

Robots in invertebrate neuroscience

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Can we now build artificial animals? A combination of robot technology and neuroethological knowledge is enabling the development of realistic physical models of biological systems. And such systems are not only of interest to engineers. By exploring identified neural control circuits in the appropriate functional and environmental context, new insights are also provided to biologists.

If we understand how an animal controls its behaviour, and comparable technology is available, it should be possible to build a robot that behaves the same way. Recent advances in both knowledge and technology have begun to make this possibility a realistic aim in invertebrate neuroscience. We have computing power of similar capacity to the nervous systems of insects, and can reproduce at least some of the capabilities of their sensor and actuator systems. Investigation of the behaviour and neurophysiology of invertebrates has produced sensorimotor 'circuit diagrams' to copy. There is now a growing number of studies in which hypotheses for the behavioural function of neural circuits are tested by implementing them as controllers for robots and evaluating the robot behaviour. Often such work reveals just how little we really know, but the results are nevertheless generating relevant insights into biology, not just robot engineering.

Several groups have been pursuing this approach for some time, such as Franceschini and colleagues¹⁻⁴ in their investigation of fly visual navigation, and Cruse and associates^{5,6} studying gait control in stick insects. Robot modelling has been used to explore the function of identified neural elements within the overall context of required behavioural output. For example, work on the 'Sahabot'^{7,8} has copied the navigation capabilities of the Saharan desert ant *Cataglyphis*⁹ using polarized light detectors based on the properties of polarization-sensitive interneurons characterized by Labhart¹⁰. Similarly, the dendritic processing thought to underlie the 'looming' detection of the lobular giant movement-detector neuron in the locust¹¹ has been tested on a robot¹². A slightly different approach is illustrated in a robot model of chemotaxis of nematode worms¹³, in which the sensor and motor mechanisms of the worm were represented by robot equivalents (Fig. 1) and the neural controller tuned by an automatic adaptive process. Biological mechanisms of adaptation are themselves studied in some robot implementations, such as the investigation of the effectiveness for robot learning of mechanisms of habituation and sensitization based on the gill-withdrawal reflex in the sea slug *Aplysia*¹⁴.

Although much of the contribution of this work in clarifying and evaluating hypotheses is similar to more conventional modelling, it differs in some important



respects. Robots are required to exist within, and interact with, the real world, unlike the simplified representation of the world used in typical computer simulations. This prevents unrealistic assumptions about the available environmental signals, the nature of 'noise', or how the consequences of actions on the environment might interact with the behaviour. Robots can potentially be tested in the same natural or experimental situation as the animal itself — for example, the 'robolobster'^{15,16} was built to do chemotaxis in the same flow tank as real lobsters, producing a better understanding of the nature of the complex chemical plume they track. Robots may also be able to represent more realistically the physics of sensors and actuators by using physical copies of them. Researchers in insect walking have built robots with the same body plan as cockroaches^{17,18}, and the antennae sensors of a real moth have been used as input devices to a robot¹⁹.

A computer simulation can sometimes include more realistic detail or represent lower-level mechanisms than a robot. Nevertheless, it is becoming more common within biology to complement simulation models with physically embodied ones, so obtaining different perspectives on a problem. A more wide-ranging review of the approach can

be found in ref. 13.

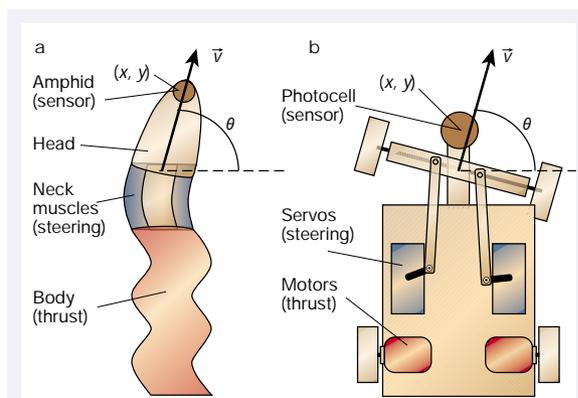


Figure 1 A robot model of chemotaxis of a nematode worm. Schematic representations of **a**, the nematode, and **b**, the robot, showing how sensory and motor systems correspond. Signal intensity is detected at a point x, y ; the direction of movement θ is controlled by head angle and the speed \vec{v} by body thrust. Reprinted with permission from ref. 13.

be found in refs 20 and 21. Here I focus on work in several areas where the neural circuits are as well explored as any in neuroscience, to show some of the insights derived from the holistic, embodied view that robots provide, and how they can produce predictions for neurophysiology. I will also discuss why invertebrate neuroethology seems particularly well suited for the robot modelling approach, providing an opportunity for real progress on issues that will translate to the wider context of behavioural neuroscience.

