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A10E3–MODELLING IN BIOMECHANICS

Organised by J.L. van Leeuwen and P. Aerts for the Biomechanics Group

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A10/E3.1–Modelling approaches in biomechanics

R. McN. Alexander, Biology, University of Leeds.

Conceptual, physical and mathematical models have all proved useful in biomechanics. Conceptual models, which have been used only occasionally, clarify a point without having to be constructed physically or analysed mathematically. Margaria's rolling egg model of human walking is an example. Physical models have been used more often. They may show that a proposed mechanism works, as Wootton's models of folding beetle wings do. They may facilitate hydrodynamic observations that would be more difficult to make on a real animal, for example Ellington's robotic model of an insect wing. Or, like McGeer's passive bipedal walker, they may serve to check the conclusions of mathematical modelling. Mathematical models have been used more often than conceptual or physical ones. Some of them are predictive, designed for example to calculate the effects of anatomical changes on jumping performance, or the pattern of fluid flow in a three-dimensional assembly of semicircular canals. Others seek an optimum, for example the best possible technique for a high jump. And a few are inverse optimisation models, attempting to discover the variable that a pattern of behaviour is designed to optimise. Mathematical models range from the extreme simplicity of some models of walking and running to the complexity of models that represent numerous body segments and muscles, or elaborate bone shapes. The simpler the model, the clearer it is which of its features is essential to the observed effect.

A10/E3.2–Cellular mechanics of plants

D.M. Bruce, Biomaterials, Silsoe Research Institute

Modelling of plant cell mechanics aims to clarify our understanding of cell and tissue mechanical behaviour. By developing and evaluating quantitative, predictive models, we can bring into focus the parameters that control mechanics under various 'duties' at which walls, cells and tissues must succeed. Given the controlling parameters, models can explore how the many levels of structure that characterise cellular biological materials are mechanically linked. The main approaches to modelling will be illustrated with two types of plant cells; thin-walled primary cells whose walls are supported by the pressure of the inter-cellular fluid, and secondary cells whose walls are stiff because they are comprise oriented cellulose fibrils bonded with hemicellulose and lignin. The mathematical description of material properties, the mechanics of membranes and of individual, isolated cells will be explained. Analytical and numerical methods for solving equations describing cell deformation will be outlined and the use of models together with experimental data to determine the material properties will be illustrated. Approaches to modelling systems of cells using structural elements and theories of foams will be described. The thick walls of secondary cells are well modelled as two-component composites of highly oriented fibres bound by a matrix material. The models explaining how these structures behave show how effective the walls are at resisting stresses imposed on the plant. Even if the structure fails, the wall and cellular structure properties contribute to avoidance of catastrophic failure.

A10/E3.3–Finite element modelling of tissue mechanics

C.W.J. Oomens and F.P.T. Baaijens, Eindhoven University of Technology, The Netherlands

To describe the mechanical behaviour of biological tissues and transport processes in biological tissues conservation laws, like conservation of mass, momentum and energy play a central role. Mathematically these are cast into the form of partial differential equations. Because of highly non-linear material behaviour, inhomogeneous properties and usually a complex geometry, it is impossible to find closed form analytical solutions for these sets of equations. The objective of the finite element method is to find approximate solutions for these very complex problems. The concepts of the method will be explained by following the procedure for a one dimensional diffusion problem. Three, well defined, steps will be followed. Transformation of the original differential equation into an integral equation by means of weighted residuals and partial integration to arrive at the weak form. The following steps are: discretisation of the solution by interpolation, linearisation and trans-

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formation of the integral equation into a linear set of equations that can easily be solved by means of a computer. Some of the aspects of the finite element solution with respect to coarseness of the finite element grid and convergence and stability of solutions will be demonstrated. To demonstrate the state of the art of Finite Element Methods the lecture will finish with an example of a moving heart valve in a flow during the cardiac cycle.

