

From Insect Vision to Robot Vision [and Discussion]

N. Franceschini, J. M. Pichon, C. Blanes and J. M. Brady

Phil. Trans. R. Soc. Lond. B 1992 **337**, 283-294

doi: 10.1098/rstb.1992.0106

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

From insect vision to robot vision

N. FRANCESCHINI, J. M. PICHON AND C. BLANES

C.N.R.S. Laboratoire de Neurobiologie, Neurocybernétique, 31 Chemin J. Aiguier, 13009 Marseille, France

SUMMARY

Airborne insects are miniature wing-flapping aircraft the visually guided manoeuvres of which depend on analogue, 'fly-by-wire' controls. The front-end of their visuomotor system consists of a pair of compound eyes which are masterpieces of integrated optics and neural design. They rely on an array of passive sensors driving an orderly analogue neural network. We explored in concrete terms how motion-detecting neurons might possibly be used to solve navigational tasks involving obstacle avoidance in a creature whose wings are exquisitely guided by eyes with a poor spatial resolution. We designed, simulated, and built a complete terrestrial creature which moves about and avoids obstacles solely by evaluating the relative motion between itself and the environment. The compound eye uses an array of elementary motion detectors (EMDs) as smart, passive ranging sensors. Like its physiological counterpart, the visuomotor system is based on analogue, continuous-time processing and does not make use of conventional computers. It uses hardly any memory to adjust the robot's heading in real time via a local and intermittent visuomotor feedback loop. This paper shows that the understanding of some invertebrate sensory-motor systems has now reached a level able to provide valuable design hints. Our approach brings into prominence the mutual constraints in the designs of a sensory and a motor system, in both living and non-living ambulatory creatures.

1. INTRODUCTION

In this paper, which is an extension of an abstract presented at the IEEE International Congress of Advanced Robotics (Franceschini *et al.* 1991) we report on our attempt to solve real-time visuomotor control problems by designing an experimental creature largely inspired by the visual behaviour and the neural networks of the housefly. This sighted mobile robot was developed in parallel with optical, electrophysiological and neuroanatomical studies on the fly visual system, with a view to adopting a bottom-up approach in the analysis of visually guided animal navigation. Features of the insect visuomotor system were mimicked at several levels:

1. The overall principle of visuomotor control based on a coarse estimation of the optic flow field in the azimuthal plane.
2. The locomotory mode based on a succession of translations followed by saccadic rotations, as observed in the free-flight behaviour of flies.
3. The logic behind the elementary motion detectors (EMDs) that participate in flow-field estimation. The functional diagram of an EMD was first established on the basis of electrophysiological analyses carried out on the housefly and then transcribed into another (optoelectronic) technology.
4. The principle of parallel computation across retinotopically projecting maps, which operates in all evolved visual systems.
5. The principle of analogue, asynchronous signal processing, which is also a basic principle of natural visual systems.

6. The compound optics design, with a panoramic but nonuniform pixel array in the azimuthal plane.

7. The invertebrate design, which favours exoskeletons over backbone constructions.

The aim of this project was not to place a unit with 'human-like intelligence' on a mobile platform that could be requested, for example, to go and search for a needle in haystack no. 12 and bring it back to its original station. The goal was simply to show whether and how the sole ability to perceive visual motion based on passive (i.e. nonemitting) sensors might suffice to steer an elementary vehicle through a complex environment and to prevent it from bumping into things on its way to a target.

Since Braitenberg's 'vehicles', the complex behaviours of which do not necessarily emerge from complex sensory-motor interactions (Braitenberg, 1982), a number of investigators have been attracted by insect-like intelligence for controlling the navigation of mobile robots (e.g. Brooks 1986; Arkin 1987; Pichon *et al.* 1989; Beer *et al.* 1990; Maes 1991). This attitude has been viewed so far with mixed feelings, however, by the traditional communities in the fields of cognitive science, artificial intelligence and robotics. The 'insect approach' has been the target of two main kinds of criticism, largely based on misconceptions.

