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## ARTIFICIAL INTELLIGENCE

## Insect-inspired AI for autonomous robots

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Autonomous robots are expected to perform a wide range of sophisticated tasks in complex, unknown environments. However, available onboard computing capabilities and algorithms represent a considerable obstacle to reaching higher levels of autonomy, especially as robots get smaller and the end of Moore's law approaches. Here, we argue that inspiration from insect intelligence is a promising alternative to classic methods in robotics for the artificial intelligence (AI) needed for the autonomy of small, mobile robots. The advantage of insect intelligence stems from its resource efficiency (or parsimony) especially in terms of power and mass. First, we discuss the main aspects of insect intelligence underlying this parsimony: embodiment, sensory-motor coordination, and swarming. Then, we take stock of where insect-inspired AI stands as an alternative to other approaches to important robotic tasks such as navigation and identify open challenges on the road to its more widespread adoption. Last, we reflect on the types of processors that are suitable for implementing insect-inspired AI, from more traditional ones such as microcontrollers and field-programmable gate arrays to unconventional neuromorphic processors. We argue that even for neuromorphic processors, one should not simply apply existing AI algorithms but exploit insights from natural insect intelligence to get maximally efficient AI for robot autonomy.

## INTRODUCTION

Autonomous mobile robots, such as drones, rovers, and legged robots, promise to perform a wide range of tasks, from autonomously monitoring crops in greenhouses to last-kilometer delivery. These applications require robots to operate for extended periods while performing complex tasks, often in unknown, changing, and complicated environments. This brings great challenges (1), among which is the difficulty of executing a rich repertoire of autonomous, robust, and adaptive behaviors with onboard resources. This challenge is exemplified by the task of navigation. The state of the art typically relies on simultaneous localization and mapping (SLAM) algorithms, which require more computational resources than can be mustered by many processors embedded onboard robots (2). More than 10 years ago, it was reasonable to anticipate that further improvements to microprocessors would soon close this performance gap. At that time, processor development still kept pace with Moore's law, which predicted a doubling of the number of transistors in a dense integrated circuit about every 2 years. However, with the end of Moore's law in sight (3, 4), we can no longer count on this. Hence, we need to explore alternative approaches to both the computing hardware and the AI of small, autonomous robots.

In this article, we argue that inspiration from insect intelligence represents an important alternative route to achieving artificial intelligence (AI) in small, mobile robots. Here, we adopt the view that AI is the "pursuit of intelligent behavior by artificial methods" (5), explicitly acknowledging that insect behaviors are intelligent (6). If we succeed in harnessing insect-inspired AI, small robots will be able to tackle difficult tasks while staying within their limited computational and memory budget. We first discuss the main aspects of insect intelligence that make it so appealing. Next, we reflect on the state of the art in this area and identify the main challenges on the road

to its more widespread adoption. Last, we discuss how insect AI can be implemented on various types of computing hardware.

## INSECT INTELLIGENCE

Insects diverged around 480 million years ago (7) within the group of arthropods. They form a dominant phylum among animals, with roughly one million species identified and an expected 5.5 million overall, compared with only 70,000 known species of vertebrates (8). Because of their proliferation, insects have developed a wide range of adaptations to different environments. These include diverse locomotion strategies such as crawling, flying, and swimming; complex visual systems (9, 10); robust navigation strategies (11–14); and even cooperative social behaviors (15, 16). Furthermore, their behaviors are implemented by a very limited number of neurons, with about 1 million neurons for the honeybee (12) and, astonishingly, fewer than 10,000 in the smallest flying wasps, *Megaphragma mymaripenne* (17). Although neurons are not identical and hence not directly comparable between species (18), these small numbers of neurons are indicative of the processing efficiency of insect intelligence. Especially in the light of this processing efficiency, insects' amazing capabilities represent a rich source of inspiration for the design of robotic solutions (19, 20).

The main property of insect intelligence is its parsimony (21), that is, the way in which insects use minimalistic yet robust solutions to achieve successful behavior in complex, dynamic, and sometimes hostile environments. "Minimalistic" here should be interpreted as a high level of efficiency in the required resources, with energy as one of the prime resources. Because the brain consumes considerable energy (22), it may come as no surprise that evolution has driven insects and other animals to achieve their repertoire of behaviors with as small a brain as possible, for which the energy consumption reaches only a few milliwatts of power. Important in achieving this parsimony is that insect intelligence—just like that of more complex animals like humans—is characterized by "embodied cognition" (23, 24). This refers to the recognition that intelligence does not depend only on the brain, but is crucially shaped by the insect's embodiment, that is, its body and sensory apparatus. Furthermore,

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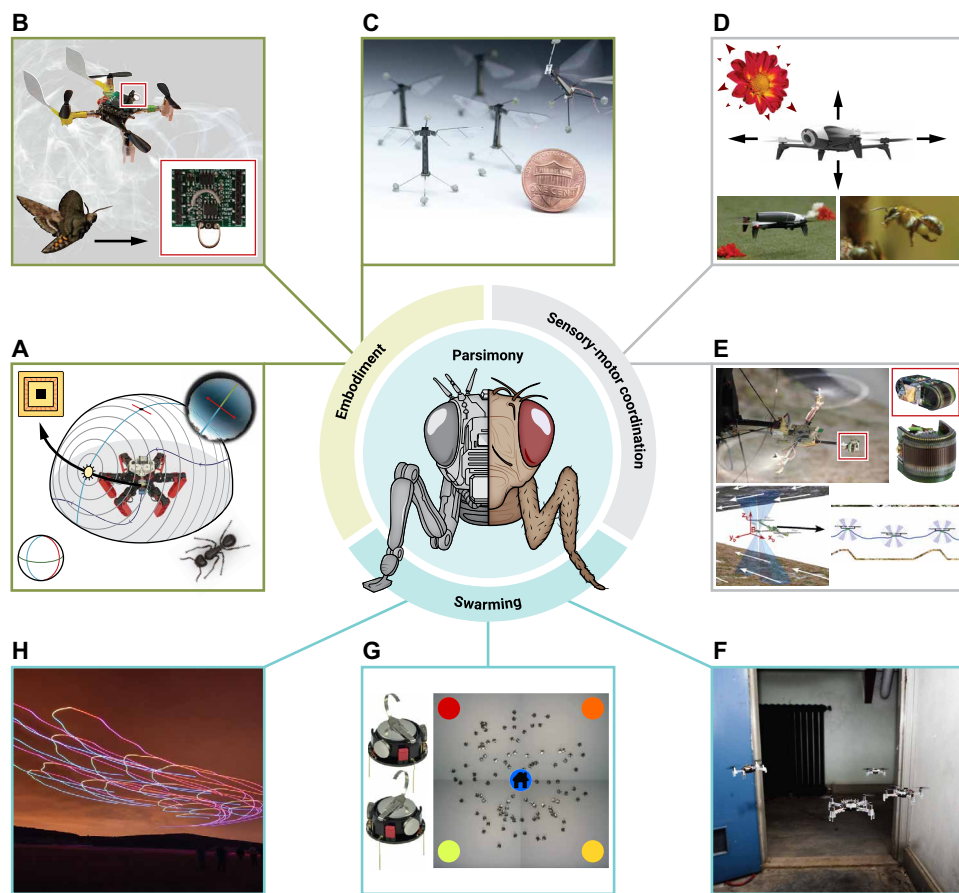
it implies that insect intelligence builds on the capability to interact with the world, combining feedback from a diverse array of sensors and exploiting the closed loop of sensory inputs and actions to simplify the cognitive operations performed by the brain. Last, social insects live together in colonies and are thus able to perform tasks that go beyond the limits of their individual capabilities. Figure 1 shows three key aspects (embodiment, sensory-motor coordination, and swarming) that contribute to the parsimony of insect intelligence. Note that these three aspects are commonly ignored in robotics studies, with a focus on developing software for standard robot hardware, passive sensing [e.g., detecting cars in prerecorded video sequences (25)], and an emphasis on single-robot intelligence. Below, we discuss the aspects from an insect point of view and illustrate them with examples from robotics.

## Embodiment

Evolution simultaneously adapts the bodies, sensory systems, and brains of animals to their ecological niche. In many cases, intelligent behavior is achieved by means of the “embodiment” itself, here interpreted as the design of the body, including the sensor and actuator apparatus. By doing so, cognitive load can be reduced or even eliminated entirely. This idea is exemplified by passive dynamic walking robots (26). In insect robotics, a decisive advance in robotic flies occurred when researchers removed active actuation of the wing angle of attack. By simplifying the mechanism to allow it to passively rotate, mass was reduced, whereas the lift-producing leading-edge vortex aerodynamics observed in insect flight were retained (27). This realized lift greater than weight at insect scale for the first time (28) and paved the way for subsequent controlled flight (29). The aerodynamics of

the flapping wings of insects can also play a role in the exploitation of passive effects. For instance, with the help of a flapping wing drone, it was shown that fruit flies passively turn into the flight direction after rapid escape maneuvers (30). Beyond purely passive mechanisms, simple neuron-mediated reflexes underlie many behaviors such as flight stabilization. Such active reflexes do depend on a coevolution of body and sensors, though. To illustrate, flight stabilization is also facilitated by mechanosensory structures on the wing, campaniform sensilla, which encode information on wing deformation and consequently on the flight dynamics (31). Hence, insect wings not only are actuators but also influence sensing and consequent active control. The scale of insects also fundamentally affects their body design and cognition. For example, the efficiency of flapping wing motion for propulsion heavily depends on the Reynolds number (viscosity of the air) (32), with small flying insects such as *Drosophila* relying on higher-frequency flapping (33) than larger ones, which even rely on gliding (34). These differences are reflected in robotic designs (29, 30, 35). Similarly, scale influences limb tip contact forces and the potential to adhere to vertical surfaces, influencing walking gaits exhibited by insects (36). Furthermore, much like how ants can carry many times their body weight, insects’ small scale protects them from collision damage. This makes occasional mistakes or inaccuracies in motion control less problematic. For example, honeybees do make crash landings (37). This has inspired collision-resilient robot designs (38–40), allowing for a less computationally expensive AI.

