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PAPER

A virtuous cycle between invertebrate and robotics research: perspective on a decade of Living Machines research

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Abstract

Many invertebrates are ideal model systems on which to base robot design principles due to their success in solving seemingly complex tasks across domains while possessing smaller nervous systems than vertebrates. Three areas are particularly relevant for robot designers: Research on flying and crawling invertebrates has inspired new materials and geometries from which robot bodies (their morphologies) can be constructed, enabling a new generation of softer, smaller, and lighter robots. Research on walking insects has informed the design of new systems for controlling robot bodies (their motion control) and adapting their motion to their environment without costly computational methods. And research combining wet and computational neuroscience with robotic validation methods has revealed the structure and function of core circuits in the insect brain responsible for the navigation and swarming capabilities (their mental faculties) displayed by foraging insects. The last decade has seen significant progress in the application of principles extracted from invertebrates, as well as the application of biomimetic robots to model and better understand how animals function. This Perspectives paper on the past 10 years of the Living Machines conference outlines some of the most exciting recent advances in each of these fields before outlining lessons gleaned and the outlook for the next decade of invertebrate robotic research.

Scientific history is littered with examples of nature inspiring new technologies—from Da Vinci's flying machines [1] to the invention of 'cat's eyes' road markers in the 1930s (www.catseyes.com/). Simultaneously, emergent technologies have advanced our understanding of natural systems by facilitating the verification of hypotheses in embodied agents, from Grey Walter's Tortoise [2] to Braitenberg's vehicles [3]. Together they have inspired a modern closed-loop research methodology aimed at accelerating our understanding of intelligent behaviour in animals, and realising similarly capable man-made artifacts [4–6]. The annual Living Machines conference was launched in 2011 to bring together leading proponents of this research method and has grown in impact ever since [7]. This review summarises the outcomes of a workshop titled 'No Backbone, No Problem: Morphology, Motion, and Minds of Invertebrate-Inspired Robots', held at the 10th anniversary Living Machines conference. Our aim is to highlight to a wider audience some of the most important contributions to the field of invertebrate robotics over the last decade, before looking at what challenges and opportunities remain for the decade ahead.

Invertebrates are ubiquitous and successful, colonising environments as diverse as deserts, rainforests, and oceans. The case is clear for their use as model systems to inspire the design of robots that must function in similarly challenging settings [8]. Broadly speaking, for many of the open technical issues in robotics (e.g. navigation, control, power, repairability, collaboration, construction), there are invertebrate specialists that inspire solutions in even the most challenging settings (e.g. monarch butterflies navigating across continents, or termites constructing elaborate structures).

At the same time, many invertebrate species lie at the intersection of animals that display intelligent behaviour, possess a relatively tractable nervous system, and are suitable for experimental interventions required to rapidly progress our understanding of their function. That is, encephalized invertebrates like arthropods and some cephalopods exhibit many of the same nervous system architectures [9–13] and behaviours as vertebrates, including foraging, grooming, sophisticated mating rituals, and social organisation. However, due to their relatively small size, arthropods typically control such behaviours with fewer neurons and synapses than their vertebrate counterparts, with clear benefits to computational neuroscience and biologically-inspired robotics, which are often resource-sensitive. Insects' small size also means that many behaviours can be observable in full in the wild (e.g. desert ants can be tracked in detail over their natural foraging range [14]), providing a corpus of benchmarking data both to inspire the construction of robots and compare their performance to that of animals. Moreover, insects are highly suitable for laboratory studies in which increasingly powerful genetic, optogenetic, neuroanatomical, and neurophysiological methods can be applied to study the structure and function of the nervous system. Due to their hardiness, they can withstand invasive experiments that probe their sensory-motor function, for example, by using experimental machinery to decouple mechanosensory feedback from the motor output in a behaving animal [15]. As a result of these and other features, insects have become some of the most important model systems for neuroscience research [16].

Invertebrates possess diverse geometries and materials that facilitate the control and execution of motion across a broad range of environments. It is hypothesized that such properties enable the smaller nervous systems described above to solve some problems via 'morphological computation' [17], in which the body's mechanics simplify the motor outputs required to perform a task relative to a naive solution. One example from insect flight is that the geometry and elasticity of insect wings and thoraxes amplify the power of flapping muscles and enable them to support the animal via simple periodic motor output ([18–21]; for a review, see [22]). Another example from the locomotion of larval insects, echinoderms, and other soft-bodied animals is that their highly compliant bodies enable them to conform to and traverse rugged terrain without the need for precise placement of appendages (e.g. for legged locomotion) [23]. Better understanding the geometries and materials of invertebrate bodies could greatly benefit the construction and control of mobile robots that crawl, walk and fly.

The invertebrate robotics community has played a key role in the establishment of the Living Machines approach [4, 24], which proceeds in the following way: First, a task or feature that is desirable for a robot is identified (e.g. navigation of barren alien worlds, structural resilience), before an exemplary species that is a master of that task or feature is identified (e.g. desert ants excel at navigating featureless desert salt pans [25], cockroaches can sustain loads over 300 times their body weight [26]). Hypothesised principles are then embedded into a simulated or robotic agent, and the agent's performance is compared to the animal's behaviour. An agent that performs as well as the animal may validate that researchers understand how the model species functions (note that it is not possible to generate positive proofs in this manner). Whereas, an agent that performs poorly provides researchers with a negative proof and thus with an opportunity to reject and then improve performance by modifying the model. Such models are quantified hypotheses for what to search for in future biological experiments. In essence, this process forms a virtuous cycle by which more biological progress facilitates more robotics progress, and more robotics progress facilitates more biological progress.