1. The disparagers of the insect approach do not have a very high opinion of insects since they are not endowed with a visual cortex. Here they may, however, be overestimating the role of the visual cortex in human visuomotor tasks. As we now know, humans have many visual systems operating in parallel and

most of them do not pass through the visual cortex (Weiskrantz 1990). We are probably not using the same visual system both when admiring Mona Lisa and when steering our body through a doorway or controlling our eye movements. It seems that sophisticated pieces of human visuomotor control operate like automatons without being linked to consciousness and can survive even quite severe lesions to the visual cortex (Goodale & Milner 1992). From the experimental viewpoint, the absence of a visual cortex in insects may be considered to be an advantage if the objective is simply understanding how a 'pure' sensory-motor creature, incapable of any intellectual feat, manages to use visual cues and neural maps to get around in the real world in real time. This particular kind of 'low-level', fast visuomotor control system has unexpectedly turned out to be in fact quite difficult to design for equipping mobile vehicles over the past 30 years. It still constitutes a major challenge for artificial intelligence and robotics and it is in this area *par excellence* that insect vision may have something to offer.

2. Others deny that insects can teach us something beyond the level of 'thermostat-like intelligence'. They vastly underestimate the level of sensory-motor intelligence at work in these humble mobile creatures which, as we now know, can attain a level of performance, complexity and organization beside which present day mobile robots look quite puny. Insect sensory-motor intelligence is prodigious and calls for an enormous number of 'high-tech' sensors, neurons, muscles, feedback loops and adaptive processes. Yet in spite of their complexity, the underlying neural networks are amenable to quantitative analysis, owing in particular to the existence of identifiable neurons, i.e. neurons that can be reliably identified in all the individuals of the species due to their structural constancy and invariant electrical response.

At the present-time, there is no visually guided mobile robot – even among those which are tethered to powerful computers – that comes anywhere near to matching the real-time visuomotor prowess of the fly. This thoroughly tested and successful natural guidance system may therefore provide an unexpected solution to a major engineering challenge and lead to the design of mobile robots capable of steering their way quickly in highly complex, alien environments.

In the next section we first review some recent findings about the visual system of the housefly, which is by now probably the best known of all the insects. The available data show how brilliantly insect neural networks can solve reflexive control problems the subtlety of which goes far beyond that of knee-jerk reactions and 'thermostat-like intelligence'.

2. REAL TIME VISUOMOTOR CONTROL IN THE HOUSEFLY

Unlike conventional aircraft, which need to keep on exploiting human perceptual and motor skills to prevent disastrous events, airborne insects several hundred millions years ago went to the expense of

flying themselves. The price paid by these early air pioneers was to install in their cockpit a sophisticated visual system collecting most of the information needed to fly the aircraft, and to link its outputs 'smartly' to the numerous actuators responsible for minutely adjusting the flight surfaces.

The housefly in particular is a self-contained aircraft that carries its own energy requirement and processes its sensory signals on-board, without dragging any cumbersome umbilical link with a super-computer. It navigates swiftly in unconstrained environments and avoids obstacles without making use of sonars, radars or laser range-finders.

Visual navigation in the housefly is achieved by a dedicated crew of on-line image- and flight-control-processors consisting of about one million neurons. These neurons, which are installed in cramped quarters called 'optic ganglia' underneath the faceted canopy (figure 1), exhibit a bewildering variety of shapes and functions but are arranged in a very orderly, crystalline manner (Cajal 1915; Strausfeld 1989, Strausfeld & Lee 1991). The neural networks perform sophisticated parallel, asynchronous processing and send analogue 'fly-by-wire' controls to a set of 17 muscles controlling the wings, via a network of descending neurons that pass through the neck of the aircraft. These constantly adjust the amplitude of the two wings, their frequency and twist. Together with additional inputs from the gyroscopic organs, they dynamically maintain the attitude of this inherently unstable flying machine, keeping it from crashing and ensuring its collision-free course even in densely cluttered and dynamic environments (Nachtigall & Wilson 1967; Götz 1983; Heide 1983; Nachtigall & Roth 1983; Zanker 1989).

An essential requisite of visually guided behaviour in flies is the ability to detect visual motion. This is particularly necessary for course control, a process which has been analysed in detail over the last few decades by investigating the optomotor responses (Götz 1968, 1972, 1983; Reichardt & Poggio 1976; Wehner 1980). The corrective manoeuvres contributing to course stabilization seem to be governed by specific sets of neurons that detect visual motion in specific directions, the layout and electrical responses of which are now known in detail (review: Hausen & Egelhaaf 1989).

