COMMENTARY

Robotics-inspired biology

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ABSTRACT

For centuries, designers and engineers have looked to biology for inspiration. Biologically inspired robots are just one example of the application of knowledge of the natural world to engineering problems. However, recent work by biologists and interdisciplinary teams have flipped this approach, using robots and physical models to set the course for experiments on biological systems and to generate new hypotheses for biological research. We call this approach robotics-inspired biology; it involves performing experiments on robotic systems aimed at the discovery of new biological phenomena or generation of new hypotheses about how organisms function that can then be tested on living organisms. This new and exciting direction has emerged from the extensive use of physical models by biologists and is already making significant advances in the areas of biomechanics, locomotion, neuromechanics and sensorimotor control. Here, we provide an introduction and overview of robotics-inspired biology, describe two case studies and suggest several directions for the future of this exciting new research area.

KEY WORDS: Robotics, Locomotion, Physical model, Biomimetics, Mechanical device

Introduction

Inspiration from biology has led to the design of robots of all shapes and sizes, many of which are inspired by the ability of animals to move and maneuver so effectively in their environment. Robots are capable of many modes of locomotion, such as running (Altendorfer et al., 2001; Grizzle et al., 2009; Hyun et al., 2014), flying (Floreano and Wood, 2015; Ma et al., 2013; Mellinger et al., 2012), crawling (Lin et al., 2011b) and swimming (Anderson and Chhabra, 2002; Guo et al., 2003; Lauder and Tangorra, 2015), as well as combinations of two or more of these modes (Fig. 1). Some bio-inspired robots seek to match a targeted biological system in form and/or function, and are often primarily exercises in design: can engineers construct a mechanical system that mimics basic biological functions such as running or swimming? Such bio-inspired robotic systems may lack direct connections to their biological counterparts other than general similarities in physical appearance, but are useful for understanding the principles of mechanical design and control, and for testing new materials or manufacturing techniques.

Other bio-inspired robots have sought to emulate both the physical appearance and the intrinsic dynamics of biological movement, resulting in robust and agile robots. Examples include Rhex (Saranli et al., 2001), Stickybot (Santos et al., 2008), iSprawl (Kim et al., 2006), the robo-cheetah (Hyun et al., 2014), insect-scale flying robots (Ma et al., 2013), and robotic swimmers such as sunfish robotic systems and the robot tuna (Anderson and Chhabra, 2002; Barrett et al., 1999; Tangorra et al., 2011). In the world of bio-inspired robots, knowledge flow has tended to move in one direction: from biological motivation to engineering output, with the goal of extracting design principles from biology (e.g. Haberland and Kim, 2015).

However, a new trend building on previous advances in biomechanics (Vogel, 1998; Wainwright et al., 1976) is emerging in which researchers flip this traditional model and use robotic and mechanical systems to develop new insights into nature (Ijspeert, 2014; Kovač, 2014). We term this approach robotics-inspired biology. Under this approach, the design of physical models and robotic systems and the study of their performance and control has directed biologists toward new experiments on animals and the discovery of new biological phenomena. Mechanical and robotic systems can offer many insights into how sensory and feedback systems enable the control of complex biological movements, how differing configurations of actuators that power movement and skeletal elements might affect locomotion, and how parameters such as stiffness or flexibility might alter propulsion on land, in the water or in air. Ideas derived from study of these mechanical systems can then drive the search for similar phenomena in animals, and suggest new hypotheses about animal function that might not have been proposed from biological studies alone.

Robotics-inspired biology lends itself particularly well to systems where dynamics, movement, sensory processes and interactions with the surrounding environment are important. The predominant work in robotics-inspired biology to date has been in locomotor biomechanics and control, where movement involves interactions between animals and complex three-dimensional fluid and topographic terrestrial surfaces. The study of how robots move in these biologically relevant scenarios presents many opportunities for inverting the traditional paradigm of bio-inspired robotics and moving towards using robotics to inspire new biological experiments.

The success of robotics-inspired biology is leveraging the booming industry of low-cost electromechanical tools now available. The decreasing cost and increasing availability of electronic components (e.g. Arduino microprocessors), actuators (components that produce movement in mechanical systems, e.g. hobby servomotors,), sensors [devices that measure motion or the environment, e.g. accelerometers and inertial measurement units (IMUs)] and fabrication equipment (3D printers and laser cutters) is enabling new contributions to robotics-inspired biology that will only increase in frequency as components decrease in cost. In addition, students in the sciences are learning computer programming skills and are exposed to electronics at younger ages. Low-cost hardware and access to open-source or inexpensive software make designing simple mechanical systems appealing for biologists. In the past, and especially from the perspective of many biologists, robotic systems can be difficult and time-consuming to

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Glossary

Physical model

An electro-mechanical system that is capable of movement and/or sensing, but that does not exhibit reactive or closed-loop behavior through active control systems involving feedback. Physical models may be passive and immobile, or powered externally through rigid components, with controlled kinematics.

