Body Caudal Undulation measured by Soft Sensors and emulated by Soft Artificial Muscles

Fabian Schwab,1 Elias T. Lunsford,2 Taehwa Hong,3 Fabian Wiesemüller,5,6 Mirko Kovac,5,6 Yong-Lae Park,3 Otar Akanyeti,2,4 James C. Liao2 and Ardian Jusufi1*

1Locomotion in Biorobotic and Somatic Systems Group, Max Planck Institute for Intelligent Systems, Heisenbergstraße 3, 70569, Stuttgart, Germany, 2Department of Biology, Whitney Laboratories for Marine Bioscience, University of Florida, Saint Augustine, Florida, 32080, U.S.A., 3Department of Mechanical Engineering, Seoul National University, Seoul, 08826, Korea, 4Department of Computer Science, Aberystwyth University, Aberystwyth, Ceredigion, SY23 3FL, UK, 5Materials and Technology Center of Robotics, EMPA, Überlandstrasse 129, Zürich, 8600, Switzerland and 6Aerial Robotics Lab (ARL), Department of Aeronautics, Imperial College London, South Kensington Campus, London, SW7 2AZ, UK
*Corresponding author. ardian@is.mpg.de, +49-711-689-3373
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Abstract

We propose the use of bio-inspired robotics equipped with soft sensor technologies to gain a better understanding of the mechanics and control of animal movement. Soft robotic systems can be used to generate new hypotheses and uncover fundamental principles underlying animal locomotion and sensory capabilities, which could subsequently be validated using living organisms. Physical models increasingly include lateral body movements, notably back and tail bending, which are necessary for horizontal plane undulation in model systems ranging from fish to amphibians and reptiles. We present a comparative study of the use of physical modeling in conjunction with soft robotics and integrated soft and hyperelastic sensors to monitor local pressures, enabling local feedback control, and discuss issues related to understanding the mechanics and control of undulatory locomotion. A parallel approach combining live animal data with biorobotic physical modeling promises to be beneficial for gaining a better understanding of systems in motion.

Key words: bio-inspired robotics, soft sensors, undulation, tail

Introduction

Animals can modulate their movements in response to dynamic external disturbances and exhibit locomotion robustness via sensory feedback in conjunction with preflexes in large part due to the morphology and passive mechanics of their compliant structures as well as integrated sensing capabilities. These aspects enable them to adjust to unanticipated changes and enhance stability (e.g. Ghazi-Zahedi (2019)), thus providing potential for the design of more resilient robots.
traversing uneven terrain (e.g. Woodward and Sitti (2018)). Tails have been shown to provide locomotion robustness in aerial, terrestrial and aquatic locomotion (Shield et al. (2021)), such as body caudal fin swimming in fishes (Colgate and Lynch (2004); Crossin et al. (2004)), twist feeding in crocodiles (Fish et al. (2007)), and slip recover (Figure 1A) or water traversal by geckos (Nirody et al. (2018)).

The research direction in biomimetic robotics has tended to be one-directional: nature’s features have been attempted to be replicated in detail in order to improve robot capabilities, with the goal of building robots with expanded locomotion efficacy across a range of environments. This research has provided a direct boost to the engineering capability, but only limited insight to the understanding of biological model system dynamics and control. However, in recent years, roboticists and biologists are increasingly collaborating, gaining insights into biological behavior and mechanisms using physical robotic models approximating animal-like capabilities (Ijspeert (2014); Kovač (2013); Long et al. (2014)). Physical models can offer powerful tools in the testing and refining of hypotheses on the evolution of locomotion patterns and appendages (McInroe et al. (2016); Nyakatura et al. (2019); Schultz et al. (2021)). Exploration of biological features through the building of robophysical models can equip biologists with platforms that may help to gain insight of animal locomotion dynamics and control under conditions relevant to understanding of the model system, by providing a physical simulation tool, and without the need of observing the animal in a complex environment using complicated field techniques such as high-speed video capture (Yeaton et al. (2020); Bostwick and Prum (2003); Nirody et al. (2018)) or on body sensors on animals which do not capture the body interaction with the environment (Aguilar et al. (2016); Aydin et al. (2019); Gravish and Lauder (2018)). Such robots can be used to provide a systems-level approach to understand locomotion where the hardware (material, morphology) and software components (sensory, control) must work
in unison to replicate movements that are seen in the wild. Furthermore, using robots offers the liberty to modify morphologies in a systematic way (larger parameter space), and perform movements that animals typically do not, or that can be dangerous for the animal.

The robotic, bio-inspired platforms have the advantage of selectively isolating and alternating interesting traits, and therefore providing a much larger parameter space for experimentation (Webb (2000)). By simplifying the complex interactions found in living organisms, abstract physical robotic models may shed new light on the interdependence of various body parts to enable locomotion, such as how climbing arboreal geckos employ an active tail reflex to dynamically respond to the loss of contact with a climbing surface (Figure 1A, Siddall et al. (2021a)), mechanisms used for mid-air reorientation (Fukushima et al. (2021); Siddall et al. (2021b)) or the study of undulatory movements produced by a single actuation point located posterior to the head of a physical robotic model (Akanyeti et al. (2016)). Additionally, physical models capture the relationship between body mechanics and coupled environmental effects, for example, the fluid dynamics of a swimming fish. Investigating the fluid-body interaction in live specimens is often time-consuming, as the animal’s behavior is frequently unpredictable.

