

ANIMAL ROBOTS

The neuromechanics of animal locomotion: From biology to robotics and back

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Robotics and neuroscience are sister disciplines that both aim to understand how agile, efficient, and robust locomotion can be achieved in autonomous agents. Robotics has already benefitted from neuromechanical principles discovered by investigating animals. These include the use of high-level commands to control low-level central pattern generator–like controllers, which, in turn, are informed by sensory feedback. Reciprocally, neuroscience has benefited from tools and intuitions in robotics to reveal how embodiment, physical interactions with the environment, and sensory feedback help sculpt animal behavior. We illustrate and discuss exemplary studies of this dialog between robotics and neuroscience. We also reveal how the increasing biorealism of simulations and robots is driving these two disciplines together, forging an integrative science of autonomous behavioral control with many exciting future opportunities.

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INTRODUCTION

Locomotion encompasses the variety of ways in which animals and robots propel themselves through their environments: underwater, on the ground, or in the air. Animals have largely solved the challenges associated with moving through a fluid (water or air) and counteracting gravitational forces to propel themselves overground by evolving appendages under active neural control, including flapping wings for flight, undulating bodies and fins, and cyclically driven legs. The resulting animal locomotion is agile, efficient, and robust enough to effectively navigate unstructured terrain and produce maneuvers that counteract unexpected perturbations. This exceptional locomotor ability arises from a synergistic coupling between neuronal elements and body mechanics, more concisely referred to as “neuromechanics.” Animals’ body morphologies, including the distribution of feedback sensors, are strongly correlated with the terrain that must be navigated. This reflects the intimate coupling between neural control and biomechanics (1); thus, locomotion cannot be fully understood by examining one without the other. This integrative perspective is shared by the field of robotics, a discipline that focuses on physical embodiment and real-time control. For these reasons, neuroscience and robotics are “sister” disciplines that can inform one another toward obtaining a better understanding of the neuromechanical mechanisms underlying autonomous locomotion and leveraging biological insights to achieve animal-level locomotor fluency in robots (2, 3).

What are some of the core principles of biological locomotor control? Years of study across species have revealed that the global organization of neural circuits for locomotion is largely conserved across vertebrates and invertebrates. This is remarkable given the evolutionary distance (4–6) across species and the differences in the number of neurons: The spinal cord (SC) of the commonly studied mouse *Mus musculus* has orders of magnitude more neurons than the ventral nerve cord (VNC) of the fly *Drosophila*

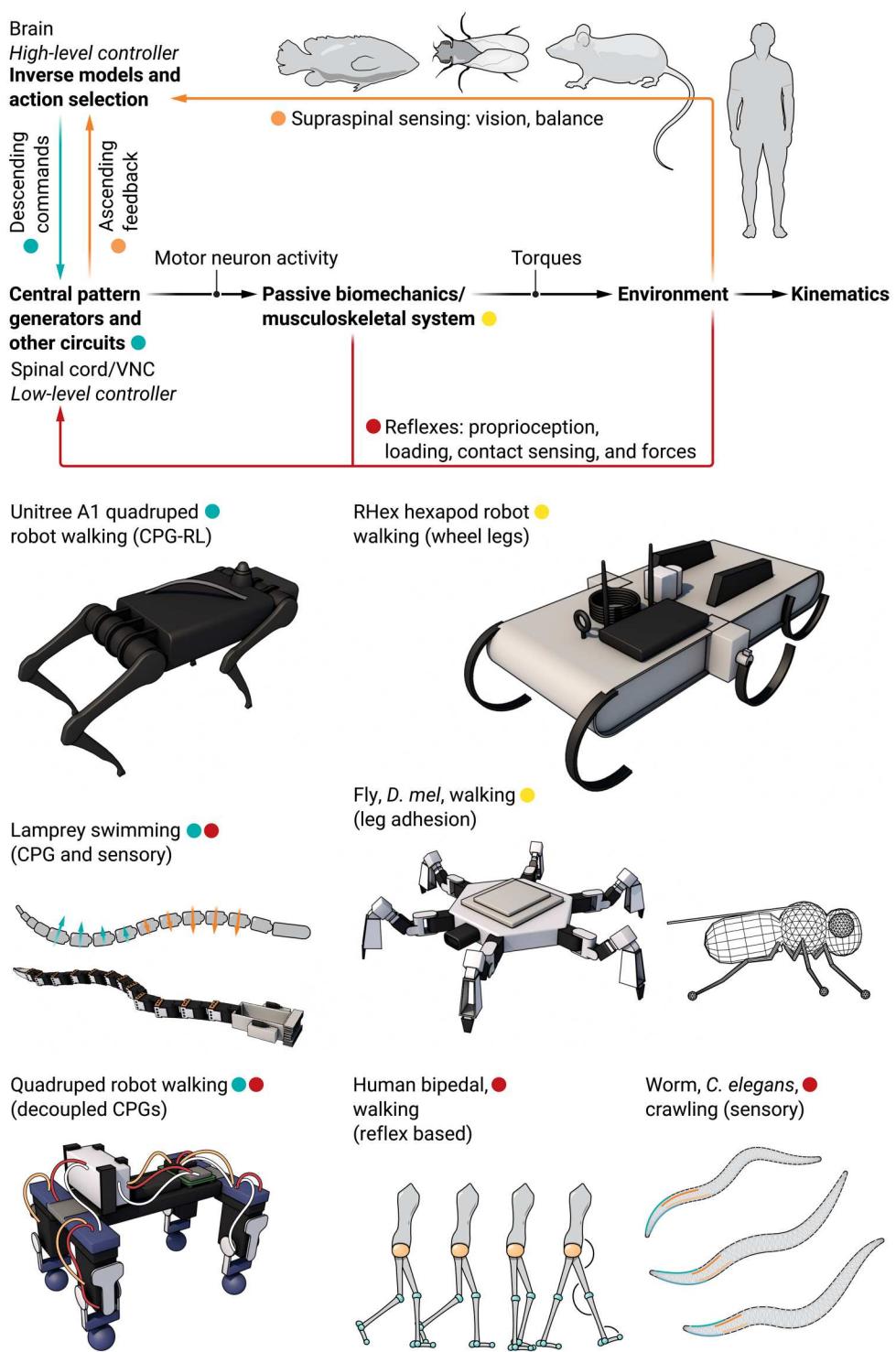
melanogaster, another popular experimental organism in neuroscience [about 10^6 (7) versus about 10^4 neurons (8), respectively]. These conserved organizational principles are schematized in Fig. 1. First, in both vertebrates and invertebrates, a relatively small number of neurons that descend from the brain are responsible for engaging downstream motor circuits in the SC and VNC (9). These are thought to engage motor systems principally by driving central pattern generators (CPGs), neurons or neuronal circuits that produce periodic bursts in the absence of a bursting input, to generate rhythmic appendage and body movements (Fig. 1, teal) (10). Descending neurons may also modulate reflexes and directly influence lower motor neurons (11). CPG-based control is capable of coordinating very different modes of locomotion, including swimming and walking (12). Second, motor circuits receive mechanosensory and proprioceptive feedback from the body and limbs (6). This feedback can be used for reflex-based control (Fig. 1, red). Third, mechanosensory feedback can be used to adjust CPG-based network dynamics to make locomotion robust against external perturbations or more effective over unstructured terrain (Fig. 1, red and teal) (13). Fourth, an animal’s awareness of its own ongoing behaviors is enabled by ascending projections from motor circuits to the brain (14, 15) and by supraspinal sensing modalities, including exteroception such as vision, smell, hearing, and the sense of balance through the vestibular system (Fig. 1, orange). Together, these inform the brain’s selection of appropriate future actions, the generation of inverse models to guide such actions, and the acquisition of learned motor skills. Last and critically, active neural control is filtered through the passive biomechanics of the body and physical interactions with the environment (Fig. 1, yellow). Embodiment has undoubtedly shaped the evolution of effective neural control strategies.

