



Lessons from Animals and Plants

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The Symbiosis of Morphological Computation and Soft Robotics

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Morphological computation is a modern perspective on intelligence that gives the physical body a stronger role [1], [2]. With respect to the traditional view, in which behavior is the result of perception, processing, and movement, with morphological computation, behavior emerges from the complex interaction of the physical body with the environment and depends heavily on the mechanical properties, the shape (or the morphology), and the arrangement of perceptual, motor, and processing units [3]. In this view, according to [2], the material properties of the structures are extremely important for control. In fact, most living organisms have soft bodies. As summarized in [4], even animals with skeletons have soft tissues; in humans, for example, the skeleton typically contributes only 11% of the body mass of an adult male. Soft bodies thus appear to be fundamental to the emergence of behavior from the interaction with the environment. In other words, morphological computation benefits from soft bodies that react and adapt to such an interaction.

Morphological computation provides principles for facing the complexity of controlling soft bodies in robotics. Their deformations are difficult to model, and typical model-based control approaches are unsuitable for this purpose. Instead, morphological computation exploits such deformations of the soft body and uses reaction forces to help achieve the desired behavior, which reduces control parameters. From the evidence of morphological computation in nature, we illustrate how animal and plant models provide principles for the implementation of morphological computation in soft robotics. In humans, despite the complexity and extent of the computing power of the brain, we found elegant simplification mechanisms in the neural circuitry of some reflexes or other sensory-motor loops, also known as *simplicity* [5]. In vertebrates, the central pattern generator (CPG) is a considerable example of the reduction of control parameters by the brain thanks to a proper arrangement of receptors, muscles, and related peripheral neural circuitry [6]. In invertebrates, we found extreme examples of the control of movements by the mechanical reactions of body parts [7]. Finally, in plants, the evidence of complex behaviors, triggered by a large number of sensing inputs, provides insight into a completely different way of computing without a brain [8].

Digital Object Identifier 10.1109/MRA.2016.2582726
Date of publication: 25 August 2016

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In this article, we show how very similar principles of morphological computation can be found in nature in apparently completely different aspects of animals and plants and how the exploitation of such principles by bioinspired robotics can achieve more efficient and effective behavior in natural environments.

Simplicity: A Form of Morphological Computation in the Human Brain?

Simplicity is the term used to indicate a collection of solutions that can be observed in living organisms that, despite the complexity of the world in which they live, allows them to act and project the consequences of their actions into the future [5]. Different from simplification, simplicity is not the adoption of a simplified model but, rather, of an approach to using simplifying principles. It does not mean the reduction of complexity but instead a reduction of the variables to set or control parameters. Considering the neural circuitry in the human brain, simplicity is what evolution reaches in tuning the morphology and connections of the neuronal networks so that perception-action loops become shorter in terms of synaptic chains, and movements are controlled with few control signals from the sensory inputs. An example is the neural circuitry that controls the saccades of human eyes. Saccades are the fundamental eye movements necessary to focus points of interest in the small area of the retina (fovea) that makes them visible. Saccades are ancestral movements and are very fast. The superior colliculus, a small area of the brain, plays a fundamental role in the perception-action loop that generates saccades from a visual stimulus that appears in the periphery of the retina. The projection of the inputs from the retina receptors onto the superior colliculus is such that an output is directly generated for the eye muscles to elicit the proper contractions that bring the eye fovea to the stimulus [9]. The overall structure of the neural circuitry is not simple, but the control of the eye movements to perform fast saccades is simple and efficient. The implementation of this model on an anthropomorphic robot head demonstrated that control of the velocity of the saccadic movement can be performed with a strict time constraint (i.e., 1 ms) [10]. Analogous with the neuroscientific model, saccadic movements are obtained by issuing velocity commands in open loop head movements. The trajectories obtained are similar to those recorded in humans, in terms of both shape and timing.

The CPG as an Example of Morphological Computation in Vertebrates

In the vertebrate spinal cord, the CPG is a neural mechanism that controls rhythmic movements with minimal parameter setting. It was discovered in the lamprey, but it is common to all vertebrates [6]. The CPG can be considered an example of morphological computation, as the arrangement of neurons and synapses, coupled with the mechanical properties of the flexible body, determines effective patterns of movements for swimming. Only two parameters are set by the brain to trigger the beginning of the movement. By this mechanism, the lamprey can control swimming without a direct use of the brain at the spinal level by using feedback from stretch receptor neurons on its skin and by excitatory and inhibitory ipsilateral and contralateral neurons, which produce an undulatory movement. From a functional viewpoint, when the body is contracted on one side, the stretch sensors detect the extension of the other side of the body, and the corresponding excitatory neurons activate the ipsilateral motoneurons, while the inhibitory neurons simultaneously inhibit the contralateral motoneurons. Therefore, because inertial movements exploit the body dynamics, a periodic swim is obtained. The brainstem gives only a start signal and a correction signal to impose the desired swimming pace. An important consequence is that the receptors begin the rhythmic signal by applying an external movement.

