Robots in invertebrate neuroscience

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Robots can be used to test hypotheses in the neuroscience of sensorimotor control. Some well explored systems in invertebrates are particularly suited to such implementations. Examples are discussed from visual motion perception, auditory localisation, chemotaxis and escape behaviour. The results provide a complementary insight into understanding these complex systems, by providing a real-world grounding and thus emphasising the contribution of the physics of environments, sensors and actuators to the control of behaviour.

If we understand how a biological system works, it should be possible to build something that works the same way. Advances in neurobiology have been accompanied by advances in technology, and there is much interest in the possibility of designing robots with the capabilities of animals. Invertebrate neuroscience in particular is providing many neural 'circuit diagrams' that can potentially be copied as sensorimotor controllers for robotics. While much of this work has a technical focus, in some cases the robot constitutes a means to test neuroscientific hypotheses, with results that can feed back to biology. This report describes some recent examples of such work and discusses what can be learnt.

One important way in which work in robotics can contribute to neurobiology is by testing models of neural systems within the constraints of real sensing, tasks and environments. Because neurobiological systems are complex, and modern modelling

methodologies allow the construction of ever more complex representations of them, validation of models has become more problematic. It can sometimes seem possible to reproduce whatever output is observed from the real system simply by tuning the many parameters, adding extra connections, or finding the right format for the model input or output. It is necessary to find ways of constraining the model if we are to have confidence that reproducing the behaviour is really a critical test of the underlying hypothesis.

It is also worth keeping in mind that producing testable predictions is not the only useful function of implementing models. A model is a powerful way to combine and summarize data that may be gathering piecemeal. Connections and gaps can be revealed in model building that otherwise may be overlooked. The logical adequacy of hypotheses to account for the data is sometimes revealed to be incomplete when they are formalised for modelling. Often alternative hypotheses present themselves during model construction and the understanding of what a particular mechanism may be capable of is improved. In these respects, different kinds of models can offer different perspectives. Analytical models provide clear statements and can often lead to useful generalisation by drawing out equivalencies between processes. Highly detailed simulations e.g. of neural biophysics, may focus attention on areas of missing data. A physical model, such as a robot, places the focus on the complete problem, that is how interaction with the world and neural systems mutually constrain each other. A consequence is that addresses how the embodiment[7] and effect of actions on the environment contribute to behaviour, rather than treating sensory processing as a unidirectional information-extracting computation. Our view and interpretation of neurobiological data is changed when we take a more holistic, task-oriented and embodied view of what the neural circuitry is doing.

Over the last decade there have been an increasing number of robots built to explore biological ideas, ranging from lego models of pre-cambrian worms[39] to humanoids[4]. But as for other problems in neuroscience, invertebrates have provided particularly fruitful model systems for this approach. This is because we have in some cases come close to having a full understanding of the specific neural connections that underlie the production of particular motor responses to particular sensory stimuli.

Insect visual control

One of the best studied areas in invertebrate neuroscience is the sensory system underlying visual motion perception, so it is not surprising that this is also an area in which a number of robot models have been built in recent years. Several authors [10;17;47] have speculated on the various ways we might exploit our understanding of the insect for robotic, in particular how some rather simple but clever algorithms apparently used by insects could be adopted for controlling mobile robots. Examples of implemented systems include: balancing lateral visual velocities to move down the centre of a corridor [44;52]using the maintenance of a constant angular velocity to slow down when approaching a tighter passageway, or landing place[46]; and using peering to extract range information[29]. Such implementations indirectly test the efficacy of the proposed controllers as an explanation of the insect's behaviour; in what follows I will discuss some examples of more explicit attempts to use the robot in evaluating hypotheses.

Collision avoidance

A leading example in this field was the work done at the end of the 1980s by Franceschini and colleagues[37]. The aim was to show how the implementation of insect-like vision could provide a mobile robot with a rapid and robust capability to steer through a complex environment. At the same time it was an investigation of how the motion detection system of the fly might be used to perform collision avoidance. This

involved both analog hardware modelling of the neural circuitry thought to perform motion detection, and analysis of the information available from motion parallax for guiding movement. Franceschini et al[12] note that by the use of a robot they were "forced to an ultimate level of concreteness in specifying the design of the complete optomotor loop" for the fly.