These conceptual neural control principles—descending drive, CPGs, sensory feedback, and embodiment—do not exist in isolation but are embedded within complex nested control loops. Therefore, although these principles were originally identified through human interpretation of experimental results (Fig. 2A), human intuition alone is not sufficient to evaluate their precise contributions to effective biological locomotion. Recent technical advances have made it possible for computational modeling and robotics to

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Fig. 1. A schematic flow diagram highlights motor control principles derived from experiments performed across diverse species and their application to neuromechanical simulations and robots. Although the precise implementation varies, including an orders-of-magnitude difference in the number of neurons, fundamental similarities in locomotor control are apparent. These principles have been tested in neuromechanical simulations and used to design the morphology and control of robots. First, low-dimensional command signals descending from the brain drive low-level motor control centers: the SC in vertebrates and the VNC in invertebrates. These descending signals then impinge on coupled CPGs to generate rhythmic movements (teal). This principle, descending control of CPGs, has been used to control quadruped robots using reinforcement learning [adapted from Bellegarda and Ijspeert (74)]. Alternatively, reflex loops based on sensory feedback have been studied in neuromechanical simulations of crawling worms [adapted from Izquierdo and Beer (41)] and walking bipeds [adapted from Geyer and Herr (47)] (red). Both CPG- and sensory feedback-based approaches have been combined as demonstrated in neuromechanical simulations of a swimming lamprey [adapted from Thandiackal *et al.* (75)] and for a quadrupedal robot [adapted from Owaki *et al.* (77)] (red and teal). Last, the output of motor circuits is filtered by passive biomechanics and interactions with the environment to give rise to observed kinematics. Biomechanical features can strongly constrain controllers, as for leg adhesion in a simulation and robot of the fly [adapted from Ramdya *et al.* (36)] and can also yield efficient design strategies as for the RHex robot with wheel-like legs (adapted from GRASP Laboratory/University of Pennsylvania) (yellow).