A10/E3.4–Modelling the mechanical regulation of cartilage biology

D.R. Carter, VA Rehabilitation R and D Center and Stanford University, Stanford, CA, USA

The growth, differentiation, and ossification of cartilage are fundamental to skeletal development, regeneration and aging. These biological processes are regulated in important ways by the local mechanical cues that are imposed during life. Using single-phase continuum material models of cartilage, it has been proposed that local intermittent hydrostatic pressure promotes cartilage maintenance. Cyclic distortional strains (or tensile) strains, however, promote cartilage growth and ossification. This basic premise has been used with finite element computer analyses to predict growth-dependent changes in bone and joint morphology, endochondral ossification patterns, and articular cartilage thickness distributions during development. Since single-phase material models can not capture the fluid exudation of the superficial layer of articular cartilage, biphasic or poroelastic solid/fluid models are often implemented. In the middle and deep layers of articular cartilage where the poroelastic analyses predict little fluid exudation, the cartilage phenotype is maintained by cyclic fluid pressure (consistent with the single-phase theory). Finite element analyses show that in superficial articular layers there is fluid exudation, which enhances joint lubrication. The chondrocytes in this layer are exposed to tangential tensile strain with high fluid pressure and the cells are ‘flattened’ due to matrix consolidation. As a result, the superficial layer assumes a more fibrous-chondroid phenotype with low proteoglycan content. Computer model results and predictions are consistent with numerous animal, cell, and molecular experiments of endochondral ossification and articular cartilage biology.

A10/E3.5–Modelling of the mechanical behaviour of skeletal muscle

M. Epstein, Engineering, The University of Calgary, Canada

The modelling of the thermo-mechanical response of skeletal muscle can and has been effected at different levels. At one end, rheological models of the Hill type attempt to provide a relatively simple phenomenological description of the macroscopic response of the muscle as a whole. This ‘black box’ approach has proved to be of immense usefulness in practical applications. On the other end, structurally based models, such as the classic Huxley paradigm, attempt to explain and quantitatively describe the observed macroscopic behaviour in terms of a more fundamental level of understanding and detail. The extraordinary progress in computational speed afforded by the modern computer has permitted the implementation of a variety of models that incorporate features of both approaches. Thus, for example, it is possible to model all the intricacies of muscle architecture while using a fibre bundle as a behavioural unit. Because the deformations of muscle are generally very large, any such models must be formulated with due attention to the demands of the laws of mechanics. In some cases, such as when internal constraints are present, somewhat counterintuitive situations can be encountered. Some of the basic principles involved in formulating kinematically correct models will be discussed and illustrated with a recently developed finite element code.

A10/E3.6–Tongues and tentacles: Modeling and optimization of protrusible muscular systems

J.L. van Leeuwen, Wageningen University, The Netherlands

The tongues of lizards and snakes and the tentacles of squid are highly deformable tissues, with a remarkable diversity in macroscopic and microscopic architectural design. Models are indispensable to improve the understanding of these complex systems. A series of models will be discussed that were designed to address the architecture and dynamics in the light of functional demands. The tentacles in squid are rapidly extended (order 30 ms) during prey capture. They have remarkably short myofilament lengths in the extensor muscles. A distributed mass model with a build in description of muscle properties shows short myofilaments to be advantageous for a high extension speed of the tentacles. This model is essentially one-dimensional by assuming a coupling between the longitudinal and the transverse motions. The chameleon captures its prey by a projection of the tongue pad off the entoglossal process. Experiments indicate that a specialized muscle loads a multi-layered tubular spring that envelops the entoglossal process. The spring releases its elastic energy while it slides over the tip of the entoglossal process. A two-dimensional distributed mass model supports the feasibility this mechanism. Snakes make complex spatial tongue flicks to explore the chemical nature of their local environment. The design and dynamics of these tongues is still poorly understood. A dynamic three-dimensional distributed mass model was constructed based on actual tongue geometry in the python to shed new light on this architectural and myocybernetic problem.