The robot carried a compound eye consisting of 100 facets around the horizontal plane. The photosensors were wired with lateral interactions to form elementary motion detectors, copied from the fly. The layout of the visual axes of the sensors followed a sine gradient from front to back; this also resembled the fly and had the attractive property of compensating for the sine law inherent in the optic flow field for forward translation. After each translational step, the distance of obstacles was extracted from the flow field and used to determine a rotation that would avoid obstacles while remaining as close as possible to the target direction. The resulting mechanism could 'slalom' the robot at 50 cm/s to a target through a random array of posts.

A problem that emerged from this work is that the range of effective vision decreases as the visual axis approaches the line of travel. In other words, the robot or animal will have trouble detecting obstacles directly ahead, obviously a problem for motor control. A solution investigated by Mura & Franceschini[34] is to introducing a scanning movement of the eye during the translation. Moreover, investigation of the fly compound eye motivated by this problem has suggested that it actually has a muscle and tendon system that carries out scanning movements of this kind[11]. In [18] a microscale sensor based on this principle is described. An alternative implementation of the same basic concept is for the robot to use a zig-zag motion, i.e. periodically changing direction to compensate for the parallax blindspot. Lewis[28] suggests that such behaviour is observed in insects and demonstrates that using it on a robot enables successful navigation through a field of obstacles.

Optomotor and tracking response

Another specific hypothesis about the neurocircuitry of the fly visual motion system was investigated in a robot model by Huber et al[21;22]. Flies show a number of reflex responses to visual stimuli. These include the optomotor reflex, producing torque in response to largefield rotation, and a fixation response to a vertical stripe. It has been suggested that a common behavioural module may underlie both these behaviours, that is, they may make use of the same sensory circuit. In particular, the fixation could be explained by the front-back asymmetry in the response of horizontal cells which integrate the output of elementary motion detectors. Because the response to (randomly generated) progressive motion is stronger than to regressive motion, the fly will end up oriented towards the stripe.

The robot implementation of this hypothesis uses a conical mirror above a video camera to get a 360-degree view, and samples five circles along the horizon, averaging vertically to get 96 sensor inputs each with an aperture of 2.1 degrees. The signals are spatially and temporally filtered by processes analogous to the large monopolar cells in the fly's lamina, motion is detected using the Hassenstein-Reichardt model of processing in the medulla and then integrated by a model of the widefield horizontal cells in the lobula plate. These signals are coupled proportionally to the motor response, such that leftward visual movement produces leftward rotation and vice-versa, but as described above, the signal (and hence the response) for front-to-back motion is stronger than the signal for back-to-front. With the normal optomotor stimulus of a striped drum, these signals are balanced and the usual compensatory rotation to stabilise the environment is seen. With a single stripe, the stronger turning for progressive motion results in the robot orienting towards the stripe, and reliably tracking towards it.

The results demonstrate that one visuomotor control mechanism can generate both responses in the fly. The expressed behaviour depends on the environmental

conditions without there being any explicit recognition of the conditions or switch between the responses. Thus the work on the robot has provided a 'critical evaluation of biological models' ([22], p.227) in this area.

Looming response

Blanchard et al[2] used a robot to investigate a different behavioural subsystem of insect vision, the 'looming' response. In locusts, an evasion response is triggered when objects approaching on a collision course exceed a threshold visual angle. An identified neuron - the lobula giant movement detector - appears to be a critical element of this behaviour[42]. A camera mounted on a miniature robot was used to provide input to a model of the anatomical and physiological organisation of this neuron[41]. The response of the neuron appears to depend on a 'race' between excitatory and inhibitory inputs, such that only rapidly expanding visual stimulus will excite it. With ideal stimuli, the rate of firing of the neuron encodes the rate of approach of the stimulus. However it was found with the robot, that even in a rather simple environment, the variation in the visual stimulus meant there was a great deal of variance in the neural response, sufficient to obscure the relationship between firing and approach rates. Nevertheless it was possible to define a threshold firing-rate level for reacting that enabled the robot to avoid collisions, albeit at varying distances from the obstacles.