Another advantage of physical models over their living equivalents is that they allow us to investigate the motion patterns that are used for effective and optimized locomotion and which forms of motion are required to support a living organism. For example, fish must maintain a water flow through their gills in order to provide oxygen to their tissue (Akanyeti et al. (2016)). Physical models are inherently devoid of such living needs, and it is possible to investigate the characteristics that are actually and exclusively advantageous for the locomotion. Similarly to how experimental observation in biology enables advancements in robotics, bio-inspired robotics expands the possibilities for testing biological hypotheses.

The main motivation for this paper is to encourage the increased utilization of multidisciplinary approaches, lending from soft robotic physical modelling and multi-scale manufacturing techniques between biologists, materials scientists, and engineers as well as hypothesis formulation from the outset, for example with respect to how undulatory locomotion might be affected by tail sensory feedback. Biorobotic models increasingly include lateral body motions, particularly back and tail bending, which is crucial for permitting undulation in fishes, amphibians, and reptiles (e.g. Thandiackal et al. (2021)). We survey the use of physical modeling in conjunction with soft robotics and sensors to monitor local pressures, enable local feedback control, and address themes pertaining to insight the mechanics and control of undulatory locomotion (e.g. Tytell and Long (2021); Thandiackal et al. (2021); Kim et al. (2020)). Biorobotics could also be used in a broader context of the comparative method, complementing the understanding of locomotion performance of extinct and extant species (e.g. Crofts et al. (2019)) or even as machines that eventually can be deployed for future space missions (e.g. Ng and Lum (2021)). The ability to observe physical systems in action would constitute a substantial benefit in complex circumstances where it may be difficult to examine them.
through live animal experimentation. A complementary approach investigating live animal data in tandem with biorobotic physical modeling would be desirable for greater understanding of systems in motion. To achieve this it would be advisable to develop interdisciplinary projects jointly from the outset, with the goal of refining hypothesis testing and possible material or device development (e.g. Miriyev and Kovač (2020)). While computational advances have steadily enhanced artificial intelligence, the physical capabilities of robots have not been improved in the same measure. Biomimetics and -robotics with more life-like capabilities (e.g. Fish (2020); Triantafyllou et al. (2020)) could help accelerate locomotion capabilities of robots by offering a different perspective.

In this paper, we examine soft sensors and biorobotics to better understand various forms of body caudal undulations. We aim to show the capabilities and possibilities of these novel soft sensors, and their potential together with soft robots for verification and exploration of locomotion traits used by living organisms. Extending on the practice of using flexible but passive structures (as seen in Lauder et al. (2012)), this paper puts the focus on active soft robotic testing platforms with incorporated soft sensing abilities. We propose that soft sensors and actuators are the next major push to enable robots to become more life-like in their capability, so that they may better emulate how animals move. Seeing that tails have many more degrees of freedom than other limbs, soft actuators are much better suited than conventional ones.

**Biorobotic physical models made of soft active materials**

To gain insight in the underlying processes of tail reflexes and passive dynamics, one can integrate stretchable strain sensors into active soft robotic platforms for sensory feedback (Figure 2B). Stretchable strain sensors have the potential to provide reliable sensory feedback that can yield robust capabilities. When intertwined with a soft actuator, the sensor can provide crucial information about traits that make efficient undulatory locomotion possible (Wright et al. (2019)).

Animal strategies such as tail usage during climbing (Figure 1A) or body stiffening during swimming (Figure 2A) can be replicated and studied using abstract active robotic platforms.

The active component of the robotic platform is important for understanding how a biological organism interacts with its surroundings. Only then can one confidently assert that the platform mimics the biological species, not just in terms of size and mass, but also in terms of material structure, mechanical composition, and compliance.

The gecko (*Hemidactylus platyurus*) uses its tail to recover from forefoot slip (Figure 1A). Inspired by that, a BioRobotic Lizard with a fully flexible, soft-sensor integrated tail was built (Figure 1B) to explore the effect of the tail for incline climbing and obstacle traversal performance in rapid locomotion (Siddall et al. (2021a)).

First, climbing trials were carried out without the robotic tail. The robot was unable to ascent at an angle greater than 45 degrees without the tail to maintain forefoot touch. With the tail attached, in contact with
Fig. 2. Flow tank experiments with a soft robotic fish. (A) Ventral view of the Bluegill Sunfish (Liao et al. (2003)). (B) Top view of soft robotic fish with soft actuator and sensor during undulation locomotion (Lin et al. (2021)) (C) Comparison of strain sensor readings and undulation tail position read from video analysis in a recirculating flow tank.

...the surface, and with a slight preload added, this angle increased to 80°, and changes from the horizontal to inclines of up to 75° became possible (Figure 1B, Siddall et al. (2021a). The BioRobotic Lizard platform gives us the possibility to do a full climbing angle parameter sweep, and measure exactly at what point the tail becomes essential for the ability to ascend.

Figure 1D shows the measurements of the soft sensors integrated in the BioRobotic Lizard’s tail during situation where the robot slips during an ascend of 70°. By incorporating a controller, we envision to actively respond to the sensor measurements of the slippage and catch the fall, resembling the active tail reflex to dynamically respond to the loss of contact with the climbing surface of geckos (Figure 1A).

A robotic platform consisting of a soft robotic fish with a backbone stiffness comparable to Bluegill Sunfish (developed in Jusufi et al. (2017) and Wright et al. (2019); Wolf et al. (2020)) was expanded to investigate closed loop responses via soft sensors in both air and water with various undulation frequencies to demonstrate the proprioceptive sensing skills required to emulate more life-like swimming with undulatory shape changes on the body (Lin et al. (2021)) (Figure 2A and B). Fish modulate an inherent cycle to preserve the necessary speed by varying the ratio of bursting to coasting while keeping the cycle length approximately constant (Li et al. (2021)). Beyond closing the loop with feedback in non-moving fluids, the next step consists of experimental validation of the closed loop controller at different water flow speeds in a recirculating flow tank (Figure 2C).