Robot (reactive) model

An electro-mechanical system capable of reactive, closed-loop, behavior and thus dynamics (i.e. behaviors not explicitly programmed) typically through feedback control systems, morphology, and interactions of flexible components with the environment. The resulting kinematics exhibited by a reactive model can be difficult to predict.

design, challenging to iterate when changes are needed, and thus require a greater degree of engineering expertise to use in extracting ideas and generating hypotheses to test in biological systems. Emerging low-cost and easy to use tools are lowering the barrier to entry for robotics-inspired biology research and enabling researchers trained as biologists to design their own mechanical systems and employ robotics for research.

In this Commentary, we aim to draw attention to the new possibilities offered by the emerging tools in robotics to inspire new ways of observing and studying organismal function. First, we briefly discuss the history of mechanical models in biology and summarize a distinction between physical models and robotic devices. We then present two case studies from the current literature where discoveries in mechanical or robotic systems have inspired new experiments on animal function. Both case studies involve examples of how robotic devices are improving our understanding of the interrelationships between morphology and dynamics in biological locomotion. Locomotion in nature occurs in environments that move and flow in response to animal movement, and mechanical devices have been instrumental in suggesting new experiments on animals in flight, swimming in the water and movement on granular media, such as sand.

Robotics-inspired biology: from physical models to reactive systems

There is a long history of biologists studying physical models of living systems to learn about organismal form, function and behavior (Koehl, 2003; Vogel, 1998; Wainwright et al., 1976; Fig. 1). Robotics-inspired biology is a natural progression along this path. We define robotics-inspired biology as the study of models of biological systems that reproduce behaviors consistent with biological observation, and more critically, that enable analysis of reactive behavior to generate new biological hypotheses of organismal function.

There are many types of systems that enable robotics-inspired biology, and it is useful to distinguish two basic types: physical models and reactive models (see Glossary). Physical models, in our view, are systems in which the motion and the shape of inputs to the

