SOFT ROBOTICS
Volume 1, Number 3, 2014
© Mary Ann Liebert, Inc.
DOI: 10.1089/soro.2014.1502

ROUNDTABLE DISCUSSION

How Does Soft Robotics Drive Research in Animal Locomotion?

Moderator: John H. Long Jr.[1]

Participants: Stacey Combes,[2] Janna Nawroth,[3] Melina Hale,[4] George Lauder,[5] Sharon Swartz,[6] Roger Quinn,[7] and Hillel Chiel[8]

Introduction

The point of this discussion is to hear from experts about the use of soft robotics in studies of animal locomotion. As early as Aristotle's ''On the Motion of Animals,'' scientists and engineers have grappled with questions about movement that still puzzle us today. Seemingly simple questions are not: How do bats fly? How does a jellyfish swim? How does an earthworm crawl? Robotics, and soft robotics in particular, provides us with tools that would have made Leonardo weep: self-propelled physical models of wings, tails, and whole bodies. How best to use and improve these models is a theme running through this discussion. We learn that animals inspire our invention of robots, and robots inspire our experiments on animals, a process of reciprocal illumination that engages biologists and engineers in soft robotics.

1. Tell us briefly how you are currently using soft robots or robotic systems in your research.

Janna Nawroth: My collaborators and I are using tissue-engineered soft robots mainly for two purposes: First, to test structure–function relationships of living organisms. For example, we reverse-engineer soft-bodied, muscle-powered swimmers using both synthetic materials and living cells, and we then quantitatively compare their swimming performance to the native organism. Through this, we can test whether we understand and are able to replicate muscle arrangement, substrate material properties, and fluid interactions well enough to achieve the kinematics and dynamics of the natural swimming mode. Further, we explore the most minimalistic tissue-engineered solution to achieve this function.

And, second, to test alternative biological designs. The idea is that natural evolution does not necessarily optimize the design of an organism for a particular function. The same body has to serve many functions and the structural and material choices for that body are limited by genetics. Other than genetic engineering and selective breeding, however, there are few options to alter the body plan of a creature to test any alternate designs. Soft robotics, in particular when using living tissue, can attempt to explore the solution space not ''discovered'' by evolution.

Sharon Swartz: Our group uses soft-winged robotic flappers as part of a research program exploring aeromechanics of bats. There are a number of kinds of topics that fall under the umbrella of this research, from analysis of functional roles of specific features of the complex and highly integrated structure of animal wings (compliant and anisotropic skin, joints with particular degrees of freedom in specific anatomical locations, wing aspect ratio), to exploring possible evolutionary pathways from nonvolant mammal quadrupeds, through controlled gliders, to fully flapping flying animals. For us, robots are ideal for at least two kinds of studies. First, they allow us to make detailed measurements that we can't obtain from living animals. A robotic wing—which will be a soft robot, because the animal wings in which we're interested are also soft—can be attached to sensitive measuring devices for quantitative assessment of lift and drag, can be the subject of particle image velocimetry studies with (relative) ease, etc. The highly complex flapping movements of bats confound many experiments, even as instrumentation costs decline and sophistication increases. And, second, just as Janna laid out above, robotic devices are a powerful means for testing alternative biological designs. Wings with various

[1]Associate Editor, Soft Robotics. Director, Interdisciplinary Robotics Research Laboratory; Professor, Biology and Cognitive Science, Vassar College, Poughkeepsie, New York.
[2]Associate Professor, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts.
[3]Technology Development Fellow for Biologically Inspired Engineering, Wyss Institute, Disease Biophysics Group, School of Engineering and Applied Sciences, Harvard University, Cambridge, Massachusetts.
[4]Professor, Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois.
[5]Professor, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts.
[6]Professor, Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island.
[7]Director, Biologically Inspired Robotics Laboratory; Professor, Department of Mechanical and Aerospace Engineering, Case School of Engineering Case Western Reserve University, Cleveland, Ohio.
[8]Professor, Department of Biology, Case Western Reserve University, Cleveland, Ohio.

configurations can be attached to a flapper apparatus to explore traits and trait combinations that we don't observe in living animals, or that are seen only in animals that aren't available to use for study.