The last decade has seen rapid progress in three key areas of invertebrate robotics: Morphologies—advances in the structure of robot bodies [23, 27, 28]; Motion Control—how those bodies are controlled [13, 29]; and Mental Faculties—how those bodies are guided through their environments [24]. The following sections describe some of the most important advances in each of these areas over the last decade, with a particular focus on the contributions of the Living Machines community. This paper also highlights examples where knowledge has transferred from scientific to industrial settings, showing the applicability of this methodology. Finally, we close with a discussion of the opportunities and challenges that remain and some of the technologies that are likely to have a significant impact. Note that is not the authors' intention to provide a comprehensive review of these subject areas for which dedicated reviews are more suited. Rather, we aim to highlight some of the most exciting advances to inspire a further decade of innovative invertebrate robotics research.

1. Morphologies: advances in invertebrate inspired robot structures

A major challenge in robotics is to deliver robots that can traverse unstructured environments, whether by crawling, flying, walking, or some other form of locomotion. The dynamics of the body can have a major impact on the types of motions that the robot can produce [17]. Although many modern commercial robots (e.g. Spot by Boston Dynamics, Cassie by Agility Robotics) are modelled after large vertebrate animals, much can also be learned about locomotion of all types from invertebrates. In the following, we summarize some areas in which robot performance was improved by incorporating compliance into their morphologies using the Living Machines approach. These efforts have been facilitated by increasingly reliable 3D printing and other recent manufacturing techniques.

Considering the compliance of invertebrate bodies has spurred an entirely new field dedicated to soft robotics [23], that is, robots without rigid components. Such robots were naturally inspired by annelids (e.g. worms) [30], echinoderms (e.g. starfish) [31], cephalopods (e.g. squid, slugs) [32], and insects in their larval stages of development (e.g. caterpillars, maggots) [33]. The diversity and success of such animals in nature suggests that they could be useful models for robots that traverse extreme terrains (e.g. tree branches [34], the bottom of the ocean [35]), handle fragile items, or safely interact with humans or other animals. Examining their morphologies closely has led to breakthroughs in crawling, flying, and walking robots.

The crawling of worms, slugs, and caterpillars has inspired the design of many robots intended to traverse and conform to unstructured substrates or to squeeze into tight spaces (for reviews, see [23, 28]). Although all these model animals crawl, they exhibit multiple underlying mechanisms, which have each been applied to the construction of robots. One such mechanism is the hydrostatic structure of worms and slugs, whose bodies exhibit turgor due to pressurised internal fluid. As a result, their motions obey a constraint of constant volume, which has been leveraged to construct robots [30, 36] and controllers [37] to mimic worm and slug crawling. In contrast, caterpillars are not hydrostats, meaning that they do not obey the same constraint and thus cannot be controlled the same way. Instead, caterpillars rely critically on gripping the substrate to lift portions of their bodies and propel themselves forward [33]. Studying these different mechanisms closely and incorporating biological details into the design of robots has led to more diverse robot morphologies that may be applied in different situations [6].

Insect-inspired flapping-wing flight of robots has also benefited from the Living Machines approach (figure 1, left). Biological studies revealed that insect wings exhibit anisometric flexural stiffness, resulting in complex deformations during flight [18]. By carefully considering how actuators and power sources scale [38] and subsequently constructing insect-scale ‘wing drivers’ that flap isolated insect wings, scientists measured how the mechanical properties of insect wings enable them to generate lift, and engineers applied these principles to construct robot wings [39]. For example, testing the wings of the moth *Manduca sexta* revealed that the lift they generate benefits from dorso-ventrally asymmetrical stiffness as well (i.e. stiffer during downstroke), helping to further explain mechanisms underlying insect flight and inspiring engineers to design wings that generate lift under simple periodic flapping [40]. Studies analysing insect wings using engineering approaches have suggested that flying insects such as moths exploit the elastic properties of their thoracic exoskeleton to amplify rhythmic flapping motions [19, 20], which may lead to more efficient robots that can operate in the field for a long time. Applying the biological principles learned has enabled the construction of robotic wings that, due to their animal-like mass, flexural stiffness, and camber, could produce animal-like lift in a flapping robot [21, 41]. This progress in extracting and applying principles underlying flapping-wing flight exemplifies the strengths of the Living Machines approach to bio-inspired robotics.

Despite their traditionally rigid construction, even legged robots have benefited from the incorporation of animal-like compliance (figure 1, right). Walking arthropods such as adult insects, crustaceans, myriapods, and arachnids do not grow as large as vertebrates for several possible reasons (e.g. limitations of their diffusion-based respiratory systems [42]). As a result, their legs have low mass and their walking motions generate low inertial forces relative to their muscles’ stiffness and elastic forces [43], requiring different control strategies than large animals like humans or large, heavy robots [44]. Incorporating elastic elements into robot joints in parallel with the actuators mimics the dynamics of small animals and serves several useful functions, for example, enabling robots to stand while exerting no energy [45], reducing the control system’s need to respond rapidly to sudden perturbations [46], and enabling bending around obstacles [47]. Incorporating elastic elements between the actuators and environment, for example, via a compliant joint drive [48] or an elastic foot [49], also has benefits such as reducing the impact forces experienced by the robot. Some legged robots are built with entirely soft legs, granting them all these benefits simultaneously [50]. Even if legged robots are not purely ‘soft robots’, they benefit