The sensory apparatus of insects is also tailored to the tasks they need to perform. Their compound eyes have a



**Fig. 1. Insect intelligence is characterized by parsimonious solutions to achieve successful behavior in complex, dynamic, and sometimes hostile environments.** Three key aspects to parsimony are embodiment, sensory-motor coordination, and swarming. These are illustrated with robotic studies. (A) Antbot is a hexapod robot, which is equipped with an ultraviolet sensor for detecting the polarization of the sky for improved navigation skills (107). (B) Smellicopter is a tiny biohybrid drone equipped with moth antennae to sense odor and fins that passively align it with the wind (54). (C) The honeybee-sized Robobee (29), which was successfully miniaturized by having a passive mechanism for varying the wing angle while only the wing stroke angle is actively controlled. (D) In (119), a drone uses the oscillations that arise during active optic flow control to estimate distances to objects in its environment. (E) In (70), an artificial compound eye is actively controlled to remain parallel to the ground surface, allowing the robot to deal with oncoming slopes. (F) The swarm gradient bug algorithm enables a swarm of tiny drones to explore unknown environments and return to the base location (96). (G) Tiny Kilobots (192) used in a study on foraging with virtual pheromone trails (93). (H) A swarm of drones flying as a flock in the presence of no-fly-zones (160).

low resolution compared with human vision, wide field of view, and a high temporal bandwidth (10, 41), exceeding a 200-Hz flicker fusion frequency in some species (42). These eyes are particularly suited for capturing fast motion cues that are relevant for agile flight, capturing prey (43), and avoiding predators (44). In robotics, it is common to have cameras with a 30-Hz frame rate, limiting response speed. Inspired by insects, lightweight artificial compound eyes with a high frame rate and wide field of view have been produced (45–47). It is also possible to use arrays of smaller cameras for an omnidirectional view (48) or down-sample a standard omnidirectional camera (49) at the cost of a heavier system. Event-based cameras are highly promising as neuromorphic vision sensors, because they asynchronously register per-pixel changes in illumination, resulting in a large dynamic range and high temporal rate (50).

Insects combine vision with multiple other sensors to achieve parsimonious motion control. They have one pair of antennae, which are sensitive to airflow and function as olfactory organs (51). In translatory motion, flies linearly combine low-latency mechanosensory feedback from their wind-sensing antennae with higher-latency visual feedback to control their flight velocity (52). A strikingly similar superposition exists for the gyroscopic mechanosensory halteres and vision in rotatory motion (53). Currently, antennae have a far superior performance for olfaction compared with artificial sensors, which has led to biohybrid robot designs incorporating live tissue from, e.g., moths, for odor source localization (54, 55). However, the antennae are also sensitive to airflow (52, 56), something that is also hard to measure onboard small robots. Promising airflow sensor designs have been demonstrated (57–59), but they are not yet widely available for robotic integration. Sensing airflow is important not only for flight control but also for tasks such as odor source localization. Flying insects like moths and fruit flies are known to find odor sources by interleaving casting (flying orthogonally to the wind direction to detect an odor) and surging (flying upwind when sensing the odor) (60–62). In (54), wind sensing and processing were bypassed by means of a physical design that passively steered the robot into the wind. In general, the robotic equivalent to the evolutionary co-development of both the body and brain can take the shape of an artificial evolution (63, 64) or an extensive investigation of existing hardware and software options (65).

### Sensory-motor coordination

The brain evolved to control motion as organisms gained the ability to move; conversely, evolution drove animals to move in such a way as to make the task of the brain easier. Active vision is an important example and entails moving the visual system to simplify visual processing (66–68). Many flying insects use their neck muscles to maintain a constant head orientation, known as gaze stabilization, during flight maneuvers. This ensures that compound eyes capture the translational and not the rotational flow, because only the former carries distance information (69). Gaze stabilization also reduces visual processing requirements, something that has been exploited in few published robotic studies because it has traditionally required heavier hardware (70–73). Interestingly, active vision in the form of microsaccades allows insects to resolve objects with an acuity beyond that expected from the coarse layout of their ommatidia (74, 75). This has been exploited on robotic platforms (76, 77). The breakthrough for this type of hyperacuity—and active vision in general—to microrobots, though, may depend on scaling down the hardware for performing these microsaccades (68, 73). Furthermore, motions

of the full body can be useful to insect and robot vision. For example, in (78), a flying robot moved actively up and down to induce clear translational flow for identifying gaps to fly through, which was similar to the peering behaviors observed in bumblebees attempting to cross a gap (79). Moreover, in (80), it was shown that the oscillations inherent to optic flow control can be used for gauging distances.

Another example of how sensory-motor coordination can simplify required processing comes from insect navigation. One theory on ant navigation postulates that they use a visual guidance in which they move toward the most familiar view (81). From time to time, ants rotate on the spot to find which viewing direction is most familiar to them. They physically perform an action (rotation of the view) that would require additional cognitive capabilities if it had to be performed mentally. Moreover, in (82), it was observed that ants often deviate from the straight-line path. Modeling this behavior has led to the insight that if the magnitude of the oscillations correlates with the uncertainty of view recognition, it leads to much more robust navigation (83, 84). In addition, in flying animals, motion is essential to navigation. For instance, honeybees and wasps perform elaborate maneuvers around their nest, termed “learning flights,” which facilitate homing in on the nest when returning (85, 86). Although the examples given here have focused on vision, insects also make use of other senses, such as that of touch (87, 88). Touching offers the possibility of active tactile sensing or even “interactive perception,” in which perception is facilitated by moving objects in the environment (89).

### Swarming

To transcend their individual limitations, social insects live together in colonies. Social insects have inspired the design of computational models (90) and have led to the field of swarm robotics (91). Swarming allows for parsimonious solutions to robotic tasks, because these can be achieved by robots with many fewer resources than a comparable single-robot system. Moreover, performing tasks with swarms holds the promise of robustness (e.g., failing robots do not immediately endanger the mission), scalability (i.e., the local perception and actions of robots allow adding more robots to, e.g., explore a larger area in an exploration task), and flexibility (just as in insect colonies, different proportions of these robots can be assigned to different tasks depending on the need). Swarm robotics examples include crossing gaps (92), shortest-path finding (93), global decision-making (94), surveillance (95), exploration of unknown cluttered environments (96), and gas source localization (97).

### Parsimony

The three aspects of embodiment, sensory-motor coordination, and swarming all feed into the parsimony of the solutions used by insects to solve complex tasks. Let us take navigation as an example. A well-known example of a highly skilled navigator is the desert ant *Cataglyphis*. It is able to forage for hundreds of meters along meandering paths and then travel back home in a straight line (98). Because of the large body of biological work in this area, it has become clear that the underlying mechanisms consist mostly of path integration (odometry) and visual guidance (99, 100). Moreover, insects’ parsimonious solution to navigation relies on the exploitation of specific characteristics of the environment. For example, when navigating outdoors, they use the polarization of the light for better path integration (101–105).

However, there is still a debate about the exact mechanisms involved in navigation in any particular exemplar species. The well-known “snapshot theory” (102, 106) proposes that ants compare



stored, coarse omnidirectional views with their current percepts, allowing them to move in directions that minimize the difference. A more recent familiarity-based theory (81) states that ants follow the most familiar view, rotating physically to move into the best matching direction. This removes the need to explicitly recall views. In a similar vein, it has been asked whether a neural network can directly map percepts to a motion direction (107). Recently, a nest-centric coordinate scheme has been proposed, which suggests how ants can travel from one feeding place to another without having traveled such a route before (99). Multiple robotics studies have drawn inspiration from these navigation schemes. Path integration has been successfully implemented onboard wheeled and legged robots with remarkable accuracy (101, 103). Several different approaches have been proposed for how to incorporate visual guidance (103, 108, 109). In one of the most advanced published studies in terms of real-world experiments (109), a robot traveled outdoor paths of ~100 m with a memory requirement of 3 megabytes (MB)/km. By comparison, a typical SLAM solution constructs three-dimensional metric maps, which requires hundreds of megabytes, even for datasets consisting of a single room (2).

Parsimonious solutions used by insects exist for many other tasks that are relevant to robotics. These include optic flow–based visual navigation for obstacle avoidance (48, 72, 110–112), target following (113), altitude control (114, 115), and landing (116). For many of these tasks, the main principles are known, but the exact mechanisms that should be implemented in robots are an area of active research. For example, it has been found that honeybees use optic flow divergence for landing (117, 118), but the algorithms for successfully executing such landings are the subject of ongoing study (119). For some tasks, such as the detection of looming objects by locusts, the neural basis is quite well understood (120–123). Understanding the locust’s lobula giant movement detector neuron has led to computationally efficient neural models, which have been tested on mobile robots and lend themselves well to implementation with neuromorphic vision sensors and processors (124–129). Detection and avoidance of dynamic obstacles is one of the areas where the low latency of event-based vision can make a difference, as has been recently demonstrated by drones capable of avoiding thrown objects or other drones (112, 130, 131). Other tasks for which relevant insect behaviors are known include odor source localization (60, 61) and various forms of learning and classification (132, 133).

The emphasis on parsimony should not be misinterpreted as an argument against cognitive capabilities. Insects and robots alike can definitely benefit from more processing, for instance, to allow for the interpretation of more complex visual information (134) or to accommodate various forms of learning, such as in the mushroom bodies (135–138). Moreover, for more advanced cognitive capabilities, insect intelligence can serve as inspiration for robot AI. For instance, a model of olfactory learning of the *Drosophila* (139) has recently been used for creating a computationally highly efficient algorithm for visual place recognition (140).

It may be clear that the parsimonious nature of insect intelligence is of considerable interest for autonomous robots. However, to fully exploit this, we need to tackle a few hard challenges.

### CHALLENGES ON THE ROAD TO INSECT-INSPIRED AI FOR AUTONOMOUS ROBOTS

We have sketched the potential of insect-inspired AI for creating autonomous, small robots with extremely limited computational

resources. However, the advantages of insect-inspired AI have been heralded before (5, 6, 141, 142). Here, we reflect on why insect-inspired AI has not yet been adopted more widely. We identify two main challenges that have been holding this approach back, but on which accelerating progress is being made.

### Designing insect-inspired AI

We have given many examples of how different aspects of insect-inspired AI have been applied to small autonomous robots. Still, it may be unclear to a designer how to apply “insect-inspired AI” to a new robotic task that has not yet been treated before in the literature. In (143), three types of design methods are discussed: manual design following the typical divide-and-conquer approach to engineering, manual design following findings from biology, and automatic design by machine learning.

The first approach typically follows a divide-and-conquer strategy, separating the solution into submodules. A commonly used division is perception, state estimation, and control modules, each of which is then developed in isolation without exploiting sensory-motor coordination. The problem with this is that it typically does not lead to a parsimonious solution in which simple elements interact in a complex manner to give rise to the desired robot behavior. Rethinking manual design methodology may be a solution. For example, in (89), it is proposed to split up the solution in submodules consisting of active sensorimotor loops, forming a hierarchy of complexity.