The results suggest that more realistic stimuli need to be used to correctly characterise the neuron's response, but also that high accuracy in sensing is not a prerequisite for effective behaviour in this case. A further issue that arose from this implementation is that when the robot reacts to avoid a collision, the visual stimulus during its reaction can provide an inappropriate input to the collision detector. This suggests there needs to be some kind of inhibitory or efferent-copy connections within the avoidance system.

Taxis

Many other sensory systems in insects are also well studied and the neural underpinnings sought. Behaviourally, a common response to various sensory signals is taxis, i.e. to orient to the source in order to find it. Many mobile robots have been built with generic taxis capabilities (particularly inspired by the 'thought-experiments' in Braitenberg[3]). Some of these robots have been designed to investigate specific hypotheses about animal taxis.

Phonotaxis

I have been involved in a series of studies using a robot implementation to elucidate the neural circuitry involved in auditory localisaton and recognition in the cricket [30;31;49-51]. Female crickets can locate a mate by moving towards the species specific song produced by the male. The behaviour, neuroanatomy and neurophysiology of this system have been studied for some years (e.g. see reviews in [19;20;38]). However to date there is not a complete, well-specified model of this system. The work on the robot has demonstrated one plausible solution, consistent with the biological observations, that is capable of producing the appropriate behaviour when tested in the same experimental conditions as the animal.

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 wavelength. The resulting vibration amplitude difference between the ears is neurally encoded both in spike rate and spike onset latency. The temporal pattern of the sound - consisting of bursts at a characteristic rate - is also apparent in the spike pattern of auditory neurons and interneurons. The issue then is how the

subsequent neural processing filters the pattern to recognise the song and compares the difference between the ears to determine the direction of the singer.

The solution proposed in [49] is that the two tasks can be linked, by making the localisation circuit dependent on having the correct pattern. In fact, a very simple neural network can be devised with the requisite properties[51]. An adapting synapse between the auditory neurons and the motor neurons means the latter receive input only at the onset of sound bursts. This requires a burst repetition rate slow enough to be clearly coded by the auditory neurons, but fast enough to allow the summation of successive motor neuron stimulations to reach the threshold for response. Thus a bandpass for the repetition rate is set, which corresponds to the parameters for 'recognition' established in experiments on the cricket. Using cross inhibition, the side of first onset will suppress the other side, and the motor output will thus generate a turn towards the louder or more clearly patterned sound.

This neural circuit was implemented in a spiking neuron simulation that ran on a robot equipped with an electronic model of the cricket's ears and capable of moving at comparable speeds to the cricket. Testing it with real or computer generated cricket song showed that it could track the sound, provided it had the correct carrier frequency and bandpass repetition rate, i.e. it appeared as selective as the cricket. Moreover, testing the robot with two sound sources it was found that this system also appears capable of 'choosing' and tracking the louder or better song. These results raise a number of issues for the cricket neurophysiology, some of which are being examined, such as whether first onset does determine turning direction, and how much of the filtering can be attributed to inherent low-pass properties of integrating neurons.

In more recent experiments[48] the phonotaxis response has been combined with an optomotor response generated by a hardware analog VLSI chip designed by Harrison[16] that mimics the optomotor visual processing of the fly described in the

previous section. Experiments on the cricket using combinations of auditory and visual stimuli had suggested a simple additive combination of the two responses would explain the behaviour. It was found, using the robot, that this would not in fact suffice when the system had realistic feedback from its actions, particularly because the dynamics of the two sensory systems differed.

Chemotaxis

Although tracking a chemical source might be considered essentially the same problem as tracking a sound source, in fact it differs substantially because of the nature of the signal. Chemicals do not usually disperse in a smooth gradient, but rather their dispersal is determined by the movement of the medium - air or water - in which they are being dispersed. The resulting 'plume' is typically directed, intermittent and turbulent. Hence a simple comparison between two spatially separated sensors is likely to be inadequate to reliably determine the turning direction that will bring the animal or robot closer to the source. This has been demonstrated at the algorithmic level in experiments with a 'robolobster'[13;14]. This robot is designed to operate underwater, in the same flow-tank as the lobster. It is scaled to the lobster in body size, spatial layout and response resolution of the sensors, and speed and pattern of locomotion. Using only tropotaxis - instantaneous comparison of the concentration between two sensors - the robot cannot effectively track a plume. It would appear necessary to include time-differentiation of the signal and/or rheotaxis (up-stream orientation) to explain the animal's behaviour.