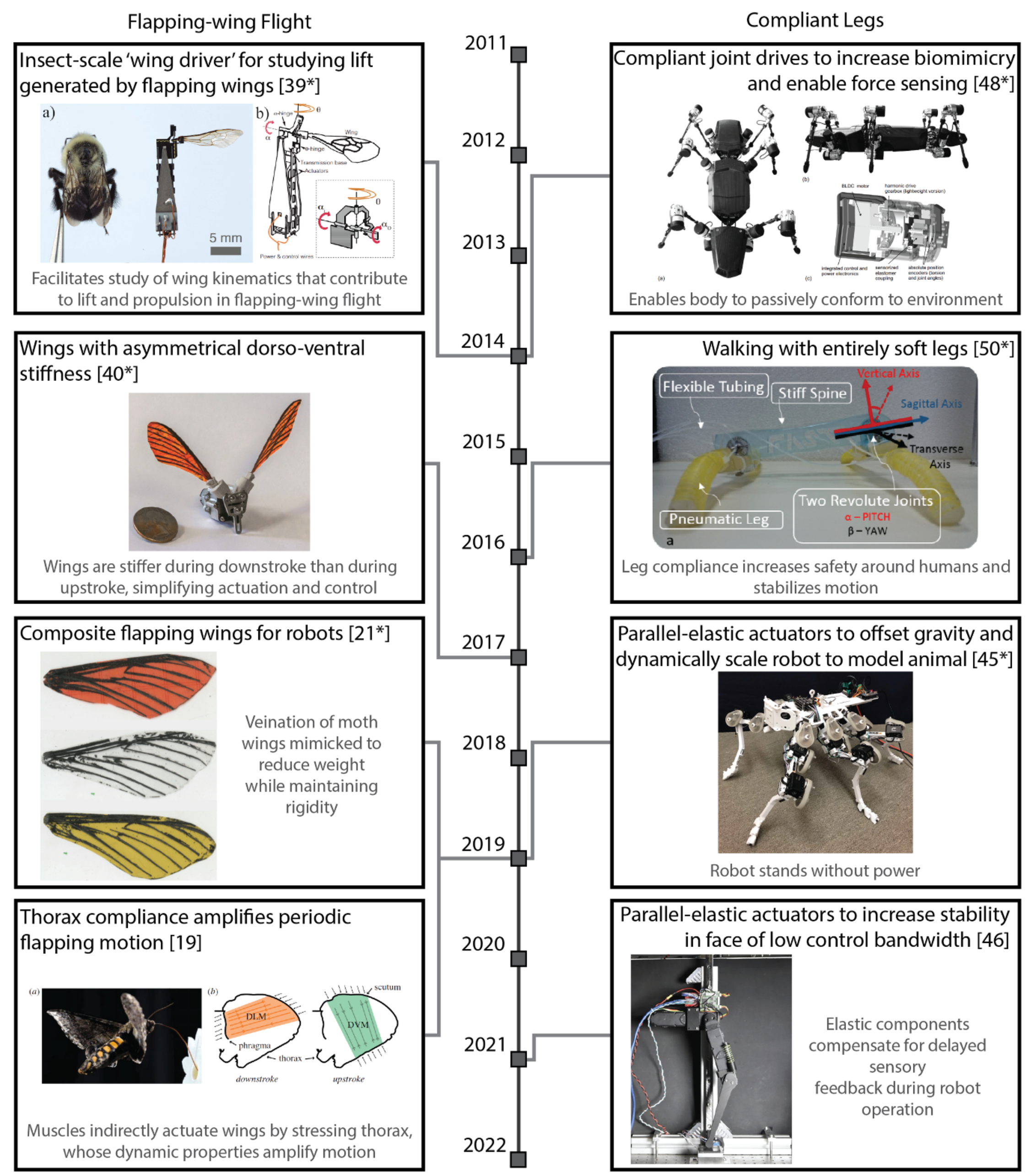

Figure 1. The progressive incorporation of invertebrate-inspired compliance into flapping-wing (left) and legged robots (right), with emphasis on those results first reported at Living Machines conferences (references marked with*). (top row, left column) Reproduced from [39], with permission from Springer Nature. (2nd row, left column) Reproduced from [40], with permission from Springer Nature. (3rd row, left column) Reproduced from [21], with permission from Springer Nature. (bottom row, left column) Reproduced with permission from [19]. © 2019 The Author(s). Published by the Royal Society. All rights reserved. (top row, right column) Reproduced from [48], with permission from Springer Nature. (2nd row, right column) Reproduced from [50], with permission from Springer Nature. (3rd row, right column) Reproduced from [45], with permission from Springer Nature. (bottom row, right column) Reproduced from [46]. CC BY 4.0.

from similar principles also extracted from invertebrate model organisms.

The explosion in soft robotic methods and applications has been greatly facilitated by additive manufacturing processes (for a review, see [27]). 3D printing enables engineers to produce a wider range of geometries than with traditional 'subtractive' methods (e.g. machining, turning), with ever-increasing precision. The fused deposition modelling technique lends itself to the construction of multi-material, multi-layered structures, enabling engineers to embed sensors and actuators within their soft-bodied robots [51]. Alternative methods such as soft lithography enable the robot to have variable stiffness throughout its geometry, which directly supports functionality such as pneumatically-actuated living hinges [31, 47, 52]. 3D printing has also enabled the rapid production of molds for casting soft robots from silicone [53]. The resulting robots possess compliance tuned to the robot's function [27] and are resilient to environmental forces due to their contained sensing and actuation [51, 54]. Advances in 3D printing have enabled engineers to mimic their model organisms and prototype their ideas more quickly, contributing to the recent growth of soft robotics.