The second approach is to draw inspiration from a biological analog of the robotic task. The main challenge here is that insects themselves are highly complex systems, for which it is difficult to reveal the exact mechanisms underlying their behaviors. Consider navigation, in which the main ingredients are clear [see (99, 144)], but many of the details that are required for devising a full algorithm or robotic implementation are not fully known. In addition, natural evolution involves implicit constraints such as those for growth and procreation, leading to, for example, courtship displays or metabolic transitions from larval to adult life stages. Such implicit constraints and the multiple objectives optimized by an insect’s body and behavior make it difficult to identify which elements may be informative for a robot design. The typical approach to drawing inspiration from biology is to identify a virtuoso, an animal that excels in some specific behavior (14). This may be a *Cataglyphis* ant (102) or honeybee (145) in the case of navigation, or a fruit fly for maneuvering (44). This must be combined with a design process in which knowledge gaps are filled by the designer. This second approach benefits from novel techniques that are accelerating the scientific endeavor of understanding insect intelligence. Advances in computing and graphics now allow us to place free-moving animals in virtual reality (52, 146), enabling us to precisely probe a mobile animal’s input-output mapping. Moreover, deep machine learning methods and tools like focused ion beam scanning electron microscopy have recently immensely accelerated the construction of obtaining full connectomes (147). This enabled the construction of a complete map of the entire central brain region of *Drosophila*, containing 25,000 neurons and 2 million synapses. Another relatively recent technique is optogenetics, which allows for more fine-grained, noninvasive control and analysis of neurons inside insects’ brains (148). For instance, this technique has revealed the neural basis for heading integration in fruit flies, which turns out to work by means of ring attractors (149). This finding has led to new computational models for path integration (129, 144). We expect that these novel techniques will fill in the

knowledge gaps more quickly and at a much more detailed level than ever before, facilitating manual insect-inspired design.

The third approach tries to circumvent the difficulties associated with complexity by automatically designing the solution. A main approach to achieving automatic design of bioinspired intelligence is to use evolutionary robotics (143, 150, 151), which typically entails evolving a neural network in simulation. There is a considerable parallel with reinforcement learning (152), although evolution can comply with all aspects of parsimonious solutions by evolving not only the controller (153) but also the sensors (154) and body (63, 64). An advantage compared with the bioinformed approach discussed previously is that evolutionary robotics can make better use of the available technological building blocks, which may be far behind their biological counterparts (e.g., olfaction and efficient parallel processing in the brain) or far ahead (e.g., efficiency of electric motors compared with muscle and capability of fast serial computations in silicon). A major challenge in evolutionary robotics is to find solutions to difficult tasks while starting evolution from scratch. As a consequence, evolution can become stuck in unsatisfying local optima. This problem can be tackled with varying success by adapting the selective pressure on evolution (151), growing the controller's size and complexity over evolution (155), scaffolded learning (156), or novelty search (157). Moreover, simulation necessarily abstracts away from many properties of the real world. This means that if a successful solution is found by evolution, it still has to cross the reality gap (158). This can be tackled by incorporating improved models of the most relevant real-world properties, combining evolution with online learning or development (159), randomizing factors that may not be modeled well (158), and abstracting away from sensory inputs and control actions in evolution so that already working low-level perception and control modules can cover the reality gap (97, 160–162). Last, both failures and successes of automatic design present challenges. On the one hand, in case of failure, the causes for this are difficult to identify. The cause may lie in the representational complexity of the solution (e.g., the size of a neural network), the learning process (e.g., the number of individuals or the mutation rate), or the sensory information available to the robot. Many choices made by the designer lead to implicit constraints on the learning process and solution, which may prevent success. On the other hand, if automatic design succeeds, it is still necessary to analyze the solution to understand how it works and characterize its weaknesses. Although such artificial solutions are more accessible than a live biological organism, the analysis of an evolved complex system can be challenging as well, potentially requiring many of the same statistical and experimental methods used in the scientific analysis of living organisms.

Figure 2 illustrates complexity at various levels, from a single neuron to networks of neurons, brain regions, and the complexity of interactions with other agents and the environment. When designing insect-inspired AI, each level plays a role.

### Full-stack autonomy solution

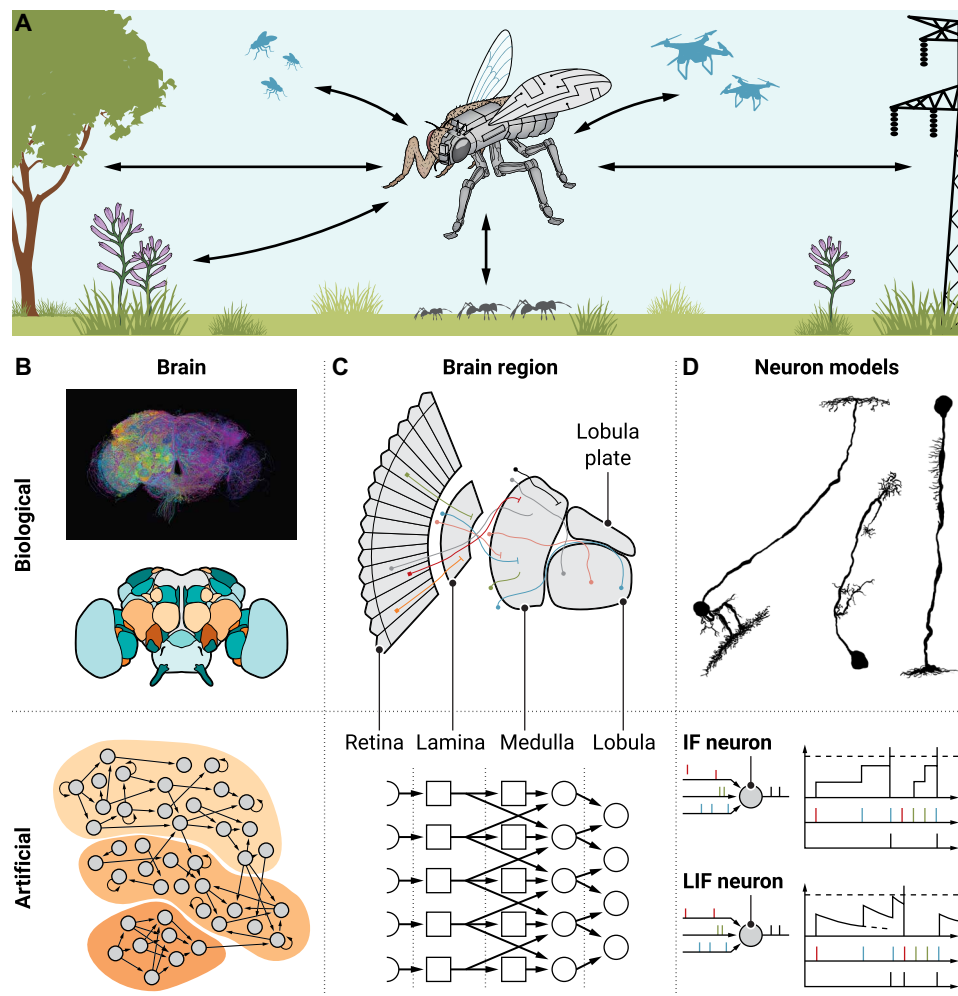
Mobile robots that autonomously perform real-world tasks need a “full-stack” autonomy solution. This means that they must be able to move, avoid collisions, and navigate to places of interest for the task including recharging, and they need to take actions to achieve their assigned goals. The mainstream approach in robotics to navigation, SLAM (163), creates a metric map of the environment and uses it for localization and motion planning. This resource-intensive process is then complemented with additional specific task capabilities.

If small, resource-constrained autonomous robots are to be fully autonomous, they will have to follow an alternative approach.

Insect-inspired AI entails one such alternative approach that avoids detailed world modeling (141). Instead, different behaviors are tightly interlinked in a sophisticated way to achieve complex tasks (164). The design of such AI—with extreme resource constraints—is challenging for single tasks, but even more so for a full-stack autonomy solution. Indeed, insect-inspired AI until now has mostly produced studies on individual tasks such as landing (116), obstacle avoidance (110, 111), or odor source finding (54). Moreover, these studies often take place in simplified environments. For example, studies on the use of optic flow often use spaces with ample texture, because optic flow becomes harder to determine when texture is lacking. Part of the reason for this is that engineered visual sensors are currently outclassed by insect eyes—they have a smaller field of view and slower update rates. Multiple successful designs for artificial compound eyes have been proposed in the academic literature (46, 165), but the lack of mass production and hence wide availability of such sensors is related to the absence of the full-stack autonomy—and hence the promise of widespread real-world application.

Most importantly, there are no scientific studies yet that demonstrate insect-inspired navigation methods working robustly over longer distances and time scales in large, real-world environments. There are multiple reasons for this. First, as stated before, the exact navigation mechanisms in different insects are still being investigated. Published theories leave out important elements that must be implemented for robotic applications. Second, most insect-inspired navigation methods have only been tested in simulation or in environments of limited size or scope, like laboratory environments. Benchmark real-world datasets that are well accepted by most of the robotics community, like the KITTI car dataset (25), are typically not suitable for using insect-based navigation. The sensors are different from those required (e.g., they use small field-of-view cameras). However, even more importantly, insect-inspired methods vitally depend on active interaction with the environment, which is not possible with a passive dataset. Last, because insect-inspired navigation makes a different choice at the highest abstraction level, different performance metrics need to be used as well. For instance, instead of the error between estimated and real position, one should look at the percentage of runs in which a robot successfully returns to within a few meters of the base station. State-of-the-art studies on insect-inspired navigation strategies, e.g., (109), are very close to having viable strategies for large real-world environments. Interestingly, they will likely have properties that mainstream SLAM research is still striving to achieve (166, 167). For example, the coarse resolution and omnidirectional vision of insects is robust against dynamic objects that may confound SLAM algorithms. Moreover, their parsimonious nature permits execution even on very small embedded processors, leaving computation resources available for other processes such as visual object recognition.

Successful navigation is the key to achieving a full-stack autonomy of robots endowed with insect-inspired AI. It will lead to more successful applications of insect-inspired AI to complex, real-world tasks. Of course, there are already such applications, with the most compelling example being the Roomba robotic vacuum cleaner, which performed a biology-inspired random walk to cover the floor of a room (168). We hope that advances in insect-inspired navigation will allow for more complex and spatially extended tasks, and stimulate the production and availability of sensing and computing



**Fig. 2. Insect-inspired AI aims to solve complicated tasks with parsimonious solutions, which rely on complex systems at multiple scales.** These systems consist of many components that interact with each other to give rise to a (desired) global behavior. Understanding and harnessing this complexity lies at the heart of the challenges faced by the insect-inspired approach. In the figure, we show biological and artificial elements side by side, where the latter are typically abstract versions of the former: **(A)** At the macroscale, the insect or robot interacts with the environment and other agents. **(B)** Different brain regions/functional neural modules connect and interact to give rise to the full behavioral repertoire. **(C)** A single part of the brain/neural network can perform a function, such as extracting global optic flow fields from local optic flow measurements. **(D)** A single biological neuron is a complex system in itself, which can implement sophisticated functions (193). In computational models, artificial neurons are typically the lowest level of complexity, and by themselves often still have relatively simple dynamics, representing simple functions. Here, an integrate-and-fire (IF) and a leaky-integrate-and-fire (LIF) neural model are shown, which lead to different dynamic behaviors and hence a different information processing capability.

hardware specifically tailored to the autonomous navigation of small robots.