George Lauder: We are using soft robotics to investigate the function of the fish body and fins during locomotion.[1,2] Fish bodies and fins are flexible, but much of the previous robotic research on fish swimming has used models that are rigid. While this makes developing and testing models of fish much simpler, it is clear that we need flexible mechanical systems to better understand the dynamics of fish motion through the water and to take advantage of increased swimming efficiency that flexibility brings under many conditions.[3,4]

To model fish bodies and fins, we are using a variety of flexible models. Some of the simplest models have proven to be the most dynamically rich. We have studied the dynamics of simple flexing panels under a variety of swimming conditions using a mechanical flapping foil control system that allows us to vary the side-to-side motion (heave), angle of attack (pitch), phase between heave and pitch, flow speed, and frequency. This approach makes it very simple to alter length, stiffness (by changing out the panel), and trailing edge shape. As a result of this work, we now have a much better idea of the effect of flexural stiffness on propulsion. In addition, the length of the panels turns out to have a substantial and nonlinear effect on swimming speed.

Recently, we have begun working (in collaboration with Jimmy Liao's Whitney Laboratory) at the University of Florida with flexible models of fish bodies using this same mechanical flapping system and studying the effects of body and head motion on locomotor efficiency and the pressures generated by the head.

Melina Hale: We investigate the neuromechanics of fish locomotion, focusing on proprioception (the sensation of movement and position in space) and sensorimotor integration. In particular, we aim to understand how proprioceptive information from the fins and body is used to modulate locomotor movement. The fins, particularly the paired fins (homologous to our arms and legs), are flexible structures. We found that fish are able to sense bending of these structures and neural signals from the fin code for the bend amplitude and speed. With such soft and flexible fin elements, effective modeling required comparably soft engineered structures. Collaborating with engineers (James Tangorra and his lab members at Drexel) and George Lauder (Harvard University), we find that soft robotic models have become critical components of our work in a number of ways. For example, the soft robots have provided platforms in which to explore observations that we've made in the biological systems. Flexible engineered fins instrumented with strain gauges have been critical for testing the functionality of mechanosensory input. Likewise, work with the engineered fin has helped to inform the questions we ask and experiments we conduct in the biological system.

Stacey Combes: We are collaborating with the Harvard Microrobotics Laboratory on a variety of questions related to the construction of insect-sized flapping micro air vehicles (MAVs; Robobees), and this collaboration plays a role in several of our research projects. One of the primary questions we have addressed using robotic systems is how the complex morphology of flexible insect wings affects force production and efficiency. Because insect wings are extremely light and move very rapidly, it is difficult to perform experimental manipulations to test hypotheses about the function of wing morphology on insects themselves. However, we have worked with members of the Harvard Microrobotics Lab to construct artificial insect wings with various features (vein configuration, anisotropic flexural stiffness, etc.) seen in real insect wings. We can then move these wings at realistic frequencies (~100–120 Hz) and directly measure fluid flow and force production.

We also have a joint postdoctoral fellow (Nick Gravish) who is using a robotic platform to investigate the fluid dynamics involved in tandem flapping, as seen in honeybees and bumblebees—where a number of bees line up in a row at the hive entrance and flap their wings in tandem to ventilate the hive. We are testing the effects of various configurations of tandem flappers to gain insight into the behavioral rules driving this phenomenon, and also to determine whether a system based on these principles could be an effective mechanism of microventilation in human-made systems.

Roger Quinn and Hillel Chiel: We are primarily interested in developing control systems for soft robots, which are particularly interesting because they are hyperredundant. Our robots are shaped like earthworms, and, also like these animals, the robots' circumferential actuators coupled with their mechanical construction allow for peristaltic locomotion; at the same time, their longitudinal actuators allow them to turn. In analyzing the equations of motion for the robot, we determined that the center of mass had constant velocity during regular waves of peristaltic motion, which could allow regular movement with relatively little additional external force; this may be a more efficient way of moving than the standard ''anchor and drag model'' for peristalsis.[5] We have demonstrated continuous peristaltic locomotion with no slipping in the robot, and this motivated us to determine if earthworms move in the same way; in particular, we focus on how they may change their movements in response to irregular or constricting terrain; what we learn from these studies will improve our locomotion controller.

We are also studying and modeling the neuromechanical basis of feeding and locomotion in the marine mollusk *Aplysia californica* to better understand neural control systems in a soft animal, because *Aplysia* is a more tractable animal for these studies. We are exploring a novel dynamical architecture for control of soft-bodied animals, which allows systems to dwell for variable times in different phases of a behavior. Thus, rather than using a limit cycle architecture, we are exploring the use of closed cycles of saddle points that form a structure known as a stable heteroclinic channel (SHCs). These can be plausibly regarded as abstractions of neural circuits and have the flexibility to incorporate sensory feedback and noise while generating rhythmic behaviors. We have used SHCs to model behaviors of *Aplysia*[6] and are using them to control our soft worm robot.