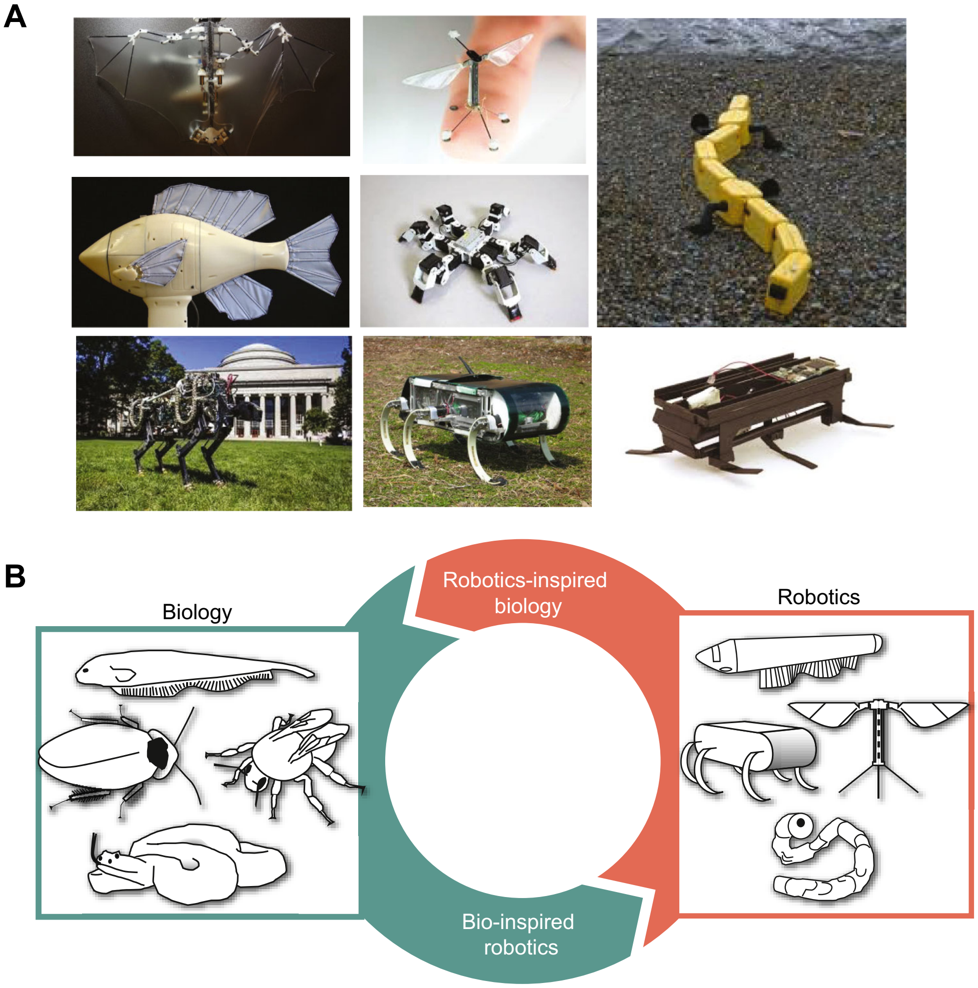

Fig. 1. Examples of bio-inspired robotic systems. (A) Bio-inspired robots that mimic flying, running, swimming and crawling organisms. Left (top down): a bat-inspired robot (Ramezani et al., 2017), a fish robot (Tangorra et al., 2011) and a cheetah robot (Seok et al., 2013). Middle (top down): a bee-inspired robot (Ma et al., 2013), a hexapedal crawling robot (Ramdya et al., 2017), a hexapedal running robot (Altendorfer et al., 2001). Right (top down): a salamander robot (Ijspeert et al., 2007), a cockroach-inspired robot (Birkmeyer et al., 2009). (B) The reciprocal illumination of research in biology and robotics includes the more traditional pathway of bio-inspired robotic systems, and we suggest here that experimental work in robotics-inspired biology is also a potentially fruitful intellectual path. All images reproduced with permission.

experimental system are strictly prescribed and the resultant output forces, kinematics (the motion of systems) or environmental responses (fluid flow for example) are measured (Fig. 2, left panel). There are no unexpected dynamics associated with the motion of these physical systems because the motion kinematics are prescribed and the system is rigid. Even though inputs are prescribed, rigid physical models can still exhibit considerable functional complexity but there is no feedback from the environment that alters the shape and dynamics of the model itself, and thus physical models, in our view, do not display reactive behavior.

The use of physical models has a long history in the study of animal function, specifically in comparative biomechanics (see Alexander, 2003a; Koehl, 2003), and examples include models used for wind tunnel studies (e.g. Denny and Blanchette, 2000; Emerson et al., 1990; Koehl et al., 2011) and to explore dynamic behavior of organisms ranging from fish to mantis shrimp to fruitflies (Corn et al., 2016; Cox et al., 2014; Dickinson et al., 1999; Paig-Tran et al., 2011). Physical models can also be manufactured from animal shells or include hard anatomical components of animals in their design which can greatly simplify construction (Denny, 1988).

By contrast, in reactive model systems, the resultant behaviors or kinematics of movement cannot necessarily be predicted *a priori* because movement is determined by interaction with the environment (for example via fluid-structure interactions), internal dynamics or feedback control systems (Fig. 2, right panel). In other words, reactive model systems treat the biological organism as a dynamic system, which experiences internal and external feedback through control systems, actuators, body mechanics and environmental forces. Examples of reactive models include flexible swimming bodies and mechanical systems that move on or within granular materials (see below), where the complex physics of granular flow make predicting movement kinematics from programmed actuation schemes challenging. Reactive systems also include sensorimotor feedback systems such as one of the earliest robotics-inspired biology experiments with robotic crickets that preferentially move towards sound (Webb, 1995).

If some of the materials used to construct reactive models are flexible and these flexible components interact with the environment, then complex dynamic behaviors can emerge, even though the input motion to the model system is prescribed. Examples of this phenomenon are commonly seen in recent studies of flexible swimming models of aquatic locomotion (e.g. Akanyeti et al., 2017; Alben et al., 2012; Lauder et al., 2012; Lim and Lauder, 2016; Lucas et al., 2015; McHenry et al., 1995) where input motions to the 'head' of a swimming simple model fish result in complex patterns of body bending and fluid flow around and behind the model due to interactions between the fluid and the structure. As another example, a simple model of terrestrial locomotion, the bristlebot (Becker et al., 2014), is designed with flexible toothbrush-like bristles serving as 'legs' that interact with the ground. These bristle legs are driven by a vibratory motor. Emerging locomotor behaviors when the driving motor causes vibration of the bristles can be very complex, difficult to predict and extremely sensitive to small changes in bristle length (Cicconofri and DeSimone, 2015); we consider such systems to be reactive even though there is not direct feedback from the bristles to the motor.