The neural underpinning of chemotaxis mechanisms is less well understood than for the auditory or visual processing discussed thus far. Several studies have thus looked at this problem at the neural level by attempting to design, train or evolve a small network of model neurons to be capable of dealing with the problems for a real robot response. In work by Kuwana et al[26], the robot is actually equipped with the same pheromone sensors as the moth it models. The antennae are dissected from the male and

attached by silver electrodes to an amplifier circuit on the robot, to detect the potential difference across the antennae caused by the female pheromone. An eight neuron recurrent network is used to connect the sensors to the motors, and can be tuned by hand or by evolutionary methods to produce the casting and turning behaviours described by Kanzaki[23].

An exception to the 'plume'-type stimulus for chemotaxis is given by the experimental conditions used to test chemotaxis in the nematode worm. In this case, a gradient of concentration is established from the center to the edge of a petri dish, and nematodes released into the dish are observed to orient themselves up the gradient to reach the center. On the other hand, the nematode's anatomy means that it samples this gradient essentially at one point only, unlike the spatially separated sensors of the lobster or moth. This environmental interface was modelled in a robot by Morse et al[33] using a light source to create the sensory gradient and a single non-directional light sensor to detect it. They also modelled the observed motor control of the nematode which moves at a near constant speed and steers by the relative contraction of muscles on each side of the head and neck.

The neural network used to control the behaviour is a simplification of identified neural properties in the nematode. The neurons are non-spiking, and can be represented as a single isopotential compartment. They are further simplified by being made linear, which makes analysis possible although at some loss of realism, e.g. the voltage-dependence of conductances and non-linear synaptic functions are not represented. The network in the nematode is known to consist of chemosensory neurons, interneurons and motor neurons which are highly interconnected. A model with one sensory neuron, three interneurons and two motor neurons (one for each side) was fully interconnected and the parameters determined using a simulated annealing algorithm. The resulting circuit could control the robot so as to approach the sensory source, and was robust to

changes in speed or the addition of turning bias. Analysis of the network enabled Ferree & Lockery[9] to describe the function in terms of a computational rule that combines klinotaxis (changing turning rate proportionally to the gradient of the stimulus) with klinokinesis (changing turning rate in response to the scalar value of the stimulus field) to best match the observed behaviour of the nematode. These strategies are thus candidate mechanisms for chemotaxis control in C. elegans.

Escape behaviour

As well as approaching certain sensory sources, another basic behaviour in many animals is to move away from or escape a sensory source - typically signalling a predator or some other risk. One well explored neural circuit for such behaviour is that involved in the wind-mediated escape response of the cricket and cockroach. These insects have two rear appendages - the cerci - that are covered in hair sensors that detect air movement. When stimulated by a puff of air, such as might be created by a predator's strike, the animal rapidly turns and runs away from the direction of the wind. The anatomical layout and neural connectivity of the sensory axons has been well described[25;36] and a small number of identified neurons well characterised. These include four pairs of 'giant' interneurons that connect the abdominal ganglion directly to the motor areas of the thoracic ganglion, and are involved in initiating and steering a rapid escape.

Chapman[6] has built a set of direction sensitive wind sensors that resemble the hair sensors on the crickets cerci, and modelled the neural system using low-level programming features in a robot's microprocessor, to produce an escape response in the robot. The neural pathway is divided into a 'trigger' system and a 'direction' system, which respond to acceleration sensitive and velocity sensitive hairs respectively. At the thoracic ganglion level, the trigger system integrates sensory input and starts a central pattern generator circuit that causes forwards or backward movement for a short time.

The direction system modulates the response by inhibiting one side or the other, causing a turn. Furthermore the network includes input from 'antennae', light and sound sensors. This enables the robot to integrate these other modalities with its escape response, e.g. to avoid obstacles and follow walls while escaping, to have heightened sensitivity for escape when light or noise levels are high, or indeed to show an escape response to sufficiently strong changes in any of these sensory cues.