A10/E3.7–Modelling secondary growth processes in plants

T. Speck, Botanical Garden, University of Freiburg; N.P. Rowe, Laboratoire Paléobotanique, Université de Montpellier 2, France

Primary and especially secondary growth processes drastically change the anatomy of plant stems and also their mechanical properties (Speck and Rowe 1999, in: The Evolution of Plant Architecture, pp. 447–479). In order to describe the changes quantitatively and to analyse their significance for mechanical stem properties, a method has be developed to calculate the contribution to the different stem tissues towards the cross-sectional area (A) and the axial or polar second moments of area (I) by using mathematical models based on polar coordinates (Speck et al. 1990, Bot. Acta 103, 111–122). The advantages of these analytical models compared to a numerical analysis of the tissue distribution using electronic image analysis systems are threefold: (1) they allow predictions of how changes in the tissue pattern, occurr e.g. during ontogeny, will influence the mechanical stem properties (Speck et al. 1998, Bot. Acta 111, 366–376, Spatz et al. 1998, Am. J. Bot., 85, 305–314), (2) A and I of the different stem tissues can be modelled and the mechanical properties can be calculated also for fossil plant material which is often deformed during fossilisation (Speck and Rowe 2001, in: Palaeobiology II, pp. 379–384), (3) if a mathematical model is formulated only a few geometrical parameters have to be measured in stem cross-sections, making this method quite efficient. In addition, we want to present a testing device and some first results of this physical model that allows to test experimentally the influence of secondary wood formation on the surrounding tissues in early lignophytes.

A10/E3.8–Oscillations of plant stems: theory and experiments

H.-C. Spatz and O. Speck, Institute for Biology III, University of Freiburg, Germany

Free oscillations of upright plant stems, or in technical terms slender tapered rods with one end free, can be modelled by considering the equilibrium between bending moments in form of a differential equation with appropriate boundary conditions. For stems with apical loads, where the mass of the stem is negligible, Mathematica 4.0 returns solutions for tapering modes $\alpha=0$, 0.5 and 1. For other values of α, including cases where the modulus of elasticity varies over the length of the stem, approximations leading to an upper and a lower estimate of the frequency of oscillation can be derived. For the limiting case of $\omega=0$, the differential equation is identical with Greenhill's equation for the stability against Euler buckling of a top-loaded slender pole. For stems without top loads, Mathematica 4.0 returns solutions only for two limiting cases, zero gravity (realized approximately for oscillations in a horizontal orientation of the stem) and for $\omega=0$ (Greenhill's equation). Approximation can be derived for all other cases. As an example for their application they are used to describe the oscillation of an *Arundo donax* plant stem.

A10/E3.9–Modelling muscle tissue in insect flight

T.L. Daniel, J.M. Macpherson, L. Kidoguchi and A. Trimble, University of Washington, Seattle

Insect flight is commonly driven by powerful muscles coupled to an elastic thorax. In this indirect system of force transduction, muscles may operate either synchronously (once contraction per activation) or asynchronously (several contractions per activation). Underlying these fundamentally different modes of flight are remarkably similar systems of contractile proteins operating in an elastic framework. We develop a three dimensional model of this acto-myosin network to explore how mechanical events at the molecular scale relate to whole muscle performance. We are particularly interested in exploring the origins of contractile asynchrony and use the model to assess how oscillatory behavior can arise from a system of couple molecular oscillators. This approach also permits us to examine how an organismal level of functional performance relates to the geometry, mechanical properties and kinetic behavior of the molecular level of organization.

A10/E3.10–Inverse and forward dynamics: models of multi-body systems

E. Otten, University of Groningen

Connected multi-body systems exhibit notoriously complex behaviour when driven by external and internal forces and torques. The problem of reconstructing the internal forces and/or torques from the movements and known external forces is called the 'inverse dynamics problem', while calculating motion from known internal forces and/or torques and resulting reaction forces is called 'the forward dynamics problem'. When stepping forward to cross the street, people use muscle forces that generate angular accelerations of their body segments and, by virtue of reaction forces from the street, a forward acceleration of the centre of mass of their body. Inverse dynamics calculations applied to a set of motion data from such an event can teach us how temporal patterns of joint torques were responsible for the observed motion. In forward dynamics calculations we may attempt to create motion from such temporal patterns, which is extremely hard to do, because of the complex mechanical linkage along the chains forming the multi-body system. To understand, predict and sometimes control multi-body systems, we may want to have mathematical expressions for them. Both Newton-Euler and Lagrangian approaches have their pros and cons. The simulation of collisions and the inclusion of muscle forces or other internal forces will be discussed. Also the possibility to perform a mixed inverse and forward dynamics calculation will be dealt with. The use and limitations of these approaches will form the conclusion of the contribution.