### COMPUTING HARDWARE

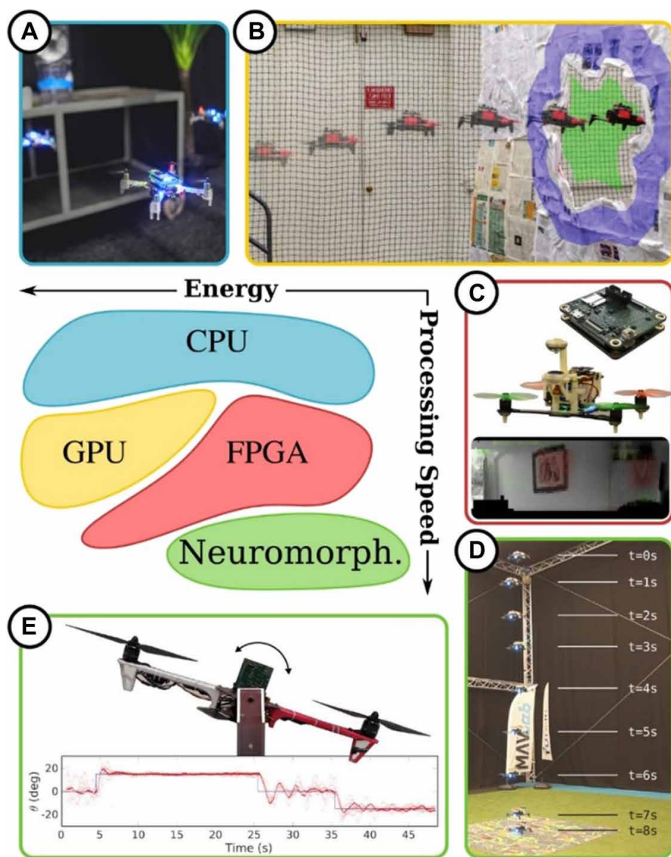
We set out to argue that drawing inspiration from insects is a way to create parsimonious solutions for the AI of small autonomous robots. This raises the question what kind of processors are suitable for a full-stack autonomy. Marr's levels of abstraction (169) help us to tease apart the problem. They are as follows: the computational level, specifying which problem is solved and why this problem is

relevant; the algorithmic level, capturing how the problem is solved, e.g., what representations are used and how they are processed; and the implementation/physical level, being the physical realization of the system. The type of processor concerns the third layer of abstraction. Choosing a processor will determine the types of autonomy algorithms that can be implemented and the corresponding time and energy efficiency. Figure 3 shows various types of computing hardware with a coarse indication of their energy expenditure and processing speed (assuming parallel computing as with neural networks). We will discuss the types of processors shown in the figure below.

Let us start with microcontrollers. Microcontrollers contain one or more central processing units (CPUs), which are general-purpose, von Neumann architectures, executing computations one after another in series. Microcontrollers draw comparatively little energy, have limited memory, and—compared with modern-day desktop/laptop processors—have a slow processing speed. For instance, an STM32F04 has 192 kB of RAM (random-access memory), has a 168-MHz processor, and draws ~0.4 W of power. For the sake of comparison, a state-of-the-art CPU such as the AMD Ryzen 9 features 12 cores (cache memory of 64 MB) with a base clock frequency as high as 3.7 GHz, drawing 105 W of power. We have shown multiple examples though, in which insect-inspired AI has enabled small robots with microcontrollers to perform complex tasks (96, 97, 170). The key here was making different choices at Marr and Poggio's first and second abstraction levels. For example, in (96), implementation of swarm exploration on a microcontroller was made possible by accepting that, in terms of navigation, the robots will only be able to come back to the base station (first level) and that behaviors are represented using a finite

state machine (second level). We think that insect-inspired AI can extend the autonomy of robots equipped with microcontrollers far beyond what is generally thought possible. The limits of microcontrollers lie largely in the processing of high-dimensional sensor data such as visual data. In principle, insect vision is characterized by low-resolution visual sensors. For instance, fruit flies have ~800 ommatidia with 8 photoreceptors per ommatidium (41, 171). Processing in the order of thousands or a few tens of thousands of pixels at the frame rate of a normal complementary metal-oxide semiconductor camera is possible, see (170), as well as with insect-inspired artificial retinas as demonstrated with the CurvACE





**Fig. 3. Computing hardware used for insect-inspired AI, illustrated with highly resource-restricted, flying robots.**

The central graph gives a very coarse indication of the energy expenditure and processing speed of different types of computing hardware, with processing speed including the parallel nature of processing in architectures such as the GPU, FPGA, and neuromorphic chips. Around the graph, examples are given in which the computing hardware is used for achieving insect-inspired AI. (A) In (97), an STM32F4 microcontroller was used for a fully autonomous swarm of tiny drones to explore an unknown cluttered environment and collaboratively localize a gas source. (B) In (78), the GPUs on an NVidia TX 2 were used to determine dense flow with a deep neural network. An active vision strategy allowed for a drone to pass through gaps of different unknown shapes. (C) Design of the MiniBee (49), which has been equipped with FPGA-based optic flow for autonomous navigation (inset, Opteran's FPGA-based visual navigation kit). (D) In (188), an onboard Loihi neuromorphic chip (Kaphoho bay) was used for controlling autonomous constant divergence optic flow landings. (E) In (189), a Loihi chip was used for the complete perception-to-action pipeline for the attitude control of a drone clamped to allow for rotation as the single degree of freedom.

(Curved Artificial Compound Eye) visual sensor (46). However, for faster sensors like event-based cameras, or more elaborate processing such as deep convolutional neural networks, the limited von Neumann processor on a microcontroller may become a bottleneck. A similar line of reasoning goes for more powerful CPUs, although the limits are less severe.

This is where parallel processing—a fundamental feature of processing in the brain—comes into the picture. Graphical processing units (GPUs) are an alternative computing architecture that is explicitly designed to perform parallel computations using many parallel processors. Notably, they can readily implement traditional (i.e., non-neuromorphic) artificial neural network inference. This

speeds up the execution of deep neural networks, making it possible to operate in real time even on onboard embedded devices such as the NVidia TX 2. For instance, in (78), a TX 2 was used to determine dense optic flow, enabling a drone to detect and fly through gaps. However, existing embedded GPUs are still relatively heavy and consume a substantial amount of energy. The NVidia TX 2 weighs 85 g and consumes 7.5 W of power, which is unacceptable for many of the small robots discussed in this article. The size and energy consumption of GPUs has been improving at a faster rate than CPUs in recent years [see (65) for a thorough investigation of various embedded processors for running deep neural networks], but both are restricted by the physical limits that limit indefinite extension of Moore's law. Exploiting potential sparsity in neural networks can make their implementation on GPUs more energy efficient, e.g., (172), but other processor architectures in which low power and high throughput have been at the core of the design from the start promise even greater gains.

An alternative for parallel processing with very high throughput is to use a field-programmable gate array (FPGA). In addition to their widespread availability on the market, FPGAs offer noise robustness and, most importantly, high implementation flexibility (173). This flexibility allows, for example, for the implementation of spiking neural networks (SNNs) (174) on FPGAs to obtain low latency and energy efficiency (173, 175–177) or computing dense optic flow (178, 179). A disadvantage of FPGAs with respect to CPUs or GPUs is that programming them is more burdensome. Traditionally, floating-point math operations were inefficient on FPGAs, but new designs now incorporate built-in floating-point units. We believe the extra effort required for FPGAs is justified if one needs to specialize beyond the traditional deep neural networks. A similar line of reasoning can be followed for application-specific integrated circuits, for which the engineering effort and especially the costs of production are orders of magnitude higher.

Neuromorphic processors represent an important alternative with substantial promise. These processors are aimed specifically at implementing the parallel, sparse, and asynchronous processing of SNNs (174) and/or exploiting other desirable characteristics of transistors. The latter includes operating in their efficient subthreshold regime (180) or using floating-gate arrays to compute the harmonic mean for low-power localization (181). SNNs have temporal dynamics that more closely model natural neurons. For instance, in the so-called leaky-integrate-and-fire model, the neurons integrate incoming weighted input currents in the membrane voltage, which decays over time and produces a spike when it exceeds a threshold (182). In real brains, spikes have likely evolved to transmit information over longer distances (22). Each spike consumes considerable energy, so the spike rate is minimized, which leads to sparse, energy-efficient processing. Examples of neuromorphic processors include Intel's Loihi (183), IBM's TrueNorth (184), HICANN (185), Neuro-Grid (186), and SpiNNaker (187). There is an increasing number of examples that show the potential of these processors both in terms of energy expenditure and in execution speed. For instance, in (188), an SNN composed of only 35 spiking neurons controlled a flying robot for performing optic flow landings, with the controller running onboard the Loihi neuromorphic processor at 265 kHz. In (189), an on-chip SNN model of a proportional, integrative, derivative (PID) controller was used to control a 1-DOF (degree of freedom) quadrotor arm at 1 kHz, with an average 0.0126 mW power consumption per time stamp for a total of 40,000 neurons. However, there remain obstacles that must be overcome to realize neuromorphic processing's



full potential, both in terms of software (how to have SNNs learn robustly, preferably online in the neuromorphic hardware) and in terms of hardware (how to interface neuromorphic processors with a robot's sensors and actuators so that the energy efficiency and execution speed is not lost).

Last, also for the choice of a processor, the scale of envisaged robots is essential. For tiny insects, the neural elements start to hit biophysical limits related to channel noise, leading to different neural solutions (17, 22). For example, the tiny wasp *Megaphragma caribea* (average body length of 170  $\mu\text{m}$ ) has many neurons without a nucleus (190). If we intend to design robots at such tiny scales, they may require custom processors that deal with similar physical phenomena and that are currently beyond the horizon.

## CONCLUSION

In this article, we have argued that drawing inspiration from insect intelligence will enable reaching higher autonomy levels, even with modest processing capabilities available on small robots and devices. To achieve this, we argue that the right approach is not to implement existing autonomy algorithms in novel processors. Instead, the robot engineer will have to strive for the same kind of parsimony that is found in insect intelligence. This will be vital for small robots with limited resources, like tiny insect-like flying drones (29, 191), but it will also be important for larger robots when they have to execute many complex tasks, when their bodies are covered with tiny sensors, and when energy efficiency is an overriding concern. Indeed, in nature, parsimony is not reserved for insects alone; it is a governing principle for all animals.