The resulting behaviour of the robot replicates a number of characteristics of the animal's escape response, such as the ability to make different kinds of initial turns depending on the stimulus direction. As well as providing a complete model of this system, a number of testable predictions could be made, for example regarding the response duration of escape runs and the lack of effect of additional stimuli during an escape run. Some interesting features of the circuit were that it delayed integration of different sensory pathways to the final pre-motor stage, and that it was found that some 'priming' effects were not possible when a linear approximation for the membrane decay function was used.

Discussion

In this report I have focussed on just a few examples of robots modelling biological systems taken from invertebrate neuroscience. There are many other similar studies to be found in the fields of invertebrate behaviour (e.g. [27;32]), and vertebrate neuroscience (e.g. [5;15;43;45]). A major motivation for the work remains the possibility of finding new solutions to engineering problems. But from the viewpoint of the biologist, what are the advantages and costs of actually building physical replicas to test hypotheses? Do robots provide a more realistic way to ascertain how a neural circuit controls behaviour?

The answer depends what is meant by 'realistic'. This can, firstly, concern how applicable the results of the robot are to the real biological system - is the model it

implements intended as "an empirical claim about some part of the physical world"[35]?
Much of the engineering end of biologically-inspired robotics is not, in this sense,
realistic modelling of any actual biological system. But as I have tried to illustrate here,
there are examples that do closely relate to biology. Provided the robot implementation
is properly assessed, it can, like other kinds of models, provide useful evaluation of and
predictions from biological hypotheses.

However a robot may be a 'realistic' biological model in this sense yet not in a
second sense: that of how detailed the model is. That is 'real' as the opposite of 'ideal'.
For example many of the models discussed above use a rather idealised notion of motor
control and do not include the details of limb movements to generate motion. They
nevertheless provide an interesting examination of real biological questions. Other
robots not discussed here attempt to replicate in more realistic detail the motor
mechanisms (e.g. for six-legged walking in insects[24;40], or for lobster locomotion[1]).
However hardware constraints on robot models can limit the realistic detail possible.
For example we still lack motor technology that is comparable to muscle in its strength
and flexibility for space and energy requirements. Thus a robot model may necessarily
be more abstract than a detailed simulation.

A third use of 'realistic' is to refer to the biological level of the mechanisms
represented in the model. As noted by Churchland & Sejnowski[8] "Not uncommonly, a
model will be criticised as unrealistic for failing to include very low-level properties"
(p.136). Here the use of the term can be highly relative - the simple spiking neurons
used in the model of escape behaviour are 'realistic' compared to most artificial network
research but not so realistic as the multicompartmental ion channel models used in
many small network simulations. Though there is no theoretical reason why such low-
level neural simulations could not be connected to a robot's actuators and effectors, in
practice there are problems, for example, with having the processing of sensory input

occur in something approximating real time. Hence there limits on the 'level of realism' possible in robot models as a consequence of the aim of building *complete* systems that connect sensors to actuators and guide behaviour in actual tasks.

It is worth noting, however, that realism in the sense of detailed or low-level mechanisms is not a guarantee of realism in a fourth sense, that of whether the mechanisms built into the model accurately represent the system being modelled. A highly detailed low-level simulation may turn out to be an incorrect explanation of the phenomenon, where a higher level or a more abstract representation in fact captures the 'real' situation. The nematode robot illustrates this point: the exact neural connectivity used in the robot probably will not map exactly to the circuit in the nematode when this is determined; whereas the analytic description of it as combining klinotaxis and klinokinesis is likely to be an accurate description of the function of whatever actual circuit is found. Robot models may be biologically plausible at one level but not at another.

A related debate is whether we can ever know that we have 'accurately represented reality' in a scientific model. Logically, we cannot, but it is apparent that some models, such as those derived from regression analysis on the data, make lesser claims to this kind of realism. On the other hand, such models can be capable of highly 'realistic' reproduction of the data. In robot models of animal behaviour, there can be a superficial sense of such 'output' realism induced by our natural reactions to seeing a real-world device moving autonomously. The robot can appear impressively 'animal-like' even when the behaviour only loosely resembles the real animal. Relying on this effect is a potential pitfall for robot modelling. It is a poor substitute for what should be a real strength of robot models - that the model can actually be tested in the same experimental situation as the animal and data collected to make direct comparisons.