A10/E3.11–Modeling the biomechanics and control of jumping

M.G. Pandy, Biomedical Engineering, University of Texas, Austin

Computer modeling and simulation has risen to new heights in recent years, mainly because of the growing belief that this approach can provide more quantitative explanations of how the neuromuscular and musculoskeletal systems interact to produce co-ordinated movement. Simulations of standing, walking, jumping, and pedaling, in particular, have provided considerable insight into how the leg muscles work together to achieve a common goal during each of these tasks. Interest in using models to study movement has been, and continues to be, fueled also by the ever-increasing performance of computers. With the computational resources available today, large-scale models of the body (i.e. models that have many segments and many muscles) may be used to perform realistic simulations of movement that are an order of magnitude more complex than those performed just 10 years ago. This presentation will review how the structures of the neuromuscular and musculoskeletal systems may be represented in a mathematical (computer) model of the body, how these elements may be integrated to simulate the dynamics of a motor task, and how model output can be analyzed to describe and explain muscle function during multijoint movement. Results obtained from a detailed, three-dimensional simulation of maximum-height jumping will be presented to illustrate the approach.

A10/E3.12–Simulation of musculoskeletal loading during active movement in man

A.J. van den Bogert, Biomedical Engineering, Cleveland Clinic Foundation

Excessive mechanical loading of tissues causes acute injuries. Strategies for prevention and rehabilitation can only be designed if the mechanisms are properly understood and tissue loading can be predicted. Such understanding is often difficult to obtain intuitively or analytically due to the complex dynamics of the musculoskeletal system. In mechanical engineering, computer aided design techniques are now standard tools for failure analysis, but their application to injury mechanics in human movement has largely been restricted to passive movements such as those that occur during vehicle collisions. In this paper we will describe our methods for development of predictive computational models for *active* movements, using multibody dynamics, muscle models, and contact mechanics. Optimization methods are used to ‘train’ these models to perform realistic movements, using information from kinematics, forces, and muscle activation in human subjects. Validation is performed by comparing predicted and actual responses to small perturbations. We also demonstrate how these models once optimized and validated, can be used to generate statistical analyses of questions related to acute injuries using a Monte Carlo simulation approach. Results will be presented from two studies: (a) anterior cruciate ligament injuries in sport, and (b) the effect of muscle activity on lower extremity injury during a vehicle collision.

A10/E3.13–Integrated modeling of neural and musculo-skeletal dynamics: The case of interceptive actions

P.J. Beek, J. Dessing and C.E. Peper, Vrije Universiteit, Amsterdam; D. Bullock, Boston University

Bullock and Grossberg’s (1988) Vector-Integration-to-Endpoint (VITE) model for the control of voluntary arm movements to a stationary target is based on a large body of behavioral and neurophysiological data. Here, we show how this model can be extended to account for arm movements towards moving targets, such as observed in the one-handed catching of a ball on a passing trajectory. Building on extant behavioral models, we propose a required velocity integration to endpoint model that prospectively insures that the hand will be at the interception point at the appropriate time. To provide a better account for the experimentally observed kinematics than the behavioral models, a parallel relative velocity channel is added. An appealing, yet admittedly not entirely complete, neural basis is given to the model. Finally, it is discussed how the motor outflow signals generated by the model may be fed into a model of the musculo-skeletal dynamics to generate actual movement trajectories.

A10/E3.14–Fluid dynamics: a physical introduction to modelling

C.P. Ellington, Zoology, University of Cambridge, UK

Novice and experienced modellers alike must choose between several approaches for estimating the forces on a body immersed in a fluid. All of these approaches have a direct physical basis, and they can be implemented either with judicious physical approximations to keep the mathematics under control, or with computationally intense methods that avoid excessive simplification.