The possibility for animals and humans to use motion parallax to assess the three-dimensional layout of the environment was discussed early by Helmholtz (1867) (see also Gibson 1958; Lee 1974; Johansson 1982; Warren & Wertheim 1990) and suggested in the case of insects by Exner in 1891 (see also Collett 1978; Wehner 1981; Buchner 1984; Horridge 1987). It is only very recently, however, that short range navigation in a flying insect, which requires at least some crude estimation of the three-dimensional layout of the environment, was shown to involve the visual processing of motion (Lehrer *et al.* 1988; Kirschner & Srinivasan 1989).

In the housefly, the front-end of the image processors consists of a two-dimensional array of 48 000 miniature photosensors (figure 2) the electrical out-

puts of which are read in parallel. Each of these photosensors delivers a low-level (0–60 mV) electrical signal to a well defined set of repeat units called second-order ('postsynaptic') neurons, which process the input signals in different ways, depending on the function they serve (Strausfeld 1989; Laughlin 1989). There are only 3000 pixels in the eye, however, each of them sensing the world with a set of eight cells

having coaxial receptive fields (Braitenberg & Strausfeld 1973). The 3000 pixels of the eye sample the visual environment in a nonuniform way, with an acute zone of vision in the front part of the eye (Beersma *et al.* 1975; Collett & Land 1975; Franceschini 1975). Each photoreceptor is a sensitive quantum detector with a very low dark count and is equipped with an integrated 'automatic gain control' (Kirschfeld & Franceschini 1969) that protects it against overstimulation and extends its dynamic range (Franceschini 1972; Howard *et al.* 1987).

The housefly retina has considerable spectral resources. The photosensors display no less than six different spectral sensitivities, from the ultraviolet (300 nm) to the red (600 nm) part of the spectrum (Franceschini 1985; Hardie 1986). The 'chromatic channels' consist mainly of the two central cells, called R7 and R8, which are arranged in tandem beneath each facet lens (figure 2). The six peripheral cells R1–6 of each facet feature an accessory, uv-sensitizing pigment that boosts their quantum collect, making these cells especially sensitive (Kirschfeld *et al.* 1977). They are known to drive in particular the neural circuits dealing with motion detection (Kirschfeld 1972).

Insects epitomize some of the general principles in sensory-motor control. They seem to use several *ad hoc* visual systems combined, each leading to a specific behaviour. For example, the male housefly, which is known to pursue the other sex on the wing (Perez 1911; Land & Collett 1974; Wehrhahn 1979), possesses a dedicated array of sex specific photosensors located on the frontal-dorsal part of the eyes (the 'love-spot', see figure 1*a*). These special receptors feature sex-specific wiring (Franceschini *et al.* 1981*b*)