In robotics, the CPG model is widely used for controlling rhythmic movements, especially locomotion, in a variety of different robots, from humanoids to four- or six-legged robots. More remarkably, the CPG has been implemented and validated on robotic models of lampreys [11] and salamanders, which were used to demonstrate how locomotion patterns change in the transition from swimming to crawling when touching the ground [12].

Role of Compliance in Morphological Computation in Invertebrates

In insects, very fast reactive behavior in unstructured environments is provided by mechanical reflexes and mechanical coupling among joints, which are the basis of the reaction of the legs to the ground and of the coordination of a high number of degrees of freedom (DoF) of the legs. The cockroach is one of the fastest running animals relative to its body length,

Preflexes effectively provide a mechanical closed loop that is sufficient to maintain stability in perturbations or terrain changes.

and it is especially fast in adapting to different terrains without stopping. This adaptation is not controlled by the brain in response to sensation; it is basically mechanical, given by a change in the shoulder angles and guided by the self-stabilization of compliant leg joints. Such so-called reflexes give an immediate response to perturbations without the involvement of the neural transmission of the signal, which would introduce longer delays. Reflexes play an important role in locomotion on uneven terrains. In particular, they allow fast transitions from smooth to uneven terrain [13]. Reflexes effectively provide a mechanical closed loop that is sufficient to maintain stability in perturbations or terrain changes.

Imitating the compliance of the leg joints of the cockroach, one of the fastest running six-legged robots, the *Sprawlita*, was developed [14]. Compliance is embedded in the leg and built with shape deposition manufacturing techniques. The robot's legs are actuated by pneumatic pistons. They are controlled three by three: the front and rear legs of the same side and the middle leg of the other side are activated together. A simple alternation of the activation of the two groups of three legs generates locomotion. The frequency and duration of activation yield the stride period and duty cycle, respectively.

The Octopus and Its Soft Body as a Model for Morphological Computation

Among invertebrates, the octopus (Figure 1) is an extreme example of morphological computation. The morphology of its body and its complex interaction with the environment give rise to a rich behavior with diverse patterns of locomotion and manipulation, which is unusual for a mollusk. An octopus' body does not contain bones or an exoskeleton, and the special arrangement of muscles, longitudinal, transversal, and oblique, in the arm's muscular hydrostat allows bending, elongation, shortening, and stiffening [15]. This huge range of arm movements, multiplied by eight arms, is controlled by a brain and peripheral nervous system, which are well developed for a mollusk but still limited in relation to the complexity of the task. Simplification mechanisms are put in place by the peripheral nervous system and by the mechanical properties of the octopus body (density and compliance) in the interaction with its special environment, which includes water. In a typical reaching movement, the strategy is to propagate a bending wave along the length of the arm. It reduces drag forces in water, exploits buoyancy to sustain the arm, and delegates control to the sequential activation of peripheral



Figure 1. (a) An *Octopus vulgaris*. (Photo by Massimo Brega, The Lighthouse.) (b) An enlarged view of an octopus arm with suckers. The picture shows the infundibulum portion (IN), with its grooves in the foreground (GR), and the orifice (O) that connects the infundibulum with the acetabulum (the latter not visible).

neurons [16]. It is controlled with only three parameters set by the brain: two for the direction of the base of the arm and the third for scaling the propagation velocity profile of the bend along the arm [17]. Food is delivered to the mouth by creating three arm segments: the distal one is passively used as a hand, while the other two, according to electromyography studies, are given by the collision of two stiffening waves, one starting at the contact point and controlled peripherally and the other starting from the arm base and controlled by the brain. An articulated structure is then created, and the fetching movement is obtained similarly to how it would be in a rigid arm with an elbow. The brain thus controls two parameters, the trigger of the stiffening wave and the elbow angle [18]. There is a strict relation between the octopus body and its behavior, and the development of its nervous system provides evidence of its embodied intelligence. The octopus lacks a central representation of the arms, and the peripheral nervous system is especially well developed in terms of neuron number, showing an organization that fits the octopus' special embodiment [7]. The octopus model provides numerous insights into morphological computation in soft robots. An octopus-like, eight-arm soft robot was built by implementing such principles. It can move in water, bend and stretch its arms, grasp objects, and reach a target [17], [19] (see Figure 2). Building a robot arm with the same density and similar morphology as an octopus arm facilitates the construction of reaching movements in water, which are very efficient in terms of control and energy [20]. A proof of concept with a passive arm, made of silicone with the same density, the same hyperelastic behavior, and the same conic morphology as an octopus arm showed that in water, acceleration at the base of the arm generates a bending wave that propagates from the base to the tip of the arm, which supports the hypothesis that the bending wave in the animal's reaching movement is given in part by the physical interaction of the arm with water. The stiffening of the proximal part

of the arm is achieved by embedding cables in the silicone arm in such a way that the longitudinal and transverse contractions are mechanically coupled. With a silicone conic arm actuated by embedded cables, Nakajima et al. demonstrated that in water, the body's dynamics perform the computation needed to control the arm and switch behavior [21]. Hauser et al. demonstrated that body nonlinearities provide computational power and that they can be modeled with mass-spring systems [22].

