on different surface types prior to the experiments. AFM further enables the measurement of quantitative forces for both adhesion and compression, to fully characterise the mechanical properties of the cement. In-situ measurements of fresh cement production will extend the understanding of the characteristics of this material and its structural changes during curing.

Wiegemann, M., Watermann, B. (2003): Peculiarities of barnacle adhesive cured on non-stick surfaces. J. Adhesion Sci. Technol. 17 (14): 1957–1977.

A7.67
Forelimb function during takeoff in *Rana pipiens*

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Hindlimb function during anuran jumping has been well studied. However, a complete understanding of jumping requires examination of forelimbs, as well. In order to determine their role during takeoff, we studied *Rana pipiens* jumping over a range of distances (15–65 cm), with an integrated setup consisting of high-speed video (250 fps), EMG, and force plates. Frogs were placed so that they bridged two separate force plates as a way of distinguishing relative contributions of fore and hindlimbs to ground reaction force. Electrodes were placed in the following muscles: *m. anconeus* (forelimb extensor); *m. coracoradialis* (forelimb flexor); *m. semimembranosus* (hindlimb extensor); and *m. coccygeoiliacus* (trunk elevator). EMG recordings indicate all four muscles are activated simultaneously during takeoff. At the onset of jumping, one third of body weight rests on forelimbs. During short jumps (e.g. 15 cm), weight is transferred from hindlimbs to forelimbs during the initial phase of jumping, but not during long jumps (e.g. 65 cm). This difference appears to result from reduced activity of *m. coccygeoiliacus* during short jumps. Caudopelvic muscles, such as *m. coccygeoiliacus*, play a key role in elevating the trunk during jumping. Reduced caudopelvic activity results in a more horizontal trajectory for the center of mass, causing greater force to be applied through the forelimbs. Synchronous activity of *m. anconeus* and *m. coracoradialis*, coupled with only minor extension at the elbow during forelimb contact, suggests forelimbs serve as a brace for balancing pelvic rotation during hindlimb extension in short jumps.
Supported by NIH AR46125, AR38404.
Keywords: Anurans, Jumping, Forelimbs, EMG, Muscle

A7.68
Biomechanics of pitcher plants: Mechanisms of prey capture in *Nepenthes bicalcarata*

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To survive in nutrient-poor habitats, *Nepenthes* pitcher plants have evolved specialized leaves capable of capturing and digesting arthropods. By investigating prey capture in *Nepenthes bicalcarata*, we discovered that the critical structure responsible for insect trapping is not a slippery waxy layer, but the pitcher peristome. Its microstructured surface is exceptional in that it is completely wettable. Only when wet, the peristome is very slippery for insects. By measuring friction forces of ants on the peristome surface, we discovered that 'aquaplaning' prevented attachment of the adhesive pads, whereas the surface microstructure was only important for the claws, which slid more easily in the direction towards the pitcher. Even though *N. bicalcarata* pitchers are highly effective ant traps, they are inhabited by colonies of the specialized ant *Camponotus schmitzi*. These ants are not only capable of running across the slippery peristomes but also of diving in the digestive pitcher fluid, hunting for prey and retrieving prey from the pitcher. Even when we maximally wetted the peristome, *C. schmitzi* never fell into the pitchers. However, high-speed video analysis of ants running rapidly on the peristome revealed that they did slide on the surface, but managed to stay attached. The ants' underwater excursions were not aided by air bubbles adhering to the body. Workers relied on bouyancy to resurface after their dives. Measurement of the buoyancy force of submerged ants showed that *C. schmitzi* were more buoyant than other ants. We are currently investigating the biomechanical adaptations involved in this fascinating ant–plant interaction.

A7.69
Locomotion and adhesion: Effects of surface texture, load and inverted running on gait kinematics and tarsal control

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Many insects combine fast locomotion with strong resistance to detachment forces. Apart from the requirement to attach and detach during running, insects have to adjust their locomotory and adhesive systems to surface texture, additional loads and substrate orientation. We investigated the mechanisms of dynamic surface attachment in weaver ants (*Oecophylla smaragdina*). Control of attachment occurs at several hierarchical levels: First, ants can adjust their gait and vary the number of feet in surface contact. When walking upside down, ants used gaits with a higher duty factor compared to upright running. Second, adhesion can be regulated by changing leg posture. Smaller angles between the

tarsus and the surface prevent adhesive pads (arolia) from peeling, thus allowing for greater attachment forces. Third, attachment is controlled at the (pre-)tarsus. Even though arolium and claws serve different functions, they are moved by the same muscle. However, the mechanical arrangement of the claw flexor system limits arolium extension on rough substrates. Arolium contact area is also regulated by active and passive mechanisms. Ants walking upside-down only used a fraction of the available contact area. When they carried loads, contact area increased by the contraction of the claw flexor and by the passive unfolding of the arolium. Rapid experimental displacements of the substrate showed that this passive pad extension occurred faster than neuronal reflexes are able to act. Our findings demonstrate that dynamic control of adhesion occurs at several levels and is strongly based on passive mechanisms inherent in the complex design of the tarsus.
Keywords: Insects, Biomechanics, Attachment control

A7.70
Biomechanics of 'waxrunning' in *Crematogaster* ant-partners of *Macaranga* trees