This leads to a final sense of 'realistic' - when it is used to refer to the nature and context of the model i.e. does it exist in and interact with the real world? It is only in this sense that robot models are, of their nature, more realistic than other kinds of simulation. Hence it is here that we should look for the advantages of such models, that may counteract some of the limitations described above. One is that by providing a real-world grounding, researchers are prevented from making unrealistic assumptions about the environment, which may mislead them about the mechanisms needed to deal with the environment, as illustrated in the work on the looming detector described above. Another is that it is sometimes easiest to represent reality with reality, as in the use of real moth antennae on a robot described above. Additionally it is important, if we are to understand the neurobiology of an animal, to understand some of the real physics of the sensors, actuators and environments that it inhabits.

In summary, then, the use of robots can offer a complementary method of modelling biological systems. The field of insect neuroscience seems particularly ripe to take advantage of the strengths of such models, as we have something approaching a holistic understanding of parts of the behaviour from sensors to control at the level of neural connectivity. As well as there being a potential technological pay-off in generalising the small and efficient mechanisms found in insects, there is also much that biologists might learn through these approaches.

1.   Ayers, J., Witting, J., Wilbur, C., Zavracky, P., McGruer, N., and Massa, D. Biomimetic Robots for Shallow Water Mine Countermeasures. *Proc. of the Autonomous Vehicles in Mine Countermeasures Symposium. Naval Postgraduate School*. (2000).

2.   Blanchard, M., Rind, F.C., and Verschure, P.F.M.J. Collision avoidance using a model of the locust LGMD neuron. *Robotics and Autonomous Systems* **30**, 17-38 (2000).

3.   Braitenberg, V. *Vehicles: experiments in synthetic psychology*. MIT Press, Cambridge, MA (1984).

4.   Brooks, R. A. and Stein, L. A. Building Brains for Bodies. A.I. Memo No. 1439. MIT Artificial Intelligence Lab (1993)

5.   Burgess, N., Donnett, J.G., and O'Keefe, J. Using a mobile robot to test a model of the rat hippocampus. *Connection Science* **10**, 291-300 (1998).

6.   Chapman, Timothy. *Morphological and Neural Modelling of the Orthopteran Escape Response.* PhD Thesis, University of Stirling (2001).

7.   Chiel, H. and Beer, R. The brain has a body: adaptive behaviour emerges from interactions of nervous system, body and environment. *Trends in Neurosciences* **20**, 553-557 (1997).

8.   Churchland, P.S. and Sejnowski, T.J. *The computational brain*. MIT Press, Cambridge, Mass. (1992).

9.   Ferree, T. C. and Lockery, S. R. Computational rules for chemotaxis in the nematode C. elegans. *Journal of Computational Neuroscience* **6**(3), 263-277 (1999).

10.   Franceschini, N. Engineering applications of small brains. *FED Journal* **7**, 38-52 (1996).

11.   Franceschini, N. and Chagneux, R. Repetitive scanning in the fly compound eye. Elsner and Wassle. *Proceedings Gottingen Neurobiology Conference*. (1997).

12.   Franceschini, N., Pichon, J.M., and Blanes, C. From insect vision to robot vision. *Philosophical Transactions of the Royal Society B* **337**, 283-294 (1992).

13.   Grasso, F., Consi, T., Mountain, D., and Atema, J. Locating odor sources in turbulence with a lobster inspired robot. In Maes, P., Mataric, M. J., Meyer, J. A., Pollack, J., and Wilson, S. W. (eds) *From animals to animats 4*. Cambridge, Mass., MIT Press. (1996)

14.   Grasso, F., Consi, T., Mountain, D., and Atema, J. Biomimetic robot lobster performs chemo-orientation in turbulence using a pair of spatially separated sensors: Progress and challenges . *Robotics and Autonomous Systems* **30**, 115-131 (2000).