## REFERENCES AND NOTES

- G. Z. Yang, J. Bellingham, P. E. Dupont, P. Fischer, L. Floridi, R. Full, N. Jacobstein, V. Kumar, M. M. Nutt, R. Merrifield, B. J. Nelson, B. Scassellati, M. Taddeo, R. Taylor, M. Veloso, Z. L. Wang, R. Wood, The grand challenges of *Science Robotics*. *Sci. Robot.* **3**, eaar7650 (2018).
- B. Bodin, H. Wagstaff, S. Saecdi, L. Nardi, E. Vespa, J. Mawer, A. Nisbet, M. Lujan, S. Furber, A. J. Davison, P. H. J. Kelly, M. F. P. O'Boyle, SLAMBench2: Multi-objective head-to-head benchmarking for visual SLAM, in *Proceedings of the 2018 IEEE International Conference on Robotics and Automation (ICRA)* (IEEE, 2018), pp. 1–8.
- M. Lundstrom, Moore's law forever? *Science* **299**, 210–211 (2003).
- T. N. Theis, H.-S. P. Wong, The end of Moore's law: A new beginning for information technology. *Comput. Sci. Eng.* **19**, 41–50 (2017).
- L. Steels, The artificial life roots of artificial intelligence. *Artif. Life* **1**, 75–110 (1993).
- R. A. Brooks, *Achieving Artificial Intelligence Through Building Robots* (MIT Libraries, 1986).
- D. Grimaldi, M. S. Engel, M. S. Engel, M. S. Engel, *Evolution of the Insects* (Cambridge Univ. Press, 2005).
- N. E. Stork, How many species of insects and other terrestrial arthropods are there on Earth? *Annu. Rev. Entomol.* **63**, 31–45 (2018).
- N. J. Strausfeld, The organization of the insect visual system (Light microscopy). *Z. Zellforsch. Mikrosk. Anat.* **121**, 377–441 (1971).
- M. F. Land, Visual acuity in insects. *Annu. Rev. Entomol.* **42**, 147–177 (1997).
- R. Wehner, Desert ant navigation: How miniature brains solve complex tasks. *J. Comp. Physiol. A* **189**, 579–588 (2003).
- R. Menzel, M. Giurfa, Cognitive architecture of a mini-brain: The honeybee. *Trends Cogn. Sci.* **5**, 62–71 (2001).
- J. D. Seelig, V. Jayaraman, Neural dynamics for landmark orientation and angular path integration. *Nature* **521**, 186–191 (2015).
- M. H. Dickinson, Death Valley, *Drosophila*, and the Devonian toolkit. *Annu. Rev. Entomol.* **59**, 51–72 (2014).
- J. H. Fewell, Social insect networks. *Science* **301**, 1867–1870 (2003).
- S. Garnier, J. Gautrais, G. Theraulaz, The biological principles of swarm intelligence. *Swarm Intell.* **1**, 3–31 (2007).
- A. A. Polillov, Small is beautiful: Features of the smallest insects and limits to miniaturization. *Annu. Rev. Entomol.* **60**, 103–121 (2015).
- P. S. Katz, R. M. Harris-Warrick, The evolution of neuronal circuits underlying species-specific behavior. *Curr. Opin. Neurobiol.* **9**, 628–633 (1999).
- B. Webb, Robots with insect brains. *Science* **368**, 244–245 (2020).
- D. Floreano, C. Mattiussi, *Bio-Inspired Artificial Intelligence: Theories, Methods, and Technologies* (MIT Press, 2008).
- R. Menzel, A short history of studies on intelligence and brain in honeybees. *Apidologie* **52**, 23–34 (2021).
- P. Sterling, S. Laughlin, *Principles of Neural Design* (MIT Press, 2015).
- M. L. Anderson, Embodied cognition: A field guide. *Artif. Intell.* **149**, 91–130 (2003).
- R. Pfeifer, C. Scheier, *Understanding Intelligence* (MIT Press, 2001).
- A. Geiger, P. Lenz, C. Stiller, R. Urtasun, Vision meets robotics: The KITTI dataset. *Int. J. Rob. Res.* **32**, 1231–1237 (2013).
- S. Collins, A. Ruina, R. Tedrake, M. Wisse, Efficient bipedal robots based on passive-dynamic walkers. *Science* **307**, 1082–1085 (2005).
- C. P. Ellington, C. Van Den Berg, A. P. Willmott, A. L. R. Thomas, Leading-edge vortices in insect flight. *Nature* **384**, 626–630 (1996).
- R. J. Wood, The first takeoff of a biologically inspired at-scale robotic insect. *IEEE Trans. Robot.* **24**, 341–347 (2008).
- K. Y. Ma, P. Chirarattananon, S. B. Fuller, R. J. Wood, Controlled flight of a biologically inspired, insect-scale robot. *Science* **340**, 603–607 (2013).
- M. Karásek, F. T. Muijres, C. De Wagter, B. D. W. Remes, G. C. H. E. de Croon, A tailless aerial robotic flapper reveals that flies use torque coupling in rapid banked turns. *Science* **361**, 1089–1094 (2018).
- B. H. Dickerson, Z. N. Aldworth, T. L. Daniel, Control of moth flight posture is mediated by wing mechanosensory feedback. *J. Exp. Biol.* **217**, 2301–2308 (2014).
- S. P. Sane, The aerodynamics of insect flight. *J. Exp. Biol.* **206**, 4191–4208 (2003).
- M. H. Dickinson, K. G. Gotz, Unsteady aerodynamic performance of model wings at low Reynolds numbers. *J. Exp. Biol.* **174**, 45–64 (1993).
- P. J. DeVries, C. M. Penz, R. I. Hill, Vertical distribution, flight behaviour and evolution of wing morphology in *Morpho* butterflies. *J. Anim. Ecol.* **79**, 1077–1085 (2010).
- J. Gerdes, A. Holness, A. Perez-Rosado, L. Roberts, A. Greisinger, E. Barnett, J. Kempny, D. Lingam, C. H. Yeh, H. A. Bruck, S. K. Gupta, Robo Raven: A flapping-wing air vehicle with highly compliant and independently controlled wings. *Soft Robot.* **1**, 275–288 (2014).
- P. Ramdya, R. Thandiackal, R. Cherney, T. Asselborn, R. Benton, A. J. Ijspeert, D. Floreano, Climbing favours the tripod gait over alternative faster insect gaits. *Nat. Commun.* **8**, 14494 (2017).
- K. Shackleton, N. J. Balfour, H. A. Toufaily, D. A. Alves, J. M. Bento, F. L. W. Ratnieks, Unique nest entrance structure of *Partamona helleri* stingless bees leads to remarkable 'crash-landing' behaviour. *Insectes Soc.* **66**, 471–477 (2019).
- A. Briod, P. Kornatowski, J.-C. Zufferey, D. Floreano, A collision-resilient flying robot. *J. F. Robot.* **31**, 496–509 (2014).
- S. Mintchev, J. Shintake, D. Floreano, Bioinspired dual-stiffness origami. *Sci. Robot.* **3**, eaau0275 (2018).
- H. V. Phan, H. C. Park, Mechanisms of collision recovery in flying beetles and flapping-wing robots. *Science* **370**, 1214–1219 (2020).
- M. F. Land, D.-E. Nilsson, *Animal Eyes* (Oxford Univ. Press, 2012).
- H. Autrum, M. Stöcker, Über optische Verschmelzungsfrequenzen und stroboskopisches Sehen bei Insekten. *Biol. Zentralbl.* **71**, 129–152 (1952).
- T. J. Wardill, S. T. Fabian, A. C. Pettigrew, D. G. Stavenga, K. Nordström, P. T. Gonzalez-Bellido, A novel interception strategy in a miniature robber fly with extreme visual acuity. *Curr. Biol.* **27**, 854–859 (2017).
- F. T. Muijres, M. J. Elzinga, J. M. Melis, M. H. Dickinson, Flies evade looming targets by executing rapid visually directed banked turns. *Science* **344**, 172–177 (2014).
- K.-H. Jeong, J. Kim, L. P. Lee, Biologically inspired artificial compound eyes. *Science* **312**, 557–561 (2006).
- D. Floreano, R. Pericet-Camara, S. Viollet, F. Ruffier, A. Brückner, R. Leitl, W. Buss, M. Menouni, F. Expert, R. Juston, M. K. Dobrzynski, G. L'Eplattenier, F. Recktenwald, H. A. Mallot, N. Franceschini, Miniature curved artificial compound eyes. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 9267–9272 (2013).
- S. Viollet, S. Godiot, R. Leitl, W. Buss, P. Breugnion, M. Menouni, R. Juston, F. Expert, F. Colonnier, G. L'Eplattenier, A. Brückner, F. Kraze, H. Mallot, N. Franceschini, R. Pericet-Camara, F. Ruffier, D. Floreano, Hardware architecture and cutting-edge assembly process of a tiny curved compound eye. *Sensors* **14**, 21702–21721 (2014).
- J. Keshavan, G. Gremillion, H. Alvarez-Escobar, J. S. Humbert, Autonomous vision-based navigation of a quadrotor in corridor-like environments. *Int. J. Micro Air Veh.* **7**, 111–123 (2015).
- A. J. Cope, A. Ahmed, F. Isa, J. A. R. Marshall, MiniBee: A miniature MAV for the biomimetic embodiment of insect brain models, in *Conference on Biomimetic and Biohybrid Systems* (Lecture Notes in Computer Science, Springer, 2019), pp. 76–87.
- G. Gallego, T. Delbrück, G. Orchard, C. Bartolozzi, B. Taba, A. Censi, S. Leutenegger, A. J. Davison, J. Conradt, K. Daniilidis, D. Scaranuzza, Event-based vision: A survey. *IEEE Trans. Pattern Anal. Mach. Intell.* **44**, 154–180 (2020).