Some of the approaches may also prove more suitable than others for estimating the rate, at which energy is lost to the fluid, which is often of great importance for locomotor mechanisms. Momentum, impulse and vortex approaches will be described and illustrated by their application to flapping flight. It is perhaps reassuring to the less mathematically inclined that relatively simple models prove quite robust for energy estimates. A new approach by Sunada and Ellington will be described that analyses flapping flight using the added mass of vortex sheets. The physical basis of the approach is easily related to earlier methods, but it avoids some of their major limitations. In particular, a unified model is applicable from hovering to fast forward flight, and the effects of most kinematic variables can be estimated.

A10/E3.15–Numerical approaches in computational fluid dynamics

J. Carling, St. George's Hospital Medical School, London

Numerical solutions of the time-dependent, incompressible, isoviscous equations of fluid dynamics (the Navier-Stokes equations) can provide useful, realistic models in many areas of biological science. The flow of blood in the circulatory system, the swimming of fish and bird flight are just some examples in which computational fluid dynamics has a role to play. In explaining how numerical solutions are obtained, it is useful to describe two approaches: the finite element method; and the finite difference method used in conjunction with an appropriate co-ordinate transformation. Whichever approach is used, the governing differential equations and boundary conditions are approximated by a system of algebraic equations which can then be solved by the techniques of computational linear algebra. In this process, it is important to bear in mind the accuracy inherent in the determination of the fluid velocity components and the fluid pressure, particularly in relation to satisfying the mass conservation constraint. It is also important to determine realistically the forces acting across and tangential to the interface between the fluid and the body or vessel with which it is in contact. To this end, it is often necessary to consider the motion of the body itself (for example, by applying Newton's laws to the body of a fish) as a separate (but interacting) computation. Here, the basis of these numerical approaches will be described and the important features illustrated by means of simple examples, which can be programmed in the matrix manipulation package MATLAB.

A10/E3.16–Cyberkelp: The integration of numerical models and tensile tests to explore the survival of giant kelps

M. Denny and B. Hale, Hopkins Marine Station, Stanford University, USA

Giant kelps can maintain a mass of 50 kg and a length of 40 m while exposed to the rapid flows and large hydrodynamic forces of ocean waves. Nonetheless, these plants are anchored to the substratum by seemingly fragile structures—stipes—with a diameter less than a centimeter and the breaking strength of rubber. This disparate set of facts presents a challenge to our understanding of how plants survive in harsh environments: can we explain the survival of giant kelps based on quantitative dynamics? Given their large size and the severity of their environment, direct experimentation on kelps is impractical, and we must resort to numerical simulations. However, simple numerical modeling is unsatisfactory because it fails to capture the complexity of the visco-elasto-plastic behavior of the materials from which plants are constructed. Here we circumvent these problems by creating a feed-back loop between real-time tests of material properties and numerical models of kelps in flow to produce a 'cyberkelp' that allows us to predict forces imposed on giant kelps. Experiments show that when waves are small and the mechanical integrity of the plant is not challenged, the stipe material behaves primarily as an elastic solid. However, when waves are large and applied forces approach the plant's limits, the stipe material exhibits augmented hysteresis, reducing the likelihood that fatigue cracks will cause breakage. The integration of numerical simulations and tensile testing allows us to highlight the otherwise obscure role of materials properties in the dynamics of a plant in flow.

A10/E3.17–Particle based simulations of swimming sperm: how stiff is the tail?

C. Lowe, Chemical Engineering Dept., Amsterdam, The Netherlands

Both the shape of a sperm's tail while it is swimming, and the resulting propulsion, result from a balance of forces. There is the frictional force exerted by the surrounding fluid on the tail, the inherent resistance of the tail to bending and the 'driving' forces generated within the tail itself. Experimentally, a great deal is known about the swimming characteristics of sperm and the elastic properties of their tails. I will describe a particle-based model for a sperm's tail, which we have used to examine how the interplay of these forces influences the swimming motion. The results suggest that there are some contradictions in the experimental results. I will discuss these contradictions and how the might possible be resolved.