In fishes, the flow-sensitive lateral line organ is comprised of a functional unit, the neuromast, which covers the head and body and lies on or near the skin surface. A neuromast is composed of a hair-like bundle that is embedded into a gelatinous cupula, which deflects when fluid moves relative to the body (Figure 3B). This triggers a mechanotransduction event in which signals from the fluid environment are translated into electric nerve signals. These signals are then transmitted to the brain via afferent neurons. Using transparent, larval zebrafish (Figure 3A), we can target afferent neurons and record their electrical signals in response to controlled mechanical deflections of a single neuromast lying on the body surface. These superficial neuromasts are sensitive to flow velocity. Neuromast deflections are generated using a fine glass pipette controlled by piezoelectric transducer, which can impose sine wave frequencies that match the...
tailbeat frequencies of freely swimming zebrafish. In adult fish, neuromasts are recessed into canals in the scales, and this mechanical filter makes them sensitive to pressure (McHenry and Liao (2014)).

It has been suggested that lateral-line activity during undulatory body motions is an important feedback link in closed-loop control of fish swimming (Roberts (1969); Roberts and Russell (1972); Ayali et al. (2009); Skandalis et al. (2021)). Similar feedback signals have been found in the spinal cord as well (Böhm et al. (2016); Picton et al. (2021)).

The soft sensory output of the robotic fish with a feedback controller is evaluated, and we show, that the sensors are fully capable of capturing the deflection of the fish in real-time (Figure 2C). This fish-inspired robotic platform allows for the discovery of the effect of tail stiffness and undulation frequency on thrust generation and with novel soft sensors can sense its environment as well as respond to perturbations. Compared to a natural fish (Figure 2A), the platform has the ability to test different frequencies and co-contractions at will and test parameters that would not be possible to find in nature.

Fish are able to modulate body and fin stiffness (Lauder et al. (2012); Long Jr (1998)), and exploit vortices found in turbulent flows (Liao et al. (2003)) to increase swimming efficiency. Experiments with physical, fish-inspired platform suggest that the timing (measured as phase difference) between yaw and side-to-side movements of the head may be key in achieving better swimming performance during steady (Akanyeti et al. (2016)) and unsteady swimming (Akanyeti et al. (2017); Long Jr et al. (2002)). The internal dynamics and the mechanisms through which soft structures are exploited for attaining this remarkable propulsive efficiency are under-explored.

To address these unknown parameters, we performed experiments with an additional submersible robotic platform, inspired by the rainbow trout, and integrated with pressure sensors. This time, a three-dimensional (3D) CAD model from scanned images of a specimen was designed and a bio-inspired physical model, consisting of a rigid head, flexible backbone and a soft body was constructed (Figure 4A) and tested. From a single actuation point located posterior to the head, undulatory movements were produced. This allowed us to assess performance in terms of thrust generation and swimming kinematics.

At first sight, the comparison between thrust (Figure 4B) and drag-producing kinematics (Figure 4C) suggest that there are favorable head movements that allow the physical model to adopt midline kinematics similar to fish and increase swimming efficiency. However, further comparison between the model and fish kinematics
Fig. 4. A) A soft physical model inspired from a rainbow trout. B) Midline reconstructions of the model for one tailbeat cycle show the body amplitude envelope for thrust-producing kinematics, which are similar to a live trout during steady swimming. C) The amplitude envelope for drag-producing kinematics is very different from the kinematics of a real trout. D) Heat map showing average propulsive force produced over one tailbeat cycle as a function of simultaneous heave and yaw movements; horizontal axis: oscillation frequency and vertical axis: timing between heave and yaw movements (0 and 180 degrees indicates in-phase and out-of-phase movements, respectively). Regions with positive (red) and negative (dark blue) values show thrust and drag producing parameters, respectively. Note the region in between the two dashed lines (light blue) show the self-propelled speed where thrust is equal to drag. E,F) A single pressure sensor placed on the side of the head near the eye (inset diagram) is enough to reveal that unique pressure profiles exist during thrust and drag-producing swimming motions shown in B) and C).

is needed to quantify similarity more objectively (Fetherstonhaugh et al. (2021)). Our results are just a proof-of-concept demonstrating that pressure profiles around the head can be linked to propulsive performance. We recognize that propulsive performance of a model may vary depending on the swimming speed and geometry and size of the physical model (for instance, see Piñeirua et al. (2017)), which warrants further investigation.

Systematic analysis on how thrust production varies as a function of oscillation frequency and phase difference (Figure 4D) suggest that by controlling the timing of head movements, the physical model can choose between slowing down (by generating drag), speeding up (by generating thrust) or swim steadily for the same flow conditions. In addition, we managed to reveal unique pressure profiles for these thrust and drag-producing swimming motions (Figure 4E,F), suggesting
that flow-relative sensory feedback can be used to enhance swimming performance.

With recent research indicating that internal mechanical sensors may be used to determine tail beat amplitude and frequency (Sánchez-Rodríguez et al. (2021)), our work on pressure sensors that detect changes in the external environment may be considered important to assure function reliability and robustness. Thus, both internal and exterior sensors are likely critical for optimizing tailbeat amplitude and frequency selection.

**Soft Sensors**

Wearable and skin-mounted sensors may help in the creation of robophysical models by offering insight into the mechanics and control (e.g. tailed model systems in (Figure 1C, reproduced from Souri et al. (2020), modified) of locomotion, including and passive mechanics, as well as potentially explaining how an organism’s muscles, sensors, motor pattern generators, and brain interact to produce coordinated movement in response to unexpected perturbations (e.g. Nishikawa et al. (2007)). We envision a robotic fish platform equipped with arrays of multi-functional soft sensors (Figure 5-left) for proprioception and flow sensors (Figure 5-right) for mechanoreception. Elastic and viscoelastic properties are critical factors for the material selection of soft robotic components in order to adapt the mechanical flexibility and multifunctionality intrinsic to natural organisms (Banerjee et al. (2021)).