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In the mutualism between ants and *Macaranga* trees in SE-Asia, waxy stems act as protective barriers that keep away foreign ants. Only the specialized ant partners of these trees are 'waxrunners' capable of climbing the slippery stems without any difficulty. We investigated the mechanisms of waxrunning in *Crematogaster* (*Decacrema*) ants by measuring attachment and running performance and by comparing skillful climbers with closely related non-waxrunners from the same species group. Comparative morphometry and kinematic analysis of ants climbing on waxy twigs showed that waxrunners not only have significantly longer legs than non-waxrunners, but they also hold them in a more sprawled posture. Longer legs and sprawled posture are mechanically advantageous for climbing ants, because they may achieve a greater normal force by grasping around the stem and the perpendicular detachment force acting on the front legs is reduced due to the longer lever arm. Ablation experiments confirmed the importance of the claws. Waxrunners were still capable of climbing waxy *Macaranga* stems even after the complete removal of all adhesive pads (arolia), but legs slipped when claw tips were removed. Waxrunning ants performed characteristic adjustments of their climbing behaviour. Not only did they change to slower gaits with higher duty factors, but they also held their body closer to the stem and groomed their front legs more often than when walking on glass rods of the same diameter. Our findings indicate that wax-running capacity in *Crematogaster* (*Decacrema*) ants is based on a combination of morphological, locomotory and behavioral adaptations.
Keywords: Kinematics, Waxrunning, Mutualism

A7.71
Burrowing mechanics and performance in a basal amphisbaenian (*Blanus cinereus*)

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Previous studies have demonstrated that relatively specialized amphisbaenians (*Amphisbaena*, *Geocalamus* and *Leposternon*) are capable of using their elongate bodies to generate spectacular forces when burrowing. Here, we investigate the mechanism of burrowing in the basal amphisbaenian *Blanus*, perhaps the most "generalized" amphisbaenians in terms of morphology and behavior. The goal of this study was to determine the mechanism used by *Blanus* to generate force during burrowing and to determine if its more generalized morphology was correlated with lower burrowing performance relative to more specialized species. We induced 10 *Blanus cinereus* (75–188 mm SVL) to push against a forceplate from artificial tunnels of different lengths. Like most amphisbaenians, the maximum force generated by *Blanus* during burrowing attempts is dependent on tunnel length. In tunnels that are very short (~10% snout–vent length) individuals produce approximately 20% of the maximum force generated in tunnels of equal or greater length than their bodies. This is consistent with the hypothesis that burrowing forces are primarily generated by the costo-cutaneous and vertebro-cutaneous muscles that run from the skin to the ribs and vertebral column. *Blanus* differs from amphisbaenians investigated previously in that it uses musculature along the entire trunk to generate pushing forces, whereas other species generally use only the musculature of the anterior half of the body to power burrowing movements. Despite its more generalized appearance and behavior, maximum pushing performance in *Blanus* (maximum forces generated as a function of body diameter) is similar to performance documented previously in more specialized genera.
Keywords: Amphisbaenian, Burrowing, Locomotion, Kinetics

A7.72
The functional morphology of locomotion in the ragworm *Nereis diversicolor*

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The study of biomechanics and functional morphology can, aside from scientific value, often be applied to mechanics. This study is part of the BIOLOCH project, which aims to biomimetically develop a self-moving endoscope to replace the current manually inserted endoscopes. Polychaetes in the family Nereididae were chosen as biological models due to their ability to move in muddy substrates similar to the mucous layer lining the intestinal walls. In a SEM study comparing parapodia and setae of 5 species we found, however, no clear correlation between substrate and morphological parameters, thus implying that setae have multiple functions. They are important during locomotion[1]. Experiments with artificial setae on a robot model suggest, together with the elaborate morphology, that they are important for generating friction with the substrate. Our SEM study indicated that swimming species in general have a smaller intersetal gap than non-swimming. According to the Cheer and Koehl model[2] gap size determines the function of hair-like structures at low Reynolds numbers. Nereids swim by forward moving body undulations coupled with the parapodia acting as paddles. This has been shown to be theoretically possibly due to the roughness caused by the parapodia[3]. However, preliminary DPIV results showed two clear backwards jets generated by the parapodia, thus making them the primary thrust producers.

Keywords: Biomimetics, Functional morphology, Flow visualisation, Locomotion, Polychaeta

1. Merz and Edwards (1998). J. Exp. Mar. Biol. Ecol. 228: 273–290.
2. Cheer and Koehl (1987). J. Theo. Biol. 129: 17–39.
3. Taylor (1952). Proc. Roy. Soc. A. 214: 158–183.

A7.73
Differential strain in an architecturally complex muscle

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Understanding the mechanical function of muscles with extensive origins and insertions is challenging. The Iliotibialis lateralis pars postacetabularis (ILPO) is the largest muscle in the hindlimb of the guinea fowl. The ILPO has a broad fleshy origin that spans the ilium and ischium with relatively short anterior fascicles inserting on an aponeurotic tendon connected to the patellar tendon and longer posterior fascicles connected more directly to the patellar tendon. The biarticular ILPO is a hip and knee extensor that undergoes active lengthening followed by active shortening during stance. The moment arm of the fascicles at the hip increases anteriorly to posteriorly whereas the moment arm at the knee remains constant. Using sonomicrometry and electromyography, we examined whether the ILPO experiences differential strain between the anterior and posterior fascicles and among proximal, central and distal portions of the posterior fascicle. The posterior fascicles experienced strains during active lengthening similar to those of the anterior fascicles. Differences in the moment arm at the hip do not completely explain the similar strains in the anterior and posterior fascicles. We hypothesize that the similar strain patterns are caused by the large aponeurosis to which the anterior fascicles attach. The aponeurosis, in series with the anterior fascicle, is predicted to stretch when the muscle is active thus reducing the strain of the anterior fascicles. Strain increases proximally to distally in the posterior fascicles during active lengthening. These proximal to distal differences may be caused by differences in sarcomere length at the start of active lengthening.

Keywords: Muscle function, Animal locomotion