A10/E3.18–Aerodynamic modelling flapping flight in birds

J.M.V. Rayner, Biology, University of Leeds

Modelling flapping flight has two main goals. One is to quantify the aerodynamic processes by which the wings generate aerodynamic force and the biomechanics of the elements of the wing and shoulder. The other is to determine the energy cost of flight for use in the understanding of flight performance. This type of model should take full account of wing aerodynamics, but effective predictions have been obtained by simplification and treating the bird as a fixed-wing aircraft. Both models may give rise to testable predictions about biophysical processes or the choices made by flying birds, but—probably because of limitations in the available measurements of body and drag—neither gives good estimates of measured flight speed or power. A range of aerodynamic tools are available for modelling wing forces in flapping flight. The most effective applied so far to birds encompass steady- or quasi-steady lifting-line theories, free vortex theories, and compromise models using flow-visualisation results to predict wing and wake vortex geometries. Panel methods have had limited success, mainly because they fail to capture the full effect of wing surface deformation, while the time-varying flows of a flapping and deforming bird wing with extensive separated vortices are too challenging for most available finite element methods. These methods, together with some of their pitfalls and some of the resulting predictions, will be reviewed.

A10/E3.19–Comparing fluid dynamics models with experimental tests

G.R. Spedding, Aerospace and Mechanical Engineering, University of Southern California

The Euler and Navier–Stokes equations are straight-forward applications of Newton's laws of motion to continuum fluids yet they are notorious in their complexity and, except in special cases, non-predictability of their solutions. Much of fluid mechanics research is thus concerned with how to make simplifications to the full equations, or to define empirical laws and relationships that allow practical devices to be built. The field of Aerodynamics is one of the more spectacular successes in dramatic simplification of potentially very complex flows, where engineering requirements have been matched by the development of very simple yet powerful mathematical models and paralleled by physical analogues. Application of these tools to animal flight mechanics has met with varying degrees of success, although the criteria for success are not always clearly defined. A number of physical and theoretical model problems will be considered and evaluated according to the context of the original problem formulation. The best models are those that allow possible modification of the formulation according to success or failure of their predictions.

A10/E3.20–Biomimetics modelling

J.F.V. Vincent, Mechanical Engineering, University of Bath

A model is only as good as the techniques, which have been used in its production. In many instances the main tool is mathematics, and we are limited by the mathematical techniques and the computing power which we have available. In addition we may be interested in only one aspect of the mechanical behaviour of a structure, and are defeated by the multifunctionality of biology. One way out of this is to make a physical model, which isolates and reproduces the essential features of the structure under investigation. If we can also model a function, which has some use in our own technology, we might be able to tap funds from industry. And we can have the fun of seeing our science applied in novel ways. The problems which have to be solved in order to achieve commercial success are not always the same as those in nature, and frequently demand advantages to the industrialist which are far greater than the few percent which nature regards as sufficient for selective advantage. Commercial successes of a biomimetic approach are, as yet, relatively few (Velcro, perhaps lotus-effect paint, drag-reduction) yet there are many ideas waiting (analogues of wood, mother-of-pearl, sensing, nanotechnology). In some instance commerce might fail because the biology has been insufficiently well understood. Ideally there would be feedback into our understanding of the biological archetype, which suggested the technology.

A10/E3.21–Physical models in biomechanics

M.A.R. Koehl, Integrative Biology, University of California at Berkeley

Physical models, like mathematical models, are useful tools in biomechanical research. Physical models permit investigators to explore parameter space in a way not possible using the comparative approach with living organisms: parameters can be varied one at a time to quantify the performance consequences of each, while values and combinations not found in nature can be tested. Experiments using physical models in the lab or field can circumvent problems posed by uncooperative or endangered organisms. Physical models also permit some aspects of the biomechanical performance of extinct organisms to be measured. Use of properly scaled physical models allows detailed physical measurements to be made for organisms that are too small or fast to be easily studied directly. Furthermore, hypotheses about the mechanisms underlying a biomechanical process can be tested by using physical models in the same was as they are by using mathematical models. These various uses of physical models will be discussed using examples from research on the evolution of gliding, the biomechanics of embryonic notochords, the feeding of copepods, the capture of odors by crustacean antennules, the hydrodynamic forces on waveswept organisms of different body designs, and the dispersal and settlement of larvae in coastal marine habitats.