John Long: **I find that one of the most exciting things about this work at the interface of soft robotics and**

animal locomotion is the exploration of the nonbiological forms and motions. Some evolutionary biologists consider one of the great questions in the field to be: Why is morphospace clumped? Soft robotic models, once developed and validated via reciprocal illumination with animals, allow us to go where no one has gone before. Morphospace: the final frontier. We could see if those occupied regions are physically impossible, just bad configurations relative to the existing biological ones, or, perhaps, globally better solutions that evolution simply has yet to explore.

It's also tremendously exciting to think about the work you are all doing on the partitioning of motion control into morphological and neural components. I know that some scientists still roll their eyes when you say, ''morphological computation.'' We've got Dickinson *et al.*[7] using the term ''preflexes.'' Or is it better to talk about ''neural control'' and ''structural control''? Once you engage in the dynamics of movement, it seems impossible to abstract away to a pure neurological system and have your explanation make any sense in terms of its involvement in motion. Nervous systems don't control movement by themselves, in absentia, or in disregard of the mechanical behavior of the system of which they are a part. I know I'm preaching to the choir here, so my apologies, but this does come up again when we talk about question 3.

In robots that are behaviorally autonomous, the morphological or structural control (whichever you prefer) can help you off-load computationally intensive ''neural'' control. That makes for much faster reaction times and automatic tuning as the interactions with the world change. Bongard and Pfiefer[8] go a step further and bring the body in as the primary mover, if you'll pardon the pun, that drives any neural control system.

2. Can we use soft robots to test hypotheses about biology? If yes, what are the pros and cons to this methodology?

Janna Nawroth: I think that soft robots can be used in similar ways, and with similar limitations, as computational models to test hypotheses about biology. On the upside, engineering the system allows full control of many parameters, allowing us to isolate and individually probe factors that cannot be easily separated in a living organism. On the downside, engineering requires simplifying the living organism to something that can in fact be built and understood, with the risk of generating behaviors that are only valid in the engineered—and therefore reduced—system. So the challenge is to choose specific questions, based on well-defined design parameters of the native organism, and if possible explore them also in another model system (computationally or experimentally).

Sharon Swartz: All tests of hypotheses have limitations. Part of scientific excellence is knowing where to draw the lines around one's tests—what is the sphere of relevance of this experiment (where the term ''experiment'' is used in a broad sense)? A soft robot that embodies relevant biological characteristics can test biological hypotheses that relate to those traits, if the hypothesis is articulated appropriately. The challenges, and hence the pros and cons, arise around where to draw the lines of applicability; there will be wide consensus that a soft robot rigorously tests hypotheses about its own function, and does not test certain far-reaching hypotheses about organisms in their natural conditions, but what about the gray areas in between?

When communicating about their work, investigators who choose to explore biological questions with soft robots need to exercise particular care in laying out both the biological hypotheses and the characteristics of the robotic system that address the hypotheses. When possible, additional links back to biology strengthen this kind of work. By this I mean that robotic tests of biological hypotheses will often generate specific hypotheses themselves, and these can be compared to biological reality. To take an example from our work, we used a soft-winged flapper to test the hypothesis that wing folding during upstroke reduces flight power in bats.[9] One finding from our work with the robot was that inertial power was reduced, and we were able to compare the reduction in inertial power in the robotic flapper to changes in inertial power computed directly from wingbeat cycle kinematics measured directly in the bat species that was the inspiration for the model.[10] In this regard, my response is similar to Janna's suggestion of further exploration in another experimental or computation system.

George Lauder: Yes, I think that soft robotic models are very useful for testing biological hypotheses. I view the interplay between robotics and biology as a system of reciprocal illumination. Biology informs us about key features that are needed in robotic models, and robotic models permit testing of hypotheses and the discovery of complex dynamical phenomena that would be extremely difficult to discover studying biology alone. For example, there is significant fish-swimming literature on the effects of growth and increasing body size on swimming capability. But as fish grow, many factors change—not just body length, but muscle mass, fin surface area, respiratory capability, and heart function all change in unknown ways and with unknown effects on locomotor capability. It is effectively impossible to study live fish that differ in the single trait of both length alone. Studying flexible swimming panels that varied in length only revealed a complex nonlinear effect of length on swimming performance that would have been impossible to discover studying live animals. And now, this work suggests that fish may grow through critical lengths at which locomotor function is decreased unless they compensate in some way. These results from studying flexible mechanical systems have thus led to new experiments on live fishes.

I've become increasingly concerned about all the uncontrolled factors present when biologists make comparisons of locomotor function among species, and using soft robotic models to generate hypotheses about the possible effects of modifying single traits is a very powerful tool that biologists can now use.