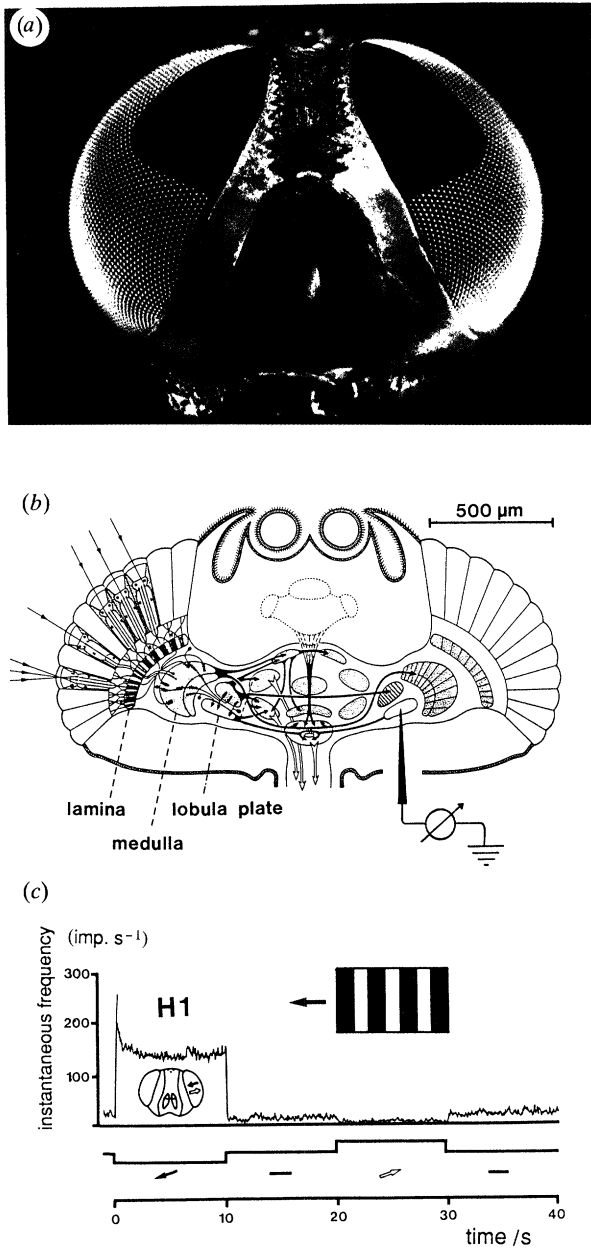


Figure 1. (*a*) Head of a male housefly observed with a Lieberkühn microscope. The shaded area delineates approximately the 'love spot', i.e. the upward looking region of the eye which is invested by male-specific photoreceptor cells that are likely to be involved in female chasing (after Franceschini 1984). (*b*) Schematic horizontal section through the head of a fly and principle of microelectrode recording from the motion sensitive neurons of the lobula plate, which play an essential role in visuomotor course control (after Kirschfeld 1979). (*c*) Response of the motion sensitive H1-neuron of the lobula plate to horizontal motion of a striped pattern presented to the ipsilateral eye in the preferred (back to front) and non-preferred (front to back) directions (after Riehle & Franceschini 1984).

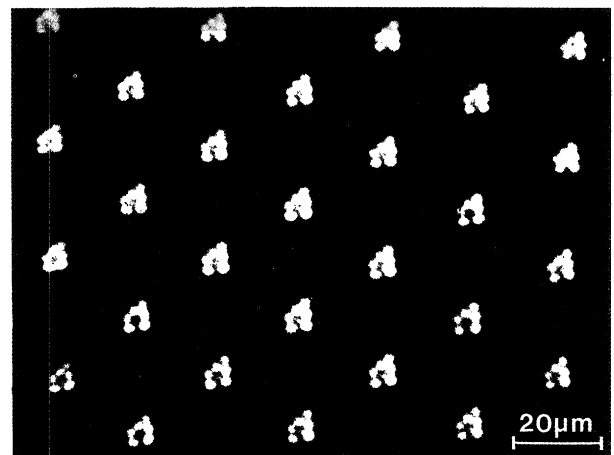


Figure 2 Photoreceptor mosaic in the compound eye of the housefly observed *in vivo* under epi-fluorescence microscopy (the corneal facets were 'optically neutralized' with a drop of water). A group of seven micrometer-sized photoreceptors (for their numbering R1–7 refer to figure 4, inset) can be seen here behind each facet lenslet. The central cell (R7) of each group usually does not display the same fluorescence colour as its six neighbours (R1–6), due to its specific visual pigments. An 8th receptor cell (R8, not seen here) lies in the prolongation of R7, with yet another spectral sensitivity. Only about 1% of the fly retinal mosaic is visible here (after Franceschini 1985).

and drive a dedicated, sex-specific neural machinery likely to be involved in the sexual pursuit behaviour (Hausen & Strausfeld 1980). Along the same lines, the fly's compound eye, like other compound eyes, possesses special uv and highly dichroic photoreceptors on its frontal dorsal rim (Hardie 1986), which are likely to be involved in polarized light navigation (Rossel 1989), possibly via polarization-opponent interneurons like those discovered in the eye of the cricket (Labhardt 1988).

Aerial insects, like many other animals, teach us that incorporating vision into a sensory-motor control loop requires some decent stabilization of the airborne platform upon which the photosensor array is mounted. In advanced insects with dynamic flight control, such as higher Diptera, no less than 21 pairs of muscle actuators quickly adjust the 3-axis head orientation system (Land 1975; Milde & Strausfeld 1986; Hengstenberg 1991). And there is the additional possibility of binocularly controlling the gaze via a pair of mos eye muscles which, by means of 'bell-cranks' and 'return springs' move the complex flexure encompassing the whole photosensor array (Franceschini *et al.* 1991).