Crawling is another complex behavior with only a few control parameters in the octopus. During crawling, each of the two arms used to push the body forward executes a four-phase cycle: shortening, attaching to the ground, elongation, and detaching. In an octopus-like robot, one DoF is enough to obtain the four phases, given the correct compliance and stiffening ability and the capability for elongation and shortening. The mechanical structure of each locomotion arm is based on a silicone cone with a flexible steel cable embedded centrally, which produces shortening and stiffening at the same time; a motor and a crack mechanism produce the four cyclical crawling phases [23] with minimal control. In swimming, the complex hydrodynamics that elicit propulsion with the pulsed jet of the octopus mantle can be obtained with one DoF, given the proper deformability of the material, the proper morphology, and the proper geometry of the mantle and the funnel [24].

Morphological Computation in the Octopus Suckers

Analogous to its body and arms, the octopus sucker is a muscular hydrostat structure with no rigid parts, in which muscles and connective tissue play the roles of structural elements and the actuation system. The musculature is arranged in radial, meridional, and circular muscular fibers that provide skeletal-like support and force for movement [25]. A single sucker consists of two general regions connected by a constricted orifice: the infundibulum, which is the disk-like

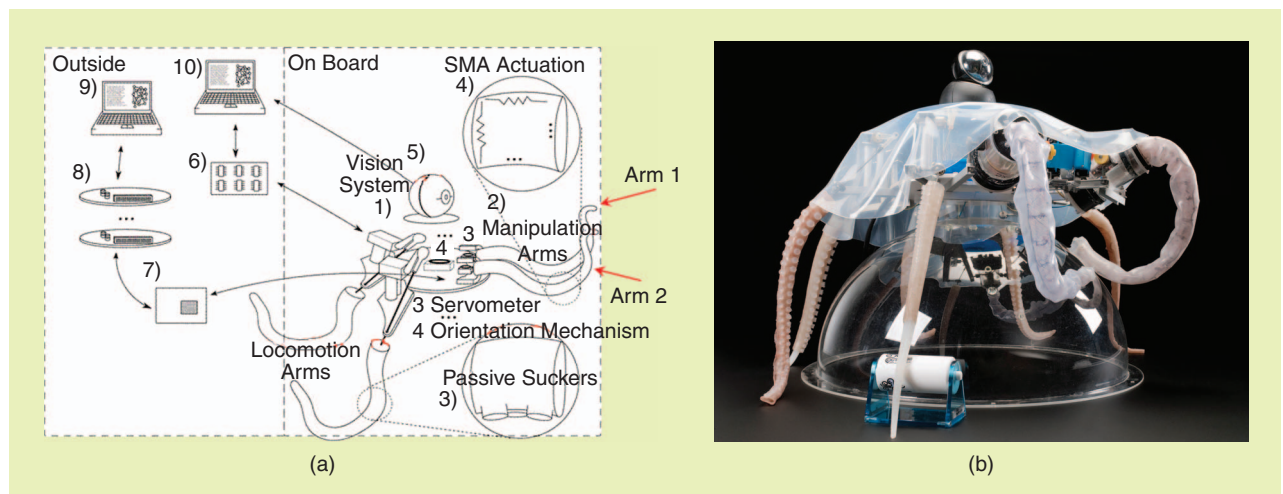


Figure 2. (a) A scheme of the octopus-like eight-arm robot developed in the OCTOPUS project (FP7-ICT 2007.8.5, FET Proactive, Embodied Intelligence, no. 231608); the two front arms are used for manipulation and employ shape memory alloy (SMA) springs as actuators; the other arms are used for locomotion and are silicone cones with a steel cable embedded centrally. (b) A picture of the octopus-like eight-arm robot. (Photo by Jennie Hills, London Science Museum.)