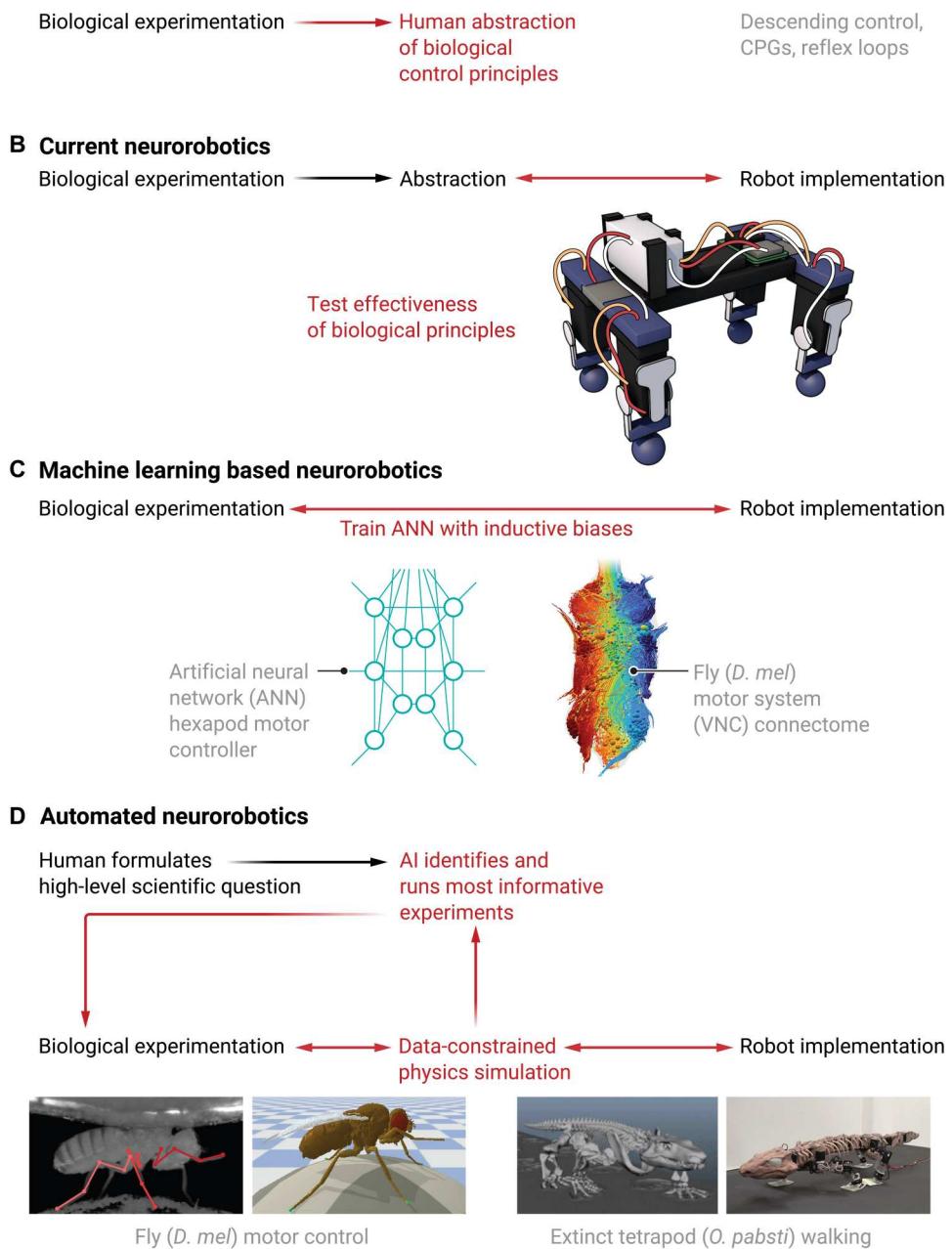


address this challenge (Fig. 2B). First, the biomechanics of animal body parts can now be modeled more realistically than before using physics simulations of interlinked structures (appendage segments) with, in some cases, experimentally defined densities, flexibilities, and degrees of freedom. Second, active movements of these structures can be controlled using artificial neural networks (ANNs) that drive simulated abstract muscle models. Third, when simulations

are unable to emulate the complex physics of how the body interacts with the environment, robots can be used as physical models of real animals.

In addition to gaining fundamental insights into the neuroscience of motor control, simulations and robots also facilitate the translation of biological insights into the design of robotic controllers. It is worth trying to replicate some of the principles of animal

A Classical neuroscience



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Fig. 2. The progression of interactions between motor control neuroscience and robotics. (A) Classically, human scientists have interpreted the results of biological experiments (measurements and perturbations) to derive abstract motor control principles. (B) Robotics has more recently been used to test the effectiveness of these principles. Image adapted from Owaki *et al.* (77). (C) In the near future, we anticipate that new principles can be found by leveraging learnable ANNs, with topologies that are potentially informed by the motor system connectomes of real animals. These may directly inspire the design of robotic controllers. (D) In the distant future, we expect neurorobotics to become fully integrated into neuroscience and partially automated, with an AI scientist using data-informed simulations and robots to identify the next most informative experiments while being guided by a human-defined high-level scientific question. The first steps in this approach are illustrated by the use of a fly biomechanical model to infer unmeasured forces and the use of a simulation and robot to explore the walking gait of an extinct tetrapod. [Images were adapted from Lobato-Rios *et al.* (110) and Nyakatura *et al.* (111).] Note that these new approaches (C and D) are expected to coexist with classical approaches (A and B).

motor control in robot design because animals typically outperform most robots in terms of locomotor agility, efficiency, and robustness. These principles may also provide a simpler implementation compared with alternative control approaches, a possibility highlighted by the conservation of neuromechanical control principles across morphologically diverse and evolutionarily distant animals that use markedly distinct locomotor styles to traverse different media. Robotics has a long tradition of taking inspiration from biology. Animals have informed robot morphologies—fish-like, snake-like, legged, and humanoid—as well as robot control. Some of the first robots, such as the tortoise robots of William Gray Walter, were driven by animal-like reflexes implemented on analog computers to perform phototaxis and obstacle avoidance (16, 17). Rodney Brooks's subsumption control architecture, linking sensing to action without the need for internal models of the world (18, 19), was also inspired by multilayered controllers hypothesized to be found in animal nervous systems. Last, the concept of embodied intelligence (20), in contrast to an artificial intelligence disconnected from the physical world, was inspired by body and body-mind interactions found in animals. However, the field of bioinspired robotics has its own challenges. First, one must decide whether a bioinspired robotics project is mainly driven by the goal to solve an engineering problem, such as improving locomotion performance, or to address a fundamental scientific question, such as identifying animal motor control principles. For engineering objectives, one must precisely define how biological inspiration can contribute to robotics. This depends on the development of good benchmarks and metrics that test whether a bioinspired approach actually improves performance over more traditional robot control architectures. Second, it is important to choose the correct level of biological abstraction and to implement key properties of an animal that are not artifacts of evolution (behaviorally irrelevant properties stemming from ancestral circuits) and that do not aim to satisfy orthogonal objectives. For instance, some limb features have evolved for mate signaling rather than for locomotion and hence might not be useful for improving robot performance. Without taking these considerations into account, a biologically inspired approach may fall into a “death valley” where it neither contributes to robotics nor advances our understanding of biology (21). A review and consideration of past successes in bioinspired robotics can help guide future work.

Bidirectional interactions between neuroscience and robotics have been reviewed before, most notably in the context of sensorimotor navigation and learning in insects and vertebrates (22–24) and in bioinspired locomotion (21, 25). In this Review, we focus more deeply on the testing and translation of biological motor control principles using simulations and robots and on highlighting opportunities for future research. First, for three core concepts—control using CPGs, reflex loops, and taking into account biomechanics—we present case studies that illustrate how robotic tools can be used to investigate the neuromechanics of animal locomotion and how bioinspiration gives rise to robot designs and controllers that, to some extent, outperform traditional engineering designs. Last, we speculate on how, in the future, a closer integration of robotics and biology might uncover new motor control principles that can be applied toward improving robotic control.

NEUROROBOTIC EVALUATION AND APPLICATION OF BIOLOGICAL MOTOR CONTROL PRINCIPLES

Neurorobotics is a research discipline at the interface between neuroscience and robotics (26–29). A neurorobotics framework, leveraging simulations and robots, can accelerate biological discovery in a number of ways. First, with these technologies, one can measure underlying quantities that might otherwise not be experimentally accessible. For example, the activities of neurons and muscles as well as torques and forces can be inferred from neuromuscular simulations rather than through difficult and invasive direct measurements in real animals. This has been demonstrated in an early work studying the role of CPGs in lamprey swimming that used embodied ANNs to predict the dynamics of underlying spinal networks (30). In addition, embodied data-inspired controllers have been used to study locomotion in invertebrates such as the stick insect (31–34). Second, simulations and robots permit perturbations that are difficult to perform on real animals—for example, the manipulation of biomechanical properties such as viscoelasticity and adhesion, the precise ablation of neurons within bioinspired ANNs, and the modification of environmental properties such as fluid viscosity and ground friction. Third, unlike physical experiments, simulations can often be performed faster than real time and increase the speed of experimentation. Simulations can be used to artificially evolve neuromechanical systems or to perform a brute-force grid parameter search. Last, although they are simplified models of real animals, experiments in simulations and robots can generate more reproducible results across experiments because, unlike real animals, their behaviors do not as heavily depend on internal states such as hunger, thirst, and fatigue. Together, these opportunities allow one to identify and test arbitrary motor control approaches, including those that may not be observed in nature. These “what-if” experiments allow one to identify criteria that may be important for animal behavior (not necessarily optimal but good enough) and to uncover non-motor constraints that may have driven the evolution of extant animal behaviors.