51. G. K. Taylor, H. G. Krapp, Sensory systems and flight stability: What do insects measure and why? *Adv. Insect Phys.* **34**, 231–316 (2007).
52. S. B. Fuller, A. D. Straw, M. Y. Peek, R. M. Murray, M. H. Dickinson, Flying *Drosophila* stabilize their vision-based velocity controller by sensing wind with their antennae. *Proc. Natl. Acad. Sci. U.S.A.* **111**, E1182–E1191 (2014).
53. M. J. Rauscher, J. L. Fox, Haltere and visual inputs sum linearly to predict wing (but not gaze) motor output in tethered flying *Drosophila*. *Proc. R. Soc. B* **288**, 20202374 (2021).
54. M. J. Anderson, J. G. Sullivan, T. K. Horiuchi, S. B. Fuller, T. L. Daniel, A bio-hybrid odor-guided autonomous palm-sized air vehicle. *Bioinspir. Biomim.* **16**, 26002 (2020).
55. Y. Kuwana, S. Nagasawa, I. Shimoyama, R. Kanzaki, Synthesis of the pheromone-oriented behaviour of silkworm moths by a mobile robot with moth antennae as pheromone sensors. *Biosens. Bioelectron.* **14**, 195–202 (1999).
56. D. Burkhardt, M. Gewecke, Mechanoreception in Arthropoda: The chain from stimulus to behavioral pattern. *Cold Spring Harb. Symp. Quant. Biol.* **30**, 601–614 (1965).
57. N. Chen, C. Tucker, J. M. Engel, Y. Yang, S. Pandya, C. Liu, Design and characterization of artificial haircell sensor for flow sensing with ultrahigh velocity and angular sensitivity. *J. Microelectromech. Syst.* **16**, 999–1014 (2007).
58. A. M. Pankonien, K. S. T. Magar, R. V. Beblo, G. W. Reich, Gust prediction via artificial hair sensor array and neural network, in *A Tribute Conference Honoring Daniel Inman* (SPIE, 2017), vol. 10172, p. 101720F.
59. S. B. Fuller, A. Sands, A. Haggerty, M. Karpelson, R. J. Wood, Estimating attitude and wind velocity using biomimetic sensors on a microbotic bee, in *Proceedings of the 2013 IEEE International Conference on Robotics and Automation* (IEEE, 2013), pp. 1374–1380.
60. F. van Breugel, M. H. Dickinson, Plume-tracking behavior of flying *Drosophila* emerges from a set of distinct sensory-motor reflexes. *Curr. Biol.* **24**, 274–286 (2014).
61. S. A. Budick, M. H. Dickinson, Free-flight responses of *Drosophila melanogaster* to attractive odors. *J. Exp. Biol.* **209**, 3001–3017 (2006).
62. R. T. Cardé, M. A. Willis, Navigational strategies used by insects to find distant, wind-borne sources of odor. *J. Chem. Ecol.* **34**, 854–866 (2008).
63. N. Cheney, J. Bongard, V. SunSpiral, H. Lipson, Scalable co-optimization of morphology and control in embodied machines. *J. R. Soc. Interface* **15**, 20170937 (2018).
64. K. Miras, E. Haasdijk, K. Glette, A. E. Eiben, Effects of selection preferences on evolved robot morphologies and behaviors, in *ALIFE 2018: The 2018 Conference on Artificial Life* (MIT Press, 2018), pp. 224–231.
65. N. J. Sanket, C. D. Singh, C. Fermüller, Y. Aloimonos, PRGFlow: Unified SWAP-aware deep global optical flow for aerial robot navigation. *Electron. Lett.* **57**, 614–617 (2021).
66. J. Aloimonos, I. Weiss, A. Bandyopadhyay, Active vision. *Int. J. Comput. Vis.* **1**, 333–356 (1988).
67. R. Bajcsy, Y. Aloimonos, J. K. Tsotsos, Revisiting active perception. *Auton. Robots* **42**, 177–196 (2018).
68. Y. Aloimonos, C. Fermüller, A bug's-eye view. *Sci. Robot.* **5**, 44 (2020).
69. H. C. Longuet-Higgins, K. Prazdny, The interpretation of a moving retinal image. *Proc. R. Soc. London B Biol. Sci.* **208**, 385–397 (1980).
70. F. Expert, F. Ruffier, Flying over uneven moving terrain based on optic-flow cues without any need for reference frames or accelerometers. *Bioinspir. Biomim.* **10**, 026003 (2015).
71. S. Mange, E. F. Helbling, N. Gravish, R. J. Wood, An actuated gaze stabilization platform for a flapping-wing microbot, in *Proceedings of the 2017 IEEE International Conference on Robotics and Automation (ICRA)* (IEEE, 2017), pp. 5409–5414.
72. J.-L. Stevens, R. Mahony, Vision based forward sensitive reactive control for a quadrotor VTOL, in *Proceedings of the 2018 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS)* (IEEE, 2018), pp. 5232–5238.
73. V. Iyer, A. Najafi, J. James, S. Fuller, S. Gollakota, Wireless steerable vision for live insects and insect-scale robots. *Sci. Robot.* **5**, eabb0839 (2020).
74. N. Franceschini, R. Chagneux, K. Kirschfeld, Gaze control in flies by co-ordinated action of eye muscles. *Göttingen Neurobiol.*, 401 (1995).
75. M. Juusola, A. Dau, Z. Song, N. Solanki, D. Rien, D. Jaciuch, S. A. Dongre, F. Blanchard, G. G. de Polavieja, R. C. Hardie, J. Takalo, Microsaccadic sampling of moving image information provides *Drosophila* hyperacute vision. *eLife* **6**, e26117 (2017).
76. L. Kerhuel, S. Viollet, N. Franceschini, The VODKA sensor: A bio-inspired hyperacute optical position sensing device. *IEEE Sens. J.* **12**, 315–324 (2011).
77. S. Viollet, Vibrating makes for better seeing: From the fly's micro-eye movements to hyperacute visual sensors. *Front. Bioeng. Biotechnol.* **2**, 9 (2014).
78. N. J. Sanket, C. D. Singh, K. Ganguly, C. Fermüller, Y. Aloimonos, Gapfly: Active vision based minimalist structure-less gap detection for quadrotor flight. *IEEE Robot. Autom. Lett.* **3**, 2799–2806 (2018).
79. J. Brebner, L. Chittka, Animal cognition: The self-image of a bumblebee. *Curr. Biol.* **31**, R207–R209 (2021).
80. G. C. H. E. de Croon, Monocular distance estimation with optical flow maneuvers and efference copies: A stability-based strategy. *Bioinspir. Biomim.* **11**, 016004 (2016).
81. B. Baddeley, P. Graham, A. Husbands, A. Philippides, A model of ant route navigation driven by scene familiarity. *PLOS Comput. Biol.* **8**, e1002336 (2012).
82. A. Wystrach, Movements, embodiment and the emergence of decisions. Insights from insect navigation. *Biochem. Biophys. Res. Commun.* **564**, 70–77 (2021).
83. F. Le Möel, A. Wystrach, Opponent processes in visual memories: A model of attraction and repulsion in navigating insects' mushroom bodies. *PLOS Comput. Biol.* **16**, e1007631 (2020).
84. A. Kodzhabashev, M. Mangan, Route following without scanning, in *Conference on Biomimetic and Biohybrid Systems* (Lecture Notes in Computer Science, 2015), pp. 199–210.
85. A. Philippides, N. H. de Ibarra, O. Riabinina, T. S. Collett, Bumblebee calligraphy: The design and control of flight motifs in the learning and return flights of *Bombus terrestris*. *J. Exp. Biol.* **216**, 1093–1104 (2013).
86. W. Stürzl, J. Zeil, N. Boeddeker, J. M. Hemmi, How wasps acquire and use views for homing. *Curr. Biol.* **26**, 470–482 (2016).
87. A. Ben-Nun, M. Guershon, A. Ayali, Self body-size perception in an insect. *Naturwissenschaften* **100**, 479–484 (2013).
88. C. Solvi, S. G. Al-Khudhairy, L. Chittka, Bumble bees display cross-modal object recognition between visual and tactile senses. *Science* **367**, 910–912 (2020).
89. N. Sanket, *Active Vision Based Embodied-AI Design for Nano-UAV Autonomy* (ProQuest Dissertations Publishing, 2021).
90. E. Bonabeau, M. Dorigo, G. Theraulaz, *Swarm Intelligence: From Natural to Artificial Systems* (Oxford Univ. Press, 1999).
91. M. Brambilla, E. Ferrante, M. Birattari, M. Dorigo, Swarm robotics: A review from the swarm engineering perspective. *Swarm Intell.* **7**, 1–41 (2013).
92. E. Tuci, R. Groß, V. Trianni, F. Mondada, M. Bonani, M. Dorigo, Cooperation through self-assembly in multi-robot systems. *ACM Trans. Auton. Adapt. Syst.* **1**, 115–150 (2006).
93. A. F. Llenas, M. S. Talamali, X. Xu, J. A. R. Marshall, A. Reina, Quality-sensitive foraging by a robot swarm through virtual pheromone trails, in *International Conference on Swarm Intelligence* (Springer, 2018), pp. 135–149.
94. A. Reina, T. Bose, V. Trianni, J. A. R. Marshall, Effects of spatiality on value-sensitive decisions made by robot swarms, in *Distributed Autonomous Robotic Systems* (Springer, 2018), pp. 461–473.
95. M. Duarte, V. Costa, J. Gomes, T. Rodrigues, F. Silva, S. M. Oliveira, A. L. Christensen, Evolution of collective behaviors for a real swarm of aquatic surface robots. *PLOS ONE* **11**, e0151834 (2016).
96. K. N. McGuire, C. De Wagter, K. Tuyls, H. J. Kappen, G. C. H. E. de Croon, Minimal navigation solution for a swarm of tiny flying robots to explore an unknown environment. *Sci. Robot.* **4**, eaaw9710 (2019).
97. B. P. Duisterhof, S. Li, J. Burgués, V. J. Reddi, G. C. H. E. de Croon, Sniffy Bug: A fully autonomous swarm of gas-seeking nano quadcopters in cluttered environments, in *Proceedings of the 2021 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS 2021)* (IEEE, 2021).
98. R. Wehner, S. Wehner, Insect navigation: Use of maps or Ariadne's thread? *Ethol. Ecol. Evol.* **2**, 27–48 (1990).
99. B. Webb, The internal maps of insects. *J. Exp. Biol.* **222**, jeb188094 (2019).
100. M. Wittlinger, R. Wehner, H. Wolf, The ant odometer: Stepping on stilts and stumps. *Science* **312**, 1965–1967 (2006).
101. J. Dupeyroux, J. R. Serres, S. Viollet, AntBot: A six-legged walking robot able to home like desert ants in outdoor environments. *Sci. Robot.* **4**, eaau0307 (2019).
102. R. Wehner, B. Michel, P. Antonsen, Visual navigation in insects: Coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129–140 (1996).
103. D. Lambrinos, R. Möller, T. Labhart, R. Pfeifer, R. Wehner, A mobile robot employing insect strategies for navigation. *Rob. Auton. Syst.* **30**, 39–64 (2000).
104. T. Labhart, Polarization-opponent interneurons in the insect visual system. *Nature* **331**, 435–437 (1988).
105. R. WEHNER, S. STRASSER, The POL area of the honey bee's eye: Behavioural evidence. *Physiol. Entomol.* **10**, 337–349 (1985).
106. B. A. Cartwright, T. S. Collett, How honey bees use landmarks to guide their return to a food source. *Nature* **295**, 560–564 (1982).
107. V. V. Hafner, R. Möller, Learning of visual navigation strategies, in *Proceedings of the European Workshop on Learning Robots* (Springer, 2001), vol. 1, pp. 47–56.
108. J. C. Knight, D. Sakhapov, N. Domcsek, A. D. M. Dewar, P. Graham, T. Nowotny, A. Philippides, Insect-inspired visual navigation on-board an autonomous robot: Real-world routes encoded in a single layer network, in *ALIFE: The 2019 Conference on Artificial Life* (MIT Press, 2019), pp. 60–67.
109. A. Stelzer, M. Vayugundla, E. Mair, M. Suppa, W. Burgard, Towards efficient and scalable visual homing. *Int. J. Rob. Res.* **37**, 225–248 (2018).
110. W. E. Green, P. Y. Oh, Optic-flow-based collision avoidance. *IEEE Robot. Autom. Mag.* **15**, 96–103 (2008).
111. A. J. Cope, C. Sabo, K. Gurney, E. Vasilaki, J. A. R. Marshall, A model for an angular velocity-tuned motion detector accounting for deviations in the corridor-centering response of the bee. *PLOS Comput. Biol.* **12**, e1004887 (2016).