3. MICROANALYSIS OF ELEMENTARY MOTION DETECTORS

Motion-sensitive neurons have long been described in the fly visual system (reviews: Hausen & Egelhaaf

1989; Strausfeld 1989). They occupy a major part of the 2nd and 3rd optic ganglia.

The accessibility of the retinal mosaic *in vivo* provides a unique opportunity of analysing the properties and working principles of an 'elementary motion detector' (EMD). For this purpose, we performed single cell recording from an identified motion sensitive neuron called H1 (Hausen 1976) located in the 3rd optic ganglion (the lobula plate) while applying optical microstimulation to single receptor cells on the retinal mosaic. The instrument specially designed for this kind of microstimulation is a hybrid between a microscope and a telescope (figure 3). It uses one of the 3000 facets of the eye as its primary objective lens (diameter $\approx 25 \mu\text{m}$; focal length $\approx 50 \mu\text{m}$) to project two microspots of light (diameter $\approx 1 \mu\text{m}$) onto two neighbouring receptor cells (diameter $\approx 1 \mu\text{m}$). Sequential stimulation of these two receptors – a procedure that simulates a micromotion in the animal's visual field – elicits a sudden discharge of nerve impulses in the H1 neuron, provided the sequence mimics motion in the 'preferred' direction (figure 4); whereas the reverse sequence corresponding to the 'non-preferred' direction does not elicit any response (Riehle & Franceschini 1984). Focusing upon the sequence-discriminating ability of these smart neural sensors highlighted the presence of a fine-grained network of lateral controls that operate in both the preferred and non preferred directions, as described in figure 5.

Using various sequences of light steps and pulses on

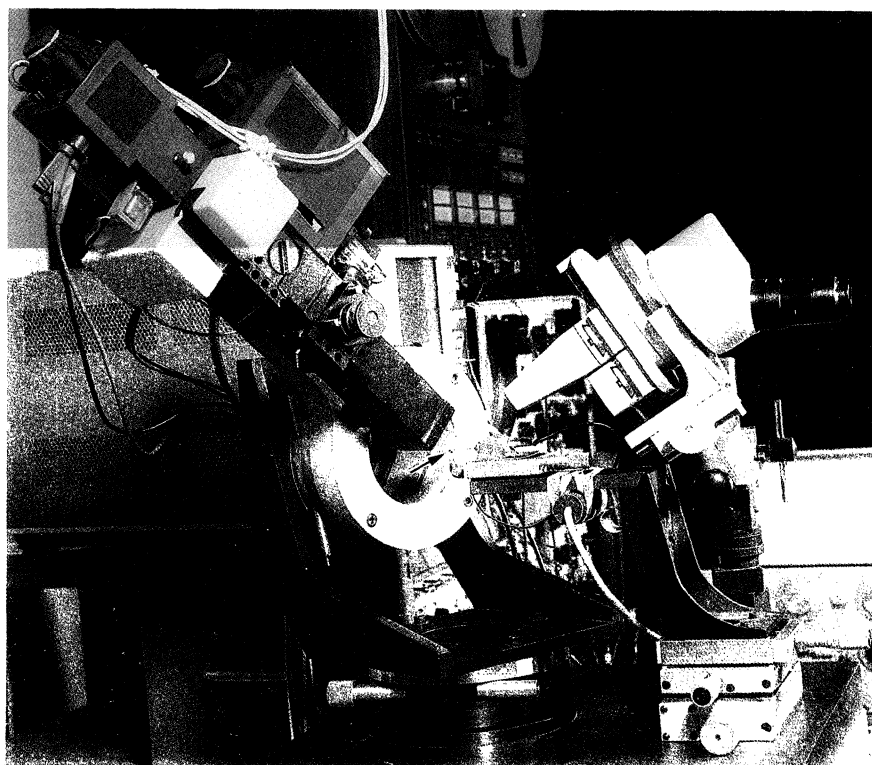


Figure 3. Triple-beam incident light 'microscope-telescope' (left) pointing at the fly's eye (arrow). This instrument was used to investigate the basic neuronal mechanism underlying directional sensitivity in a motion detecting neuron. It can deliver a sequence of $1 \mu\text{m}$ spots to two different photoreceptor cells within a single facet in association with microelectrode recording from single, identifiable neurons, such as H1, in the lobula plate (cf. figure 1*b,c*).