In this section, we present case studies that illustrate how experimentally derived principles of motor control have been tested and exploited in scientific and engineering studies, respectively, using this neurorobotic framework. We focus on crawling, swimming, and walking as a function of CPG-based control, reflex loops from sensory feedback, and features of embodiment. From the many studies in this rapidly growing field, we have chosen this subset because we feel that they reflect well a general framework that can guide future work. For each subsection, we indicate whether the presented work informs fundamental science or the engineering of robots.

Biomechanics, morphological design, and control

Locomotion emerges from passive interactions between the body and the environment, as well as from the concerted activity of myriad neural circuit elements. Many modern studies of locomotion focus on the latter, primarily by recording neural activity in explant tissues or in behaving animals. However, neural controllers have evolved in the context of body mechanics and world physics. Therefore, it is also necessary to understand how the viscoelastic properties of tissues (muscles, tendons, and bones or exoskeletons) and the physics of the environment sculpt controlled movements. This gap in biomechanical knowledge is a fundamental impediment

toward reproducing animal behaviors in simulations or robots—a benchmark for how well we understand biological motor control. Because it is difficult to measure and perturb these biomechanical properties in real animals, this gap must also be addressed through experiments with simulated agents and robots. Here, we highlight two research efforts that have used this approach to investigate and engineer locomotor controllers that focus on the roles of biomechanics and morphology in control (Fig. 1, yellow).

Leg adhesion and fast insect walking gaits (informing fundamental science)

Walking and running can be characterized by “locomotor gaits” defined by the relative phases of leg movements. Gaits differ widely across species and can depend, for example, on the relative importance of drag and inertial forces (35). Large vertebrates such as horses locomote fastest using dynamically stable gaits—often with flight phases in which every leg is off the ground. By contrast, insects walk fastest using a statically stable tripod gait in which each front leg moves in phase with its contralateral mid- and ipsilateral hind leg. Thus, even if the insect were to pause while using the tripod gait, its stance would remain stable. One possible explanation for this key difference in fast locomotor gaits across vertebrates (dynamically stable gaits) and insects (statically stable gaits) is that many insects must locomote in three dimensions (sideways and upside down) using adhesive pads and claws on their leg tips. Testing this hypothesis in real animals is difficult. Therefore in (36), the authors developed a simulation of an adult *D. melanogaster* fly in which walking gaits were defined by the phase relationship between each of six continuously actuated legs (without a neural network controller). This allowed the authors to focus purely on the role of biomechanical adhesion in the generation of fast locomotor gaits. They optimized the walking speed of this fly model under different simulation conditions in which they could run hundreds of experiments. They found that statically stable tripod gaits emerged as the fastest when optimizing for vertical walking on the wall with leg adhesion. By contrast, for fast ground walking without leg adhesion, a dynamically stable hexapod “bipod” gait not seen in nature emerged. Bipod locomotion was also quicker for a large hexapod robot. This study suggests that the requirement for three-dimensional (3D) locomotion using leg adhesion may have driven this difference in fast locomotor gaits between insects and vertebrates. It also highlights how even abstract simulations and robots can inform our understanding of the interplay among biomechanics, ecological goals, and locomotor control strategies.

Robust, open-loop hexapodal robot control inspired by cockroach locomotion (informing engineering)

The importance of mechanics in locomotion is also well illustrated in the design of RHex, a hexapod robot with six rotational limbs whose design was inspired by the study of fast cockroach gaits (37, 38). A key insight into its development was that stable locomotion can be obtained using an open-loop tripod gait under the control of a simple clock as long as leg stiffness is properly tuned. Its control principles were derived from studies showing that, in cockroaches generating fast gaits, motor patterns measured through electromyography did not vary between flat and highly irregular terrains (39). This suggests that these fast gaits are controlled in open loop. With properly tuned limb stiffness, this approach can be used to generate stable robotic locomotion on complex terrain (38). The RHex robot was later commercialized by Boston Dynamics and deployed in very complex terrains—mud, sand, and dense

vegetation—that would have been very difficult to traverse using traditional robots with wheels or continuous tracks. Thus, RHex is an excellent example of bioinspiration leading to one of the sturdiest robots with outstanding traversability in multiple types of environments.

Control via reflex loops with sensory feedback

Both the SC in vertebrates and the VNC in invertebrates contain reflex loops in which inputs from sensory neurons, including mechanoreceptors, project to motoneurons (directly or indirectly via interneurons) to trigger fast motor responses. These feedback loops ensure fast reactions to perturbations but may also generate rhythmic motor patterns through a chain of movements triggered by preceding sensory signals. As we will discuss in the next section, neuromechanical simulations have been used to show how invertebrate crawling and human walking may rely on such sensory feedback loops (Fig. 1, red).

Worm crawling can be explained by sensory feedback loops (informing fundamental science)

Limbless animals can propel themselves forward or backward in a viscous media by performing undulatory movements. For example, the worm *Caenorhabditis elegans* uses dorsoventral axial undulations to move through soil. *C. elegans* is a popular experimental organism in neuroscience because it offers genetic access to individual neurons that can be identified across animals. Thus, in the worm, one can express genetically encoded indicators to record neural activity of chosen neurons or genetically encoded actuators to drive neural activation or silencing of specific neurons. Moreover, the connectivity (“connectome”) of the worm’s nervous system was the first to be mapped (40). The simplicity of the worm and its behavior lends itself well to the comprehensive investigation and modeling of locomotion. Recently, Izquierdo and Beer (41) used neuromechanical simulations to test the degree to which a control strategy depending only on sensory feedback and biomechanical properties can give rise to worm-like locomotion without the need for centrally generated rhythmic oscillations. This question was also previously explored in (42), which developed a 2D neuromechanical model of the worm. Here, they populated this model with a connectome-inspired neural network that included circuits for head motoneurons and the VNC. This network could then actuate damped spring-like muscles with Hill-like force-length and force-velocity properties. They performed evolutionary optimization to obtain neural and muscle parameters that could best replicate the recorded average velocity of real worms crawling on an agar plate. Two features of the resulting successful networks are noteworthy. First, a large majority of neuromuscular solutions could reproduce worm crawling (both average speed and body kinematics) by generating oscillations that did not rely on CPGs but instead on stretch-receptor feedback signals arising from mechanical deformations of the body. Because this work was performed in a neuromechanical model, the authors could pinpoint these mechanisms by measuring the activities of simulated stretch sensors and motor units. Second, traveling waves along the body remained intact even after neural units in body segment subsets were artificially silenced. This was due to the passive propagation of mechanical curvature on one side of the body to neighboring segments. Similar control principles based on proprioceptive stretch feedback have been tested on a robot inspired by *C. elegans* (43), allowing the

robot to successfully navigate a terrain lined with pegs without the need for exteroception.