112. N. J. Sanket, C. M. Parameshwara, C. D. Singh, A. V. Kuruttukulam, C. Fermüller, D. Scaramuzza, Y. Aloimonos, Evdodgenet: Deep dynamic obstacle dodging with event cameras, in *Proceedings of the 2020 IEEE International Conference on Robotics and Automation (ICRA)* (IEEE, 2020), pp. 10651–10657.
113. F. Colonnier, S. Ramirez-Martinez, S. Viollet, F. Ruffier, A bio-inspired sighted robot chases like a hoverfly. *Bioinspir. Biomim.* **14**, 36002 (2019).
114. F. Ruffier, N. Franceschini, Visually guided micro-aerial vehicle: Automatic take off, terrain following, landing and wind reaction, in *Proceedings of the 2004 IEEE International Conference on Robotics and Automation (ICRA'04, 2004)* (IEEE, 2004), vol. 3, pp. 2339–2346.
115. C. Planta, J. Conrad, A. Jencik, P. Verschure, A neural model of the fly visual system applied to navigational tasks, in *International Conference on Artificial Neural Networks* (Lecture Notes in Computer Science, 2002), pp. 1268–1274.
116. B. Herissé, T. Hamel, R. Mahony, F.-X. Russo, Landing a VTOL unmanned aerial vehicle on a moving platform using optical flow. *IEEE Trans. Robot.* **28**, 77–89 (2011).
117. M. V. Srinivasan, S. Zhang, J. S. Chahl, Landing strategies in honeybees, and possible applications to autonomous airborne vehicles. *Biol. Bull.* **200**, 216–221 (2001).
118. E. Baird, N. Boeddeker, M. R. Ibbotson, M. V. Srinivasan, A universal strategy for visually guided landing. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 18686–18691 (2013).
119. G. C. H. E. de Croon, C. De Wagter, T. Seidl, Enhancing optical-flow-based control by learning visual appearance cues for flying robots. *Nat. Mach. Intell.* **3**, 33–41 (2021).
120. F. C. Rind, P. J. Simmons, Orthopteran DCMD neuron: A reevaluation of responses to moving objects. I. Selective responses to approaching objects. *J. Neurophysiol.* **68**, 1654–1666 (1992).
121. P. J. Simmons, F. C. Rind, Orthopteran DCMD neuron: A reevaluation of responses to moving objects. II. Critical cues for detecting approaching objects. *J. Neurophysiol.* **68**, 1667–1682 (1992).
122. S. Judge, F. Rind, The locust DCMD, a movement-detecting neurone tightly tuned to collision trajectories. *J. Exp. Biol.* **200**, 2209–2216 (1997).
123. F. C. Rind, S. Wernitznig, P. Pölt, A. Zankl, D. Gütl, J. Sztarker, G. Leitinger, Two identified looming detectors in the locust: Ubiquitous lateral connections among their inputs contribute to selective responses to looming objects. *Sci. Rep.* **6**, 35525 (2016).
124. F. C. Rind, D. I. Bramwell, Neural network based on the input organization of an identified neuron signaling impending collision. *J. Neurophysiol.* **75**, 967–985 (1996).
125. S. Yue, F. C. Rind, A collision detection system for a mobile robot inspired by the locust visual system, in *Proceedings of the 2005 IEEE International Conference on Robotics and Automation (IEEE, 2005)*, pp. 3832–3837.
126. S. Yue, F. C. Rind, Collision detection in complex dynamic scenes using an LGMD-based visual neural network with feature enhancement. *IEEE Trans. Neural Netw.* **17**, 705–716 (2006).
127. Q. Fu, C. Hu, T. Liu, S. Yue, Collision selective LGMDs neuron models research benefits from a vision-based autonomous micro robot, in *Proceedings of the 2017 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS)* (IEEE, 2017), pp. 3996–4002.
128. L. Salt, D. Howard, G. Indiveri, Y. Sandamirskaya, Parameter optimization and learning in a spiking neural network for UAV obstacle avoidance targeting neuromorphic processors. *IEEE Trans. Neural Networks Learn. Syst.* **31**, 3305–3318 (2019).
129. X. Sun, S. Yue, M. Mangan, A decentralised neural model explaining optimal integration of navigational strategies in insects. *eLife* **9**, e54026 (2020).
130. D. Falanga, K. Kleber, D. Scaramuzza, Dynamic obstacle avoidance for quadrotors with event cameras. *Sci. Robot.* **5**, eaa29712 (2020).
131. N. J. Sanket, C. D. Singh, C. M. Parameshwara, C. Fermüller, G. C. H. E. de Croon, Y. Aloimonos, EVPropNet: Detecting drones by finding propellers for mid-air landing and following. *Proceedings of Robotics: Science and Systems*. 10.15607/RSS.2021.XVII.074 (Sanket-RSS-21, 2021).
132. S. Dasgupta, C. F. Stevens, S. Navlakha, A neural algorithm for a fundamental computing problem. *Science* **358**, 793–796 (2017).
133. R. Huerta, T. Nowotny, M. Garcia-Sanchez, H. D. I. Abarbanel, M. I. Rabinovich, Learning classification in the olfactory system of insects. *Neural Comput.* **16**, 1601–1640 (2004).
134. A. G. Dyer, C. Neumeyer, L. Chittka, Honeybee (*Apis mellifera*) vision can discriminate between and recognise images of human faces. *J. Exp. Biol.* **208**, 4709–4714 (2005).
135. M. Heisenberg, Mushroom body memoir: From maps to models. *Nat. Rev. Neurosci.* **4**, 266–275 (2003).
136. D. Smith, J. Wessnitzer, B. Webb, A model of associative learning in the mushroom body. *Biol. Cybern.* **99**, 89–103 (2008).
137. M. N. Modi, Y. Shuai, G. C. Turner, The *Drosophila* mushroom body: From architecture to algorithm in a learning circuit. *Annu. Rev. Neurosci.* **43**, 465–484 (2020).
138. J. E. M. Bennett, A. Philippides, T. Nowotny, Learning with reinforcement prediction errors in a model of the *Drosophila* mushroom body. *Nat. Commun.* **12**, 2569 (2021).
139. C. Pehlevan, A. Genkin, D. B. Chklovskii, A clustering neural network model of insect olfaction, in *Proceedings of the 2017 51st Asilomar Conference on Signals, Systems, and Computers* (IEEE, 2017), pp. 593–600.
140. B. Arcanjo, B. Ferrarini, M. Milford, K. D. McDonald-Maier, S. Ehsan, An efficient and scalable collection of fly-inspired voting units for visual place recognition in changing environments. *IEEE Robot. Autom. Lett.* **7**, 2527–2534 (2022).
141. R. A. Brooks, Elephants don't play chess. *Rob. Auton. Syst.* **6**, 3–15 (1990).
142. N. Franceschini, J.-M. Pichon, C. Blanes, From insect vision to robot vision. *Philos. Trans. R. Soc. London Ser. B Biol. Sci.* **337**, 283–294 (1992).
143. V. Trianni, S. Nolfi, M. Dorigo, Evolution, self-organization and swarm robotics, in *Swarm Intelligence* (Springer, 2008), pp. 163–191.
144. A. J. Cope, C. Sabo, E. Vasilaki, A. B. Barron, J. A. R. Marshall, A computational model of the integration of landmarks and motion in the insect central complex. *PLOS ONE* **12**, e0172325 (2017).
145. M. Srinivasan, S. Zhang, M. Lehrer, T. Collett, Honeybee navigation en route to the goal: Visual flight control and odometry. *J. Exp. Biol.* **199**, 237–244 (1996).
146. J. R. Stowers, M. Hofbauer, R. Bastien, J. Griessner, P. Higgins, S. Farooqui, R. M. Fischer, K. Nowikovsky, W. Haubensak, I. D. Couzin, K. Tessmar-Raible, A. D. Straw, Virtual reality for freely moving animals. *Nat. Methods* **14**, 995–1002 (2017).
147. L. K. Scheffer, C. S. Xu, M. Januszewski, Z. Lu, S. Y. Takemura, K. J. Hayworth, G. B. Huang, K. Shinomiya, J. Maitlin-Shepard, S. Berg, J. Clements, P. M. Hubbard, W. T. Katz, L. Umayam, T. Zhao, D. Ackerman, T. Blakely, J. Bogovic, T. Dolafi, D. Kainmueller, T. Kawase, K. A. Khairy, L. Leavitt, P. H. Li, L. Lindsey, N. Neubarth, D. J. Olbris, H. Otsuna, E. T. Trautman, M. Ito, A. S. Bates, J. Goldammer, T. Wolff, R. Svirskas, P. Schlegel, E. Neace, C. J. Knecht, C. X. Alvarado, D. A. Bailey, S. Ballinger, J. A. Borycz, B. S. Canino, N. Cheatham, M. Cook, M. Dreher, O. Duclos, B. Eubanks, K. Fairbanks, S. Finley, N. Forknall, A. Francis, G. P. Hopkins, E. M. Joyce, S. J. Kim, N. A. Kirk, J. Kovalyak, S. A. Lauchie, A. Lohff, C. Maldonado, E. A. Manley, S. McLin, C. Mooney, M. Ndama, O. Ogundeyi, N. Okeoma, C. Ordish, N. Padilla, C. M. Patrick, T. Paterson, E. E. Phillips, E. M. Phillips, N. Rampally, C. Ribeiro, M. K. Robertson, J. T. Rymer, S. M. Ryan, M. Sammons, A. K. Scott, A. L. Scott, A. Shinomiya, C. Smith, K. Smith, N. L. Smith, M. A. Sobeski, A. Suleiman, J. Swift, S. Takemura, I. Talebi, D. Tarnogorska, E. Tenshaw, T. Tokhi, J. J. Walsh, T. Yang, J. A. Horne, F. Li, R. Parekh, P. K. Rivlin, V. Jayaraman, M. Costa, G. S. X. E. Jefferis, K. Ito, S. Saalfeld, R. George, I. A. Meinertzhagen, G. M. Rubin, H. F. Hess, V. Jain, S. M. Plaza, A connectome and analysis of the adult *Drosophila* central brain. *eLife* **9**, e57443 (2020).
148. T. Riemensperger, R. J. Kittel, A. Fiala, Optogenetics in *Drosophila* neuroscience, in *Optogenetics* (Springer, 2016), pp. 167–175.
149. S. S. Kim, H. Rouault, S. Druckmann, V. Jayaraman, Ring attractor dynamics in the *Drosophila* central brain. *Science* **356**, 849–853 (2017).
150. S. Nolfi, J. Bongard, P. Husbands, D. Floreano, Evolutionary robotics, in *Springer Handbook of Robotics* (Springer, 2016), pp. 2035–2068.
151. S. Doncieux, N. Bredeche, J.-B. Mouret, A. E. G. Eiben, Evolutionary robotics: What, why, and where to. *Front. Robot. AI* **2**, 4 (2015).
152. R. S. Sutton, A. G. Barto, *Reinforcement Learning: An Introduction* (The MIT Press, 2018).
153. D. Floreano, C. Mattiussi, Evolution of spiking neural controllers for autonomous vision-based robots, in *International Symposium on Evolutionary Robotics* (Springer, 2001), pp. 38–61.
154. L. Lichtensteiger, R. Salomon, The evolution of an artificial compound eye by using adaptive hardware, in *Proceedings of the 2000 Congress on Evolutionary Computation. CEC00 (Cat. No. 00TH8512)* (IEEE, 2000), vol. 2, pp. 1144–1151.
155. K. O. Stanley, R. Miikkulainen, Evolving neural networks through augmenting topologies. *Evol. Comput.* **10**, 99–127 (2002).
156. J. C. Bongard, Morphological and environmental scaffolding synergize when evolving robot controllers: Artificial life/robotics/evolvable hardware, in *Proceedings of the 13th Annual Conference on Genetic and Evolutionary Computation (ACM, 2011)*, pp. 179–186.
157. J. Lehman, K. O. Stanley, Exploiting open-endedness to solve problems through the search for novelty, in *Proceedings of the Eleventh International Conference on Artificial Life (ALIFE XI)* (MIT Press, 2008), pp. 329–336.
158. N. Jakobi, P. Husbands, I. Harvey, Noise and the reality gap: The use of simulation in evolutionary robotics, in *Lecture Notes in Computer Science (including subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)* (Springer, 1995), vol. 929, pp. 704–720.
159. J. Kodjabachian, J.-A. Meyer, Evolution and development of neural controllers for locomotion, gradient-following, and obstacle-avoidance in artificial insects. *IEEE Trans. Neural Netw.* **9**, 796–812 (1998).
160. G. Vászárhelyi, C. Virágh, G. Somorjai, T. Nepusz, A. E. Eiben, T. Vicsek, Optimized flocking of autonomous drones in confined environments. *Sci. Robot.* **3**, eaat3536 (2018).
161. K. Y. W. Scheper, G. C. H. E. de Croon, *Abstraction as a Mechanism to Cross the Reality Gap in Evolutionary Robotics* (Springer, 2016), vol. 9825 LNCS.
162. G. Francesca, M. Brambilla, A. Brutschy, V. Trianni, M. Birattari, AutoMoDe: A novel approach to the automatic design of control software for robot swarms. *Swarm Intell.* **8**, 89–112 (2014).
163. J. Fuentes-Pacheco, J. Ruiz-Ascencio, J. M. Rendón-Mancha, Visual simultaneous localization and mapping: A survey. *Artif. Intell. Rev.* **43**, 55–81 (2015).