portion of the sucker that contacts the substrate, and the acetabulum, the upper hollow portion. The infundibulum is covered by epithelium with superficial radial grooves and ridges [25]. These structures are fundamental to increasing the adhesion capability of the infundibulum. The network of grooves allows low pressure, which is generated in the acetabular chamber, to be transmitted to almost the entire sucker-substrate interface. The acetabulum, on its roof, has an evident protuberance that protrudes toward the orifice and fills approximately 80% of the total acetabular volume [26]. The protuberance is characterized by a rough surface, whereas all of the remaining portions of the acetabulum are completely smooth. The protuberance seems to play an important role in the adhesion and detachment of the sucker [26], and it was recently discovered that it is completely covered by a dense network of hair-like micro-outgrowths [27] that may provide an additional adhesive mechanism that works in concert with suction. The discovered surface structures, together with the role of the mechanical properties and the morphology of the materials, are also relevant to biomimetics, with the

aim of developing novel artificial suction cups with improved adhesion on nonsmooth surfaces. The measurements of the mechanical properties of the octopus sucker tissues demonstrated that they are very soft, as proven by their mean elasticity moduli (7.7 and 18.1 kPa for the infundibulum and the acetabular protuberance, respectively [28]). The study of the material's mechanical properties is crucial because the first step in the adhesion process is passively assured by the infundibulum, as the compliance of its tissues achieves a perfect seal when the sucker comes into contact with substrates of various degrees of roughness. The morphology of the sucker plays a fundamental role as well. We hypothesize that the process of continuous adhesion is achieved by sealing the orifice between the acetabulum and infundibulum via the acetabular protuberance, wherein the infundibulum forms a completely flat shape, and by sustaining adhesion through the preservation of the sucker's configuration [26]. We used noninvasive techniques (i.e., ultrasonography and magnetic resonance imaging) to make a three-dimensional (3-D) reconstruction of sucker morphology aimed at obtaining a computer-aided