Capacitive soft sensors are made out of conductive materials, and change their capacitance between the two deformable layers when deformed (Ponce Wong et al. (2012); Atalay et al. (2018); Li et al. (2016); Kim et al. (2019)). Other kinds of soft sensors are based on optical properties, such as light intensity (To et al. (2018); Larson et al. (2016); Xu et al. (2019a); Jung et al. (2020)) and different wavelengths (Xu et al. (2018); Zhuang et al. (2018)).

Resistive soft sensors transduce external mechanical stimuli into electrical signals. Although various sensors of this type based on different mechanisms have been proposed, such as conductive polymers (Wang et al. (2017)), conductive fabrics (Atalay et al. (2018)), and thin-metal-film coated polymers (Firouzeh and Paik (2015)), we focus on a particular class of resistive soft sensors made of highly deformable elastomer embedded with conductive liquids, where the electric resistance of liquid-filled microchannels in an elastomer matrix changes when the matrix structure is stretched, compressed, or bent (Park et al. (2010); Majidi et al. (2011); Park et al. (2012); Vogt et al. (2013); Shin et al. (2020)), (Figure 5 A-C).

These sensors are extremely useful in soft robotics due to their high sensitivity, stretchability, and ability to deform dynamically. Since the main sensing medium is a liquid that can be easily formed in any shape without limiting or degrading the existing range of motion and degrees of freedom of the host structures, these sensors can be easily attached to or embedded in any body parts of a soft robot. This makes them especially suitable for measuring movements that are inspired by animal locomotion and performed by soft robotic platforms and to detect contacts made by external environments, as demonstrated by artificial proprioceptors (Wirekoh et al. (2019); Park et al. (2020)) and mechanoreceptors (Kim et al. (2018); Shin et al. (2019)), respectively.
Fig. 5. Examples of liquid-embedded soft sensors. A multifunctional soft sensor with a combination of microfluidic, optical, and piezoresistive sensing mechanisms Kim et al. (2020) (left) and a biomimetic flow sensor composed of ionic gel microchannels and a hair-like structure Shin et al. (2019) (right).

One of the most commonly used conductive liquids in the sensors is eutectic gallium-indium (eGaIn) (Dickey et al. (2008); Chiechi et al. (2007)), a metal alloy that maintains a liquid state at room temperature. The high electrical conductivity makes it ideal for stretchable sensors and circuits when embedded in elastomer. Moreover, the high surface tension and viscosity makes the material not only easy to be injected but also stable in microchannels even with large deformations.

Although eGaIn is known to be nontoxic unlike mercury, its safety has not been fully investigated on the absorption by humans. If biocompatibility or optical clarity are needed in the system, an alternative to liquid metals is ionic liquid. Ionic liquids, for example saline solutions, are biocompatible but still electrically conductive, and can be used as a replacement of eGaIn for soft sensors (Chossat et al. (2013, 2015)). Moreover, the optical transparency of ionic liquid makes it possible to use the liquid-filled microchannel as an optical waveguide for additional functionalities (Kim et al. (2020)).

Bio-Inspiration for Multi-Modal Sensing

If multiple sensing mechanisms can be integrated in a single sensor structure, multi-modality can be accomplished easily while retaining design and fabrication simplicity. Examples of it can again be found in biology, e.g. on a larval zebrafish (Figure 3). Sensory neurons called low-threshold mechanoreceptors (LTMRs) are one type of the mechanoreceptors connected to hair follicles, which detect physical stimuli applied to the skin. It is known that the LTMRs are functionally distinct and triggered by particular types of physical stimuli (Abraira and Ginty (2013)). In detail, the LTMRs of the hairy skin are categorized...
into three subtypes Aβ-, Aδ-, and C-LTMRs, which are distributed around follicles of three different types of hairs, such as guard, zigzag, and awl/auchene hairs, as a form of a bundle. The bundles at the follicles are composed of different combinations of the subtypes of the LTMRs. When a physical stimulus is applied to the skin, it excites the bundles by moving hairs on the skin, and the bundles generate electrical signals.

By interpreting the distinct electrical signals activated by the LTMR combinations, the central nervous system can distinguish the difference of the stimuli near the skin, such as pressure, friction, or even both. As depicted in Figure 6, the multifunctional soft sensor is available to detect three different deformation modes, bending, compressing, and stretching, which can be interpreted based on the signals from the three sensing mechanisms. By integrating the information from the three signals, the unique pattern can be determined. The presented multifunctional sensor is capable of not only detecting three individual deformations but also decoupling combined ones.

Since robotic platforms for robotic-inspired biology normally operate in unstructured environments, e.g., water or rough terrain, there will be various information

**Fig. 6.** Comparison between innocuous touch sensing of hairy skin using low-threshold mechanoreceptors and proposed soft multi-modal sensing.
from both the inside and the outside of the body, such as bending angle, thrust, pressure, and drag force, useful for controlling the robot with stability and safety. The multi-functioning sensor mimics the function of animal LTMRs, which can decompose multiple mixed signals while sharing a single structure skin. Therefore, acquiring various sensor signals can be important in this study, which can be achieved through different types of soft sensors distributed in the body.