Similar sensory-driven locomotion was also investigated for crawling in the larval stage of the fly *D. melanogaster*. The brain of a *Drosophila* larva has also been mapped (44), and specific neurons can be identified across individual animals, genetically targeted, and manipulated (45). Unlike undulating worms, fly larvae crawl using axial peristaltic movements that travel along the body segments. Using an elegant mathematical and phenomenological analysis of the behavior of a neuromechanical model, Loveless *et al.* (46) found that many simulated instances of their model resembled real larval crawling trajectories. Crawling emerged mostly from local (segmental) sensory-motor positive feedback loops and long-range (intersegmental) inhibition. As for the *C. elegans* worm, these mechanisms circumvent the need for centrally coordinated CPGs. These findings again highlight the power of neuromechanical models for the integrative mechanistic study of animal locomotion.

Reflex loops can control bipedal locomotion in a human neuromechanical model (informing both fundamental science and engineering)

Akin to the distributed control principle for invertebrate locomotion described above, Geyer and Herr (47) developed an influential model of human locomotion that demonstrates the importance of biomechanics and the fact that a limited number of reflexes can generate locomotion as a limit cycle without the need for CPGs. Their model includes a 2D musculoskeletal model of the human body, including seven muscles and three rotational degrees of freedom per limb. In their model, a set of negative and positive feedback loops representing spinal reflexes are active either during stance or swing to control muscle activation, and a simple balance controller keeps the torso upright. This neuromechanical simulation produces sagittal plane gaits that are remarkably human-like, with a good match to human joint kinematics, ground reaction forces, and even muscle activities. The gaits are also robust to small perturbations like encountering sloped terrain. The model has been extended in various ways by Geyer and other research groups, for instance, to produce 3D running gaits (48), to modulate gaits (49–51), to modulate speed by adding CPG circuits (52), to study different pathologies (53–55), and to explore walking in other bipedal animals such as simulated dinosaurs (56). Although the model was not originally designed to control robot locomotion, its key ideas, simulating muscle dynamics and reflex control, have been successfully used to control wearable robots and bipedal robots. For instance, they were used to control an ankle prosthesis (57, 58), an ankle-and-knee prosthesis (59), exoskeletons (60), and a simulated torque-controlled bipedal robot (61). Interesting properties of these reflex loop–based systems include robust human-like locomotion, modularity, active compliance, and fast learning/optimization of controllers due to domain knowledge embedded in the reflex loops.

Control Via CPGs

Animal motor control appears to be modular, with actions being generated by combinations of “movement primitives”: sensorimotor control modules that are activated in sequence and in superimposition to generate rich movements (62–65). A useful analogy is to view biological locomotor circuits as organized similar to a puppet on strings (66), in which complex movements planned in the brain (the puppeteer) are produced by modulating the amplitude and

timing of a limited number of descending pathways (pulling a few strings) to the SC or the VNC. Downstream circuits in the SC and VNC then generate movement primitives from a “vocabulary” of possible movements. These movement primitives are thought to be implemented by low-level circuits in the SC and VNC, including CPGs that can produce periodic activity without the need for periodic inputs and discrete pattern generators or force fields that mediate point-to-point movements. Spinal circuits are composed of multiple CPGs, typically one pair of oscillators per pair of antagonistic muscles, that are distributed and coupled together. CPG oscillations can be modulated by inputs from descending pathways to change locomotor speed or gaits. CPGs can be viewed as kinds of feedforward controllers that transform simple high-level commands, such as a desired speed, into multiple periodic signals that can be sent to muscles. This principle has been exploited for low-level robotic control in several ways (Fig. 1, teal).

Dynamical movement primitives inspired by the modularity of animal locomotion (informing engineering)

In robotics, the concepts of modularity and movement primitives have led to the design of dynamical movement primitives (DMPs): pattern generators based on nonlinear dynamical systems with well-defined attractor properties (67). DMPs approximate the functions of pattern generators in the SC or VNC and can generate either discrete or rhythmic movements like reaching or locomotion, respectively. They can be trained on the basis of human demonstrations using locally weighted regression. Once they have learned a particular movement, they can replay the movement while being robust against perturbations and can be reused in new conditions, such as for targeting a new point in space by modulating simple command signals. DMPs are now often used for trajectory generation and have been used for different types of motor tasks in humanoid robots (68–70).

Reinforcement learning of high-level controllers for low-level CPGs (informing engineering)

How high-level controllers in the brain learn and plan movements while taking into account the constraints of downstream SC or VNC circuits remains largely mysterious. In the puppet on strings analogy mentioned above, we know that strings may have either global or local effects. For example, descending pathways may either project to multiple locations in the SC/VNC to affect whole-body movements or project locally to influence the movements of only a few joints. In addition, some descending inputs drive rhythmic movements and some discrete movements; some inhibit reflexes, whereas others amplify them (13). Therefore, descending commands are very different from desired joint angles or torques (as in robotics) and from muscle contraction signals (as is sometimes assumed in neuroscience). A combination of reinforcement learning, CPG models, and robots has been used to explore how brain commands might orchestrate motor circuits and also how to simplify learning on legged robots (71–73). For example, deep reinforcement learning has been used to train policies representing higher brain modulation to control the omnidirectional locomotion of a quadruped robot controlled by an abstract CPG model (74). The advantages, compared with more traditional reinforcement learning using policies in joint angle space, include simpler rewards for good controllability (including omnidirectional locomotion and the ability to change postural height and ground clearance), simpler transfer to the real world, and more natural-looking gaits. The disadvantage is that the approach is possibly

less generic and, in this case, specific to periodic movements. Still, this work highlights the benefits of CPGs as good building blocks for fast learning, in contrast to traditional reinforcement learning approaches that require complicated reward functions and millions of training episodes to learn a control policy.

Combining CPGs and sensory feedback for robust motor control

Although CPGs can generate oscillations in isolation, they also receive input from sensory feedback. Thus, in animals, CPGs and reflexes are tightly integrated. To achieve animal-like locomotion, it is likely that robotics will require the proper integration of feed-forward CPGs and feedback control loops. Neuromechanical models and robots have been used to decipher the respective contributions of these mechanisms when they are combined to achieve locomotor control (Fig. 1, red and teal).