In the coming years, we expect to see robots whose designs increasingly leverage compliance and additive manufacturing to approach the control efficacy and efficiency of their biological counterparts. With recent advances in modelling and controlling soft robots [55], they may gain more predictable performance and may become more practical for deployment in real-world scenarios, e.g. exploring disaster sites or monitoring hard-to-access infrastructure. Improved modelling methods may also reduce the computational power required to control soft robots by facilitating the design of robots with increased morphological computational power. Such robots could use their mechanics to solve the unique, high-dimensional control challenges they naturally face due to their structure and material properties if designed correctly [17]. Increased inclusion of compliant components, even within traditional jointed robotic arms and legs, may further increase the efficiency of robot locomotion by enabling robots to temporarily store work done on the robot by actuators or the environment and convert it to kinetic energy at a later time. However, such efficiency benefits may depend upon improvements in the way invertebrate-inspired robots control their motion.

2. Motion control: how simple systems control complex mechanics

For a robot to control the motion of a complex morphology (either nature-inspired or engineered), it must be equipped with a control system capable of coordinating its action in unpredictable real-world environments. The structure and function of invertebrate nervous systems have inspired the control of such robots for several reasons. First, many invertebrates have relatively large neurons that can often be identified between individuals, facilitating scientists' understanding of how control networks function [56]. Second, due to the robustness of many invertebrate species to experimentation, many key principles of nervous system function were first discovered and explored in invertebrate species. One notable example that has been particularly impactful in robotics is the discovery that many rhythmic motions are controlled by local pattern-generating networks whose phasing could be altered by sensory feedback (e.g. locust wingbeat [57], leech heartbeat [58], lobster chewing [59]). The emergence of coordinated behaviour from apparently decentralised control networks inspired the control systems of early invertebrate-inspired which had control systems based on these networks implemented as finite state machines (FSMs), in which each body segment could complete one action at once (e.g. flex or extend the leg [60–62]), and actions were selected by comparing sensory signals to specific thresholds. Such robots were capable of impressive feats of motion but were challenged by their tendency to miss specific sensory transition cues when conditions changed, for example, due to altered terrain.

More recent approaches have addressed this challenge by leveraging increased neurobiological knowledge about hexapod [63] and other invertebrate control networks [64] to control the legs of walking robots (figure 2, left). In particular, many newer controllers now mimic the distributed structure of invertebrate nervous systems [65], incorporate the dynamics of neurons and synapses [66], or both [64, 67–69]. Due to the increased compactness of computers and availability of graphical processing units for performing vector calculations, many studies have directly applied simulations of invertebrate control networks (e.g. [70, 71]) to the control of walking robots [64–68]. Such studies have increased the capability and autonomy of walking robots while simultaneously testing how effectively models of the peripheral nervous system function in the real world.

To further increase the autonomy of walking robots, for example, enabling them to autonomously avoid obstacles as they walk, additional principles from the nervous systems of invertebrates have been applied (figure 2, right). Recent work has shown that cockroaches walk along paths of varying curvature by altering the phasing between joints in the leg [71], and that such alterations are driven by neural activity in higher control centres (i.e. the central complex) [72]. This mechanism has been incorporated into the control of stepping of hexapod robots, causing each robot to alter the stepping motion of each leg depending on its heading [70, 73, 74]. This mechanism can be combined with a biomimetic visual processing network to autonomously determine the robot's heading, and thus, the coordination of the leg joints [75]. In particular, the visual network may extract information about obstacle locations, change the heading of the robot to prevent a collision, and send this information to the local leg control networks to alter stepping and direct the robot away from obstacles [75].

Finally, advanced neural controllers mimic the dynamics of the nervous system to better understand the dynamic interplay between central rhythms and peripheral sensory feedback. Such control networks may share the organization of FSM controllers of the past, but incorporate neural dynamics, e.g. leaky integration and slow-fast dynamics [69, 71], which enable controllers to generate rhythmic outputs or adapt their responses to sensory input over time. In some controllers, pattern-generating networks adapt their oscillation to match incoming sensory signals, facilitating the identification of sensory information that deviates from nominal conditions and triggering corrective action [76]. Such controllers simultaneously test the effectiveness of biological models of learning and endow robots