**Discussion and Outlook**

In this article we present soft sensors for soft robotic platforms to investigate body caudal undulation locomotion and tail usage. By combining bio-inspired soft robotic platforms with integrated sensing capabilities, we are able to perform systematic experimental validation of tail and undulation locomotion concepts that would be extremely difficult to execute in living organisms. Environmental variables can be controlled to obtain repeatable outcomes and by abstracting complex actions to single traits, the influence of the tail can be measured separately and its importance evaluated.

The comparison in swimming performance of our soft fish model compared to fishes shows that our fish has a greater ratio of lateral to thrust force generation (nearly 5:1), whereas fishes swimming with an undulatory body wave typically show a 2:1 ratio (see Lauder et al. (2012)). This indicates that our model is most likely a substantially lesser efficient swimmer than swimming fish like mackerel or bluegill. We would like to investigate this in the future and propose using particle image velocimetry to compare the fish’s swimming performance with a soft robot of similar size.

Beyond comparative biomechanics research, applications of stretchable sensors could potentially extend to include diagnostics. More detailed artificial lateral line analysis based on variable stiffness, soft sensing feedback (e.g. soft strain or pressure sensor) can be done in the future. We envision to adapt the sensors and place them on real animals, to revolutionize the way we can measure locomotion, movements and muscle activity.

In addition, shape sensors could be relevant for identifying morphological changes for impulsive and dynamic aquatic locomotion, such as in squid where it has been shown that changes in body cross-section can lead to thrust peaks of up to a factor of 2.6 (Steele et al. (2017)). Similarly, flying fish exhibit very fast undulation of their tail for aquatic escape (with speeds of up to 10-20m/s (Park and Choi (2010))). This shape morphing happens relatively quickly (in less than 1 s) and will require appropriately matched sensor dynamics to measure the time-independent changes in body shape. It has been shown that microfluidic soft sensors can detect a sinusoidal input of 20% strain with a response time of less than 0.1 seconds and up to 5 Hz. Therefore, they could potentially be used for such fast motions although dynamic effects on changing fluid forces during the motion could potentially influence the measurements (Xu et al. (2019b)). Future work could target tailored methods for high-speed proprioception and closed-loop control for fast-moving aquatic systems where the environmental interaction and forces are unsteady and dynamic.

We intend to do more study on the effect of active body stiffness adjustment on fish swimming speed and performance. It is assumed that, regardless of
the hydrodynamic load, the body's normal driving frequency decreases the force needed to induce a given motion.

The robotic platforms can be developed further; a scaled-down version of the soft fish, disturbance rejection for situational awareness and obstacle clearance with sensory feedback (e.g., soft strain or pressure sensor), or soft sensor integration for flow sensing with velocity and angular sensitivity are only a few of the many possibilities for using physical robotic platforms to gain insight into biological processes.

Ultimately, new insights into behavior, neuromuscular regulation, and mechanosensory receptivity can be obtained by recording the biological activity of animals' caudal appendages using soft robotic systems equipped with advanced soft sensing capabilities. Our approach demonstrates that bio-inspired robots are effective tools for investigating natural performance.

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References

Abraira, V. E. and Ginty, D. D. (2013). The sensory neurons of touch. Neuron, 79(4):618–639.

Aguilar, J., Zhang, T., Qian, F., Kingsbury, M., McInroe, B., Mazouchova, N., Li, C., Maladen, R., Gong, C., Travers, M., Hatton, R. L., Choset, H., Umbanhowar, P. B., and Goldman, D. I. (2016). A review on locomotion robophysics: the study of movement at the intersection of robotics, soft matter and dynamical systems. Reports on Progress in Physics, 79(11):110001.

Akanyeti, O., Putney, J., Yanagitsuru, Y. R., Lauder, G. V., Stewart, W. J., and Liao, J. C. (2017). Accelerating fishes increase propulsive efficiency by modulating vortex ring geometry. Proceedings of the National Academy of Sciences, 114(52):13828–13833.

Akanyeti, O., Thornycroft, P. J., Lauder, G. V., Yanagitsuru, Y. R., Peterson, A. N., and Liao, J. C. (2018). Fish optimize sensing and respiration during undulatory swimming. Nature Communications, 7(1):1–8.

Atalay, O., Atalay, A., Gafford, J., and Walsh, C. (2018). A highly sensitive capacitive-based soft pressure sensor based on a conductive fabric and a microporous dielectric layer. Advanced Materials Technologies, 3(1):1700237.

Ayali, A., Gelman, S., Tytell, E. D., and Cohen, A. H. (2009). Lateral-line activity during undulatory body motions suggests a feedback link in closed-loop control of sea lamprey swimming. Canadian Journal of Zoology, 87(8):671–683.

Aydin, Y. O., Rieser, J. M., Hubicki, C. M., Savoie, W., and Goldman, D. I. (2019). Physics approaches
to natural locomotion: Every robot is an experiment.

In Walsh, S. M. and Strano, M. S., editors, *Robotic Systems and Autonomous Platforms*, pages 109–127. Woodhead Publishing.

Banerjee, H., Kalairaj, M. S., Ren, H., and Jusufi, A. (2021). Strong, ultra-stretchable hydrogel based multi-layered soft actuator composites enhance biologically-inspired pumping systems. *Advanced Engineering Materials*, n/a.

Bostwick, K. S. and Prum, R. O. (2003). High-speed video analysis of wing-snapping in two manakin clades (pipridae: Aves). *Journal of Experimental Biology*, 206(20):3693–3706.

Böhm, U., Prendergast, A., Djenoune, L., Nunes Figueiredo, S., Gomez, J., Stokes, C., Kaiser, S., Suster, M., Kawakami, K., Charpentier, M., Concordet, J., Rio, J., Del Bene, F., and Wyart, C. (2016). CsF-contacting neurons regulate locomotion by relaying mechanical stimuli to spinal circuits. *Nature Communications*, 7:10866.