A10/E3.22–Analytical and physical models of semicircular duct systems

M. Muller and J.H.G. Verhagen, Experimental Zoology Group (EZO), University of Wageningen, The Netherlands

The system of three hydrodynamically interconnected semicircular ducts in the inner ear of vertebrates is a sensor of angular movement. Rotation of the head in space induces endolymph flow in the ducts, which can be described by a system of differential equations of the sixth order. At least thirteen morphological, geometrical and physical parameters are required to specify position in space, shape of the system and endolymph flow. Solving the complete system-equations leads to unacceptable long formulae for the description of endolymph movements. Also computer simulations can only give a limited overview of the physical behaviour of the system because of the many parameters involved. A simplification procedure is presented which provides surveyable analytical formulae, which describe the essentials of the physical behaviour of the system thus giving insight in its biological functioning. Crucial steps in this procedure are: (1) considering only two coupled ducts; (2) considering only the fast part of the transduction process; (3) considering only maximum endolymph displacements and time constants and (4) taking lengths and radii of the two ducts equal. Understandable features become: (1) the optimisation of shape (lengths, curvatures and radii) of the ducts; (2) the optimal positioning of the ducts in the head; (3) co-operation between left and right labyrinths; (4) optimal combinations of mechanical signals which are transferred to the brain, (5) the distribution of flow in the system for all possible rotations.

A10/E3.23–Particle based methods applied in models of growth and form of sponges and corals

J.A. Kaandorp, Section Computational Science, Amsterdam

In previous work [1,2] a method has been developed for modelling the hydrodynamic environment around complex-shaped marine sessile organism as for example a sponge or a stony coral, using a particle based method, known as the lattice Boltzmann method. With this method the distribution of suspended material determined by a combination of flow and diffusion in the external environment around a rigid organism can be described for low Reynold's numbers. Recently many new insights have become available on the genetic regulation of the growth process in sponges and stony corals. During this presentation we will present three dimensional models of growth and form, where the growth process is regulated by gradients of morphogens or other chemical agents and the availability of suspended food particles in the environment. In the model both the biological regulation and the external hydrodynamic environment are captured using the lattice Boltzmann method. Furthermore, it will be discussed how these models can be coupled with a particle-based model of a flexible object.

1. J.A. Kaandorp and J.E. Kuebler, The algorithmic beauty of seaweeds, sponges and corals, Springer-Verlag, Heidelberg, New York, 2001.
2. J A Kaandorp, P M A Sloot, Morphological models of radiate accretive growth and the influence of hydrodynamics, J. Theor. Biol., 209:257–274, 2001.

A10/E3.24–The (non-)adaptive nature of behaviour revealed by whole body modelling: lizard bipedalism

P. Aerts and R. Van Damme, Biology, Antwerp University

Dynamic bipedalism has evolved on numerous occasions in lizards. Traits that pop up repeatedly in independent evolutionary lines are often considered adaptive, but the exact advantages of bipedal locomotion in lizards remain debated. Earlier claims that bipedalism would increase maximal running speed or that it would be energetically advantageous have been questioned. We suggest a non-adaptive solution to the riddle, using 'whole body' mechanical modelling. Starting point is the intermittent running style combined to the need for a high manoeuvrability characterising many small lizard species. Manoeuvrability benefits from a caudal shift of the centre of mass of the body (body-COM), since forces to change the heading and to align the body to this new heading do not conflict with each other. The caudally situated body-COM, however, might result in a lift of the front part of the body when accelerating (intermittent style), thus resulting in bipedal running bouts. Adopting a momentum-impulse approach, the effect of acceleration is quantified for *Cylindroconus*, a model based on the morphometrics of *Acanthodactylus erythrurus* (a small lacertid lizard). Biologically relevant input results in considerable distances (beyond the acceleration distance) passively covered bipedally as a consequence of the acceleration. In this way, no functional explanation of the phenomenon of lizard bipedalism is required.