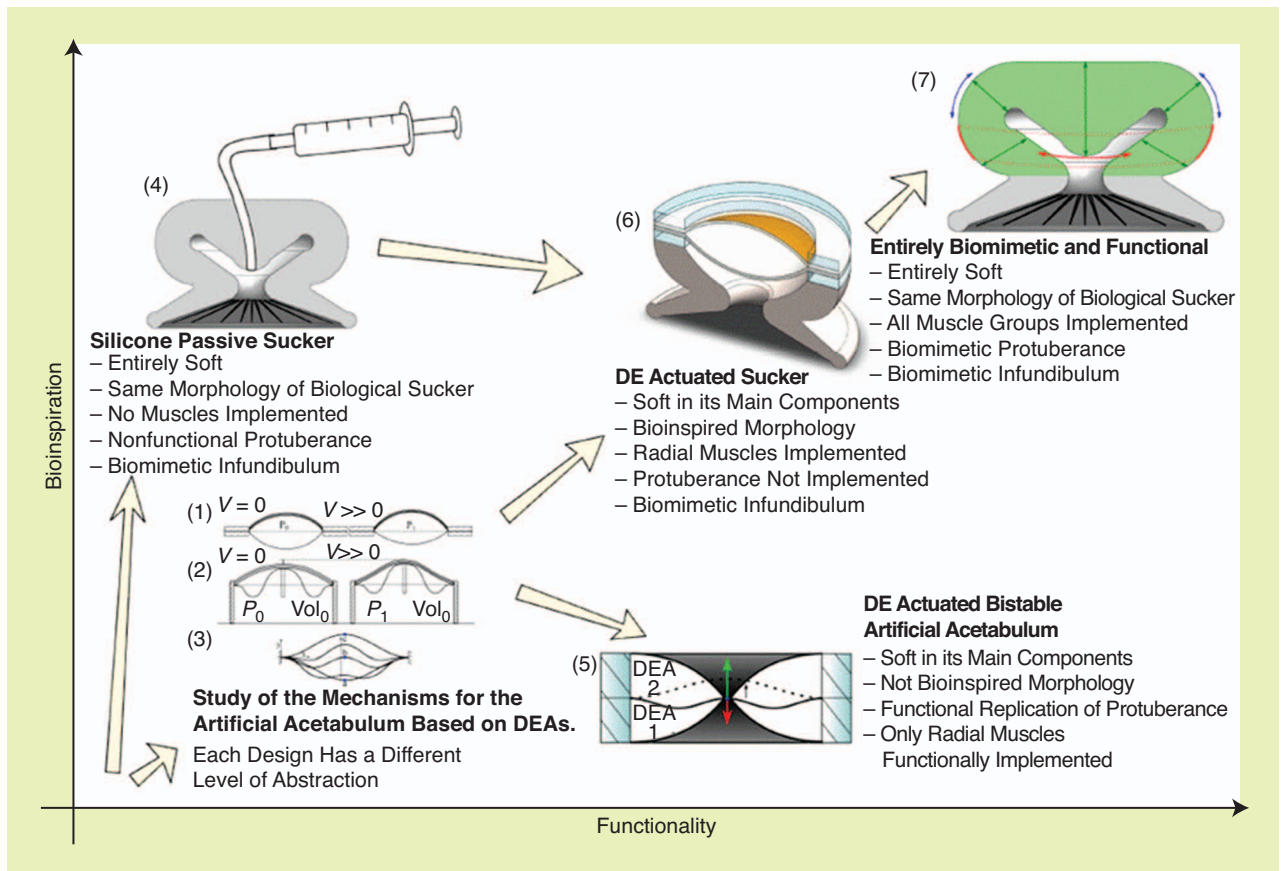


Figure 3. A schematic of the design process of the artificial suction cup. The different phases of the process and the relative devices and concepts are represented in a Cartesian space defined by the bioinspiration and functionality axis. (1)–(3) An actuation mechanism of the artificial infundibulum; (1) a hydrostatically coupled dielectric elastomer (DE) membranes; (2) ADE actuator coupled with a negative spring-rate element; (3) A bistable buckled beam mechanism; (4) A silicone sucker from the reconstruction of the biological sucker, actuated by a syringe; (5) A bistable buckled beam actuated by two DEAs for the implementation of the artificial infundibulum, capable of maintaining the pressure difference without energy consumption; (6) An artificial sucker with biomimetic infundibulum and artificial acetabulum made of hydrostatically coupled DEAs; (7) Ideal artificial suction cups morphologically and functionally comparable to the biological sucker. (Maurizio Follador, Ph.D. dissertation, 2015.)

design model perfectly equivalent to the octopus sucker in size and anatomical proportion. The 3-D information was used to develop the first passive prototypes of the artificial suction cups made of silicone [29] that are able to achieve adhesion in wet conditions. These capabilities demonstrate the importance of the role of morphology, material compliance, and interaction with the environment.

From a technological perspective, an effort has also been made to develop the first soft actuation unit integrated into the artificial suction cup based on dielectric elastomer actuators (DEAs). The actuation unit imitates the role of the acetabular radial muscles in creating suction and moving water from the infundibulum–substrate interface toward the acetabulum, enhancing attachment. The device works in a wet environment and is able to produce up to 6 kPa of pressure, reaching a maximum pressure in less than 300 ms [30]. Figure 3 shows the approach used in designing the artificial sucker. The two axes represent the level of abstraction of the solution found, with bioinspiration and functionality increasing in the direction of the arrows.

How Plants and Plant-Inspired Robots Exploit Morphological Computation

Different from animals, which are determinate in growth and reach a final size before they are mature, plants exhibit indeterminate growth and continue to add new organs and tissues

for their entire life span. This also implies that they continuously adapt their morphology and physiology in response to variability within their environment, showing considerable plasticity, particularly in foraging for resources [8], [31]. These properties are particularly evident in the plant root system, which is able to explore the soil and penetrate the environment with a number of sensorized apices, resulting in capillary searching of the entire volume of the medium. This exploratory ability of plant roots emerges from the complex and dynamic interaction between their morphology, sensory-motor control, and environment, which represents the basic principle of morphological computation. The motion of plant roots is coordinated and efficiently shaped to exploit soil resources and avoid hazards. In the soil, the roots are exposed to multiple stimuli, many of which can potentially elicit such movements. The overall apex bending movement is a combination of both active bending and passive deflection. The elongation rate of the root apex is determined by both the root apex growth pressure and by the reaction force of the soil to its deformation [32], [33]. For example, the mechanical strength of soil may increase with drying and thereby restrict root elongation [34]. The mechanical properties of the plant roots and the morphology of their structure have been considered in developing the first level of control embedded in the mechanical structure of the first robot inspired by plant roots, which is named *PLANTOID* [35], [36] (Figure 4).

An extreme representation of morphological computation in plants generated by the interaction of the body, materials, and environment is given by their passive movements. As stated by Zahedi and Ay [37], “the consensus is that morphological computation is the contribution of the morphology and the environment to the behavior that cannot be assigned to a nervous system or a controller.” Plant materials are optimized to reduce energy consumption during motion because of the sedentary nature of plants that obliges them to make the most of resources available in the environment. Different from animals, plants cannot move when resources fundamental to survival are not more available. To address these limitations, they have developed energetically efficient solutions to exploit the interaction with changing environmental conditions, especially humidity and temperature variations. Examples of these movements are found in pinecones, which release their ripe seeds by opening their scales in drying ambient air conditions and closing their scales in a wet environment [38]. This is possible due to the organization of plant cell walls, which are composed of a soft matrix (consisting of hemicelluloses, pectin, structural proteins, and/or lignin, which are able to swell and desorb humidity) and stiff cellulose fibrils embedded in this pliant medium, which drive the movement of the plant organ. This actuation principle is implemented by a wide variety of species in their seed dispersal units so that seeds are able to fly, drill, or bend.