Chiechi, R. C., Weiss, E. A., Dickey, M. D., and Whitesides, G. M. (2007). Eutectic gallium-indium (egain): A moldable liquid metal for electrical characterization of self-assembled monolayers. *Angewandte Chemie*, 47(1):142–144.

Chossat, J.-B., Park, Y.-L., Wood, R. J., and Duchaine, V. (2013). A soft strain sensor based on ionic and metal liquids. *IEEE Sensors Journal*, 13(9):3405–3414.

Chossat, J.-B., Shin, H.-S., Park, Y.-L., and Duchaine, V. (2015). Soft tactile skin using an embedded ionic liquid and tomographic imaging. *ASME Journal of Mechanisms and Robotics*, 7(2):021008.

Colgate, J. and Lynch, K. (2004). Mechanics and control of swimming: A review. *IEEE Journal of Oceanic Engineering*, 29(3):660–673.

Crofts, S. B., Shehata, R., and Flammang, B. E. (2019). Flexibility of heterocercal tails: What can the functional morphology of shark tails tell us about ichthyosaur swimming. *Integrative Organismal Biology*, 1.

Crossin, G. T., Hinch, S., Farrell, A., Higgs, D., Lotto, A., Oakes, J., and Healey, M. (2004). Energetics and morphology of sockeye salmon: Effects of upriver migratory distance and elevation. *Journal of Fish Biology*, 65(3):788–810.

Dickey, M. D., Chiechi, R. C., Larsen, R. J., Weiss, E. A., Weitz, D. A., and Whitesides, G. M. (2008). Eutectic gallium-indium (egain): A liquid metal alloy for the formation of stable structures in microchannels at room temperature. *Advanced Functional Materials*, 18(7):1097–1104.

Fetherstonhaugh, S. E. A. W., Shen, Q., and Akanyeti, O. (2021). Automatic segmentation of fish midlines for optimizing robot design. *Bioinspiration & Biomimetics*, 16(4):046005.

Firouzeh, A. and Paik, J. (2015). The design and modeling of a novel resistive stretch sensor with tunable sensitivity. *IEEE Sensors Journal*, 15(11):6390–6398.

Fish, F., Bostic, S., Nicastro, A., and Beneski, J. (2007). Death roll of the alligator: Mechanics of twist feeding in water. *Journal of Experimental Biology*, 210:2811–2818.

Fish, F. E. (2020). Advantages of aquatic animals as models for bio-inspired drones over present auv technology. *Bioinspiration & Biomimetics,*
Fukushima, T., Siddall, R., Schwab, F., Toussaint, S., Byrnes, G., Nyakatura, J., and Jusufi, A. (2021). Inertial tail effects during righting of squirrels in unexpected falls: From behavior to robotics. *Integrative and Comparative Biology*, page icab023.

Ghazi-Zahedi, K. (2019). *Morphological Intelligence*. Springer International Publishing, Cham.

Gravish, N. and Lauder, G. V. (2018). Robotics-inspired biology. *Journal of Experimental Biology*, 221(7).

Ijspeert, A. (2014). Biorobotics: Using robots to emulate and investigate agile locomotion. *Science*, 346(6206):196–203.

Jung, J., Park, M., Kim, D., and Park, Y.-L. (2020). Optically sensorized elastomer air chamber for proprioceptive sensing of soft pneumatic actuators. *IEEE Robotics and Automation Letters*, 5(2):2333–2340.

Jusufi, A., Vogt, D. M., Wood, R. J., and Lauder, G. (2017). Undulatory swimming performance and body stiffness modulation in a soft robotic fish-inspired physical model. *Soft Robotics*, 4(3):202–210.

Kim, T., Lee, S., Hong, T., Shin, G., Kim, T., and Park, Y.-L. (2020). Heterogeneous sensing in a multifunctional soft sensor for human-robot interfaces. *Science Robotics*, 5(49).

Kim, T., Park, J., J. Yoon, S., H. Kong, D., Park, H., and Park, Y. (2019). Design of a lightweight inflatable sensing sleeve for increased adaptability and safety of legged robots. In *2019 2nd IEEE International Conference on Soft Robotics (RoboSoft)*, pages 257–264.

Kim, T., Yoon, S. J., and Park, Y.-L. (2018). Soft inflatable sensing modules for safe and interactive robots. *IEEE Robotics and Automation Letters*, 3(4):3821–3827.

Kovač, M. (2013). The bioinspiration design paradigm: A perspective for soft robotics. *Soft Robotics*, 1:28–37.

Larson, C., Peele, B., Li, S., Robinson, S., Totaro, M., Beccai, L., Mazzolai, B., and Shepherd, R. (2016). Highly stretchable electroluminescent skin for optical signaling and tactile sensing. *Science*, 351(6277):1071–1074.

Lauder, G. V., Flammang, B., and Alban, S. (2012). Passive robotic models of propulsion by the bodies and caudal fins of fish. *Integrative and Comparative Biology*, 52(5):576–587.

Li, B., Gao, Y., Fontecchio, A., and Visell, Y. (2016). Soft capacitive tactile sensing arrays fabricated via direct filament casting. *Smart Materials and Structures*, 25(7):075009.

Li, G., Ashraf, I., François, B., Kolomenskiy, D., Lechenault, F., Godoy-Diana, R., and Thiria, B. (2021). Burst-and-coast swimmers optimize gait by adapting unique intrinsic cycle. *Communications Biology*, 4(1):40.