Robot phonotaxis

Many mobile robots have been built with generic 'taxis' capabilities to approach sensory sources, often inspired by the 'thought experiments' described by Braitenberg²². Taxis behaviours have also been well studied by neuroethologists, and there is much specific data available about particular animal responses to particular signals, and the neural pathways involved. Consequently this would seem a promising area for robot modelling. Cricket phonotaxis is one example where the behaviour, neuroanatomy and neurophysiology have been studied for many years^{23–28}. Robotic implementations of this system have been investigated over the past decade^{29–32}, and improved copies of the sensory and neural processing mechanisms³³ now allow us to draw direct comparisons to the cricket.

Female crickets can locate a mate by orienting towards the species-specific calling song produced by the male. The cricket's ears are connected by a tracheal tube and thus function as pressure-difference receivers. That is, the vibration of the ear drums is the sum of direct and delayed inputs and hence is dependent on relative phase, which varies with sound-source direction for a given wavelength³⁴. The resulting difference in vibration amplitude between the ears is neurally encoded both in spike rate and spike onset latency. The characteristic temporal pattern of the sound is preserved in the spike pattern of auditory neurons and interneurons^{25,35}. The question is how the subsequent neural processing can filter the pattern to recognize the song and compare the difference between the ears to determine the direction of the singer.

The main hypothesis tested on the robot so far is that the tasks of recognition and localization may be closely interlinked. For example, using an electronic circuit to model the tracheal delays in the cricket auditory system, it was shown that a selective approach to particular carrier frequencies can result from tuning the delays to give maximal directionality for particular wavelengths of sound³¹. Use of a spiking neural network, which mimicked the temporal coding properties of identified auditory interneurons, showed that a circuit reacting to the relative latency of activation on each side would respond only to particular temporal patterns, in a way that resembled the female cricket's preference³³.

Using a robot demonstrated that this explanation of phonotaxis is viable for a real sound source in a noisy environment. It was also relatively straightforward to test the model with multiple sound sources, repeating experiments carried out on the cricket to look at the choice between similar but not identical songs, the behaviour when a song was played directly above the robot, and the reaction to a song split between two directions. The robot results were surprisingly similar to the cricket in the first two cases, suggesting that no additional recognition or decision mechanism is needed to explain these behaviours. But the results differed in the case of split song, highlighting some limitations of the model and directions for further work.

The cricket robot is intended as a test-bed for evaluating hypotheses, rather than as an engineering project with a fixed target. For example, a well-characterized pair of mutually inhibitory auditory interneurons in the cricket was not included in the model described above. How these connections might change the functionality of the system is the subject of current investigation focusing on the problems of more realistic sound fields. This means testing the robot outdoors, dealing with a large range of signal amplitudes, background noise and signal distortion from reverberation. It would be difficult to build adequate simulation models of

such environmental factors, but they can be easily replicated in the real world. Phonotaxis outdoors also raises the problem of how the auditory response can be integrated with other sensorimotor responses needed for movement through a complex environment. Some work in this direction is discussed below.

Robot optomotor reflex

One of the best studied areas in invertebrate neuroscience is the sensory system underlying visual motion perception in insects, so it is not surprising that this is also an area in which a number of robot models have been built. Several authors^{3,36,37} have speculated on how some rather simple but clever algorithms apparently used by insects could be adopted for controlling mobile robots, and a number of systems have been implemented. Additionally, some new discoveries in biology have been made as a result of the task-oriented perspective enforced by robotics. For example, an insect (or robot) can use motion parallax as an efficient way to avoid collisions in cluttered environments². However, such a means for detecting obstacles has the drawback that the range of effective vision decreases as the visual axis approaches the line of travel (that is, obstacles directly ahead are the hardest to see). One solution is to oscillate the direction of motion (producing a zig-zag path) or make scanning movements of the eye itself. Lewis³⁸ reports examples of zig-zag paths in insects and uses this behaviour successfully on a robot to navigate through a field of obstacles. And in a detailed investigation of the compound eye, motivated by the results of robot modelling, Franceschini and Chagneuz report³⁹ a muscle and tendon system behind the fly's eye that could produce the required scanning movement. A microscale sensor has been built based on this principle⁴⁰.