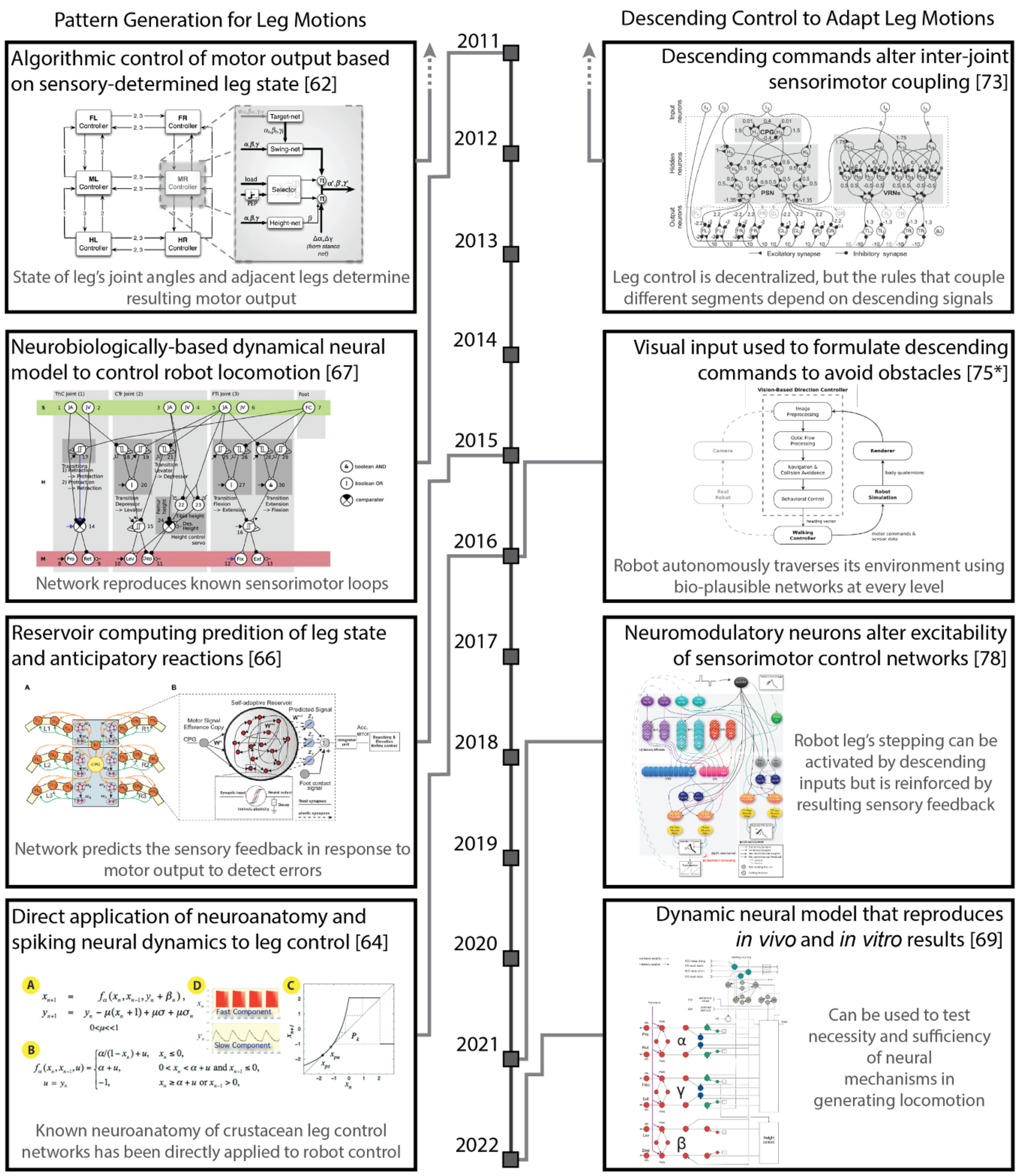

Figure 2. The progressive incorporation of invertebrate- and neural-inspired control mechanisms into the control of legged robots, both for controlling individual leg motions (left) and adapting those motions using descending signals. Results first reported at Living Machines conferences are marked with*. (top row, left column) [62] Taylor & Francis Ltd. http://tandfonline.com. (2nd row, left column) Reprinted from [67], Copyright (2012), with permission from Elsevier. (3rd row, left column) Reproduced from [66]. CC BY 4.0. (bottom row, left column) Republished with permission of ASME, from [64]; permission conveyed through Copyright Clearance Center, Inc. (top row, right column) Reprinted from [73], Copyright (2008), with permission from Elsevier. (2nd row, right column) Reproduced from [75], with permission from Springer Nature. (3rd row, right column) Reproduced from [78]. © IOP Publishing Ltd. All rights reserved. (bottom row, right column) Reproduced from [69]. CC BY 4.0.

with adaptive motion. Other robots' control systems achieve flexibility through other means, e.g. changing the dynamics of sensory feedback through an artificial endocrine system. In this type of system, simulated neuromodulators that alter pattern generation and sensory processing are added into the simulated circulatory system, where they affect neural processing until they dilute from the blood [77, 78]. Robot controllers whose dynamics are designed using the Living Machines approach both lead to new flexibility in robot behaviour and enable rigorous testing of biological models of learning and adaptation.

In the coming years, we expect to see the incorporation of even more details from neuroscience into robot control, in particular, how the local motor control networks communicate with the brain to direct and reinforce locomotion. Due to the genetic tools available for the roundworm *Caenorhabditis elegans* and the fruit fly *Drosophila* *melanogaster*, scientists have constructed more complete and detailed connectomes of the brain and nerve cord than ever before, providing insight into how information is shared between portions of the nervous system [79–81] and in some cases directly linking network structure to behavioural function [82]. Although connectomes do not answer all questions about how the nervous system functions, they are a crucial first step toward a much deeper understanding of the system.

Furthermore, we expect to see the application of more sophisticated, continuous learning algorithms based on the details of actual nervous systems. Although elements such as the adaptive frequency oscillators [76] discussed previously represent online, long-term adaptation in robots, there is still a long way to go before robots may learn continuously from the world around them without forgetting what they have already learned [83, 84]. However, we would expect to see robots that can learn motions required to perform crucial tasks in an unsupervised manner, using architectures that mirror those in the nervous systems of invertebrates. This includes learning with multiple mechanisms in different levels of the nervous system. Motor circuits with these capabilities could serve as a natural foundation for robot Mental Faculties to interface with.

3. Mental faculties: revealing the neural basis of invertebrate behaviour

For the invertebrate-inspired robots described above to complete useful work in the real world safely and autonomously, they must possess some level of cognitive function, that is, the ability to solve problems adaptively using learning and memory. To probe these questions in invertebrates, many researchers have focused on navigation tasks for several reasons. First, robust navigation requires multiple aspects of intelligent behaviour from perception, to learning, memory, and decision-making. Second, the observable behaviour of navigating animals provides a direct window into the animal's current knowledge about its location in the world. And finally, many insect species are famous navigators piloting through environments over ranges as large as entire continents [89].

This section focuses on visual processing because vision has been shown to be fundamental for navigation across insects and is highly desirable for robots. Two aspects of vision-based navigation have advanced significantly over the last decade and provide instructive examples to the potential applications of invertebrate research to engineering: position tracking based on insect path integration (PI) behaviour (figure 3 Left), and visual navigation inspired by insect route following (figure 3 Right). In both cases, we have seen an advance from algorithmic to biologically-constrained sensory and neural models that offer much deeper insights into how animals solve these complex tasks.