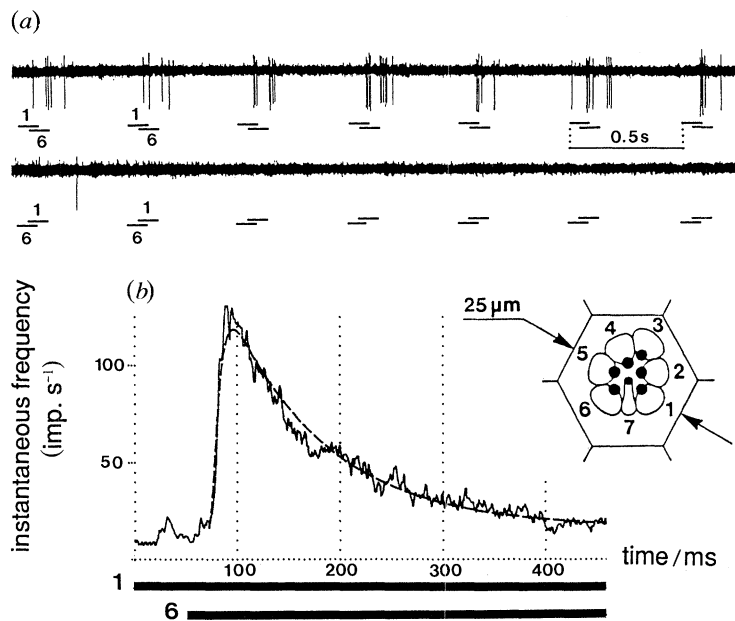


Figure 4. Sequence discrimination by a fly elementary motion detector (EMD) that drives the H1 neuron. (a) Sequentially presenting two flashes (each with a duration of 100 ms) to the pair of receptor cells R1 and R6 (inset) consistently induced a prominent spike discharge in H1 provided the sequence mimicked motion in the preferred direction (top trace). Note that the opposite (non-preferred) sequence induced no response (bottom trace) (after Riehle & Franceschini 1984). (b) A sequence of light steps (or dark steps, not shown here), with 50 ms delay, presented to the two receptor cells R1 and R6 produces a prominent but transient response in H1, provided the delay is such as to simulate a micromotion in the preferred direction (the dotted line shows the response of a first-order highpass filter with a time constant of 94 ms in series with a first-order lowpass filter with a time constant of 5 ms). To a first approximation the global response to motion of a largefield pattern (such as the striped pattern shown in figure 1c) results from the nonlinear spatiotemporal summation of thousands of transient responses that are qualitatively similar to this one.

the two receptors, we determined the kinetics of the (nonlinear) filters present within the 'direct' and 'lateral' branches of an EMD (Franceschini *et al.* 1989; Franceschini 1992).

Directionally selective motion-detecting neurons have been known for 30 years to exist in the visual system of many species among both vertebrates (Letting *et al.* 1959; Hubel & Wiesel 1959) and invertebrates (Waterman *et al.* 1964; Horridge *et al.* 1965). The fly, however, is the only animal in which the network of motion detectors has been analysed with the high degree of spatial and temporal resolution afforded by single neuron recording combined with single photoreceptor stimulation on a retinal mosaic.

4. REACTIVE MOBILE ROBOT WITH AN INSECT-LIKE, ON-BOARD VISUAL PROCESSOR

In an attempt to take up the challenge of the fly's visually guided behaviour and explore how motion-detecting neurons might possibly help to solve collision avoidance and ensure the vehicle's survival, we designed an experimental creature the sole purpose of which is to move around and avoid obstacles by evaluating exclusively the relative motion between itself and the (optically contrasted) environment (Pichon *et al.* 1989).