A recent study with a number of interesting features is the implementation of an optomotor aVLSI (analog very-large-scale integration) chip by Harrison and Koch^{41,42}. They use a new technology to build a physical replica of the insect's visual motion detection system, and test it by direct substitution for the insect in an experimental apparatus, and by controlling a mobile robot in an everyday environment. The technology, pioneered by Carver Mead⁴³, uses transistor circuits in the sub-threshold domain to do highly efficient, specialized calculations that exploit the inherent exponential dynamics of the silicon substrate. Harrison's circuit implements the Hassenstein-Reichardt⁴⁴ model of elementary motion detection. Each detector correlates the response at one photoreceptor with the delayed response from a neighbouring receptor. This is implemented on the chip by a multiplier operation on signals delayed by inherent lags in temporal low-pass filters. By subtracting the outputs of detectors for opposite directions, a strong direction-selective response is produced. Summing the response across all the detectors provides a signal representing full-field motion, which resembles the response of certain tangential cells in the lobular plate of the fly brain. This output is a measure of self-rotation, and is used by the fly to produce compensatory torque responses to correct deviations in heading direction — the well-known optomotor reflex.

The advantage of reproducing this model in hardware is that it performs the computationally demanding task in real time, with very low power consumption, using parallel analog computation to reduce the large bandwidth of visual input to a single, meaningful output. Hence it is possible to test the response of this system with stimulation identical to that used for experiments on the fly. The fly's optomotor response is often tested in a closed-loop flight simulator, in which the torque movements of a tethered fly in response to visual motion are fed back to control the motion of the visual scene. In this situation, flies can compensate for an imposed drift in the direction of motion (Fig. 2). Individual trials show a characteristic oscillation in torque during this behaviour. If the fly and the torque meter are then replaced by the optomotor chip, so that it receives the equivalent visual stimulus, the output from the chip can be used as a torque signal fed back to the flight simulator. In this situation, similar compensation for the imposed rotation was produced (slightly larger drift is

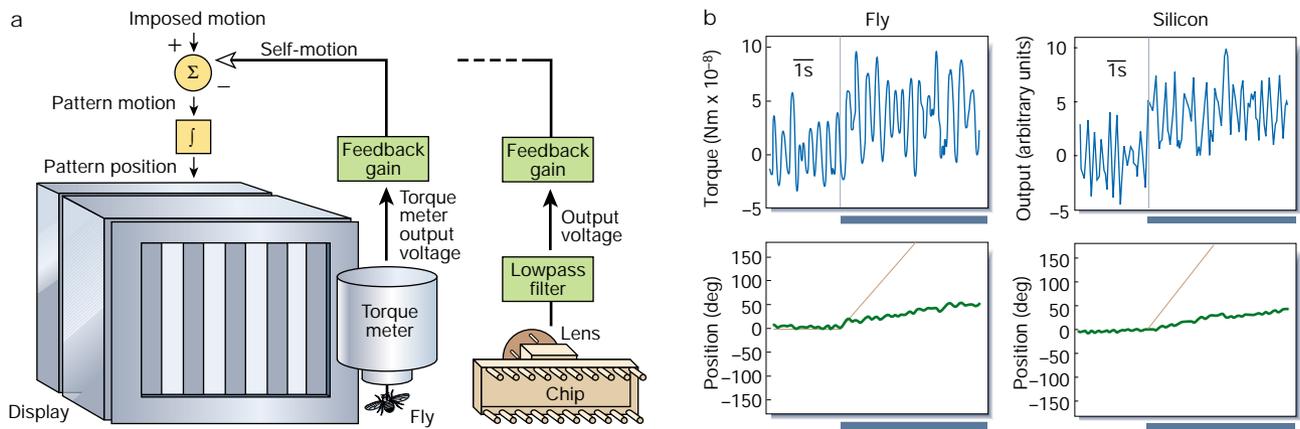


Figure 2 Replicating an insect's visual motion detection system using an optomotor chip. **a**, Experimental set-up used to test the optomotor response in the fly and in a model implemented on a silicon chip in vLSI. **b**, The fly can produce torque that stabilizes the visual environment (thick line) against imposed drift (thin line); the chip produces similar results. Reprinted with permission from ref. 41.

recorded for the chip, but this is most likely a consequence of the much smaller visual angle it sees compared with the fly). This indicates that relatively straightforward connections between the output from the fly's tangential cell and its motor system are sufficient to explain this behaviour, without additional processing. Moreover, the same oscillatory behaviour was also observed, suggesting that this is a natural result of the inherent feedback lags in the system.