15.   Hannaford, B., Winters, J., Chou, C.-P., and Marbot, P.-H. The anthroform biorobotic arm: a system for the study of spinal circuits. *Annals of Biomedical Engineering* **23**, 399-408 (1995).

16.   Harrison, R.R. and Koch, C. An analog VLSI model of the fly elementary motion detector . In Jordan, M.I., Kearns, M.J., and Solla, S.A. (eds*.) Advances in Neural Information Processing Systems 10*. MIT Press, Cambridge, MA (1998).

17.   Horridge G.A., Loughuet-Higgins H.C., and Horridge G.A. What can engineers learn from insect vision. *Philosophical Transactions of the Royal Society B* **337**, 271-282 (1992).

18.   Hoshino K, Mura F, and Shimoyama I. Design and performance of a micro-sized biomorphic compound eye with a scanning retina. *Journal Of Microelectromechanical Systems* **9**(1), 32-37. (2000).

19.   Huber, F. Behavior and neurobiology of acoustically oriented insects. *Naturwissenschaften* **79**(9), 393-406. (1992).

20.   Huber, F. and Thorson, J. Cricket Auditory Communication. *Scientific American* **253**, 47-54 (1985).

21.   Huber, S. A. and Bulthoff, H. H. Simulation and robot implementation of visual orientation behaviour of flies. In Pfeifer, R., Blumberg, B., Meyer, J. A., and Wilson, S. W. (eds) *From animals to animats 5*. Pp. 77-85. Cambridge, Mass., MIT Press. (1998)

22.   Huber, S., Franz, M.O., and Bulthoff, H.H. On robots and flies: modeling the visual orientation behaviour of flies. *Robotics and Autonomous Systems* **29**, 227-242 (1999).

23.   Kanzaki, R. Behavioral and neural basis of instinctive behavior in insects: odor-source searching strategies without memory and learning. *Robotics and Autonomous Systems* **18**(1-2), 33-43. (1996).

24.   Kindermann, T, Cruse, H, and Dean, J. Biologically motivated controller for a six-legged walking system. *IECON (Industrial Electronics Conference). 4*, 2168-2173. (1998).

25.   Kohstall-Schnell, D. and Gras, H. Activity of giant interneurons and other wind sensitive elements of the terminal abdominal ganglion in the walking cricket. *Journal of Experimental Biology* **193**, 157-181 (1994).

26.   Kuwana, Y, Shimoyama, I, and Miura, H. Steering control of a mobile robot using insect antennae. *IEEE International Conference On Intelligent Robots And Systems 2*, 530-535. (1995).

27.   Lambrinos, D., Moller, R., Labhart, T., Pfeifer, R., and Wehner, R. A mobile robot employing insect strategies for navigation. *Robotics and Autonomous Systems* **30**, 39-64 (2000).

28.   Lewis, A. Visual navigation in a robot using zig-zag behaviour. In Jordan, M.I., Kearns, M.J., and Solla, S.A. (eds.) *Advances in Neural Information Processing Systems 10*. MIT Press, Cambridge, MA (1998).

29.   Lewis, M. A. and Nelson, M. E. Look before you leap:peering behaviour for depth perception. Pfeifer, R., Blumberg, B., Meyer, J. A., and Wilson, S. W. *From animals to animats 5*. 98-103.Cambridge, Mass., MIT Press. (1998).

30.   Lund, H.H., Webb, B., and Hallam, J. A robot attracted to the cricket species *Gryllus Bimaculatus*. In Husbands, P. and Harvey, I. (eds.) *Fourth European Conference on Artificial Life*. MIT Press, Cambridge MA (1997).

31.   Lund, H.H., Webb, B., and Hallam, J. Physical and temporal scaling considerations in a robot model of cricket calling song preference. *Artificial Life* **4**, 95-107 (1998).

32.   Melhuish, C., Holland, O., and Hoddell, S. Collective sorting and segregation in robots with minimal sensing. Pfeifer, R., Blumberg, B., Meyer, J. A., and Wilson, S. W. *From animals to animats 5*. Cambridge, Mass., MIT Press. (1998).

33.   Morse, T. M., Ferree, T. C., and Lockery, S. R. Robust spatial navigation in a robot inspired by chemotaxis in Caenorrhabditis elegans. *Adaptive Behaviour* **6**(3/4), 393-410. (1998).