Vertebrate swimming via coupled oscillators and sensory feedback (informing fundamental science)

As for crawling, undulatory movements are also used to swim. Thus, a related question arises: To what extent do undulations arise from central CPG-based or peripheral sensory feedback-based mechanisms? Thandiackal *et al.* (75) addressed this question using an abstract neuromechanical simulation (and a robot) based on the lamprey. They outfitted the simulation and robot with force feedback sensors communicating with intersegmentally coupled oscillators. This allowed them to perturb one or more neural components to measure their relative contribution to swimming speed. They found that swimming can be produced using either central feedforward or peripheral feedback mechanisms. By varying parameters in their model, they observed that traveling undulatory waves can be generated over a large range of oscillator intrinsic frequencies and feedback strengths. However, controllers that combine both central and peripheral mechanisms are more robust against neuronal lesions than those that use only one of these mechanisms. This result was also confirmed in a real aquatic robot.

Distributed and fault-tolerant control using an insect-inspired decentralized approach (informing engineering)

Insect legs are embedded and covered with proprioceptive and tactile sensors that are thought to play an important role in decentralized locomotor control (33). One group implemented this feedback mechanism for interleg coordination in robots. They termed this approach "Tegotae," a Japanese concept that describes how well a perceived reaction (sensory information) matches an expectation (an intended motor command) (76). Controllers were made of distributed oscillators that do not have direct couplings (like typical CPG models) but rather receive local sensory feedback signals. This led to the emergence of gaits via the synchronization of oscillators through physical interactions with the environment. For instance, a Tegotae feedback loop that slows down the phase of oscillators when limbs are loaded can lead to stable gaits on a quadruped robot (77). Similar types of load-dependent reflex loops are found in mammals, including cats (78). Interestingly, when the frequency of the oscillators is increased, this leads to gait transitions among walking, trotting, and galloping (79), as has been observed in cat experiments (80). Similar ideas have been used to control snake-like crawling (81), bipedal locomotion (76), salamander-like walking (82), and, as reviewed above, swimming (75). Compared with the traditional view of biological CPGs, emphasizing the importance of inter-oscillator coupling to generate

synchronized gaits, the Tegotae principle suggests that sensory feedback to oscillators for actuated joints (or pairs of muscles in animals) might be more important than (strong) direct intersegmental couplings for interlimb synchronization. This lends more importance to the embodiment of the controllers and to physical interactions with the environment. Such a bioinspired control approach is particularly interesting for robotics: It can offer robust locomotor control implemented in a distributed manner on different microcontrollers with higher fault tolerance and lower computational cost.

THE FUTURE OF NEUROROBOTICS AND MOTOR CONTROL

These aforementioned examples highlight how some core motor control principles have been tested to gain insights into fundamental science and leveraged to improve our engineering of robots. However, because these long-standing principles were obtained from human interpretation of biological experiments, they probably exclude additional undiscovered control principles that might be instrumental to reach the goal of more agile, efficient, and robust robotic locomotion. To discover such principles in the future, we may complement human abstraction with machine learning (Fig. 2C) and a direct dialog between experimental data and realistic simulations of the (animal or robot) system under consideration (Fig. 2D). For engineering applications, such a learnable controller might have a generic architecture, as in the case of deep reinforcement learning of robotic control (83). Alternatively, to gain neuroscientific insights, controllers might have strong inductive biases that are based on the connectivity of an animal's real nervous system (as for the *C. elegans* neuromechanical simulation described above). Such a detailed, nearly one-to-one mapping between models and data would permit the use of simulations to generate hypotheses that can then be tested by recording, activating, or silencing specific neural circuits in a behaving animal (84–88). This latter vision has not yet been achieved thus far, and in most of the studies described above, the high level of abstraction of computational models has made it challenging to generate fine-grained experimental predictions. Note that we do not advocate abandoning more abstract, low-order, models successfully used so far (Fig. 2, A and B), but rather, we see opportunities for exploring additional new avenues thanks to several recent technological developments (Box 1).

First, because interaction forces between body parts and the environment are fundamentally important in the study of motor control, physics simulation environments must accurately replicate the internal and external forces that an animal or robot experiences in the real world. For instance, although it is computationally expensive to model the compliance of an insect's cuticle-based exoskeleton, its mechanical properties may play a key role in the sensing of limb loading to perform corrective movements. Thus, it is important to design more realistic morphological meshes that emulate (in a data-informed manner through careful mechanical characterization) passive elastic and stiffness properties. These would be embedded within more realistic physics environments and simulations that can model body physics, collisions, and other interaction forces at increasingly small time steps while retaining accuracy and robustness against numerical errors. These challenges have been addressed by the development of improved physics engines, including Bullet, Havok, MuJoCo, ODE, and

Box 1. Technological advances enabling the integrative identification of biological motor control principles.**Neuromechanical simulations**

Physics simulators: New physics simulators permit a more realistic modeling of collisions with the appropriate scaling to accurately represent the physics of animals of different sizes. This can help address the “sim-to-real” problem: the difficulty of ensuring that the physical realism (and experimental results) of simulations accurately mimic biological or robotic systems.

Computation: Compute capacity and GPU-based parallelization enable more rapid and even faster than real-time exploration of parameter space for neuromechanical motor controllers.

Parameterization: Statistical optimization approaches can instantiate hundreds of open parameters in numerical neuromechanical models for which biological data are often missing.

Biological data and tools

Digitization of body morphologies: CT enables the accurate recapitulation of geometric constraints and joint degrees of freedom.

Pose estimation: The rapid collection of precise 3D kinematic data by deploying trained deep neural networks on video data has supplanted arduous marker-based motion capture or manual annotations in small animals.

Connectomes: Descriptions of the connectivity of all neurons in a fragment or entire nervous tissue can be used to build biologically inspired and constrained ANN controllers.

Genetic tools: Enable investigators to repeatedly record, activate, and silence the same neurons, neural circuits, and muscles across individual animals. Optogenetics uses light of different wavelengths for activating or deactivating genetically labeled neurons and microscopes for recording their activity. Chemogenetics uses chemicals to modulate the activity of genetically labeled neurons.

Bioinspired robots

Materials and manufacturing techniques: 3D printing and other approaches pioneered in the field of soft robotics can facilitate building robots that are more biologically accurate. This includes replicating muscle-like actuation and flexible sensory organs such as touch-sensitive skin.