The optomotor chip is straightforward to interface to a real motor-control mechanism such as a mobile robot platform. This enables the same circuit to be tested with realistic natural input and feedback simply by driving it around in an everyday environment⁴⁵. The output of the motion processor is sufficient to instantaneously correct for as much as a 5:1 bias in left–right motor gearing, converting tight-circling behaviour without the optomotor control into straight-line motion. An unexpected bonus is that interfacing this sensory capacity to the cricket robot is also simple, allowing tests of how these behaviours might best be combined.

Combining sensorimotor systems

The examples so far illustrate the use of robots to investigate single-modality sensorimotor systems. A necessary advance is to use embodied models to address more complex behaviours, such as the combination of output from several systems. To take a specific case, can the stabilizing optomotor signal be used to improve the directness of approach to a sound source, or would the sensory systems interfere? Studies on the cricket suggest that it does more efficient taxis in the light than the dark⁴⁶. Böhm, Schildberger and Huber⁴⁷ recorded the orientation behaviour of crickets when an optomotor stimulus was varied in direction and amplitude in the context of a specific phonotaxis stimulus, and vice versa. They found “a turning tendency that can be explained as the weighted sum of the turning tendencies evoked by the two individual stimuli”. Taking this as a starting point, Webb and Harrison⁴⁸ assessed the effectiveness of such a mechanism for controlling a robot equipped with both phonotaxis and optomotor systems.

The output from the network model of phonotactic processing was motor commands to change the speed of the robot's left and right wheels, either making a turn towards the sound or moving forward. The optomotor chip output was added to this at the motor command stage by increasing the speed of one wheel and decreasing the other by an amount proportional to any detected visual rotation.

It quickly became clear that a problem with just adding these two outputs is that if the robot turned in response to a sound it would immediately turn away again in response to the optomotor signal

produced during the turn. Indeed, the potential for interference of ‘automatic’ corrections with ‘intended’ deviations is a well-known problem, having inspired the concept of ‘efferent copy’ as a solution. This is the proposal that a signal corresponding to an intended motor command is sent directly to the sensory system to cancel out the expected sensory feedback from that motor action.

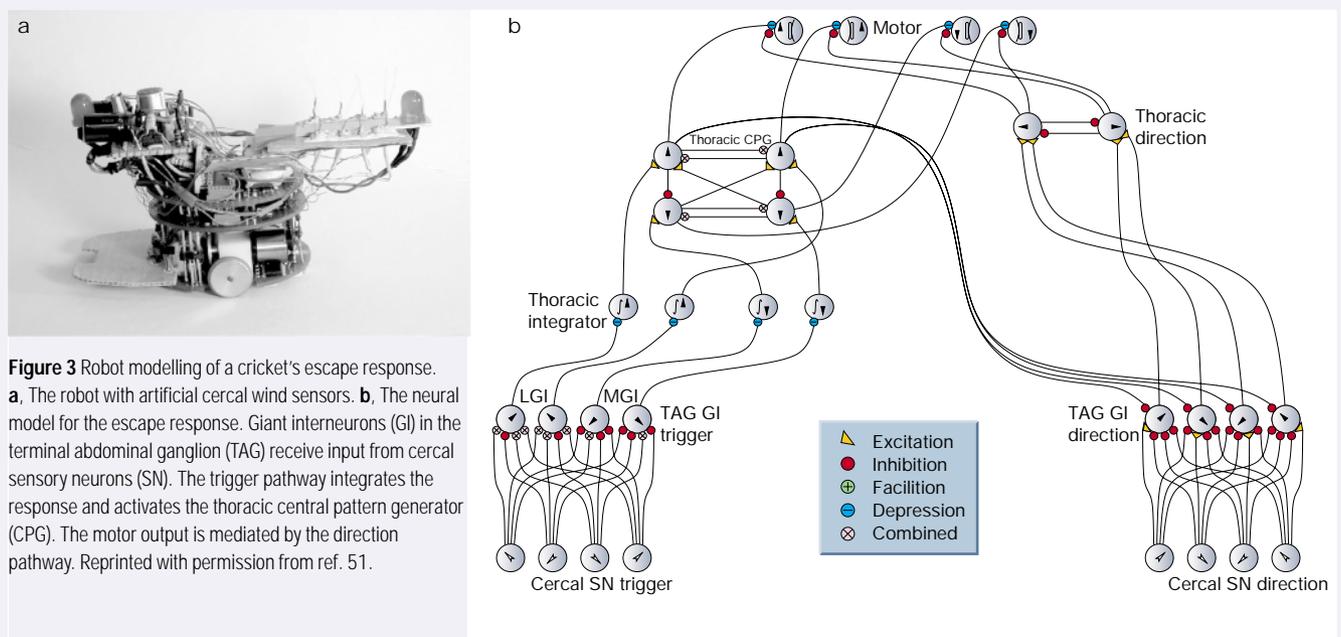
A simpler solution than this — just inhibiting the optomotor response during turns in response to sound — was found to be sufficient. In trials using real sound sources and an everyday visual environment, the robot was able to correct for a motor bias while approaching the sound source⁴⁸, and including the optomotor control resulted in a significant decrease in the variance of phonotactic tracks. This algorithm also produces results consistent with those of Böhm and co-workers⁴⁷ for the cricket tested in ‘open-loop’ behaviour on a treadmill, although efferent copy or simple addition are also consistent with their results, which suggests a more fine-grain analysis of the response is needed to distinguish between these possibilities.