Melina Hale: I think soft robotics can be important for hypothesis testing as long as we are thoughtful in coming up with appropriate hypotheses to test. Such experiments need to be framed with biological testing, and, as with hypothesis testing in biological systems, we have to be careful about the interpretation of results. Robots can be fabulously useful for reducing the complexity of the system being tested and for taking precise data during an experiment. The difficulties of controlling and instrumenting organisms and determining how such manipulative procedures impact the movement make it unrealistic to get comparable data in living systems. If hypotheses tested are specific and focused on the elements of the system that can be reasonably modeled, such experiments can complement work in biological systems nicely. I tend to think of this relationship between robotics and biology in exploring a biological system as an iterative process: each approach informing the next steps taken with the other. In this process, hypothesis testing in the robot is not performed in isolation, but rather organism and robot reinforce or perhaps cause us to question our understanding of the other.

Stacey Combes: I agree with the other panelists that we can use robotic systems to test hypotheses in certain limited cases. I find this approach particularly effective for testing functional hypotheses concerning particular features of complex structures (such as insect wings), where the real structures are overwhelmingly complex and contain so many different features with a variety of biological functions (e.g., force production, thermoregulation, protection, and signaling) that it is nearly impossible to pick them apart within the biological system. In trying to isolate the physical function of one particular feature, it is very helpful to use a simplified robotic model where you can alter only this feature and observe the results.

Roger Quinn and Hillel Chiel: Yes. The scientific method can include modeling to test biological hypotheses. Models have the advantage that they can start with simplifications and complexity can be added as needed. The simplest model that tests the hypothesis is the goal. However, one should never trust the model. The model should be used as a tool to guide biological experiments that test/confirm the hypothesis. These models can include both physics-based software models and hardware models. Software models have the advantage of being able to be rapidly modified and adapted, but have the disadvantage that it is difficult to model physics with great fidelity in common situations such as when a robot contacts the environment—which is an especially difficult problem for soft robots. Hardware models have the advantage that the physics is guaranteed to be correct and the disadvantage that it can be difficult and time-consuming to build the model with the fidelity necessary to capture an animal system of interest. For example, in studying peristaltic locomotion, we found that the cost of transport was lower if the model used a peristaltic wave and a controller that was sensitive to sensory feedback (e.g., when encountering a constriction in the tube through which it was moving). We are now carefully analyzing movies of worm movements to see if the biological system uses a similar mechanism for transport. Preliminary results suggest that worms may use a combination of wave motion and ''anchor and drag,'' and thus the biological system raises new questions that we can address by refining and further improving our models.

***John Long:* Several of you have made the point, in different ways, that the testing of biological hypotheses with robots has limits. That's a great point, and one worth pondering. Those limits would seem to start with this constraint: not all biological hypotheses are testable with robots. Janna mentioned the negative of having to simplify the system in order to model it. But isn't that one of the virtues of modeling? We simplify in order to manipulate a few variables of interest, to hold constant or eliminate other variables, and, perhaps most importantly, to be able to understand the mechanisms underwriting the behavior of interest. Melina, Stacey, and George seem to take this line regarding simplicity, and I agree. I know that my physicist and mathematician friends get stoked by what they call an ''elegant'' equation or model. They want very much to isolate a principle so that they can abstract it and then see what else it might explain or predict. (I don't mean this to be physics envy, by the way.)**

Back to Janna's point. Does it follow that if we must simplify to model, we can never test hypotheses that relate to the full complexity of the biological system? I see Sharon addressing this question when she talks about the gray area between tests of a robotic system clearly addressing its own functioning and clearly not addressing a fully complex biological system. One of the criticisms that I routinely get from biologists is that robots aren't ''realistic'' because they lack whatever features that person thinks are essential. So we are landing right on Sharon's point about interpretation, and the problems therein. She, Melina, and George point to the reciprocal illumination, the iterative hypothesis generation, between robotic and biological systems. We may start with a hypothesis formed from our knowledge of animals. Then we test that animal-inspired hypothesis in a robot. In so doing, we learn something new from the robotic system that causes us to create a new hypothesis about how the animal works. Then we test that robotically inspired hypothesis in the animal. If I've got that right, then we are saying that the robotic modeling is part of the process of studying biology. The connections between the robot and the animal are then the hypotheses themselves, correct?

3. What are the most important questions in research on animal locomotion? How can we use soft robots to answer them?

Janna Nawroth: Personally, I am very interested in microscale and microfluidic animal locomotion, a regime that becomes more and more accessible to engineering with the advent of new microfabrication tools such as 3D printing of many materials, even living cells. Right now, I focus on cilia-driven propulsion and pumping, and the modularity of the mechanism means that many different flow and locomotion modes can be achieved using different arrangements of identical units (the individual cilia). If we could build and actuate these units, or control the assemble of living ciliated cells, we could better understand, and even customize, swimming and pumping at low Reynolds numbers, for example, for the use of microfluidic devices.