These systems do not require additional control or energy, and this makes them an interesting source of inspiration in robotics and in actuation technologies that are not necessarily muscle-like. Following this principle, a soft actuator



Figure 4. A prototype of the *PLANTOID* robot. The figure shows two functional roots, a trunk containing a microcontroller main board and a spool of the material used to grow the robotic root in polypropylene (nominal diameter $d = 2.5$ mm), and an aerial portion with branches that include polymeric artificial leaves (based on controllable hygromorphic plant-inspired material moving in response to humidity, see [39]).

with bending capabilities inspired by the pinecone scale was recently proposed [39]. A simple way to obtain anisotropic motion in an artificial actuator is to couple a humidity-responsive material (active layer) with an elastic material that is insensitive to environmental humidity (passive layer). The main function of the passive layer is to convert the water-driven swelling of the active layer into a bending actuation. In the proposed plant-inspired hygromorphic actuator, the moisture-sensitive material is a well-known conjugated conductive polyelectrolyte complex known as poly(3,4-ethylenedioxythio-phenylene):poly(styrenesulfonate) (PEDOT:PSS), which has the capability to absorb water with its hydrophilic PSS portion, while the passive layer is a thick humidity-inert elastomer, such as poly-dimethylsiloxane, which acts as a structural material. When the pinecone scale-like system is subjected to a high-humidity environment, the PEDOT:PSS layer absorbs water vapor and swells passively, increasing its volume (isotropically) and generating a bending movement due to the constraints of the passive layer. The original equilibrium of the system is quickly recovered upon drying in ambient air. The influx and efflux of water in the cell wall-like structures causes changes in the system's geometry. Because PEDOT:PSS is a conductive polymer with a reasonable conductivity (up to hundreds of S/cm), the system can also be controlled by applying an electric current, which induces a localized joule-heating effect, sufficient to release the fraction of water absorbed at the equilibrium with humidified air. The drying of the active portion results in its shrinking, which induces a bending movement in the reverse direction with respect to that observed in passive conditions. The actuation is perfectly reversible and, upon removing the stimulus (electrical current), the system quickly comes back to the original equilibrium state. These soft plant-inspired systems couple sensing (i.e., humidity detection) and motion (i.e., bending) capabilities, with a consequent advantage in terms of integration and energy optimization. This system represents an interesting example of morphological computation and an innovative view in the artificial world.

Conclusions

Despite the widespread use of soft robotics worldwide, criticism may be raised as to when and to what extent robotics technologies or applications benefit from the use of soft materials, deformability, and compliance. The development of physical structures and behaviors that are more similar to those of living organisms can help robots to better negotiate real-world environments and accomplish real-world tasks [4]. However, the use of soft materials and continuum deformations and stiffening make control more difficult in computational terms using traditional model-based robot control approaches. Therefore, the robots of tomorrow will benefit from the interconnection and interaction between morphological computation and soft robotics.

Bioinspired principles of morphological computation offer a new way to build control schemes and behavioral architectures based on simplification mechanisms that exploit the

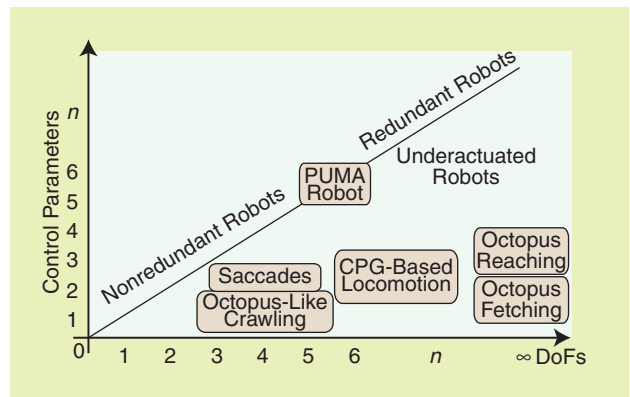


Figure 5. A graphical representation of a number of control parameters versus controlled DoFs. In traditional robots, they are the same, except for underactuated robots, which, however, represent a form of morphological computation [41]. Animals and soft robots controlled with the morphological computation simplification mechanisms are grouped in the bottom part of the plot, where two or three parameters are sufficient for control, in some cases even well on the right side, which corresponds to the many actuators activated.

physical body and its interaction with the environment. The greatest contribution to robotics is that the number of control parameters can be lower than the number of motor activations (see Figure 5). However, the design of the physical body becomes complex as the number of design parameters is very large to account for the morphology, the geometry, the mechanical properties of materials, and the dynamic interaction with the environment. Evolutionary algorithms have been proposed to explore such large design parameter spaces and to design morphological computation in soft robots that is beyond the creativity of a human designer [40]. The full potential of soft robotics in terms of technological advancement and scientific progress is still unexplored and offers interesting and demanding research challenges. A variety of application scenarios have been developed, presenting scientists with more challenges that can further contribute to the development of soft robotics overall.