Reactive model systems enable new insights into biological systems because they may highlight new movement behaviors and emergent dynamics that cannot be predicted from knowledge of organismal morphology and actuation patterns alone (see Glossary). The progression from physical to reactive models has taken place over the past 30 years. Physical models have enabled an engineering and physics approach to study the function of biological systems, pioneered by biomechanists such as Steve Vogel (1988, 1998), Steve Wainwright (Wainwright et al., 1976; Wainwright, 1988) and R. McNeill Alexander (1983, 2003b). As physical models became increasingly complex there was a natural progression towards experiments with 'reactive' systems: physical models that can respond to changes in the environment implemented with feedback

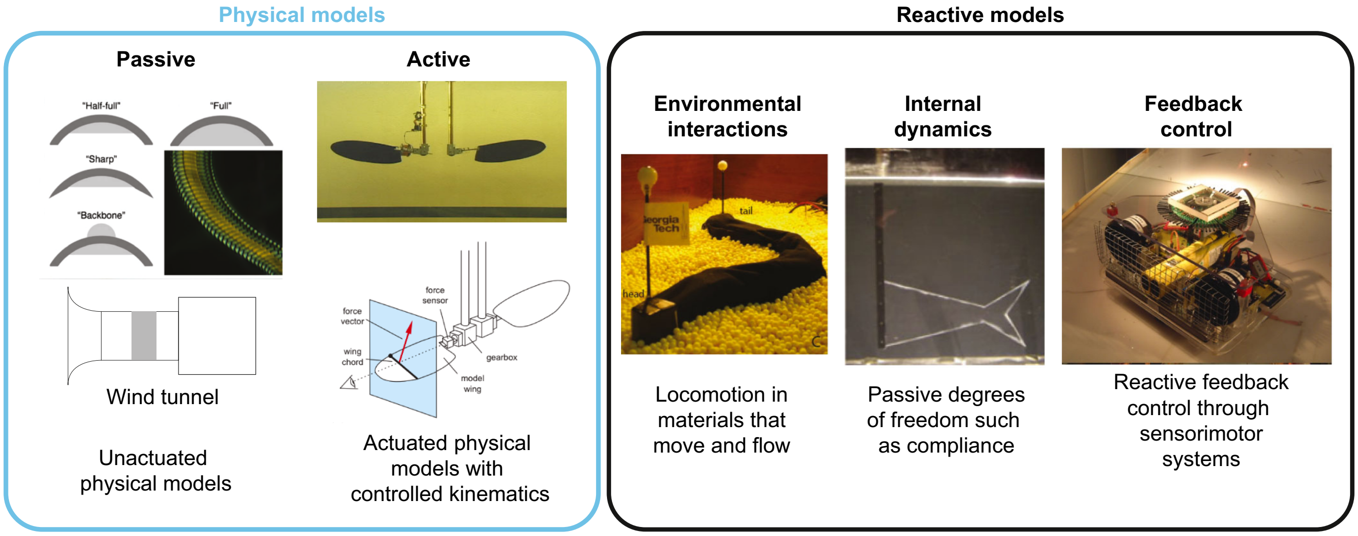

Fig. 2. Overview of selected physical and reactive models employed in robotics-inspired biology research. Components used in robotics-inspired biology can be divided into physical and reactive model systems (see Glossary). Physical models (left) may be unactuated (passive) to investigate flows or forces, such as how snake cross-section affects lift and drag during glide (Miklasz et al., 2010). They may also be actuated (active) with prescribed kinematics such as in the robofly experiments (Dickinson et al., 1999) with rigid wings. Reactive models (right) have dynamics associated with their motion due to feedback and/or flexible components, and may react to their environment in various ways, including nonlinear interactions with the environment (left) (Maladen et al., 2009), internal degrees of freedom (middle) (Feilich and Lauder, 2015) and sensorimotor dynamics (right) (Fuller and Murray, 2011). All images are reproduced with permission.

control systems. Barbara Webb performed one of the first robotics-inspired biology experiments, demonstrating how simple sensorimotor feedback loops can describe organismal behaviors (Webb, 1995). The addition of sensors (either external or attached to actuators or moving components) and feedback systems opened up whole new avenues of modeling biology, allowing mechanical systems to adjust their behavior depending on input from the environment. And better tools for manufacturing and adding flexible components to mechanical models allowed the development of relatively simple reactive systems that better respect the bendable and non-rigid nature of biological materials.