Sharon Swartz: As animal locomotion research matures, it is appealing to think that there will be more efforts to identify broad-scale processes and phenomena, and not only to continue to accumulate a large number of (admittedly very interesting) individual case studies. I think soft robots could potentially be useful and even very powerful tools in efforts to identify principles that govern the function of animal locomotion. Robotic devices, soft and rigid, are well suited, for example, to exploration of scale effects over multiple orders of magnitude, and in a manner that is much more difficult to assess in living animals. Similarly, as physical and biological sciences are better integrated, roles of mechanical properties of materials will be an important topic in animal locomotion in the coming decade. Again, robots offer ideal test beds for exploration of biomaterial functional significance, for both the range of variation of material properties observed in mechanically important tissues today, and to possible variation in these characteristics that we don't see today because of extinction or because materials with particular properties have not (or not yet) evolved.

George Lauder: We have made tremendous progress in the design of mechanical systems for locomotion. While we can continue to explore new materials and methods of integrating disparate materials into functional mechanical devices, I think that the most important questions now concern control. How do we control complex biomimetic robotic devices, and how can we simplify our control algorithms so that our mechanical systems respond in a robust manner to environmental perturbations? Much of the control may be in the peripheral mechanics as Bob Full at UC Berlely has been suggesting for some time, and this does indeed very much simplify the central control problem. But this important idea has yet to be fully explored and tested for aquatic swimming systems.

Melina Hale: Dianna Padilla and Brian Tsukimura recently articulated a relevant grand challenge in organismal biology that biologists need to leverage engineering and mathematical approaches to examining the question: ''How do organisms walk the tightrope between stability and change?''[11] This question and control theory that underlies it (discussed in the associated article by Noah Cowen and colleagues[12]) can be applied in a wide range of biological contexts. In fact, even just in locomotion it could be applied in a range of ways. Some of the most compelling to me are how the nervous system and biomechanical plant are integrated to adapt to rapid changes in environment such as unsteady flows or perturbations and how the nervous system generates changes, such as transitions between stable, steady locomotor gaits. These seem to me to be ideal contexts for using robotics to inform how we explore the biological system. Sharon mentioned scaling in her response, and that is another really interesting idea. One of the problems with looking at effects of scaling in organisms is that size generally isn't the only thing that is changing. Particularly during development, many aspects of the organism's morphology and physiology confound questions of how size impacts performance. The ability to simplify the robotic system to dissect apart the different aspects of change that occur during growth is really appealing.

Stacey Combes: I feel like one of the biggest questions we keep running up against in our work on animal locomotion concerns variability. When I began studying this field, many articles were published that quantified the kinematics of one or two locomotory cycles (e.g., a wing stroke) in one or two individuals, and extrapolated from these to assert general mechanisms of locomotion in the organism. As our capabilities for filming, analysis, and data storage have grown, we have seen again and again that most types of locomotion are extremely variable—between species, between individuals, in different behavioral contexts, and even from cycle to cycle. Is this variability an inevitable result of imperfect control systems or environmental heterogeneity, or does it provide some benefit to the organism (e.g., by producing unpredictable trajectories that could allow an animal to evade a predator)? Which aspects of variability in locomotion are purposefully encoded by the nervous system, and which are simply noise in the system? What is the best way to collect data (e.g., long sequences, multiple sequences per individual, and multiple individuals) in order to understand the important features of locomotory variability, without becoming bogged down in endless data analysis?

One way that working with robotic systems is helpful in answering these questions is that they help us determine which features are inherently noisy, simply due to the physics of the system. When we originally began working with flapping MAVs, I was excited to use this system as a way of standardizing locomotory kinematics (which is not possible with live insects) to really understand how particular motions and morphological features affect force generation. What we've seen over a number of years is that when an MAV is as tiny as an insect and is flapping its wings back and forth over a hundred times per second, it's nearly impossible to produce perfectly standardized motions; given the same control inputs, the kinematic output varies from flap to flap, and this variability is similar in some ways to what we see in real insects. This has led us to think about kinematics as less of an optimization problem (e.g., what are the ''ideal'' flapping kinematics to achieve a particular performance goal?) and as more of a shifting range of variables, where the mean value and/or variability of the range can perhaps be shifted by control mechanisms (e.g., by tightening accessory muscles), but where there is always some noise. As mentioned above, we have also started to think about the potential benefits of having a slightly ''noisy'' locomotory system in real-world situations, where there is spatial and temporal variability in the physical environment, and where animals are engaged in complex behavioral interactions with other organisms.