Figure 6 shows how an observer O moving at speed V_O can assess the distance D to an obstacle P if it is

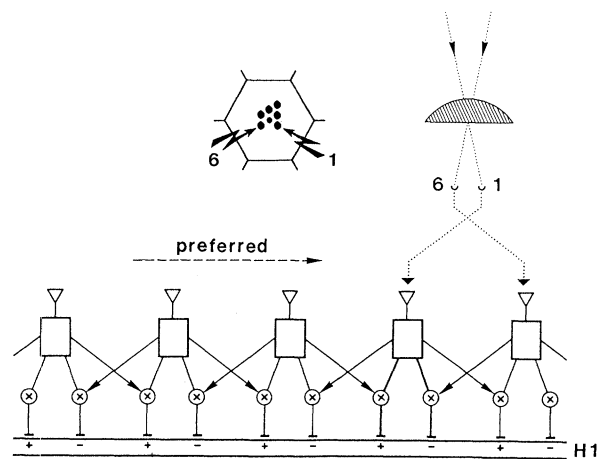
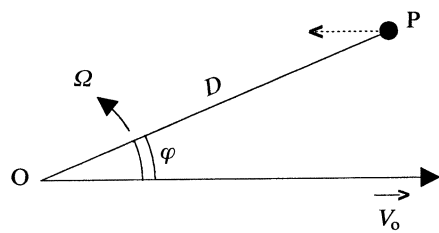


Figure 5. Basic topology of the lateral interactions leading to directionally selective motion detection in the H1 neuron of the fly, as inferred from electrophysiological experiments involving single neuron recording combined with optical microstimulation of only two photoreceptors (R1 and R6) in a single facet with the microscope-telescope shown in figure 3. Each 'puppet' in this array describes the signal flow from one lamina cartridge down to the H1 neuron. An essential point is that each puppet drives H1 with two legs whose transmittance is controlled by signals from the adjacent puppets (one on each side). The two legs of a given puppet drive H1 with opposite polarities (after Franceschini *et al.* 1989).



$$\Omega = \frac{V_o}{D} \cdot \sin \varphi$$

Figure 6. Principle of motion parallax. Any agent (fly, human, robot, etc.) translating at speed V_o can gauge the distance to a contrast point P located at azimuth φ if it is equipped with a passive sensor able to measure the angular speed Ω of P when this point crosses its visual field due to the agent's own movement.

equipped with a sensor able to evaluate the angular speed Ω of the contrast point P when this point crosses the visual field due to the observer's movement. The resulting formula was established by Whiteside & Samuel (1970) in the context of aerial navigation.

A genuine compound eye with as many facets (100)

as the fly's eye in its equatorial plane was installed on a wheeled, synchro-drive mobile platform (Real World Interface, Massachusetts) (figures 7*a,b* and 11). An array of electro-optical EMDs the principle of which was closely copied from those of the fly was wired down with fine grain underneath the photosensor layer (figure 7*b,c*). All these EMDs operate concurrently, using analogue signals, i.e. signals that are graded in amplitude and continuous in time. They drive an obstacle avoidance algorithm which is implemented on-board the vehicle as a parallel, analogue network the architecture of which was inspired by that of natural nervous systems. This network integrates the signals delivered by the EMDs and controls the steering of the mobile platform in real time.

An essential feature of the system is the robot's locomotory mode, which consists of a series of purely translational steps of size ΔL , each of which is dedicated to visual acquisition (figures 9 and 10). Imposing bouts of rectilinear motion upon the creature is in fact an easy compromise which makes it possible to selectively recover the translational component of the optic flow field: the only component that matters for gauging the distance to obstacles and assessing the three-dimensional layout of the environ-