References

- [1] R. Pfeifer and J. C. Bongard, *How the Body Shapes the Way We Think: A New View of Intelligence*. Cambridge, MA: MIT Press, 2007.
- [2] C. Paul, "Morphological computation: A basis for the analysis of morphology and control requirements," *Robot Automat. Syst.*, vol. 54, pp. 619–630, 2006.
- [3] D. Zambrano, M. Cianchetti, and C. Laschi, "The morphological computation principles as a new paradigm for robotic design," in *Opinions and Outlooks on Morphological Computation*, H. Hauser, Ed. Zurich: University of Zurich, 2014, pp. 214–225.
- [4] S. Kim, C. Laschi, and B. Trimmer, "Soft robotics: A bioinspired evolution in robotics," *Trends Biotech.*, vol. 31, no. 5, pp. 287–294, 2013.
- [5] A. Berthoz, *Complexity: Simplifying Principles for a Complex World*, G. Weiss, Trans. New Haven, CT: Yale Univ. Press, 2012.
- [6] S. Grillner, "Control of locomotion in bipeds, tetrapods and fish," in *Handbook of Physiology*, vol. 2. Bethesda, MD: American Physiological Society, 1981, pp. 1179–1236.

- [7] B. Hochner, "An embodied view of octopus neurobiology," *Curr. Biol.*, vol. 22, no. 20, pp. R887–R892, 2012.
- [8] A. Hodge, "The plastic plant: Root responses to heterogeneous supplies of nutrients," *New Phytologist*, vol. 162, no. 1, pp. 9–24, 2004.
- [9] B. Girard and A. Berthoz, "From brainstem to cortex: Computational models of the saccade generation circuitry," *Progress in Neurobiology*, vol. 77, no. 4, pp. 215–255, 2005.
- [10] C. Laschi, F. Patanè, S. E. Maini, L. Manfredi, G. Teti, L. Zollo, E. Guglielmelli, and P. Dario, "An anthropomorphic robotic head for investigating gaze control" *Advanced Robotics*, vol. 22, no. 1, pp. 57–89, 2008.
- [11] C. Stefanini, S. Orofino, L. Manfredi, S. Mintchev, S. Marrazza, T. Assaf, L. Capantini, E. Sinibaldi, S. Grillner, P. Wallén, and P. Dario, "A novel autonomous, bioinspired swimming robot developed by neuroscientists and bioengineers," *Bioinspiration Biomimetics*, vol. 7, no. 2, p. 025001, 2012.
- [12] A. J. Ijspeert, A. Crespi, D. Ryczko, and J. M. Cabelguen, "From swimming to walking with a salamander robot driven by a spinal cord model," *Science*, vol. 315, no. 5817, pp. 1416–1420, 2007.
- [13] R. J. Full, D. R. Stokes, A. N. Ahn, and R. K. Josephson, "Energy absorption during running by leg muscles in a cockroach," *J. Exp. Biol.*, vol. 201, no. 7, pp. 997–1012, 1998.
- [14] J. G. Cham, S. A. Bailey, J. E. Clark, R. J. Full, and M. R. Cutkosky, "Fast and robust: Hexapedal robots via shape deposition manufacturing," *Int. J. Robotics Res.*, vol. 21, no. 10–11, pp. 869–882, 2002.
- [15] W. M. Kier and M. P. Stella, "The arrangement and function of octopus arm musculature and connective tissue," *J. Morphol.*, vol. 268, pp. 831–843, 2007.
- [16] G. Sumbre, G. Fiorito, T. Flash, and B. Hochner, "Neurobiology: Motor control of flexible octopus arms," *Nature*, vol. 433, no. 7026, pp. 595–596, 2005.
- [17] C. L. Huffard, F. Boneka, and R. J. Full, "Underwater bipedal locomotion by octopuses in disguise," *Science*, vol. 307, p. 1927, 2005.
- [18] Y. Gutfreund, "Patterns of arm muscle activation involved in octopus reaching movements," *J. Neuroscience*, vol. 18, no. 15, pp. 5976–5987, 1998.
- [19] M. Cianchetti, M. Calisti, L. Margheri, M. Kuba, and C. Laschi, "Bio-inspired locomotion and grasping in water: The soft eight-arm OCTOPUS robot," *Bioinspiration Biomimetics*, vol. 10, no. 3, p. 035003, 2015.
- [20] C. Laschi, M. Cianchetti, B. Mazzolai, L. Margheri, M. Follador, and P. Dario, "Soft robot arm inspired by the octopus," *Advanced Robotics*, vol. 26, no. 7, pp. 709–727, 2012.
- [21] K. Nakajima, T. Li, H. Hauser, and R. Pfeifer, "Exploiting short-term memory in soft body dynamics as a computational resource," *J. R. Soc. Interface*, vol. 11, no. 100, pp. 1–22, 2014.