Roger Quinn and Hillel Chiel: How do animals actually manage to control complex peripheries, especially those that are soft, and thus have fewer constraints on their many degrees of freedom? The studies we have pursued suggest several approaches to answering this and related questions. First, local compliance can simplify some aspects of control (it is much easier, for example, to grasp objects with a compliant manipulator that conforms to the surface, and avoids the oscillations that occur when a rigid manipulator attempts to grasp something rigid, and it may crush soft and fragile objects).[13] Although the hyperredundance of soft robots and animal bodies is challenging, there may be groupings of activation (e.g., the peristaltic wave for locomotion) that simplify the control. The advantage of the excess degrees of freedom is that, in novel environments, the animal or robot may be able to ''ungroup'' them to allow for greater flexibility. Understanding how this is done is an important challenge for the future.

We agree with Stacey Combes that variability is an important challenge, but we note that it has several different aspects. First, there is the problem of coping with noisy sensors, actuators, and control elements. Second, there is the challenge of actually using noise as the basis for control (which is an exciting aspect of the SHC dynamical architecture, which in fact requires some noise or sensory input to function properly). Third, external changes in sensory input need to be tracked, and this of course generates variability. The most fundamental issue for thinking about this problem may be the difference between an ''optimal solution'' and ''good enough'' solutions;[14] for survival and reproduction, animals need to be able to generate fast solutions that work well enough, and this allows them to adjust as the environment rapidly changes.

Soft robotics confronts us with these issues immediately because of the large number of degrees of freedom. By relating the models to experimental results in tractable animals, we can repeatedly test and refine our ideas of how control of these challenging peripheries is actually done.

John Long: **Great stuff here gang! Following up on Melina's reference to the grand challenges issue of *Integrative and Comparative Biology*, I did a quick search in that journal using the keyword ''robot'' and didn't turn up anything related to those grand challenges. Short of reading all 10 articles, which I haven't done, I'm guessing that robots aren't the first word rolling off the tongue of biologists when they are thinking about the important and open questions. Thanks to you all for being the first, as far as I can tell, willing to begin to put together what amounts to some grand-challenge-type questions at the interface of animal locomotion and soft robotics.**

Here's what I'm seeing in your statements as challenging areas where soft robotics can help us gain traction (forgive me if I've misconstrued your ideas).

- **Locomotion and fluid flow at low Reynolds numbers by micromodular systems**
- **The functional interaction over a wide size range of materials, material properties, and locomotor mechanisms**
- **The neural and structural control of locomotor systems with many degrees of freedom undergoing a range of environmental perturbations and unstable transitions between stable states**
- **The intentional and accidental causes of variation in the kinematics, control, and dynamics of locomotor systems**

4. How do you justify the use of robots to biologists, particularly those serving as reviewers of your articles and grant proposals?

Janna Nawroth: Robots constitute a type of model system, such as *in silico*, *in vitro*, and *in vivo* approaches, and as such, they have specific advantages and downsides that need to be considered and reflected in the experimental design and interpretation of the data. In general, I think any biological study benefits from using at least two different model systems, to complement each other and overcome the limitations of any single model system.

Sharon Swartz: I like John's idea of a new piece of vocabulary for this approach, and would be tickled if *in robo* started to catch on. I don't find justification of use of robots fundamentally any different than justifying computational modeling, or indeed, in some cases, *in vivo* work in laboratory settings. In practice, I've spent more time responding to reviewers' concerns about the validity of results obtained from studying animals flying in wind tunnels for natural flight than I have convincing reviewers that our work employing robotic wings is meaningful in addressing biological topics. It's important that any article or proposal be clear about the goals of robotics with respect to biological understanding, however. Robotics sheds tremendous light on specific kinds of questions, and very little or none on others, hence making claims that go beyond the data can quickly damage credibility.

George Lauder: I argue that robotic devices give biologists control over experimental variables to a degree just not possible with biological systems, and that it is thus important to study both mechanical devices and live animals. This is also true of computational approaches, which are a key third avenue to studying biological function.

Melina Hale: In general, when I give talks on our collaborative projects with robots and show James Tangorra's videos of robotic fins flapping, that's when I get the ''ooohs'' and ''aaaahs.'' I think biologists are naturally inclined to find engineered devices that reflect biological systems super exciting. In terms of grant proposals, I would argue that the mutually beneficial volley of ideas and results in a biology–engineering collaboration is a compelling way to approach exploring a biological system.

Stacey Combes: I agree with George's comments, and haven't had much trouble arguing for the benefit of robotic approaches to biologists when I point out which variables are impossible to control in the living organism. I also think that robotics (which I often refer to as ''physical modeling'') is a logical alternative or addition to computational modeling approaches in reducing complexity to answer targeted biological questions.

