

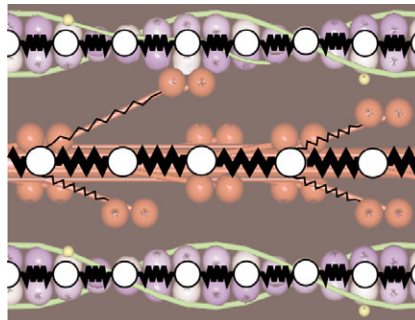
Inside JEB is a twice monthly feature, which highlights the key developments in *The Journal of Experimental Biology*. Written by science journalists, the short reports give the inside view of the science in JEB.

Inside JEB

BIOMECHANICS OF SWIMMING AND FLIGHT

While airborne birds routinely defy gravity and aquatic creatures glide with ease through water, man has largely been restricted to land for all but the last century. How birds and fish manoeuvre with such freedom in their fluid environments has always fascinated humans, and more recently it has become clear that many of the principles that keep birds and insects aloft apply also to fish and other agile swimmers. With this in mind, Johan van Leeuwen and Andy Biewener have compiled and edited a collection of papers investigating the biomechanics of both flight and swimming. Focusing initially on the machinery that powers locomotion, other papers discuss the biomechanics of swimming and flight, as well as general aerodynamic principles that can be applied to either flight or swimming.

MUSCLE IN LOCOMOTION



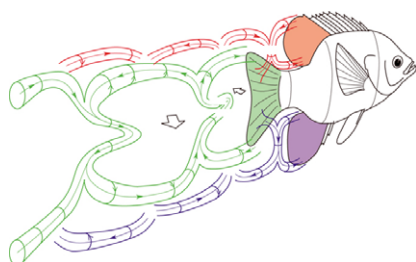
Ultimately, muscle powers all flight and swimming in the animal world. Muscular contraction is driven by myosin heads that consume ATP and slide actin filaments along myosin filaments. While much is known about functional specialisation in vertebrate muscle, the approaches that invertebrates have adopted to modulate muscle performance are less well known. William Kier and Frederick Schachat (p. 164) discuss some unusual adaptations found in squid. Squid mantle, fin and arm muscles are obliquely striated (with Z disks linking actin filaments inclined at an angle) and tend to be characterised by long myosin and actin filaments, which are capable of a large contraction range while generating high tensile stresses. However, the tentacle extensor muscle is more similar to cross striated vertebrate skeletal muscle, but with much shorter myofilaments. The result is that the tentacle extensor muscle can contract very rapidly, but generates small tensile stresses. According to Kier and Schachat, the molecular components of both muscle types are virtually indistinguishable, and it is mainly the different architecture that

gives rise to the muscles' different properties.

Where as squid tentacles have to act fast to grab passing prey, the major muscles involved in flapping bird flight must generate great force while contracting repeatedly as birds take off and remain aloft. Yet, according to Bret Tobalske and Andy Biewener, little is known about the mechanical properties of the second largest flight muscle in birds, the supracoracoideus muscle (p. 170), which was thought to be responsible for flipping the wing upwards at the beginning of an upstroke (supination) during flight. Measuring muscle activity, and bone and muscle strain, in freely flying pigeons, Tobalske and Biewener confirmed that the muscle does indeed flip the wing at the beginning of the upstroke. Also the muscle's elastic tendon stores up to 60% of the muscle's work, presumably releasing the energy later to reduce the metabolic cost of flight. However, two of the team's predictions were not born out; strain in the supracoracoideus muscle was much greater and the power generated by the muscle was less than the team had predicted. Tobalske and Biewener say 'it is sobering that our predictions of function from anatomy were only partially correct,' but van Leeuwen describes the team's findings in freely flying birds as 'quite an experimental achievement'.

Concluding the discussion of muscle function in locomotion, Bertrand Tanner, Michael Regnier and Tom Daniel describe their theoretical work on a three dimensional molecular model of muscle. By modelling the kinetics and molecular structure of half a sarcomere, the team successfully predicts muscle function for *Manduca sexta* (p. 180). Knowing that the major flight muscle only operates at 40% maximal power and that extra power required for manoeuvres during flight was probably generated by 'shifting activation phase [timing] to produce higher mechanical output', the team were also able to model how the timing of activation influences the energetics of contraction. Calculating ATP consumption as well as mechanical work done, power and efficiency, Daniel and colleagues found that the mechanical work generated and ATP consumption vary depending on the timing of myosin activation. Daniel says 'to our knowledge, no prior study has shown that myosin cross-bridge ATPase rates vary with phase of activation'.