Liao, J. C., Beal, D. N., Lauder, G. V., and Triantafyllou, M. S. (2003). The kármán gait: Novel body kinematics of rainbow trout swimming in a vortex street. *Journal of Experimental Biology*, 206(6):1059–1073.

Lin, Y.-H., Siddall, R., Schwab, F., Fukushima, T., Banerjee, H., Baek, Y., Vogt, D., Park, Y.-L., and Jusufi, A. (2021). Modeling and control of a soft robotic fish with integrated soft sensing. *Advanced
Long, J. H., Combes, S., Nawroth, J., Hale, M., Lauder, G., Swartz, S., Quinn, R., and Chiel, H. (2014). How does soft robotics drive research in animal locomotion. *Soft Robotics, 1*(3):161–168.

Long Jr, J. H. (1998). Muscles, elastic energy, and the dynamics of body stiffness in swimming eels. *American Zoologist, 38*(4):771–792.

Long Jr, J. H., Adcock, B., and Root, R. G. (2002). Force transmission via axial tendons in undulating fish: A dynamic analysis. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 133*(4):911–929.

Majidi, C., Kramer, R., and Wood, R. J. (2011). A non-differential elastomer curvature sensor for softer-than-skin electronics. *Smart Materials and Structures, 20*(10):105017.

McHenry, M. J. and Liao, J. C. (2014). The hydrodynamics of flow stimuli. In Coombs, S., Bleckmann, H., Fay, R. R., and Popper, A. N., editors, *The Lateral Line System*, pages 73–98. Springer New York, New York, NY.

McInroe, B., Astley, H., Gong, C., Kawano, S., Schiebel, P., Rieser, J., Choet, H., Bloh, R., and Goldman, D. (2016). Tail use improves performance on soft substrates in models of early vertebrate land locomotors. *Science, 353*(6295):154–158.

Miriyev, A. and Kovač, M. (2020). Skills for physical artificial intelligence. *Nature Machine Intelligence, 2*(11):658–660.

Ng, C., S. X., and Lum, G. Z. (2021). Untethered soft robots for future planetary explorations. *Advanced Intelligent Systems, n/a:2100106.

Nirody, J. A., Jinn, J., Libby, T., Lee, T. J., Jusufi, A., Hu, D. L., and Full, R. J. (2018). Geckos race across the water’s surface using multiple mechanisms. *Current Biology, 28*(24):4046–4051. e2.

Nishikawa, K., Biewener, A., Aerts, P., Ahn, A., Chiel, H., Daley, M., Daniel, T., Full, R., Hale, M., Hedrick, T., Lappin, A., Nichols, T., Quinn, R., Satterlie, R., and Szymbik, B. (2007). Neuromechanics: An integrative approach for understanding motor control. *Integrative and Comparative Biology, 47*(1):16–54.

Nyakatura, J. A., Melo, K., Horvat, T., Karakasiliotis, K., Allen, V. R., Andikfar, A., Andrade, E., Arnold, P., Lauströer, J., Hutchinson, J. R., Fischer, M. S., and Ijspeert, A. J. (2019). Reverse-engineering the locomotion of a stem amniote. *Nature, 565*(7739):351–355.

Park, H. and Choi, H. (2010). Aerodynamic characteristics of flying fish in gliding flight. *Journal of Experimental Biology, 213*(19):3269–3279.

Park, M., Jeong, B., and Park, Y.-L. (2020). Hybrid system analysis and control of a soft robotic gripper with embedded proprioceptive sensing for enhanced gripping performance. *Advanced Intelligent Systems, page 2000061.

Park, Y.-L., Chen, B.-R., and Wood, R. J. (2012). Design and fabrication of soft artificial skin using embedded microchannels and liquid conductors. *IEEE Sensors Journal, 12*(8):2711–2718.

Park, Y.-L., Majidi, C., Kramer, R., Bérard, P., and Wood, R. J. (2010). Hyperelastic pressure sensing with a liquid-embedded elastomer. *Journal of Micromechanics and Microengineering, 20*(12):125029.
Schwab et al.

Picton, L. D., Bertuzzi, M., Pallucchi, I., Fontanel, P., Dahlberg, E., Björnfors, E. R., Iacoviello, F., Shearing, P. R., and El Manira, A. (2021). A spinal organ of proprioception for integrated motor action feedback. Neuron, 109(7):1188–1201.e7.

Pineira, M., Thiria, B., and Goody-Diana, R. (2017). Modelling of an actuated elastic swimmer. Journal of Fluid Mechanics, 829:731–750.

Ponce Wong, R. D., Posner, J. D., and Santos, V. J. (2012). Flexible microfluidic normal force sensor skin for tactile feedback. Sensors and Actuators A: Physical, 179:62–69.

Roberts, B. (1969). The response of a proprioceptor to the undulatory movements of dogfish. Journal of Experimental Biology, 51(3):775–785.

Roberts, B. and Russell, I. (1972). The activity of lateral-line efferent neurones in stationary and swimming dogfish. Journal of Experimental Biology, 57(2):435–448.

Schultz, J. T., Beck, H. K., Haagensen, T., Proost, T., and Clemente, C. J. (2021). Using a biologically mimicking climbing robot to explore the performance landscape of climbing in lizards. Proceedings of the Royal Society B: Biological Sciences, 288(1947):20202576.

Shield, S., Jericevich, R., Patel, A., and Jusufi, A. (2021). Tails, flails, and sails: How appendages improve terrestrial maneuverability by improving stability. Integrative and Comparative Biology.

Shin, G., Jeon, B., and Park, Y.-L. (2020). Direct printing of sub-30 µm liquid metal patterns on three-dimensional surfaces for stretchable electronics. Journal of Micromechanics and Microengineering, 30(3):034001.