Ant species inhabiting barren salt-pans forage for food over distances of up to 1 km before returning home by the bee-line once they find a food morsel [86, 90]. This is achieved by integrating their direction and speed to constantly calculate an estimate of their position relative to the nest [90]. It is directly analogous to the odometry problem in robotics, which remains an open area of research due to the accumulative drift that arises from iteratively adding noisy sensory information [91]. Insects have been shown to use a variety of cues to monitor their heading direction (e.g. polarised light, magnetic fields, terrestrial visual cues, self-motion (for review see [92])), and speed of travel (e.g. step-counting and optic flow [93]). However, only recently have the neural architectures that govern this behaviour been revealed. Specifically, a series of mutually-instructive neuroanatomical [94–97] and computational modelling [98, 99] studies have pinpointed the PI circuit to the fan-shaped body region of the insect central complex. At the same time, neuroanatomoical [94] and opto-genetic [97, 100–102] tools have traced the insect head-direction system to the ellipsoid body of the same neuropil. Computational modelling played a vital role in identifying a steering circuit in the fan-shaped body that could minimise the difference between the animal's current and desired heading and thus replicate realistic PI. Indeed, there is now broad agreement that the Central Complex acts as a vector engine for different types of navigation [103]. More recently, these deep brain models have been augmented with biologically plausible perception systems capable of generating a compass signal from polarised light accurate to less than one degree in ideal conditions [104] through a matched-filter-like process [105]. Robotic implementations of these models have been instantiated and provide the necessary real-world verification of hypotheses and inspiration for engineers [106–109].

Similar advances have occurred in our understanding of invertebrate visual navigation. Central-place foraging insects such as ants, bees, and wasps shuttle between feeding and nest sites by routes guided by visual features in their surroundings such as trees, shrubs, and buildings (for review see [110]). Inspired by the observation of ants pausing and rotating before choosing a direction of travel [111], Baddeley *et al* [112] demonstrated that route following could emerge from simply moving in the most familiar direction at all times. The key insight was that views captured when travelling along a path inherently encode the direction of travel and that by simply rotating until the most familiar view is found, the agent will recover the same orientation, later. This is a fundamentally simpler problem than place recognition commonly used in robotics; essentially, it simply asks 'have I seen this scene before?' rather than 'where have I seen this place before?'.