A10/E3.25–Optimizing motor patterns to a growing skeletomotor system: A primitive-based modeling approach

W.J. Kargo, Neurosciences Institute, San Diego CA

Experimental studies show that different-sized frogs use different motor patterns to produce hindlimb wiping: smaller frogs activate muscle groups (motor primitives) sequentially while larger frogs activate the same primitives synchronously. Both motor pattern types drive the wiping tool (the ankle) to the same final target. In the present study, I examined whether motor pattern variations reflect: (1) motor equivalent solutions to reach the target, (2) size-dependent solutions to minimize muscle forces and energy expenditure, or (3) size-dependent solutions for dealing with unexpected (unseen) objects in the hindlimb's workspace. I used a primitive-based modeling approach in combination with a SIMM model of the frog and Zajac–Hill type models of the hindlimb muscles to test these alternatives. I scaled model size by 1.5–2.5 times and incorporated appropriate scaling relationships for the hind limb actuators. The 'neural system' of each sized model performed a multi-objective optimization algorithm. Larger models settled on synchronous motor pattern solutions in order to minimize muscle activations and avoid saturation. Smaller models settled on sequential motor pattern solutions in order to minimize reaching time in the presence of unknown path obstacles. The results provide evidence that the neural system tunes primitive activation parameters (onset and amplitude) based on multiple task goals, which are solved differently with different physical plants.

A10/E3.26–Computational fluid dynamics of an anguilliform swimmer

T. Williams and J. Carling, St. George's Hospital Medical School, London

This workshop complements presentation A10.15, 'Numerical approaches in computational fluid dynamics'. In this session we will illustrate the kinds of data that can be obtained by computational fluid dynamics. We will present results of modelling an anguilliform swimmer in a tank of water. The time-dependent body shape of the creature, but not its position, is provided to the computer code. The pressure and components of water velocity are computed throughout the three-dimensional domain of the tank, by solving the full Navier–Stokes equations. In parallel and interactively with this computation, Newton's Laws of Motion are solved for the body of the fish, to determine the time course of the position and orientation of the creature. Stills and animated sequences will be shown which allow the viewer to visualise the water movements as well as the pressure and drag forces exerted on the body of the creature as it propels itself forward through the tank.

A10/E3.27–Finite element analysis or bent cardboard? Approaches to the modelling of insect wings

R.J. Wootton, P.G. Young and R.C. Herbert, University of Exeter

Insect wings undergo appreciable strains in flight. Their deformations are largely elastic responses to aerodynamic, inertial and impact loads, modulated remotely by muscles in the thorax. Many mechanisms involved invisible deformations can be investigated and demonstrated by quick, crude models using everyday materials. Such models can take no account of the mechanical properties and structural details of the actual wing, or the sensitivity of the mechanisms to real conditions, but they can provide a useful starting point for sophisticated, but far more time-consuming, finite element modelling, which can properly address these factors. We compare the application of simple mechanical and complex analytical models to the functioning of a selection of wings and wing components.

A10/E3.28–How to perform measurements in a hovering animal's wake: Physical modelling of the vortex wake of the hawkmoth, *Manduca sexta*

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Current models of flying animals' wakes suggest that the wakes consist of a linked vortex ring series. From measurements in the wake, it should be possible to estimate the impulse and circulation around a hovering animal's wings. To investigate the feasibility of this approach, we studied the evolution of a single isolated vortex ring. Based on existing kinematic and morphological data, a piston and tube vortex ring generator was constructed to produce circular vortex rings with the same size and disc loading as those in the wake of a hovering hawkmoth, *Manduca sexta*. Results show that the artificial rings were initially laminar, but developed turbulence due to an azimuthal wave instability. The initial impulse and circulation were accurately estimated for laminar rings using particle-imaging velocimetry (PIV); after the transition to turbulence, initial circulation was underestimated. The underestimate for turbulent rings can be corrected the time of its transition to turbulence and its velocity profile are accurately known, but this correction will not be feasible for experiments on real animals. It is therefore crucial that measurements are made while the wake vortices are still laminar. Based on the scaling of ring Reynolds number, animals about the size of hawkmoths probably are the largest animals with wakes that stay laminar for sufficiently long to perform measurements during hovering.