Onboard computing: The miniaturization of computing hardware allows for the real-time processing of sensory feedback that better mimics motor control in biological nervous systems.

data (92–94). With these data, one might test the explanatory power of an arbitrary motor controller by assessing the degree to which it can accurately reproduce measured animal behaviors. As an additional biological constraint, ANN motor controllers can be designed on the basis of animal nervous system connectomes or graphs of neural connectivity (95–97) and physiological measurements from identified cell types. Connectomes are becoming available thanks to advances in automated electron microscopy, image segmentation, and neuron reconstruction. By combining these data, one might use imitation learning of real measured limb kinematics to parameterize a connectome-based ANN motor controller. However, it remains difficult to instantiate hundreds of open parameters—synaptic weights, sensory gains, and muscle parameters—in numerical neuromechanical models in the absence of biological data. The dynamics of a model are typically highly dependent on these parameters. This important challenge in high-dimensional models can possibly lead to ill-defined problems, with multiple sets of parameters generating similar behavior. Thus, how to set parameters (through inference from biological data or through optimization), identify which parameters are biologically relevant, and assess parameter sensitivity are important open questions. It is likely that algorithms for parameterizing ANNs will have a strong statistical component, enabling the identification of families of well-performing solutions and distributions of effective parameters (98). Once parameters have been set, network solutions represent predictions about real biological neural controllers. These predictions can then be tested using genetic tools to precisely target specific neurons or neural populations and then to record, activate, or silence these neurons through optogenetic or chemogenetic means—methods that use particular wavelengths of light or exogenous chemicals to perturb specific neurons (45).

Once these kinds of data-driven, and likely more complex, motor control networks are identified from a dialog between animal experiments and simulations, the accessibility of ANNs then makes it possible to investigate, distill, and abstract their core features for implementation as robotic controllers. However, some of these biological motor control principles may not be readily and efficiently emulated using conventional hardware. For example, fast real-time processing of sensory feedback may require implementation on miniaturized onboard computing. In addition, neuromorphic chips may be needed to replicate spiking neural networks. These have already been used in event-based cameras (99) to confer interesting properties such as very high temporal resolution, very high dynamic range, and low power consumption. In addition, to test and apply the results from bioinspired simulations in a real robot, one must overcome the so-called “sim-to-real gap”—differences between simulation and real-world physics cause a robot’s behavior to deviate from that of its associated simulation (100). Although this gap is being steadily narrowed with increasingly accurate physics engines and realistic simulation environments, it remains challenging to scale robots down to the size of smaller experimental animals such as insects and rodents. This scaling is needed to represent the physics of animals of different sizes. For example, the relative importance of inertial and viscous forces strongly determines the behavior of a system in motion, and small animals such as insects experience stronger viscous forces (low Reynolds number). It also remains challenging to replicate biomechanical properties in engineered materials, for example, fabricating exoskeleton cuticle for robotic models of insects or fabricating

PhysX—each with their own advantages and disadvantages for different applications (89). Improved realism comes with a tremendous increase in computational cost. This is partially addressed by an improved computing power of workstations and the enabling of graphics processing unit (GPU)–based parallelization. The latter also unlocks the possibility to more rapidly (even faster than real time) explore the parameter space of neuromechanical controllers in physics simulations such as Nvidia’s Isaac Gym (90).

Advanced biological tools and data are also necessary to generate meaningful comparisons between simulated or robotic agents and their animal counterparts. For example, one should have precise morphological and kinematic measurements of the animal under study. The increased accessibility of 3D computerized tomography (CT) scans has made it possible to digitize the body morphologies of small animals, such as insects and rodents, to model their morphologies, geometric constraints, and joint degrees of freedom in simulations and robots (91). Similarly, recent advances in markerless pose estimation using deep neural networks have made it possible to rapidly collect precise 3D kinematic data by deploying trained deep neural networks on videography, x-ray, and cineradiography

hair, scales, muscles, fat, tendons, and bones for robotic models of vertebrates. Materials and manufacturing techniques such as 3D printing, pioneered in the field of soft robotics (101), can help overcome this challenge by building robots that are more accurately endowed with the viscoelastic properties of biological tissues. Similarly, the development of fast direct-drive motors without gears can allow one to simulate muscle dynamics and proprioception in software rather than with complex hardware.

Moving beyond passive properties, animals also have an unparalleled number of mechanical sensors covering their bodies: hairs in mammals and bristles in insects. These likely play an important role in the ability of animals to sense and respond to their environments. Currently, although vision is well replicated, tactile sensing in robots is still relatively primitive, with many fewer and less diverse sensors, although there is fast progress in this area (102–105). Small sensors—such as cameras, accelerometers, and inertial measurement units—can be more cheaply fabricated thanks to mass production of smart phones and other portable devices. Last, more rigorous benchmarks will be needed to establish that robotic behaviors can be improved using biologically inspired algorithms. These include defining and quantifying concepts such as “agility” that include performance across multiple locomotor conditions including non-steady-state behaviors. First attempts at quantitatively measuring agility exist through specific measurements, benchmarks, or competitions (106–109) but more are needed, ideally with the same scoring methods for both animals and robots.

First steps toward automating the science of motor control

New opportunities in motor control can be found through the integration of the aforementioned computational, biological, and robotics tools. In our opinion, one of the most exciting opportunities involves automated scientific inference using machine learning. As for other domains such as computer vision, we envision that machine learning can be leveraged to overcome human biases and to accelerate discovery by making new and better use of data. Because of the importance of embodiment and interactions with the environment, this approach must be taken in tandem with physically realistic simulations. In this section, we discuss several recent studies that illustrate how realistic simulations and robots can be coupled with machine learning/computational optimization to advance the science of motor control.

