Introduction

A moving topic: control and dynamics of animal locomotion

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Animal locomotion arises from complex interactions among sensory systems, processing of sensory information into patterns of motor output, the musculo-skeletal dynamics that follow motor stimulation, and the interaction of appendages and body parts with the environment. These processes conspire to produce motions and forces that permit stunning manoeuvres with important ecological and evolutionary consequences. Thus, the habitats that animals may exploit, their ability to escape predators or attack prey, their capacity to manoeuvre and turn, or the use of their available energy all depend upon the processes that determine locomotion. Here, we summarize a series of 10 papers focused on this integrative research topic.

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As pointed out in a recent review by Dickinson et al. (2000), animal locomotion is deceptively simple—Newton’s laws govern the dynamics of body forces and accelerations that result from the interaction of animals with their surrounding environment. But those dynamics turn out to be exquisitely complex: the physical rules governing emergent forces in media such as air, water or even soil have challenging mathematical underpinnings that are only recently being tackled by collaborations among engineers and biologists. The advent of new computational and experimental resources makes this undertaking more tractable.

Understanding the control of movement also demands a deeper look into the role of sensory information acquisition and processing. Indeed, without appropriate sensory processing, motion cannot be controlled, at least over long time scales. Thus, while passive dynamic mechanical responses to perturbations may provide stable responses over short time scales, sensory systems are indisputably critical for long- and short-term course control and stable motion.

Sensory information acquisition and processing determine, in turn, patterns of motor activation. Activation of muscles that interact with the external forces an animal produces to move through (or over) its environment, sets the stage for how appendages move and how energy is used (as a brake, a clutch or an actuator). The time-varying oscillatory nature of appendage and body movement during locomotion means that the dynamics of muscle activation in relation to force and movement are critical for determining how muscles shift their roles to accomplish varying motor tasks.

These three processes—sensory processing, motor control and animal–environment interaction—constitute the theme of control and dynamics of animal locomotion in this issue of Biology Letters. Together, these papers show how the combination of engineering, biology, experiments and computation provide an understanding of the control of locomotion on land, in air and in water.

In the first group of three papers, the authors address the challenging issues surrounding animal–environment interactions, with a focus on the physics of the environment as an important determinant of locomotion. Nawroth et al. (2010) show that temperature and body size play key roles in determining the fluid dynamics associated with aquatic locomotion. Using a combination of computational and experimental methods in a study of jellyfish locomotion, they show that developmental changes in body morphology compensate for associated changes in fluid dynamic properties (e.g. viscosity and Reynolds number) as animals develop. Lentink et al. (2010) continue this theme through a study of the interactions of the vortical flows shed by flapping wings and fins. Here, they reveal complex wake structures, signatures of forces on flapping appendages that arise from different patterns of wing or fin motions. Their results suggest that subtle changes in how appendages are controlled may lead to significant changes in the emergent flows and forces, which are likely to be enhanced at the frequencies and cruising speeds that many swimming and flying animals employ. The third paper by Mazoucheva et al. (2010) grapples with an enigmatic animal–environment interaction involving locomotion over granular substrates (e.g. sand). Neither entirely fluid nor entirely solid, this medium has physical

One contribution of 11 to a Special feature on ‘Control and dynamics of animal movement’. 
properties that depend upon the forces it experiences. Here, they examine the locomotion of hatchling loggerhead sea turtles (Caretta caretta), showing that compaction of loose sand by the flipper enables equally effective locomotion as that obtained by traction using their flipper’s claw when moving over a solid sandpaper substrate.

The second group of three papers is concerned with sensory information processing in the control of animal locomotion. All three papers focus on the ability of nervous systems to encode information at rates and magnitudes that are critical for movement control. In a study of the lateral line in larval zebrafish, Liao (2010) combines single cell imaging and electrophysiological methods with biomechanical manipulations to reveal fine-tuned sensitivity of mechanosensory cells to local flow direction and velocity. In a similar vein, but at a larger scale of motion, Sane et al. (2010) question how mechanosensory information determines flight paths in migratory insects. Using a combination of field behaviour and experimental manipulation of sensory systems, they show that long-distance migration requires mechanosensory input mediated through antennae in addition to visual information. Vision, in turn, is the focus of the paper by Theobald et al. (2010). Using a flight simulator that provides abrupt perturbations to otherwise smooth motion in the visual world of a tethered fruitfly, these authors show that compensatory reflexive responses to sideways motion depends upon the overall visual flow experienced by the animal as a result of its own body movement (forward, backward or sideways).

The final group of papers focuses on the emergent motions of animal appendages and their role in locomotion. Dadda et al. (2010) question whether motor output may be lateralized in the brain of fish. Using a time-tested experimental paradigm of escape locomotion in fish subject to mechanical stimulation, they show lateralization—determined by turning direction preference—leads to lower latency in the motor output associated with escape. That may be a consequence of either motor-patterning or sensory processing. In terrestrial systems, motor-patterning combined with the biomechanics of limbs plays a key role in gaits that may conserve energy and provide stability. Thus, Daley & Usherwood (2010) use a theoretical approach to explore how limb compliance combined with the control of limb positions (extensions and velocities) allows for effective control of stability during locomotion over uneven terrain while maintaining appropriate bounds on energy utilization.

This theme of limb control continues into the air with two additional papers on insect flight, both focusing on manoeuvrability. Hedrick & Robinson (2010) draw on prior work that has shown that, as an animal turns, the interaction between wing-flapping and body rotation leads to a counter torque that provides inherent stability, without any special asymmetry in wing-flapping. In their paper here, they show that this stabilizing dynamic applies across multiple wing strokes in a continuous sustained turn. In the paper by Combes et al. (2010), the focus turns more towards the ecological implications of flight performance in relation to wing-flapping dynamics. Interestingly, many studies have shown that animals are capable of flying with incredible reductions in wing area. However, none have clearly shown whether flight is somehow compromised by wing damage. Using a combination of experimental manipulations on dragonflies, they ask if the damage that naturally occurs to wings has any measureable fitness consequences. By directly measuring prey capture success of dragonflies with and without partial wing loss, they provide the first clear demonstration of an ecological consequence of natural wing reductions.

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