There are many outstanding examples of robotic devices that take inspiration from a great diversity of organisms ranging from insects to fish, birds and mammals (Ayers and Witting, 2007; Goldman and Hu, 2010; Ijspeert et al., 2007; Jayaram and Full, 2016; Lin et al., 2011a; Long et al., 2011; Neveln et al., 2013; Ritzmann et al., 2004; Sefati et al., 2013; Tangorra et al., 2011). Such robotic systems have the advantage of relatively complex control systems and reactivity, and hence serve as excellent platforms for testing the effects of morphology, body–environment interactions and feedback control for locomotion. Such hypotheses are extremely difficult to test in living biological systems, where altering individual structural features often has unwanted and uncontrolled side effects.

Robotics-inspired biology

The leading-edge vortex: from mechanical systems to biology

The leading edge vortex (LEV) in flapping wing flight is perhaps the most well-developed example of the impact physical models may have in understanding animal mechanical function. An LEV is an area of low pressure that arises on the upper surface of propulsive surfaces such as insect wings (where air flow separates as it moves over a sharp leading edge). Low pressure within the LEV generates increased lift compared with that in wings without an LEV. Ellington et al. (1996) first used a mechanical model to generate and visualize the LEV as a mechanism allowing flying insects to generate sufficient lift to support their weight against gravity. While the Ellington et al. (1996) study included some images of smoke trails moving over the wing of a hawkmoth, the key contribution of that study was the use of a mechanical flapper with a 1.03 m wingspan that enabled smoke visualization of the LEV and understanding of its formation and evolution during the flapping wing stroke (Fig. 3). The large size of the mechanical device allowed a slow flapping frequency of 0.3 Hz to maintain a similar Reynolds number to that of flying moths, and the wing included tubing to allow smoke injection. Use of this mechanical device was critical to visualization of flow over a moving wing-like surface and firmly established the LEV as fundamental to understanding insect flight.

One limitation of the Ellington et al. (1996) flapping mechanism was the lack of measured forces, so that the direct effect of the LEV on lift could not be measured. An important paper by Dickinson et al. (1999) resolved this by describing use of a sophisticated mechanical fly model with two rigid wings and force sensors embedded in a tank of mineral oil (Fig. 3). This mechanical system allowed, for the first time, quantification of the time course of forces during the wing stroke, and suggested specific mechanisms that insects might use to enhance lift. This experimental system also allowed the use of a quantitative flow visualization technique to measure fluid velocity around the moving wing and reveal the magnitudes of fluid motion in and around the LEV. Further study using this mechanical ‘robofly’ system clarified the shape of the LEV and described details of its structure that were not previously possible to visualize using smoke trails (Birch and Dickinson, 2001; Lentink and Dickinson, 2009).

These two mechanical systems, the Ellington flapper and the Dickinson robofly, opened the door to numerous investigations of LEVs in a wide variety of animals. Without these fundamental discoveries from the analysis of wing performance in mechanical models and the tremendous insights gained into the physical mechanisms of locomotion, there is no doubt that biologists would not have undertaken the studies that they did on a diversity of animals and plants. One might even suggest that something of an LEV ‘cottage industry’ has arisen in the years following publication of the initial Ellington and Dickinson papers, with numerous groups working to identify the presence of an LEV on their particular biological study system.

The presence of an LEV has now been identified as a key feature of the flight performance of some plant seeds (Lentink et al., 2009), in bird flight (Lentink et al., 2007), on bat wings (Muijres et al., 2008), the feet of paddling birds (Johansson and Norberg, 2003), insect wings (Bomphrey et al., 2006, 2005), swimming fishes (Borazjani and Daghooghi, 2013; Bottom et al., 2016) and on pieces of shark skin moved by a mechanical flapper to understand the dynamics of shark skin function during locomotion (Oeffner and Lauder, 2012). In Fig. 3, we include an analysis showing the presence of an LEV on the tail of a swimming bluegill sunfish. The presence of the LEV on the tail of swimming fishes may enhance leading edge suction, and thus improve thrust generation and locomotor efficiency.

Moving on and in flowing media: from robotic systems to biology

The robotic physical models described above have enabled biologists to reproduce animal body movements and to study the fluid mechanics and biomechanics of LEVs. Physical models illustrate how control of kinematics enables study of the resultant forces and flows associated with animal movement. However, organisms generate movement by producing internal forces (via muscles in most cases) that act against external forces from the environment and body mechanics such as inertia and internal stiffness. Thus, the study of movement in responsive environments that can flow and fail during locomotion requires reactive robotic systems that model limb and body actuation to observe the emergent movement behaviors.