Using a morphologically realistic simulation of *Drosophila* to infer unmeasured collisions and forces (informing fundamental science)

To automate the discovery of biological motor control principles, it will be useful to first generate more realistic neuromechanical models of the animal in question—specifically, to have as close to a direct mapping between simulated and real body parts and, if also required, neuronal elements. This approach is particularly interesting for studying the adult fly *D. melanogaster*: Its brain and VNC connectomes are already or becoming available, neural activity in the brain and VNC can be recorded in tethered behaving animals, and large collections of transgenic flies are available for testing computational predictions by recording or perturbing the activity of identifiable subsets of neurons. A neuromechanical simulation of the fly may be used as a platform for synthesizing diverse datasets and generating experimental predictions. Toward this long-term vision, Lobato-Ríos *et al.* (110) performed a CT scan of an adult

female fly and digitally reconstructed its biomechanical hull. They then enabled limb degrees of freedom on the basis of measurements of real limb kinematics during grooming and walking. By replaying these limb kinematics in their biomechanical model, they could infer unmeasured torques and ground reaction forces during walking and body part collision forces during antennal grooming (Fig. 2D). Importantly, altering the size and shape of the model’s forelimbs disrupted the kinematic replay of grooming, illustrating the importance of morphological realism. The authors then leveraged the neuromechanical capabilities of their model to explore locomotor controllers. They used a genetic algorithm to optimize a simple neural controller for fast and stable walking. In the future, such a network will be constrained by the fly’s VNC connectome (Fig. 2C) (96).

Using simulations and robots to infer locomotor characteristics of an extinct quadruped (informing fundamental science)

Simulations and real robots can also be used to inform our understanding of motor control in extinct species. Nyakatura and colleagues (111) explored possible walking gaits of a tetrapodal stem amniote, *Orobates pabsti*, for which a well-preserved fossil and fossilized footprints have been found. To assess gaits in a quantitative way, the authors first used a 3D skeletal digitization to design a kinematic simulation, a robot, and a robotic simulation (Fig. 2D). They then used x-ray motion analysis and ground reaction force measurements from extant tetrapod sprawling species—salamander, skink, iguana, and caiman—to define and populate a 3D sprawling gait space in which different sprawling gaits could be compared. They performed grid search of dynamic OroBOT and kinematic *Orobates* simulations to match fossil trackways assigned to *Orobates*. This revealed a wide range of possible gaits that could be classified according to metrics including energy consumption, the amount of roll and pitch (balance) of the gait, and the precision of walking on the track. These results revealed that *Orobates* likely had a more erect and advanced locomotor pattern than expected from previous studies of earlier tetrapods. This work illustrates how biologically informed robots and simulations can be used to quantitatively study the behavior of an extinct species.

Designing motor controllers using deep reinforcement learning (informing engineering)

Reinforcement learning, inspired by the principles of biological motor learning, can be used to design unique locomotor controllers thanks in large part to advances in simulators and computation (Fig. 2C). For instance, Hutter’s group (112–114) has designed a series of locomotion controllers for the quadruped robot ANYmal that have tackled increasingly complex scenarios. These learned controllers could cope with substantial perturbations like pushes, make maneuvers to self-right after falling, and produce robust gaits in challenging environments such as walking through rivers and over slippery ground. Several key contributions were the use of neural networks to learn actuator dynamics with supervised learning and to facilitate sim-to-real transfer, the use of neural networks to learn control policies with reinforcement learning, curriculum learning in randomized terrains of increasing complexity, and the use of the Isaac Gym simulator to run thousands of simulated robots in parallel on GPUs. The trained neural networks can be analyzed like biological circuits to examine and understand underlying control policies. This addresses the challenge of interpretability in deep learning. Interestingly, the learned controllers exhibited the

emergence of animal-like reflexes, such as the foot trapping reflex—a stumbling-correction reaction that leads to a fast retraction and extension of the limb when it hits something during swing (113)—as well as internal models that estimate how slippery the ground is (114). The learned controllers are starting to outperform model-based controllers and have contributed to winning the DARPA Subterranean Challenge (109). Reinforcement learning can also be an interesting way to make robots imitate animal gaits. For instance, Peng and colleagues (115) have used reinforcement learning to allow a quadrupedal robot to imitate gaits recorded from a real dog. This was accomplished by designing a reward function composed of several terms that reward both a similarity to the reference motion and the ability to move forward at a desired speed (without falling). The approach is interesting both for robotics (by using reference motions to constrain the search of possible gaits) and potentially for neuroscience as a method for reverse-engineering control circuits underlying animal behavior.

A future vision for the neurorobotics of motor control

Animals and robots in the loop (informing fundamental science)

The aforementioned approaches to constrain models with data are currently performed offline after animal or robot experiments and data preprocessing. In the more distant future, with gains in the speed of computation and model updating, we envision that bio- and neuromechanical simulations could run “in the loop” in real time with ongoing animal experiments. This will unlock new types of animal experiments in which neural, mechanical, or visual perturbations can be performed in closed loop in a state-dependent manner. For example, complementing existing experimental systems in neuroscience with closed-loop visual virtual reality (116, 117), ongoing simulations of measured animal kinematics might be used to infer unmeasured internal states like joint torques and trigger leg perturbations at particular torque values. A similar more high-level approach has previously been taken using robots to manipulate social behaviors in swimming fish (118), congregating cockroaches (119), and other organisms (120). Ultimately, in-the-loop experiments may even include a high-level robot scientist (121–124) that fine-tunes whole-organism neuromechanical models using incoming data, then generates a new hypothesis, and lastly performs experiments in an optimal way in terms of information theory by performing the minimal number of simulated and real experiments to test the validity of a hypothesis (Fig. 2D).

Bioinspired robotics taken to the limit (informing engineering)

Thanks to our better understanding of animal locomotion and advances in key scientific and engineering aspects, we envision increasing contributions of bioinspiration to robotics, for instance, in field robotics, wearable robots, and assistive robots. Bioinspired robots are especially well suited for complex outdoor environments to perform repetitive, dirty, or dangerous tasks such as inspection, transport, and environmental monitoring. Bioinspiration offers the possibility to create better hardware than traditional robotics: with better sensing using tactile skins; better efficiency using approaches taken by animals like eels that can travel thousands of kilometers without food; and a better mix of hard and soft components to emulate animals that can squeeze through small spaces, endure high physical impact, and still provide high torques and forces.

We envision future bioinspired robots that are highly fault tolerant, can self-repair like a salamander regrowing a limb, and possibly even split into different parts and keep functioning like flatworms.

In terms of control, bioinspiration can lead to robots that approach the agility and multifunctionality of animals. Indeed, we need robots that, like animals, can rapidly switch between different modes of locomotion, rarely get stuck, and use their limbs for multiple functions. We can also benefit from robots that improve over time, learn new motor skills, and possibly transfer skills from one robot to another. Last, we should also explore the possibility of going beyond biology, taking good ideas from nature, and applying them without the genetic and physiological constraints that burden animals. For instance, while still taking inspiration from biology, we can design humanoid robots with more arms, more eyes, and more types of sensing, including electric and magnetic senses. Nature has given us an incredible library of solutions to problems that robots need to solve, and we are just beginning to explore and exploit them.

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