Roger Quinn and Hillel Chiel: We argue that three different modeling approaches should be used in parallel: animal, physics-based software, and hardware. They each have their pros and cons as discussed above. As pointed out by S.C., biologists understand that animal experiments are limited by the variable that cannot be controlled. Whereas the animal is the ''truth,'' the other models are tools for guiding the animal experiments. However, as described by M.H., when a new biological principle is demonstrated in a robot, it is very convincing and produces the ''wow'' factor.

John Long: **Melina's point about the wow factor of videos is a great one and often applies to videos of critters too. For those of working on animal locomotion, it does seem like the similarities in movement between the target (animal) and the model (robot) really help capture attention and, almost automatically, instill a sense of verisimilitude between the two in the mind of the viewer (and reviewer?). But some reviewers, perhaps the ones that Sharon has in mind, seem to be looking for something else to validate the approach. So, right, we have to own up to the shortcomings and yet also argue for the power of the approach.**

5. Do you find that a biocentric approach to soft robotics is a good way to engage engineers?

Janna Nawroth: I'd rather say it's a good way to engage nonengineers, such as biologists, to start thinking in terms of engineering. However, I also find that many engineers enjoy the challenge of adapting technical approaches to biological questions, in particular, when there is a component of playfulness in it, as is the case for building robots.

Sharon Swartz: I find that collaborations across disciplinary boundaries succeed best when the proposed work has the potential for scientific advances within all the contributing disciplines individually, as well as the integrated whole. As soft robotics has become gained in prominence in engineering, we've seen more colleagues outside of biological sciences interested in conversing and collaborating, in part because they more readily perceive an audience for work they may do in partnership with us. Our group is entering a major new collaboration on this subject with engineers from several subdisciplines, which has taken several years to gel. But the challenge until now has not, I think, been engaging engineers as much as funding significant work.

George Lauder: I find that most engineers are intrinsically interested in biological systems that move due to the obvious complexity and performance of swimming, flying, and running animals. Almost anyone interested in how things work is drawn to the area of biomechanics. So much progress has been made in the dynamics of human-engineered wings and propellers, for example, that the many novel biological features present in organisms are an obvious source of intellectual interest for engineers. So I have not observed any need to specifically ''engage'' engineers…most are immediately engaged.

On the other hand, I feel that many biologists experience some discomfort with a focus on studying engineered mechanical systems. The sense seems to be that there is a movement away from biological complexity, and that such studies might be ''missing something'' or ''leaving out'' key biological features. I have found that it can take more effort to engage biologists and explain why this is an important avenue of study. Biologists are more prone to believe that the whole organism with all its complexity intact is the appropriate level of study, and to show some resistance to studying the effects of isolated traits with mechanical devices.

Melina Hale: I haven't actually been in the situation of trying to engage engineers in research who weren't already sympathetic to biological questions and systems. With locomotion, there is such an easy overlap of interests and points of common understanding that I think the biologists and engineers generally get why we all care about movement systems. In contrast, I have at times found it hard to explain neuromechanics of locomotion (particularly for studies of aquatic systems) to other biologists who work at the molecular and genetic levels and for whom the organismal systems approach is far outside their area of research.

Stacey Combes: I agree that there seems to be no problem with engaging engineers in creating bioinspired robots. In fact, I've started to feel the opposite—that there is almost too much of this type of work going on, with engineers creating robots based on almost every conceivable organism, often without any clear justification for why we would want a robot based on that particular organism or of what important question the robot will help answer. I worry that this has become such a trend that it could eventually backfire, if funding agencies start looking at what has come out of previous bioinspired robotics work, and decide that there is not as much substance coming out of this approach as had been anticipated. One of the best ways to avoid this problem is by forming strong collaborations between biologists and engineers, where each side is bringing hypotheses and questions to the table for the other group to test, rather than biologists simply advising engineers on how to create the next cute, animal-mimicking robot.

Roger Quinn: As an engineer, I can say that the biocentric approach fascinates me despite my previous noninterest in biology through school and the early part of my career. Biologists convinced me. The fact is that robot capabilities pale in comparison to animals'. It would be foolish for an engineer trying to design and control soft-bodied robots to ignore animals that are so successful in the behaviors of interest. There are many beautiful natural solutions to these problems. I agree strongly with S.C.'s concern about what is promised by the biorobotics community versus what is achieved and that we must be careful in that regard, and that the way to avoid the problem is to have strong engineering–biology collaborations.