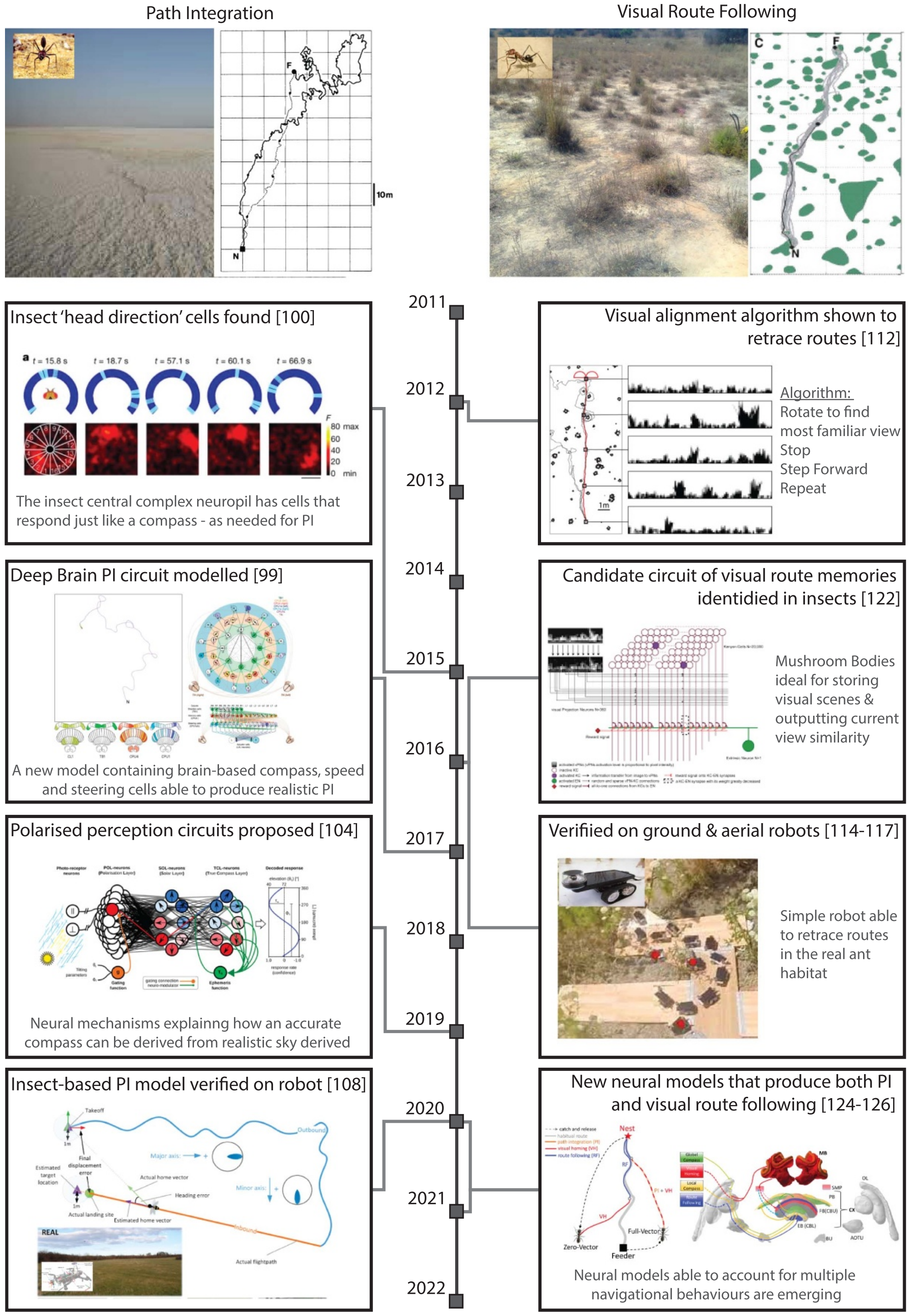

Figure 3. The progression from algorithmic to neural models of insect navigation. The left column highlights four studies from neurophysiology, computational modelling, and robotics that greatly contributed to a new in-depth understanding of insect path integration (ant image adapted from [85], salt-pan image credit to A Savin, WikiCommons, PI behaviour example adapted from [86] with authors permission). The right column similarly describes the advance from algorithmic to brain-based models that increasingly accurately replicate visual navigation behaviours (desert ant image and environment images credited to Michael Mangan & Hugh Pastoll, behavioural example adapted from review [87], original data [88]). (top row, left column, PI data) Reproduced with permission from [86]. (top row, left column, ant photo) Reproduced from [85], with permission from Springer Nature. (top row, left column, desert photo) This 'Salt pan at Lake Karum in Ethiopia' image has been obtained by the author(s) from the WikiCommons website where it was made available by A Savin under a CC BY-SA 4.0 licence. It is included within this article on that basis. It is attributed to A Savin. (2nd row, left column) Reproduced from [100], with permission from Springer Nature. (3rd row, left column) Reprinted from [99], Copyright (2017), with permission from Elsevier. (4th row, left column) Reproduced from [104]. CC BY 4.0. (bottom row, left column) Reproduced from [108], with permission from Springer Nature. (top row, right column, desert photo) Image taken by Michael Mangan. (top row, right column, ant photo) Image taken by Michael Mangan. (top row, right column, route data) Reprinted from [87], Copyright (2013), with permission from Elsevier. (2nd row, right column) Reproduced from [112]. CC BY 4.0. (3rd row, right column) Reproduced from [122]. CC BY 4.0. (4th row, right column) Reproduced from [114], with permission from Springer Nature. (bottom row, right column) Reproduced from [124]. CC BY 4.0.

Follow-up robotic studies have explored extensions ranging from the compact encoding of visual scenes [113], to scanning-free route following [114], applicability to aerial navigation [115], and even the use of temporal cues to improve visual place recognition [116, 117]. Moreover, direct insights were drawn towards the function of the observed learning walks and flights of insects [118] as they begin foraging [119]. Ablation studies in freely navigating animals implicated the Mushroom Body [120] and Central Complex [121] neuropils in visual navigation. This hypothesis has since been upheld by computational models that have shown that Mushroom Body neuropils are particularly well suited to storing visual memories [122, 123], which could drive navigation using the central complex steering circuit [124–126]. Verification of these increasingly biologically realistic algorithms on real robots in complex environments represents the next logical step.

We have shone a light on two specific aspects of invertebrate navigation but there are many complementary research avenues that are being actively pursued and that will have similar impacts. Within the visual domain there have been various studies looking at the potential benefits of compound eye-inspired sensing (e.g. [127–129], and low-level processing for tasks such as collision avoidance [130–132] and flight control [133, 134]. Integration of such reactive faculties with more deliberative navigation strategies will require cue integration and decision-making algorithms. Brain-inspired models are emerging [124, 135] that can account for cue integration in ants [136] and decision-making in flies [137], but more dedicated behavioural and robotic studies are required to verify if insects actually utilise the same strategies.

A further avenue for research lies in multimodal navigation. Insects utilise a suite of sensory cues from across domains to navigate including odour, tactile, taste, as well as vision (for review see [92]). Tantalisingly, some of the models developed for visual navigation have been shown capable of being repurposed for navigation in other domains (e.g. [138]) and indeed the visual navigation model in Ardin *et al* [122] was adapted from an odour association model. Targeted neuroscientific studies will continue to constrain and inspire new computational models, and as new sensors become available (e.g. miniaturised odour sensors) it will become possible to verify their function in real environments and readiness for translation to engineering solutions.

4. Translating bio-inspired knowledge into real-world applications

The translation of knowledge from biomimentic research to bioinspired applications offers a metric to assess the success of invertebrate robotics research. There have been a number of notable examples of commercialisation projects based on the three subcategories of invertebrate robot research discussed above.

Firstly, inspired by the bodies of flying insects that are structurally robust to collisions with objects a new generation of drones are under development that possess novel morphologies. Specifically, drones are being augmented with external shells that ensure safe movement through cluttered, human environments as they can bounce off of obstacles without damaging themselves or obstacles (or even a human) before continuing to their goal [139]. Such modifications not only increase safety for the drone, user, and environment, but may also be key in gaining regulatory approval as they reduce the need for an unrealistically precise, and provably capable, control system that functions perfectly in all scenarios. Drones with such non-standard morphologies [140, 141] are now being commercialised by companies such as Dronistics (https://dronistics.epfl.ch) for applications in last-mile delivery drones.