- [22] H. Hauser, A. J. Ijspeert, R. M. Fuchsli, R. Pfeifer, and W. Maass, "Towards a theoretical foundation for morphological computation with compliant bodies," *Biol. Cybern.*, vol. 105, pp. 355–370, 2011.
- [23] M. Calisti, M. Giorelli, G. Levy, B. Mazzolai, B. Hochner, C. Laschi, and P. Dario, "An octopus-bioinspired solution to movement and manipulation for soft robots," *Bioinspiration Biomimetics*, vol. 6, p. 036002, 2011.
- [24] F. Renda, F. Giorgio-Serchi, F. Boyer, C. Laschi, J. Dias, L. Seneviratne, "A unified multi-soft-body dynamic model for underwater soft robots," *Int. J. Robotics Res.*, to be published.
- [25] W. M. Kier and A. M. Smith, "The morphology and mechanics of octopus suckers," *Biol. Bull.*, vol. 178, pp. 126–136, 1990.
- [26] F. Tramacere, L. Beccai, M. Kuba, A. Gozzi, A. Bifone, and B. Mazzolai, "The morphology and adhesion mechanism of *Octopus vulgaris* suckers," *PLoS One*, vol. 8, no. 6, p. e65074, 2013.
- [27] F. Tramacere, E. Appel, B. Mazzolai, and S. N. Gorb, "Hairy suckers: The surface microstructure and its possible functional significance in the *Octopus vulgaris* sucker," *Beilstein J. Nanotechnol.*, vol. 5, no. 1, pp. 561–565, 2014.
- [28] F. Tramacere, A. Kovalev, T. Kleinteich, S. N. Gorb, and B. Mazzolai, "Structure and mechanical properties of *Octopus vulgaris* suckers," *J. R. Soc. Interface*, vol. 11, no. 91, p. 20130816, 2014.
- [29] F. Tramacere, L. Beccai, F. Mattioli, E. Sinibaldi, and B. Mazzolai, "Artificial adhesion mechanisms inspired by octopus suckers," in *Proc. 2012 IEEE Int. Conf. Robotics and Automation (ICRA)*, Saint Paul, MN, pp. 3846–3851.
- [30] M. Follador, F. Tramacere, and B. Mazzolai, "Dielectric elastomer actuators for octopus inspired suction cups," *Bioinspiration Biomimetics*, vol. 9, no. 4, p. 046002, 2014.
- [31] A. Trewavas, "What is plant behaviour?" *Plant Cell Environ.*, vol. 32, pp. 606–616, 2009.
- [32] E. Greacen and J. Oh, "Physics of root growth," *Nature*, vol. 235, pp. 24–25, 1972.
- [33] L. Clark, W. Whalley, and P. Barraclough, "How do roots penetrate strong soil?" *Plant Soil*, vol. 255, pp. 93–104, 2003.
- [34] W. Whalley, L. Clark, D. Gowing, R. Cope, R. Lodge, and P. Leeds-Harrison, "Does soil strength play a role in wheat yield losses caused by soil drying?" *Plant Soil*, vol. 280, pp. 279–290, 2006.
- [35] A. Sadeghi, A. Tonazzini, L. Popova, and B. Mazzolai, "A novel growing device inspired by plant root soil penetration behaviors," *PLoS ONE*, vol. 9, no. 2, p. e90139, 2014.
- [36] B. Mazzolai, L. Beccai, and V. Mattoli, "Plants as model in biomimetics and biorobotics: New perspectives," *Frontiers Bioengineering Biotechnology*, vol. 2, p. 2, 2014.
- [37] K. Zahedi and N. Ay, "Quantifying morphological computation" *Entropy*, vol. 15, no. 5, pp. 1887–1915, 2013.
- [38] I. Burgert and P. Fratzl, "Actuation systems in plants as prototypes for bioinspired devices," *Philos. Trans. R. Soc. London A, Math. Phys. Sci.*, vol. 367, no. 1893, pp. 1541–1557, 2009.
- [39] S. Taccola, F. Greco, E. Sinibaldi, A. Mondini, B. Mazzolai, and V. Mattoli, "Toward a new generation of electrically controllable hygro-morphic soft actuators," *Adv. Mater.*, vol. 27, pp. 1668–1675, 2015.
- [40] F. Corucci, M. Calisti, H. Hauser, and C. Laschi, "Novelty-based evolutionary design of morphing underwater robots," in *Proc. 2015 Annu. Conf. Genetic and Evolutionary Computation*, pp. 145–152.
- [41] F. Iida, R. Pfeifer, and A. Seyfarth, "AI in locomotion: Challenges and perspectives of underactuated robots," in *50 Years of Artificial Intelligence*, M. Lungarella, F. Iida, J. Bongard, and R. Pfeifer, Eds. Berlin, Germany: Springer-Verlag, 2007, pp.134–143.

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