Reactive models enable the study of emergent patterns of locomotion when the movement dynamics and the flow of the surrounding environment are coupled. There are many examples of animal movement in flowing environments, flight and swimming through fluids, and legged and limbless locomotion on flowable ground (Fig. 4). In many cases, animal movement results in changes to the surrounding environment such as fluid flow or soil failure, which, in turn, affects the animal’s movement. The feedback loop between animal movement and the flow and force response from the surrounding environment can lead to non-intuitive and novel movement biomechanics that can be studied with robots.

When an animal such as a sprinting zebra-tailed lizard pushes off of the granular substrate (Li et al., 2012) or a sandfish lizard oscillates its body below the granular substrate (Maladen et al., 2009) the ground may either flow or remain solid. Complex physics underlie this material response and the flow or solidification of the ground underfoot determines the locomotor success. Solidification of granular media is beneficial for surface-moving animals (Li et al., 2009; Mazouchova et al., 2010) whereas flowing granular media

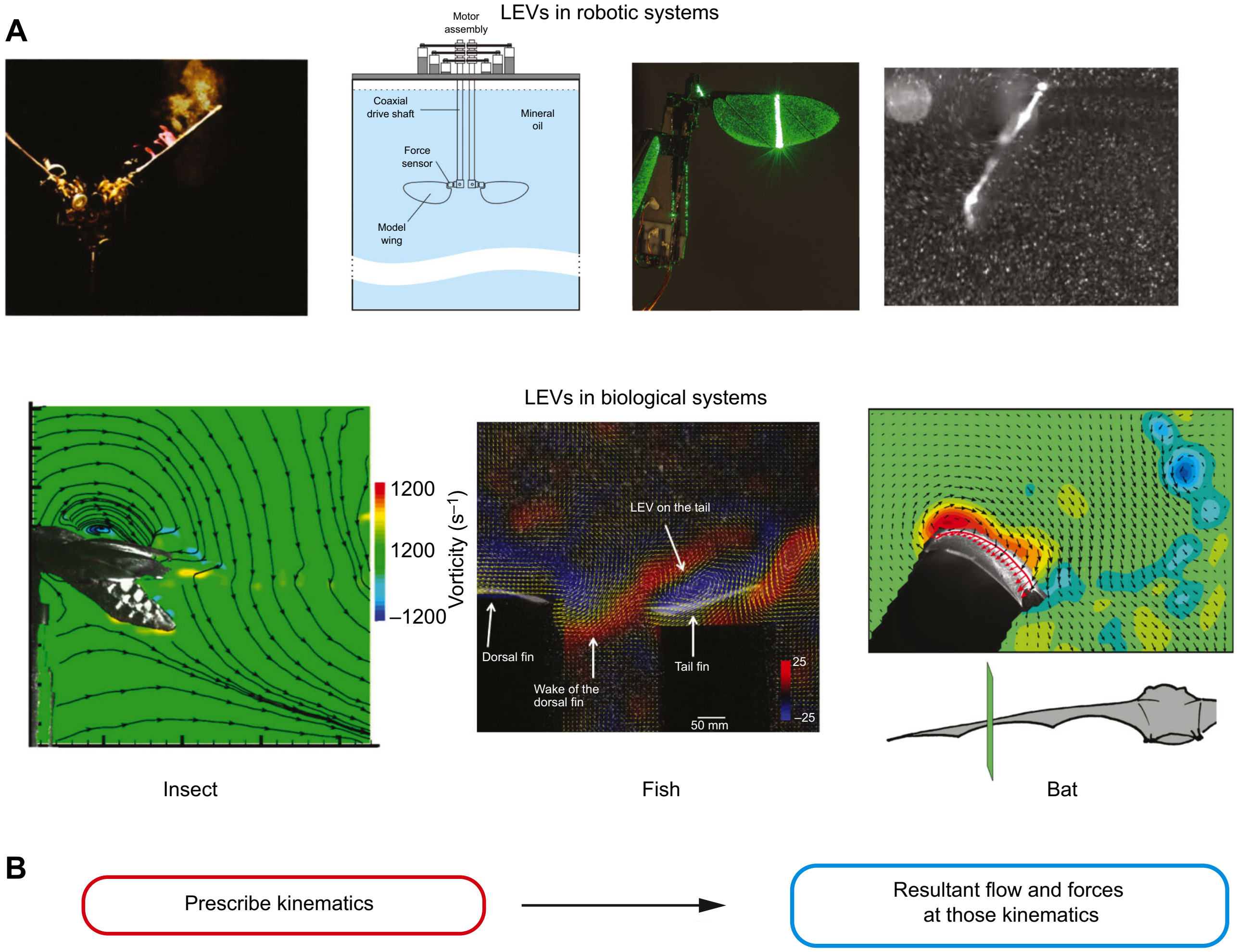

Fig. 3. The leading edge vortex (LEV): from mechanical systems to biology. (A) LEVs observed remaining attached to robotic experimental systems (top) led to biologists searching for and discovering LEVs in oscillatory locomotion through fluids (bottom). Top row shows results from four different LEV experiments with robots. From left to right: LEVs on a model hawkmoth wing (Ellington et al., 1996), the robofly experimental apparatus (Dickinson et al., 1999), a bee-sized robot with attached vortex (Gravish et al., 2015). The bottom row shows LEVs observed in flying organisms: *Manduca sexta* (left) (Bomphrey et al., 2005), the tail of a freely swimming bluegill sunfish, *Lepomis macrochirus* (middle, our unpublished results) and in bat flight (Muijres et al., 2008). (B) Conceptual diagram of physical model experiments. All images are reproduced with permission.

can be advantageous in the case of swimming lizards such as the sandfish and other burrowing reptiles (Li et al., 2012). Recent experiments with robots moving across and within sand have highlighted the complicated interactions that occur between locomotors and deformable substrates and in the spirit of robotics-inspired biology have generated new hypotheses regarding animal locomotion (Fig. 4).