34.   Mura, F. and Franceschini, N. Obstacle avoidance in a terrestrial mobile robot provided with a scanning retina. In Aoki, M. and Masaki, I. (eds.) *Intelligent Vehicles II*. MIT Press, Cambridge, MA (1996).

35.   Orzack, S.H. and Sober, E. A critical assessment of Levin's The strategy of model building in the social sciences (1966). *Quarterly Review of Biology* **68**, 533-546 (1993).

36.   Paydar, S., Doan, C., and Jacobs, G. Neural mapping of direction and frequency in the cricket cercal system. *Journal of Neuroscience* **19**, 1771-1781 (1999).

37.   Pichon, J-M, Blanes, C., and Franceschini, N. Visual guidance of a mobile robot equipped with a network of self-motion sensors. Wolfe, W. J. and Chun, W. H. *Mobile Robots IV*. 44-53. (1989)

38.   Pollack, G.S. Neural Processing of Acoustic Signals. In Hoy, R.R., Popper, A.N., and Fay, R.R. (eds.) *Comparative Hearing: Insects.* Springer, New York: Berlin (1998).

39.   Prescott, T.J. and Ibbotson, C. A robot trace-maker: modelling the fossil evidence of early invertebrate behaviour. *Artificial Life* **3**, 289-306 (1997).

40.   Quinn, R.D. and Ritzmann, R.E. Construction of a hexapod robot with cockroach kinematics benefits both robotics and biology. *Connection Science* **10**, 239-254 (1998).

41.   Rind, F. C. and Bramwell, D. I. Neural network based on the input organization of an identified neuron signalling impending collision. *Journal of Neurophysiology* **75**, 967-985. (1996).

42.   RIND, FC. The role of an identified brain neuron in mediating optomotor movements in a moth. *Journal of Experimental Biology* **102**, 273-284. (1983).

43.   Rucci, M, Wray, J, and Edelman, GM. Adaptation of orienting behavior: from the barn owl to a robotic system. *Proceedings Of IEEE International Symposium On Computational Intelligence In Robotics And Automation*, 91-93. (1997).

44.   Santos-Victor, J., Sandini, G., Curotto, F., and Garibaldi, S. Divergent stereo in autonomous navigation: from bees to robots. *International Journal of Computer Vision* **14**, 159-177 (1995).

45.   Shibata, T. and Schaal, S. Robot gaze stabilisation based on mimesis of oculomotor dynamics and vestibulocerebellar learning. *Advanced Robotics* **13**, 351-352 (1999).

46.   Srinivasan, M.V., Chahl, J.S., Weber, K., and Venkatesh, S. Robot navigation inspired by principles of insect vision. *Robotics and Autonomous Systems* **26**, 203-216 (1999).

47.   Srinivasan, M.V. and Venkatesh, S. *From Living Eyes to Seeing Machines*. Oxford University Press, Oxford (1997).

48.   Webb, B. and Harrison, R.R. Integrating sensorimotor systems in a robot model of cricket behavior .*Sensor fusion and Decentralised Control in Robotic Systems III*. SPIE, Boston Nov 6-8 (2000).

49.   Webb, B. Using robots to model animals: a cricket test . *Robotics and Autonomous Systems* **16**, 117-134 (1995).

50.   Webb, B. and Hallam, J. How to attract females: further Robotic Experiments in Cricket Phonotaxis. In Maes, P, Mataric, M J., Meyer, J-A, Pollack, J., and Wilson, S. W. *From Animals to Animats 4: Proceedings of the Fourth International Conference on the Simulation of Adaptive Behaviour*. 75-83.Cambridge, MA, MIT Press. (1996)

51.   Webb, B. and Scutt, T. A simple latency dependent spiking neuron model of cricket phonotaxis. *Biological Cybernetics* **82**, 247-269 (2000).

52.   Weber, K, Venkatesh, S, and Srinivasan, MV. An insect-based approach to robotic homing. Jain, A. K., Venkatash, S., and Lovell, BC. *Fourteenth International Conference on Pattern Recognition*. 297-299 Los Alimitos, CA, IEEE. (1998)

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