BIOMECHANICS OF SWIMMING



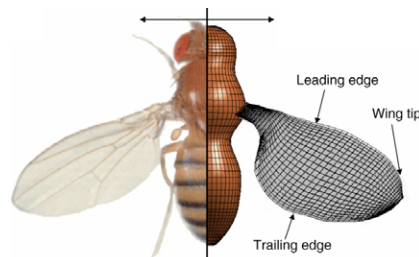
Over the last 10 years, our understanding of the biomechanics of swimming has been revolutionised by the development of particle imaging velocimetry (PIV), which has revealed details of the complex fluid flow patterns around fish and in their wake. Eric Tytell, Emily Standen and George Lauder briefly review the current understanding of the fluid dynamics associated with fish swimming (p. 187), but also sound a note of caution. Pointing out the consistency found in the wakes of fish ranging from eels to mackerel, they warn that the simplified two dimensional PIV view could have obscured more complex fluid flows occurring in three dimensions. Expanding PIV techniques into the third dimension, the team discuss their work on the bluegill sunfish, brook trout and yellow perch, analysing the fishes' dorsal, anal and median fin motions during manoeuvres and free swimming. Identifying complex interactions between flow from different fins, the team say that 'these data demonstrate that, while fish do move primarily in the horizontal plane, neither their bodies nor their motions can be accurately simplified in a two-dimensional representation'.

Scaling down from adult to larval fish, Ulrike Müller, Jos van den Boogaart and van Leeuwen point out that the sticky environment experienced by miniature swimmers is very different from the more fluid environment experienced by their adult counterparts (p. 196). Analysing fluid flow patterns as larval fish accelerated from stationary, swam steadily and came to a halt, the team found that tiny larval zebrafish swim with a wide body amplitude. They also found that the larvae are hugged by a relatively thick boundary layer, unlike the adult's relatively thin layer, and that the wake dies off quickly. When setting off, the larvae bend themselves into a C shape followed by a propulsive stroke, and when stopping they gradually reduce their tail beat frequency and amplitude.

While much has been learned from *in vivo* studies of swimmers, studies of robotic fins and wings can also teach us a great

deal about the hydrodynamics of swimming. With the aim of developing robotic submarine vehicles, Promode Bandyopadhyay, David Beal and Alberico Menozzi, working at the Naval Undersea Warfare Center in Rhode Island, USA, have designed and built a robotic fin, loosely based on a penguin fin, which they can control while directly recording forces exerted on the moving limb (p. 206). Based on measurements from the moving fin, the team have developed a model that allows them to calculate the lift and drag exerted on a stiff, penguin-like fin, and to calculate optimised oscillation parameters for the fin during swimming. Surprisingly, the rigid fin's wake was remarkably similar to an eel's, shedding vortex rings alternately to the left and right (although the robotic fin's vortices die off more rapidly than the eel's). The team have also compared the performance of the rigid penguin-like fin with the sunfish's flexible pectoral fin and concluded that although the sunfish's fin confers greater hydrodynamic variation, penguin fin analogues may be better suited to propel biorobotic vehicles.

BIOMECHANICS OF FLIGHT



As largely earth-bound creatures, humans can take to the water, yet routine human-powered flight remains an elusive dream. While engineers have a well developed understanding of machine-powered flight, the realms of viscosity encountered by jets, large birds and insects differ hugely. Although viscosity effects can be disregarded on fixed wing jets, flapping birds are prey to the effects of lift, drag and turbulence, which drastically alter aerodynamic performance. Despite the apparent complexity of flapping bird flight, Geoffrey Spedding, Anders Hedenström, John McArthur and Mikael Rosén have compared the aerodynamics of birds, ranging in size from the thrush nightingale to the robin, with the forces acting on fixed wings (p. 215) and found that the birds' wakes were only slightly more complex than fixed wing wakes. The team adds that 'this observation suggests that simple aerodynamic models might help to understand many features of bird flight' but warn that their results may not apply to larger birds.

Following Spedding's discussion of the aerodynamics of bird wings, Fritz-Olaf Lehmann reviews wake-wing interactions in insects to understand 'how oscillating [insect] wings interact with the surrounding fluid' (p. 224). Working with large scale Plexiglas™ insect wing models immersed in mineral oil (to simulate the air viscosity experienced by an insect), Lehmann has modelled wing-airflow interactions in two and four winged insects. He explains that wing-wing and wing-wake interactions can significantly enhance lift with only minimal modifications to a wing stroke pattern, improving an insect's efficiency, and possibly contributing to the insect's flight control.