Two conclusions are evident from these studies. First, a precise efferent copy is impossible to produce, as it requires the system to predict the exact visual input that will occur, which is not known in a natural environment. Second, the temporal dynamics of the sensory processing and of the feedback through motor actions in the environment are critical factors to consider in evaluating the integration of different modalities. Additional constraints that may come from considering a more neurally plausible implementation of the integration mechanisms are currently being studied.

Robot escape

The implementation of neural circuits to control a robot places an emphasis on behavioural output that can sometimes be forgotten in the detailed analysis of sensory circuits. For example, in investigating phonotaxis it was noticeable that much of the reliability of the behaviour may be explained by the fact that the animal can constantly correct its movements during the approach to sound. By contrast, avoiding a stimulus, although logically the opposite of taxis, typically requires a different behavioural response.

A cricket stimulated by a puff of air, such as might be created by a predator's strike, rapidly turns and runs away from the direction of the wind, producing a complete behaviour sequence in response to a short-lived stimulus. The cricket has two rear appendages (the cerci) covered in hair sensors that detect air movement. The anatomical layout and neural connectivity of the sensory axons from the cercal wind sensors has been well described^{49,50} and a small number of identified neurons well characterized. These include



four pairs of 'giant' interneurons connecting the abdominal ganglion to the motor areas of the thoracic ganglion, which are involved in initiating and steering a rapid escape. Chapman⁵¹ has built a set of direction-sensitive wind sensors that resemble the hair sensors on the cricket's cerci (Fig. 3a), and modelled the neural system using a dynamic spiking neural simulation (Fig. 3b) to produce a cricket-like escape response in a robot.

In this model, the neural pathway is divided into a 'trigger' system and a 'direction' system, which respond to 'acceleration-sensitive' and 'velocity-sensitive' hairs, respectively. The cricket has cercal hairs that vary in length, resulting in different mechanical properties, with longer hairs best deflected by a constant wind, and short hairs by a rapid puff⁵². The mechanical model hairs (essentially a fine wire attached to a spring, which when deflected in a specific direction briefly closes a contact switch) can be similarly classified. Each closure of a switch is treated as a 'spike' from a sensory neuron. This results in a low-bandwidth signal from an array of sensors that can be detected and processed at a millisecond timescale.