One example of robotics-inspired biology comes from recent studies of sidewinding snakes such as the sidewinder rattlesnake, *Crotalus cerastes*. Rattlesnakes move deftly across sandy desert slopes, and sidewinding is a complex three-dimensional movement in which a horizontal and vertical traveling wave are propagated along the body. In similar sandy environments a sidewinding bio-inspired robot was found to move readily on horizontal surfaces but quickly failed when climbing slopes (Marvi et al., 2014). This led to a study of how snakes are modifying their sidewinding movement to enable them to climb. Snakes ascending slopes compensated for the slope angle by modifying the amplitude of the vertical traveling wave along their body, and they decreased the amplitude of the vertical traveling wave and thus were able to engage more contact area with the slope as they climbed, which prevents slipping. When Marvi et al. (2014) performed similar control modifications in their robot, they found that it could successfully climb slopes where it previously failed.

The story could end here: an observation from biomechanics experiments on snakes was tested on a robot which verified that a simple wave modulation control strategy can enable climbing of slopes. But simultaneous experiments performed on the robot began to illustrate to these researchers that more broad movement control such as turning and reversing direction could be realized by relatively simple modulations of the amplitudes and timing of the vertical and horizontal traveling sidewinding waves (Gong et al., 2016). Follow-up experiments of turning and other directional locomotion of snakes demonstrated use of this similar gait modulation in maneuvering (Astley et al., 2015). This approach involving reciprocal illumination and experimentation between biology and mechanical systems (Fig. 1) highlights how close-knit robotic and biological experiments can lead to a research feedback loop whereby robots can be used for generation of biological hypotheses. The end result of this intellectual feedback loop is that roboticists expanded their control capabilities using wave modulation, and biologists, in turn, were able to develop and test new control strategy hypotheses for maneuvering snakes.