Meanwhile, there are a host of new companies looking to build complete nature-inspired propulsion and control systems. For example, UK-based Animal Dynamics (www.animal-dynamics.com/) has created a small (sub 200 g) drone called SKEETER that features a dragonfly-inspired flapping-wing system in place of multi-rotor systems. The company is targeting applications for short-range surveillance, search and rescue, and surveying. Similarly, HEBI Robotics (www.hebirobotics.com/), a spin-out from the Carnegie Mellon University Biorobotics Lab, is commercialising modular motor and control systems inspired by decentralized control in crawling robots. Interestingly, the company is finding that these insights generalise not just to other nature-inspired robots, such as hexapods, but also to hybrid robots with radial arms fitted with tracks. These technologies are opening applications in fields that were not possible using previously available engineered solutions.

Lastly, invertebrate neuroscience is also starting to impact commercial applications. For example, spin-out company SenseFly (www.sensefly.com/) commercialised an unmanned air vehicle landing system inspired by the optical flow processing system of flying insects leading to an acquisition by drone manufacturer Parrot. More recently, the University of Sheffield spin-out Opteran Technologies (https://opteran.com/) has been pioneering commercialisation of Natural Intelligence. Initial offerings include solutions for obstacle avoidance and decision-making created by reverse engineering how invertebrates sense, perceive, and process information and then decide how to move safely and efficiently through the world as a result.

The examples above clearly demonstrate the growth in the translation of knowledge derived from invertebrate robotics to commercial settings in the last decade. While the field remains in its infancy, the opportunity for industrial applications appears to be increasing, revealing a positive view of bioinspired solutions from investors, industries, and customers. Indeed, end-users returned positive views of the role that swarms of bioinspired robots could play in their specific domain [142] promising a bright future for such systems as they step into the real world.

5. Summary and outlook

The last decade (aligning with ten years of Living Machines conferences) has seen a rapid acceleration in our understanding of the role that individual morphology, motion control, and mental faculties play in generating the array of adaptive behaviours observed in invertebrates. In this Perspectives paper, we have tried to capture some of the most significant advances made in this exciting research area with a focus on new fundamental scientific knowledge and its translation into real-world robots. Morphologies have shifted from rigid to highly compliant, even soft bodies for robots; motion controllers have advanced from sensory-driven FSMs to closed-loop, dynamical neural controllers that can deal with unpredictable or changing conditions; and mental faculties have advanced from algorithmic models to neural models mapped to specific brain regions.

In the main text, we outlined some of the clear near-term goals for morphology, motion control, and mental faculty research, but what the next decade might bring in regard to emergent areas is prime for exploration and exploitation. One area for clear expansion is in invertebrate-inspired materials. Human-made materials such as metals and plastics are typically strong until the point of failure when significant, and often irreparable damage occurs. This contrasts with the organic structures of invertebrates' bodies that fail under less stress but are far less brittle and are easy to repair through a cyclic process. The exoskeletons of many invertebrates also possess complex networks of embedded sensors (e.g. dragonfly wings [143]) that can warn the animal of potential damage before it occurs. Bio-inspired materials that possess some of these characteristics would usher in an area of robots built from sustainable materials that can be deployed for extended periods of time without human intervention or repair (e.g. [144]).

Allied to any advance in materials is the need for advances in lightweight and resilient propulsion and power systems. Large, loosely bio-inspired legged robots (e.g. Boston Dynamics, Agility Robotics) are becoming increasingly common but their large, heavy power units still limit them. Insect-inspired electrostatic [145] or polymer [146] based actuators offer promise for lighter, lower-power propulsion systems for insect scale robots. And while research into gut-inspired power generation is ongoing, it is tantalising to consider the possibilities of solar-driven robots inspired by photosynthesising aphids [147].

Another direction for future research is for hypotheses to be verified in the outdoor environments in which animals evolved rather than in sanitised laboratory conditions. This will require a series of interlocking issues to be addressed concurrently whose mutual resolution may in itself create a virtuous cycle. Firstly, real-world verification requires the hypothesis to be embedded in a physical system complete with its own sensing, processing, and motion control systems. Such a closed-loop test bench will more closely replicate the problems faced by the animals that we wish to understand and mimic and will allow researchers to unpick the details of biological function across levels. The component parts that could be combined to realize this goal are already under development: biologically-based visual systems have been developed (see CURVAce and DVS cameras); neuromorphic hardware is allowing biologically constrained neural circuits to be implemented on low-power devices; and as outlined above, smaller and lighter robot structures are being developed at pace. A new era of in-the-field Living Machines, in which behavioural, neuroscientific, and modelling are combined in closed loop will further accelerate the pace of scientific advancement and translation to engineering needs.

Similar opportunities will become available in the area of biohybrid systems, in which a natural system (here, the invertebrate) is augmented by technology to useful effect. There are already numerous examples of insects being steered by neural stimulation (for review see [148]), and as the control packs are made smaller and more portable, this could offer a more direct means of realising miniature, deployable systems in the wild (e.g. small, rugged search and rescue systems).

We note that as the capability of biomemetic artefacts increases, researchers will encounter questions that, to this point, have been purely hypothetical. For example, what is the trade-off between the number of neurons and intelligent behaviour? And is there a necessary (or at least, best) substrate for brain models to succeed? Such substrates could range from standard digital computing devices to analogue neuromorphic chips, or even wet-ware (e.g. biological computing hardware). Questions like these may interest those from fields as diverse as artificial intelligence, neuroscience, and philosophy.

It is clear that invertebrate robot research offers benefits to both neuroscientists and engineers alike. As experimental tools and technologies continue to advance, neuroscientists will be able to delve deeper into the brain and body structures, map behaviour in increasing detail, and embody hypotheses into more capable robots than before. Although it is impossible to predict with any confidence what the robots of the future will look like, we suspect that they will borrow many morphologies, motor control principles, and mental faculties from invertebrate animals.

Data availability statement

No new data were created or analysed in this study.

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