The neural simulation exploits the robot's microprocessor for maximum efficiency while maintaining sufficient detail to copy appropriate neuron properties. For example, synaptic delays (axon lengths) are represented by shifting a bit (a spike) along a byte. It uses a single-compartment neuron representation based on a simplified 'integrate and spike' model, and includes synaptic depression and facilitation effects. At the level of the 'thoracic ganglion' (Fig. 3b) the trigger system integrates sensory input and starts a central pattern generator circuit for forwards or backwards movement. The direction system modulates this response by inhibiting one side or the other, causing a turn. The combined output produces different kinds of turn-and-run sequences, depending on the direction of the wind stimulus, that closely resemble the cricket's behaviour⁵³. The complete network (not shown) includes input from 'antennae' (close-range distance sensors), light and sound sensors, enabling the robot to integrate these other modalities with its escape response. Thus it can avoid obstacles and follow walls while escaping, show heightened sensitivity for wind-evoked escape when light or noise levels are high, and produce an escape response to sufficiently strong changes in any one of these additional sensory cues.

This robot represents the most complete model of this neural system to date. It combines in a single coherent circuit many aspects of escape behaviour that have previously been simulated separately^{49,54}, and places the circuit within the sensorimotor-environment

loop, generating the complete behavioural response. By combining physical, behavioural and physiological constraints, particular solutions to the possible pathways become more plausible than others. Sometimes simple solutions remove potential problems. For example, by providing the robot with a cardboard buffer to make its shape more like the body of a cricket, the need for highly reliable obstacle detection was reduced as it was less likely to get stuck when it hit something. Finally, this robot shows a more complex behavioural output than the largely reactive responses of the systems described previously, by incorporating mechanisms for context-dependent plasticity of the response.

Conclusion

Robot implementations have become an accepted method for exploring issues in invertebrate neuroscience. I have described a few specific examples in detail, to show how the idea of physical modelling can contribute interesting new insights into neurobiological systems. Many other invertebrate systems have been explored in this way, and similar work is being done on a variety of vertebrate systems, including snakes, rats, fish and humans. But invertebrate systems have been a particularly successful area for the approach. Invertebrate behaviours tend to be more stereotyped and thus easier to analyse comprehensively. The number of neural connections between sensing and action is orders of magnitude less than for vertebrates, making the possibility of complete pathway mapping plausible. We should have comparable processing power available in modern computers to that in insect brains, so failure to replicate their behavioural capabilities will indicate areas in which we lack knowledge of how the systems work.

In addition, although the importance of 'embodiment' is still debated for higher cognitive processes, there is little doubt that the efficient functioning of invertebrates is highly dependent on the nature of the physical interface between their neural control systems and their environment. This is an area where robotic models have particular advantages. In a box-and-arrow, mathematical or computer model, the included constraints are only those we can think of in advance. Robot implementations introduce us to constraints inherent to the sensorimotor problem that we might otherwise fail to consider. □

1. Pichon, J.-M., Blanes, C. & Franceschini, N. in *Mobile Robots IV* (eds Wolfe, W. J. & Chun, W. H.) 44-53 (Society of Photo-optical Instrumentation Engineers, Bellingham, 1989).
 2. Franceschini, N., Pichon, J. M. & Blanes, C. From insect vision to robot vision. *Phil. Trans. R. Soc.*