Hillel Chiel: As a biologist, it was very exciting to work with engineers, because I had always felt that one could make general statements in qualitative terms, but that to really test a hypothesis rigorously, you needed to formulate it mathematically, or as a computer model, or as an actual physical device. The result of doing this sharpens the kinds of experiments one does, and in turn forces the biologist to argue for including or not including a particular biological detail. What makes the problem so tricky and challenging is that the significance of many biological details depends on context, and so in one context, the detail can (and should) be ignored, and in another it may be critical. To take a concrete example, if a muscle is slack or fully stimulated, adding one spike from a neuron will have no effect, but if the muscle is at the peak of its length–tension curve, adding a single spike can have a huge effect. Creating and testing biological ideas using models—whether in the computer or in the physical world—should become part of the regular set of tools that biologists use to test their ideas.

John Long: **You all report good relations with engineers who are eager to engage and tackle the nifty puzzles presented by animal locomotion. It's the biologists who need the engagement. Interesting. I wonder if theirs is a discomfort with models in general or robots in particular? To George's point about discomfort with simplicity (or lack of complexity), I can't help but think of this quote from Weiner and Rosenblueth: "The best material model of a cat is another, or preferably the same, cat."[15] Out of context, that comes close to where I think at least some antirobotic biologists are coming from; they don't like mathematical models either.**

I wonder how biologists would react if NSF's biology directorate opened up a biorobotics panel? Or, thinking

about Stacey's point, would it be better to create a new NSF directorate of robotics that is meant to support multidisciplinary teams? These teams might embody the reciprocal illumination approach in a different way from what we've discussed above. Instead of robot–animal iterative illumination, we could have engineer–biologist iterative illumination.

On behalf of editor-in-chief Barry Trimmer and the *Soft Robotics* journal, I sincerely thank you all for your powerful perspectives. Best wishes in your important work.

References

1. Curet OM, Patankar NA, Lauder GV, MacIver MA. Mechanical properties of a bio-inspired robotic knifefish with an undulatory propulsor. Bioinsp Biomim 2011;6:026004.
2. Esposito CJ, Tangorra JL, Flammang BE, Lauder GV. A robotic fish caudal fin: effects of stiffness and motor program on locomotor performance. J Exp Biol 2012;215: 56–67.
3. Lauder GV, Lim J, Shelton R, Witt C, Anderson EJ, Tangorra J. Robotic models for studying undulatory locomotion in fishes. Marine Tech Soc J 2011;45:41–55.
4. Lauder GV, Flammang BE, Alben S. Passive robotic models of propulsion by the bodies and caudal fins of fish. Integr Comp Biol 2012;52:576–587.
5. Boxerbaum AS, Shaw KM, Chiel HJ, Quinn RD. Continuous wave peristaltic motion in a robot. Int J Robotics Res 2012;31:302–318.
6. Shaw KM, Lyttle DN, Gill JP, Cullins MJ, McManus JM, Lu H, Thomas PJ, Chiel HJ. (2014) The significance of dynamical architecture for adaptive responses to mechanical loads during rhythmic behavior. J Comput Neurosci, in press.
7. Dickinson MH, Farley CT, Full RJ, Koehl MAR, Kram R, Lehman S. How animals move: an integrative view. Science 2000;288:100–106.
8. Pfeifer R, Bongard J. How the Body Shapes the Way We Think: A New View of Intelligence. Cambridge, MA: MIT Press, 2006.
9. Bahlman JW, Swartz SM, Breuer KS. How wing kinematics affect power requirements and aerodynamic force production in a robotic bat wing. Bioinsp Biomim 2014; 9:025008.
10. Riskin DK, Bergou AJ, Breuer KS, Swartz SM. Upstroke wing flexion and the inertial cost of bat flight. Proc R Soc B 2012;279:2945–2950.
11. Padilla DK, Tsukimara B. A new organismal systems biology: how animals walk the tight rope between stability and change. Integr Comp Biol 2014;54:218–222.
12. Cowan NL, Ankarali MM, Dyhr JP, Madhav MS, Roth E, Sefati E, Sponberg S, Stamper SA, Fortune ES, Daniel TL. Feedback control as a framework for understanding tradeoffs in biology. Integr Comp Biol 2014; 54:223–237.
13. Mangan EV, Kingsley DA, Quinn RD, Sutton GP, Mansour JM, Chiel HJ. A biologically inspired gripping device. Industrial Robot 2005;32:49–54.
14. Loeb GE. Optimal isn't good enough. Biol Cybern 2012; 106:757–765.
15. Rosenblueth A, Wiener N. The role of models in science. Phil Sci 1945;12:316–321.

Address correspondence to:
John H. Long, Jr.
Department of Biology
Department of Cognitive Science
Interdisciplinary Robotics Research Laboratory
Vassar College
P.O. Box 513, 124 Raymond Avenue
Poughkeepsie, NY 12604-0513

E-mail: jolong@vassar.edu