164. R. Brooks, A robust layered control system for a mobile robot. *IEEE J. Robot. Autom.* **2**, 14–23 (1986).
165. S. Wu, T. Jiang, G. Zhang, B. Schoenemann, F. Neri, M. Zhu, C. Bu, J. Han, K. D. Kuhnert, Artificial compound eye: A survey of the state-of-the-art. *Artif. Intell. Rev.* **48**, 573–603 (2017).
166. X. Chen, A. Milioto, E. Palazzolo, P. Giguere, J. Behley, C. Stachniss, Suma++: Efficient lidar-based semantic (SLAM), in *2019 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS)* (IEEE, 2019), pp. 4530–4537.
167. Z. Wang, Q. Zhang, J. Li, S. Zhang, J. Liu, A computationally efficient semantic (SLAM) solution for dynamic scenes. *Remote Sens. (Basel)* **11**, 1363 (2019).
168. J. L. Jones, Robots at the tipping point: The road to iRobot Roomba. *IEEE Robot. Autom. Mag.* **13**, 76–78 (2006).
169. D. Marr, *Vision: A Computational Approach* (Freeman & Co., 1982).
170. C. De Wagter, S. Tijmons, B. D. W. Remes, G. C. H. E. de Croon, Autonomous flight of a 20-gram Flapping Wing MAV with a 4-gram onboard stereo vision system. *Proc. IEEE Int. Conf. Robot. Autom.*, 4982–4987 (2014).
171. N. Franceschini, K. Kirschfeld, Les phénomènes de pseudopupille dans l'œil composé de *Drosophila*. *Kybernetik* **9**, 159–182 (1971).
172. J. Lee, J. Lee, D. Han, J. Lee, G. Park, H.-J. Yoo, An energy-efficient sparse deep-neural-network learning accelerator with fine-grained mixed precision of FP8–FP16. *IEEE Solid State Circuits Lett.* **2**, 232–235 (2019).
173. L. P. Maguire, T. M. McGinnity, B. Glackin, A. Ghani, A. Belatreche, J. Harkin, Challenges for large-scale implementations of spiking neural networks on FPGAs. *Neurocomputing* **71**, 13–29 (2007).
174. W. Maass, Networks of spiking neurons: The third generation of neural network models. *Neural Netw.* **10**, 1659–1671 (1997).
175. Q. Wang, Y. Li, B. Shao, S. Dey, P. Li, Energy efficient parallel neuromorphic architectures with approximate arithmetic on FPGA. *Neurocomputing* **221**, 146–158 (2017).
176. H. Fang, Z. Mei, A. Shrestha, Z. Zhao, Y. Li, Q. Qiu, Encoding, model, and architecture: Systematic optimization for spiking neural network in FPGAs, in *Proceedings of the 2020 IEEE/ACM International Conference On Computer Aided Design (ICCAD)* (IEEE, 2020), pp. 1–9.
177. V. Sakellariou, V. Paliouras, An FPGA accelerator for spiking neural network simulation and training, in *Proceedings of the 2021 IEEE International Symposium on Circuits and Systems (ISCAS)* (IEEE, 2021), pp. 1–5.
178. F. Aubépart, N. Franceschini, Bio-inspired optic flow sensors based on FPGA: Application to micro-air-vehicles. *Microprocess. Microsyst.* **31**, 408–419 (2007).
179. Opteran, Opteran Development Kit 2.
180. G. Indiveri, B. Linares-Barranco, T. J. Hamilton, A. van Schaik, R. Etienne-Cummings, T. Delbruck, S.-C. Liu, P. Dudek, P. Häflicher, S. Renaud, J. Schemmel, G. Cauwenberghs, J. Arthur, K. Hynna, F. Folowosele, S. Saighi, T. Serrano-Gotarredona, J. Wijekoon, Y. Wang, K. Boahen, Neuromorphic silicon neuron circuits. *Front. Neurosci.* **5**, 73 (2011).
181. P. Shukla, A. Muralidhar, N. Iliev, T. Tulabandhula, S. B. Fuller, A. Trivedi, Ultra-low power localization of insect-scale drones: Interplay of probabilistic filtering and compute-in-memory. *IEEE Trans. Very Large Scale Integr. (VLSI) Syst.* **30**, 68–80 (2022).
182. R. B. Stein, A theoretical analysis of neuronal variability. *Biophys. J.* **5**, 173–194 (1965).
183. M. Davies, N. Srinivasa, T. H. Lin, G. Chinya, Y. Cao, S. H. Choday, G. Dimou, P. Joshi, N. Imam, S. Jain, Y. Liao, C. K. Lin, A. Lines, R. Liu, D. Mathaikutty, S. McCoy, A. Paul, J. Tse, G. Venkataramanan, Y. H. Weng, A. Wild, Y. Yang, H. Wang, Loihi: A neuromorphic manycore processor with on-chip learning. *IEEE Micro* **38**, 82–99 (2018).
184. P. A. Merolla, J. V. Arthur, R. Alvarez-Icaza, A. S. Cassidy, J. Sawada, F. Akopyan, B. L. Jackson, N. Imam, C. Guo, Y. Nakamura, B. Brezzo, I. Vo, S. K. Esser, R. Appuswamy, B. Taba, A. Amir, M. D. Flickner, W. P. Risk, R. Manohar, D. S. Modha, A million spiking-neuron integrated circuit with a scalable communication network and interface. *Science* **345**, 668–673 (2014).
185. J. Schemmel, D. Brüderle, A. Gröbl, M. Hock, K. Meier, S. Millner, A wafer-scale neuromorphic hardware system for large-scale neural modeling, in *Proceedings of the 2010 IEEE International Symposium on Circuits and Systems (ISCAS)* (IEEE, 2010), pp. 1947–1950.
186. B. V. Benjamin, P. Gao, E. McQuinn, S. Choudhary, A. R. Chandrasekaran, J. M. Bussat, R. Alvarez-Icaza, J. V. Arthur, P. A. Merolla, K. Boahen, Neurogrid: A mixed-analog-digital multichip system for large-scale neural simulations. *Proc. IEEE* **102**, 699–716 (2014).
187. S. B. Furber, F. Galluppi, S. Temple, L. A. Plana, The spinnaker project. *Proc. IEEE* **102**, 652–665 (2014).
188. J. Dupeyroux, J. Hagenaars, F. Paredes-Vallés, G.C.H.E. de Croon, Neuromorphic control for optic-flow-based landings of MAVs using the Loihi processor, in *Proceedings of the 2021 IEEE International Conference on Robotics and Automation (ICRA)* (IEEE, 2021).
189. R. K. Stagsted, A. Vitale, A. Renner, L. B. Larsen, A. L. Christensen, Y. Sandamirskaya, Event-based PID controller fully realized in neuromorphic hardware: A one DoF study, in *Proceedings of the 2020 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS)* (IEEE, 2020), pp. 10939–10944.
190. A. A. Polilov, The smallest insects evolve anucleate neurons. *Arthropod Struct. Dev.* **41**, 29–34 (2012).
191. Y. M. Chukewad, J. James, A. Singh, S. Fuller, RoboFly: An insect-sized robot with simplified fabrication that is capable of flight, ground, and water surface locomotion. *IEEE Trans. Robot.* **37**, 2025–2040 (2021).
192. M. Rubenstein, C. Ahler, R. Nagpal, Kilobot: A low cost scalable robot system for collective behaviors, in *Proceedings of the 2012 IEEE International Conference on Robotics and Automation (IEEE, 2012)*, pp. 3293–3298.
193. A. Gidon, T. A. Zolnik, P. Fidzinski, F. Bolduan, A. Papoutsis, P. Poirazi, M. Holtkamp, I. Vida, M. E. Larkum, Dendritic action potentials and computation in human layer 2/3 cortical neurons. *Science* **367**, 83–87 (2020).

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