- Lond. B* **337**, 283–294 (1992).
3. Franceschini, N. Engineering applications of small brains. *FED J.* **7**, 38–52 (1996).
 4. Mura, F. & Franceschini, N. in *Intelligent Vehicles II* (eds Aoki, M. & Masaki, I.) 47–52 (MIT Press, Cambridge, MA, 1996).
 5. Cruse, H., Bartling, C., Cymbalyuk, G., Dean, J. & Dreifert, M. A modular artificial neural network for controlling a six-legged walking system. *Biol. Cybern.* **72**, 421–430 (1995).
 6. Cruse, H., Kindermann, T., Schumm, M., Dean, J. & Schmitz, J. Walknet—a biologically inspired network to control six-legged walking. *Neural Networks* **11**, 1435–1447 (1998).
 7. Lambrinos, D. *et al.* An autonomous agent navigating with a polarized light compass. *Adapt. Behav.* **6**, 175–206 (1997).
 8. Lambrinos, D., Moller, R., Labhart, T., Pfeifer, R. & Wehner, R. A mobile robot employing insect strategies for navigation. *Robot. Auton. Syst.* **30**, 39–64 (2000).
 9. Wehner, R. in *Neural Basis of Behavioural Adaptations* (eds Schildberger, K. & Elsner, N.) 103–143 (Fischer, Stuttgart, 1994).
 10. Labhart, T. Polarization-opponent interneurons in the insect visual system. *Nature* **331**, 435–437 (1988).
 11. Rind, F. C. & Simmons, P. J. Signalling of object approach by the DCMD neuron of the locust. *J. Neurophysiol.* **77**, 1029–1033 (1997).
 12. Blanchard, M., Rind, F. C. & Verschure, P. F. M. J. Collision avoidance using a model of the locust LGMD neuron. *Robot. Auton. Syst.* **30**, 17–38 (2000).
 13. Morse, T. M., Ferree, T. C. & Lockery, S. R. Robust spatial navigation in a robot inspired by chemotaxis in *Caenorhabditis elegans*. *Adapt. Behav.* **6**, 393–410 (1998).
 14. Dampier, R. L., French, R. L. B. & Scutt, T. W. ARBIB: an autonomous robot based on inspirations from biology. *Robot. Auton. Syst.* **31**, 247–274 (2000).
 15. Grasso, F., Consi, T., Mountain, D. & Atema, J. in *From Animals to Animals 4: Proc. Sixth Int. Conf. Simul. Adapt. Behav.* (eds Maes, P., Mataric, M. J., Meyer, J. A., Pollack, J. & Wilson, S. W.) 104–112 (MIT Press, Cambridge, MA, 1996).
 16. Grasso, F., Consi, T., Mountain, D. & Atema, J. Biomimetic robot lobster performs chemo-orientation in turbulence using a pair of spatially separated sensors: progress and challenges. *Robot. Auton. Syst.* **30**, 115–131 (2000).
 17. Quinn, R. D. & Ritzmann, R. E. Construction of a hexapod robot with cockroach kinematics benefits both robotics and biology. *Connect. Sci.* **10**, 239–254 (1998).
 18. Delcomyn, F. & Nelson, M. E. Architectures for a biomimetic hexapod robot. *Robot. Auton. Syst.* **30**, 5–15 (2000).
 19. Kuwana, Y., Shimoyama, I. & Miura, H. in *Proc. IEEE Int. Conf. Intell. Robots Syst.* 530–535 (IEEE Computer Society Press, Los Alamitos, CA, 1995).
 20. Webb, B. What does robotics offer animal behaviour? *Anim. Behav.* **60**, 545–558 (2000).
 21. Webb, B. Are 'biorobots' good models of biological behaviour? *Behav. Brain Sci.* (in the press).
 22. Braitenberg, V. *Vehicles: Experiments in Synthetic Psychology* (MIT Press, Cambridge, MA, 1984).
 23. Huber, F. Behavior and neurobiology of acoustically oriented insects. *Naturwissenschaften* **79**, 393–406 (1992).
 24. Huber, F. & Thorson, J. Cricket auditory communication. *Sci. Am.* **253**, 47–54 (1985).
 25. Wohlers, D. W. & Huber, F. Processing of sound signals by six types of neurons in the prothoracic ganglion of the cricket *Gryllus campestris* L. *J. Comp. Physiol.* **146**, 161–173 (1981).
 26. Schildberger, K. Behavioural and neuronal methods of cricket phonotaxis. *Experientia* **44**, 408–415 (1988).
 27. Wendler, G. in *Sensory Systems and Communication in Arthropods* (eds Gribakin, F. G., Wiese, K. & Popov, A. V.) 387–394 (Birkhäuser, Basel, 1990).
 28. Pollack, G. S. in *Comparative Hearing: Insects* (eds Hoy, R. R., Popper, A. N. & Fay, R. R.) 139–196 (Springer, New York, 1998).
 29. Webb, B. in *From Animals to Animals 3: Proc. Third Int. Conf. Simul. Adapt. Behav.* (eds Cliff, D., Husbands, P., Meyer, J.-A. & Wilson, S. W.) 45–54 (MIT Press, Cambridge, MA, 1994).