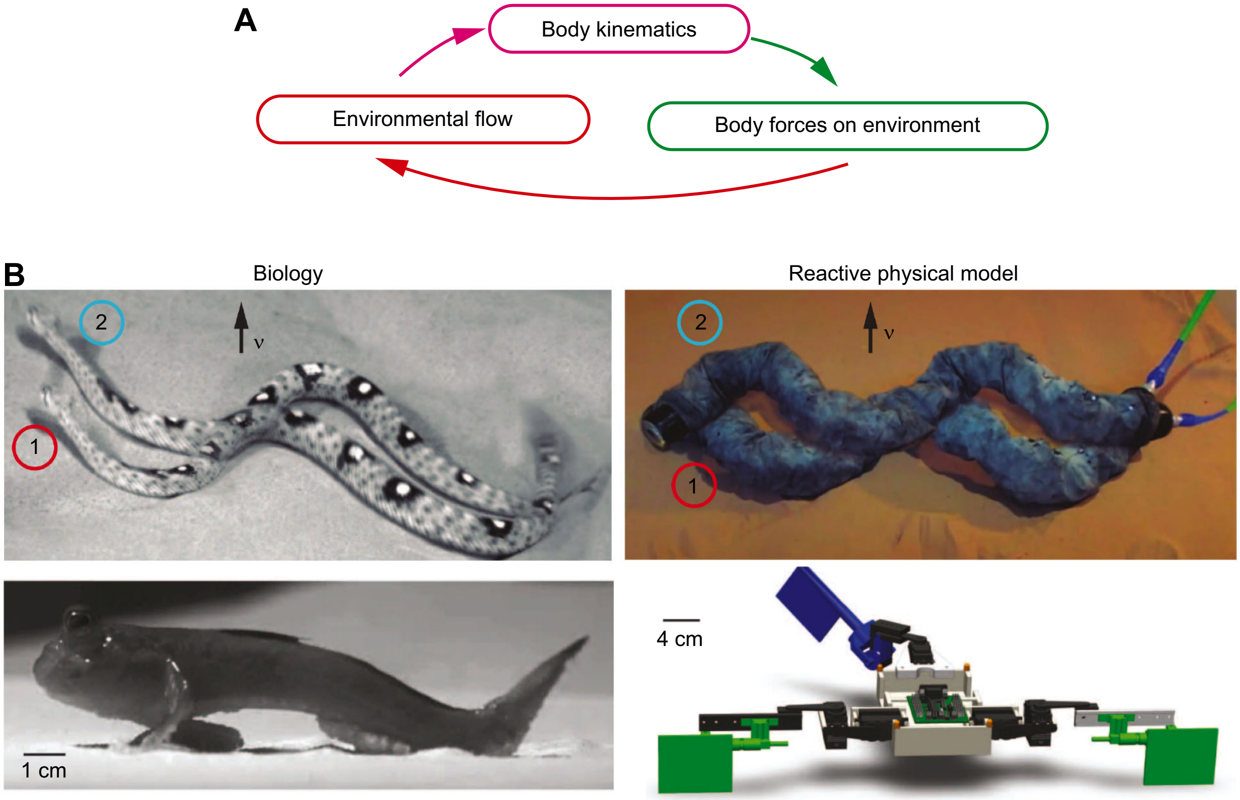

Fig. 4. Locomotion in flowable and reactive environments. Examples of locomotion on and within flowable substrates. (A) Locomotor dynamics and control on flowable substrates, such as sand and water, are complicated because appendages can slip, which modifies body kinematics, in turn altering force production on the external environment which then affects flow of environmental media. (B,C) Examples of biological locomotor systems (left) and robotic locomotor systems (right) on complex, reactive media. (B) Snapshots of two time instances (1 and 2) are overlaid. *v* indicates the direction of travel. Sidewinding motion of the snake *Crotalus cerastes* is shown on the left with its robotic counterpart on the right. Marvi et al. (2014) demonstrated that by varying the traveling wave amplitude and phase along the robot or snake's body they are able to climb slopes and maneuver. (C) The mudskipper (*Periophthalmus barbarous*) (left) with its robotic counterpart on the right (McInroe et al., 2016). Locomotion studies of tail use in a bio-inspired robot enable understanding of how early tetrapods may have transitioned from water to land. All images are reproduced with permission.

Conclusions

The future of robotics-inspired biology is bright, with research in many areas currently incorporating ideas from mechanical devices into biological investigations. For example, biologists studying collective behavior have been using robots to model the swarming of insects and the schooling of fish and to derive rules for inter-individual interaction (Butail et al., 2013). Robots are poised to make a big impact on collective behavior research in which interactions with the environment, with conspecifics and with predators can be explored (Swain et al., 2012), and where hypothesized mechanisms are tested with data on natural biological swarms (Couzin et al., 2005; Polverino et al., 2012). The decreasing cost of new aerial drones and swarm robot platforms such as the kilobots (Rubenstein et al., 2014) will likely increase the adoption of robot experiments by collective behavior biologists.

An additional area that promises to provide new ways in which mechanical and biological systems interact is evolutionary robotics (Long, 2012). Evolutionary algorithms have long been used to optimize parameters in the search for optimal designs, but modification of robotic devices and selecting variants for further comparative testing over multiple generations is an approach that is still in its infancy (Long et al., 2006). Biological systems are extremely diverse and capturing this diversity in mechanical devices is challenging; doing so within an evolutionary and phylogenetic context, is even more challenging. And yet, the ability to generate multiple physical variants and conduct comparative testing of these models promises new insights into the principles that have governed the diversification of biological systems.

The aim of robotics-inspired biology research is to 'close the loop', and use both physical models and reactive robotic systems to generate new hypotheses for biological investigation. We hope that this approach enables the next generation of biologists and engineers to exploit the rich dynamics of mechanical systems for biological ends. A potential side-effect of this trend is that robotics-inspired biology can serve as an access point for future biologists who may be lured by the value of using increasingly accessible mechatronic systems to simplify biological complexity. Robotics-inspired biology is leading to a better understanding of organismal function, and extrapolation into the future suggests that we will uncover many new avenues of study and features of organismal design that biologists might not have considered without inspiration from physical models and robotic devices.

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Competing interests

The authors declare no competing or financial interests.

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