Shin, H.-S., Kim, T., Bergbreiter, S., and Park, Y.-L. (2019). Biomimetic soft airflow sensor with printed ionogel conductor. In 2019 2nd IEEE International Conference on Soft Robotics (RoboSoft), pages 611–616. IEEE.

Siddall, R., Fukushima, T., Bardhi, D., Perteshoni, B., Morina, A., Hasimja, E., Dujaka, Y., Haziri, G., Martin, L., Banerjee, H., and Jusufi, A. (2021a). Compliance, mass distribution and contact forces in cursorial and scansorial locomotion with birobotic physical models. Advanced Robotics, 35(7):437–449.

Siddall, R., Ibanez, V., Byrnes, G., Full, R. J., and Jusufi, A. (2021b). Mechanisms for mid-air reorientation using tail rotation in gliding geckos. Integrative and Comparative Biology.

Skandalis, D. A., Lunsford, E. T., and Liao, J. C. (2021). Corollary discharge prevents signal distortion and enhances sensing during locomotion. bioRxiv, page 2021.02.15.431323.

Souri, H., Banerjee, H., Jusufi, A., Radacsi, N., Stokes, A. A., Park, I., Sitti, M., and Amjadi, M. (2020). Wearable and stretchable strain sensors: Materials, sensing mechanisms, and applications. Advanced Intelligent Systems, page 2000039.

Steele, S. C., Weymouth, G. D., and Triantafyllou, M. S. (2017). Added mass energy recovery of octopus-inspired shape change. Journal of Fluid Mechanics, 810:155–174.

Sánchez-Rodríguez, J., Celestini, F., Raufaste, C., and Argentina, M. (2021). Proprioceptive mechanism for bioinspired fish swimming. Phys Rev Lett, 126(23):234501.

Thandiackal, R., Melo, K., Paez, L., Herault, J., Kano, T., Akiyama, K., Boyer, F., Ryczko, D.,
Ishiguro, A., and Ijspeert, A. J. (2021). Emergence of robust self-organized undulatory swimming based on local hydrodynamic force sensing. *Science Robotics*, 6(57):eab6354.

To, C., Hellebrekers, T., Jung, J., Yoon, S. J., and Park, Y.-L. (2018). A soft optical waveguide coupled with fiber optics for dynamic pressure and strain sensing. *IEEE Robotics and Automation Letters*, 3(4):3821–3827.

Triantafyllou, M. S., Winey, N., Trakht, Y., Elhassid, R., and Yoerger, D. (2020). Biomimetic design of dorsal fins for auvs to enhance maneuverability. *Bioinspiration & Biomimetics*, 15(3):035003.

Tytell, E. D. and Long, J. H. (2021). Biorobotic insights into neuromechanical coordination of undulatory swimming. *Science Robotics*, 6(57):eabk0620.

Vogt, D. M., Park, Y.-L., and Wood, R. J. (2013). Design and characterization of a soft multi-axis force sensor using embedded microfluidic channels. *IEEE Sensors Journal*, 13(10):4056–4064.

Wang, T., Zhang, Y., Lui, Q., Chen, W., Wang, X., Pan, L., Xu, B., and Xu, H. (2017). A self-healable, highly stretchable, and solution processable conductive polymer composite for ultrasensitive strain and pressure sensing. *Advanced Functional Materials*, 27(7):1705551.

Webb (2000). What does robotics offer animal behaviour. *Animal Behaviour*, 60(5):545–558.

Wirekoh, J., Valle, L., Pol, N., and Park, Y.-L. (2019). Sensorized flat pneumatic artificial muscles (sfpam) embedded with biomimetic microfluidics sensors for proprioceptive feedback. *Soft Robotics*, 6(6):768–777.

Wolf, Z., Jusufi, A., Vogt, D., and Lauder, G. (2020). Fish-like aquatic propulsion studied using a pneumatically-actuated soft-robotic model. *Bioinspiration & Biomimetics*, 15(4):046008.

Woodward, M. and Sitti, M. (2018). Morphological intelligence counters foot slipping in the desert locust and dynamic robots. *Proceedings of the National Academy of Sciences*, 115(36):E8358–E8367.

Wright, B., Vogt, D. M., Wood, R. J., and Jusufi, A. (2019). Soft sensors for curvature estimation under water in a soft robotic fish. In *2019 IEEE International Conference on Soft Robotics (RoboSoft) COEX, Seoul, Korea, April 14-18, 2019*, pages 367–371. IEEE.

Xu, L., Liu, N., Ge, J., Wang, X., and Fok, M. P. (2018). Stretchable fiber-bragg-grating-based sensor. *Optics Letters*, 43(11):2500–2506.

Xu, P. A., Mishra, A. K., Bai, H., Aubin, C. A., Zullo, L., and Shepherd, R. F. (2019a). Optical lace for synthetic afferent neural networks. *Science Robotics*, 4(34).

Xu, S., Vogt, D. M., Hsu, W.-H., Osborne, J., Walsh, T., Foster, J. R., Sullivan, S. K., Smith, V. C., Rousing, A. W., Goldfield, E. C., and Wood, R. J. (2019b). Biocompatible soft fluidic strain and force sensors for wearable devices. *Advanced Functional Materials*, 29(7):1807058.

Yeaton, I. J., Ross, S. D., Baumgardner, G. A., and Socha, J. J. (2020). Undulation enables gliding in flying snakes. *Nature Physics*, 16(9):974–982.

Zhuang, W., Sun, G., Li, H., Lou, X., Dong, M., and Zhu, L. (2018). Fbg based shape sensing of a silicone octopus tentacle model for soft robotics. *Optik*, 165:7–15.