 30. Webb, B. Using robots to model animals: a cricket test. *Robot. Auton. Syst.* **16**, 117–134 (1995).
 31. Lund, H. H., Webb, B. & Hallam, J. in *Fourth Eur. Conf. Artif. Life* (eds Husbands, P. & Harvey, I.) 246–255 (MIT Press, Cambridge, MA, 1997).
 32. Lund, H. H., Webb, B. & Hallam, J. Physical and temporal scaling considerations in a robot model of cricket calling song preference. *Artif. Life* **4**, 95–107 (1998).
 33. Webb, B. & Scutt, T. A simple latency dependent spiking neuron model of cricket phonotaxis. *Biol. Cybern.* **82**, 247–269 (2000).
 34. Michelsen, A., Popov, A. V. & Lewis, B. Physics of directional hearing in the cricket *Gryllus bimaculatus*. *J. Comp. Physiol. A* **175**, 153–164 (1994).
 35. Schildberger, K. Temporal selectivity of identified auditory interneurons in the cricket brain. *J. Comp. Physiol.* **155**, 171–185 (1984).
 36. Horridge, G. A., Loughet-Higgins, H. C. & Horridge, G. A. What can engineers learn from insect vision? *Phil. Trans. R. Soc. Lond. B* **337**, 271–282 (1992).
 37. Srinivasan, M. V. & Venkatesh, S. *From Living Eyes to Seeing Machines* (Oxford Univ. Press, Oxford, 1997).
 38. Lewis, A. in *Advances in Neural Information Processing Systems 10* (eds Jordan, M. I., Kearns, M. J. & Solla, S. A.) 822–828 (MIT Press, Cambridge, MA, 1998).
 39. Franceschini, N. & Chagneux, R. in *Neurobiology: From Membrane to Mind. Proc. 25th Gottingen Neurobiol. Conf.* (eds Elsner, N. & Wasse, H.) (G. Thieme, Stuttgart, 1997).
 40. Hoshino, K., Mura, F. & Shimoyama, I. Design and performance of a micro-sized biomorphic compound eye with a scanning retina. *J. Microelectromech. Syst.* **9**, 32–37 (2000).
 41. Harrison, R. R. & Koch, C. A silicon implementation of the fly's optomotor control system. *Neural Comput.* **12**, 2291–2304 (2000).
 42. Harrison, R. R. & Koch, C. in *Advances in Neural Information Processing Systems 10* (eds Jordan, M. I., Kearns, M. J. & Solla, S. A.) 880–886 (MIT Press, Cambridge, MA, 1998).
 43. Mead, C. *Analog VLSI and Neural Systems* (Addison-Wesley, Reading, MA, 1989).
 44. Hassenstein, B. & Reichardt, W. Systemtheoretische Analyse der Zeit-, Reihenfolgen-, und Vorzeichenauswertung bei der Bewegungsperzeption des Rüsselkäfers. *Chlorophanus. Z. Naturforsch.* **11b**, 513–524 (1956).
 45. Harrison, R. R. & Koch, C. A robust analog VLSI motion sensor based on the visual system of the fly. *Auton. Robot.* **7**, 211–224 (1999).
 46. Weber, T., Thorson, J. & Huber, F. Auditory behaviour of the cricket I. Dynamics of compensated walking and discrimination paradigms on the Kramer treadmill. *J. Comp. Physiol. A* **141**, 215–232 (1981).
 47. Böhm, H., Schildberger, K. & Huber, F. Visual and acoustic course control in the cricket *Gryllus bimaculatus*. *J. Exp. Biol.* **159**, 235–248 (1991).
 48. Webb, B. & Harrison, R. R. in *Proc. SPIE Symp. Sensor Fusion and Decentralized Control in Robotic Systems III* (eds McKee, G. T. & Schenker, P. S.) 113–124 (SPIE, Boston, MA, 2000).
 49. Kohstall-Schnell, D. & Gras, H. Activity of giant interneurons and other wind sensitive elements of the terminal abdominal ganglion in the walking cricket. *J. Exp. Biol.* **193**, 157–181 (1994).
 50. Paydar, S., Doan, C. & Jacobs, G. Neural mapping of direction and frequency in the cricket cercal system. *J. Neurosci.* **19**, 1771–1781 (1999).
 51. Chapman, T. *Morphological and Neural Modelling of the Orthopteran Escape Response*. Thesis, Univ. Stirling (2001).
 52. Shimozawa, T. & Kanou, M. The aerodynamics and sensory physiology of range fractionation in the cercal filiform hair of the cricket *Gryllus bimaculatus*. *J. Comp. Physiol. A* **155**, 495–505 (1984).
 53. Tauber, E. & Camhi, J. The wind-evoked escape behaviour of the cricket *Gryllus bimaculatus*: integration of behavioral elements. *J. Exp. Biol.* **198**, 1895–1907 (1995).
 54. Ezrachi, E., Levi, R., Camhi, J. & Parnas, H. Right-left discrimination in a biologically oriented model of the cockroach escape system. *Biol. Cybern.* **81**, 89–99 (1999).