Staying with insect aerodynamics, Jane Wang discusses a theoretical study where she develops a computational model to investigate the efficiency and power output of six different hovering wing beat patterns (p. 235). Defining each wing beat in terms of four parameters Wang calculates the work each wing beat does to support a unit weight over a unit time as the parameters vary. The results are power surfaces for each wing beat pattern, revealing the most efficient combination of wing beat parameters that fall at the lowest point on the surface. While the surfaces that she generates seem to agree with recorded hovering wing beat patterns, Wang adds that for a specific wing shape, many wing beat patterns may occur close to the optimal pattern.

Taking a completely different theoretical approach, Hikaro Aono, Fuyou Liang and Hao Liu describe their ground-breaking computational fluid dynamic simulation of a hovering fruit fly (p. 239). Computationally reproducing the shape and motion of the insect's wings and body, the team simulated fluid flow patterns around the insect revealing a horseshoe-shaped vortex wrapped around the wing early in both the down- and upstrokes, which subsequently develops into a doughnut shaped ring resulting in a strong downwash jet which keeps the hovering insect aloft. According to Liu, this innovative simulation agrees well with experimental observations of hovering fruit flies.

Finally, Graham Taylor, Adrian Thomas and colleagues describe recent developments in experimental approaches in the biomechanics of flight in their Oxford labs. Discussing the merits and pitfalls of tethered flight analysis, the team describe a novel virtual-reality insect-flight arena that they have developed (p. 258). The arena not only simulates the insect's global view, but also stimulates all of the insect's sensory systems (including the

gyroscopic halteres) by mounting the insect on a six-component force–moment balance, which moves the insect as if it were flying freely. Taylor and Thomas then go on to describe their work on free-flying birds, collecting inertial observations and combining them with photographic records of wing and tail movements during flight. Although both systems will provide state-of-the-art experimental data to produce advanced models of flight control, Taylor and Thomas add that ‘details of the underlying physiology remain opaque’.

GENERAL FLUID DYNAMIC APPROACHES



Having discussed the current understanding of the fluid mechanics of both swimming and flight, van Leeuwen and Biewener’s collection of articles concludes with three papers considering general fluid dynamic approaches. David Lentink and colleagues from Wageningen University and Delft University of Technology describe a soap-film technique (p. 267), which allows the team to directly visualise wake vortices generated by a flapping structure. Designing a small 2D wing, the team move

it through a thin flowing soap film, generating eddies and vortices that can be visualised by light diffraction. Using this form of direct visualisation, the team have revealed the range of wake complexity found for a variety of wing beat patterns. Describing the wing beats in terms of ‘dimensionless wavelengths’, the team have derived general principles that can be applied across all flapping structures, revealing the relatively simple wakes generated at high dimensionless wavelengths and the increasingly complex vortex interactions that are generated as the dimensionless wavelength declines.

Returning to robotic techniques in flapping motion simulation, Alexandra Techet has been inspired to understand the fluid dynamics of flapping-fin locomotion with the intention of designing highly manoeuvrable aquatic vehicles. Basing her fin’s design on turtle and aquatic penguin fins (p. 274), Techet controls the fin’s roll and pitch motions over a range of flapping frequencies while measuring the hydrodynamic efficiency and forces acting on it. Her intention is to find combinations of kinematic parameters that maximise lift and efficiency.

Concluding the collection, Jifeng Peng and John Dabiri introduce the Lagrangian approach to analysing digital PIV (p. 280). By tracking individual particle trajectories, Dabiri and Peng determine the boundary of

the vortex associated with a flapping fin, the momentum of the wake vortex and its added mass in order to determine instantaneous locomotive forces. Dabiri and Peng explain that when a fin or flipper moves through a fluid and generates an attached vortex, the vortex also displaces fluid as the limb is moved. The inertia of the surrounding fluid imparts an ‘added-mass’ to the vortex, and this must also be considered when calculating instantaneous locomotive forces. Applying the method to the two dimensional wake of the bluegill sunfish, the team emphasise that the accuracy of the technique will improve when applied to three dimensional DPIV recordings.

SUMMARY

Having compiled the collection of 14 articles, van Leeuwen is enthusiastic and says that the collection gives ‘a nice impression of the state-of-the-art view of swimming and flight in 2007’. Although he admits that the papers gathered in this issue only offer a glimpse of the fast developing world of fluid locomotion, he hopes that the novel approaches described will inspire anyone fascinated by fish, birds and insects to tackle some of the more arduous questions that have so far eluded us.

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Kathryn Phillips
kathryn@biologists.com
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