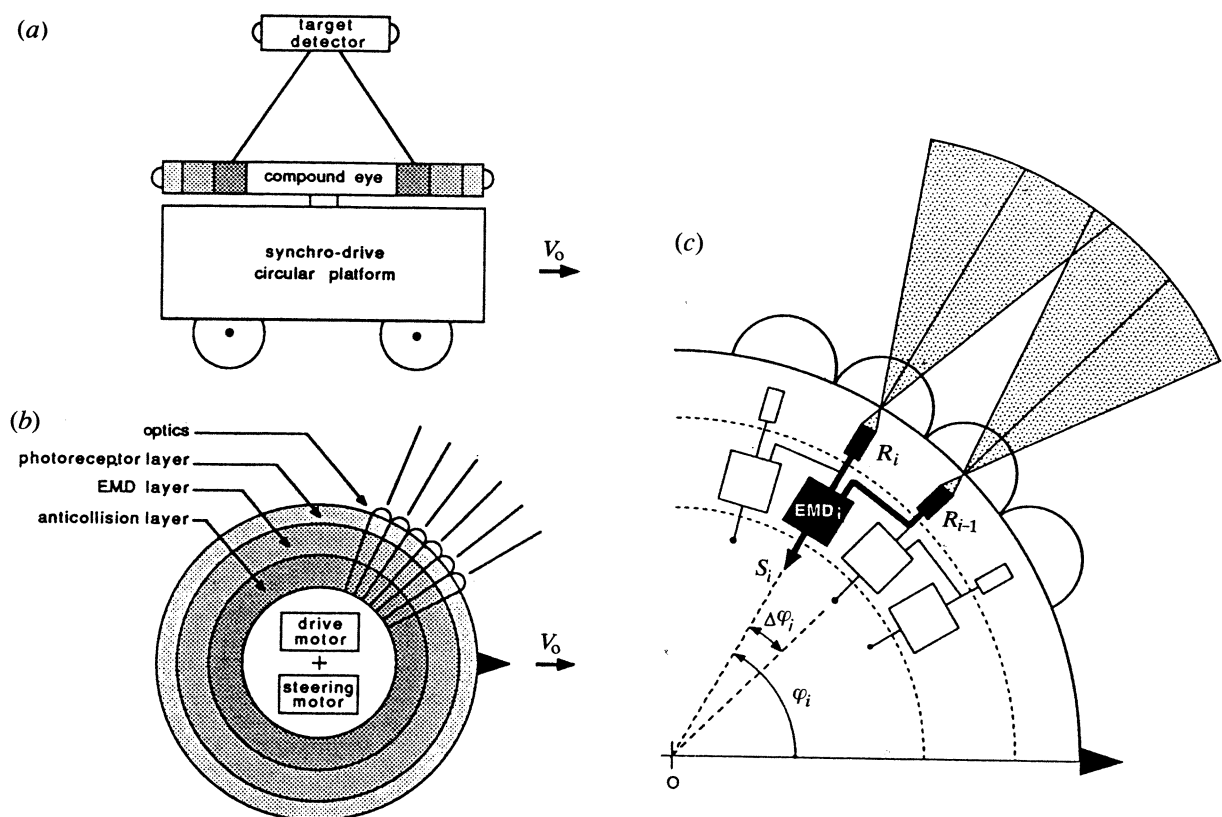


Figure 7. (*a,b*) The mobile robot is equipped with a panoramic compound eye in charge of collision avoidance and with an accessory visual system (on top) that constantly surveys the horizon and constantly informs the vehicle about the bearings of the target lamp. The compound eye and target detector are mounted onto a neck which is integral with the steering of the three-wheeled synchro-drive mobile platform. The compound eye is based on parallel and analogue processing circuits the layered and columnar organization of which is reminiscent of insect optic ganglia. (*c*) The principle of collision avoidance is based on motion parallax (cf. figure 6) and makes use of an array of elementary motion detectors (EMDs) that are wired down with fine grain underneath the receptor mosaic. Their principle was closely copied from the fly (cf. figure 5) (after Pichon *et al.* 1989).

ment (Koenderink & van Doorn 1976; Longuet-Higgins & Prazdny 1980; Prazdny 1980).

Another essential feature of the system, also inspired by the fly (Franceschini 1975), concerns the nonuniform layout of the visual axes in the eye. A sine gradient in interommatidial angle was installed in the eye, such that sampling of the visual space is finer towards the front than laterally. This gradient can be said to compensate for the sine law inherent in the optic flow field (figure 6) and ensures that any contrast point located inside a given circle of vision with radius R_v (dotted circle in figure 8) will be detected with certainty, upon translation by ΔL . The introduction of a sine gradient leads to considerable data reduction and allows the underlying EMD array to be built uniformly, each of them displaying the same temporal properties as its neighbours. These advantages are so conspicuous that they may in retrospect contribute to explain the gradient in resolution that is observed in the peripheral retina of so many creatures, including humans and flies.

A visual feedback control loop is implemented to control the subsequent steering angle of the vehicle from the numerous motion signals delivered by the EMDs. An intermittent steering command is delivered in this way at the end of each translational step (figure 9). The obstacle avoidance algorithm is simple and local. It relies on a 'snap map' of obstacles in polar coordinates, which is available at the end of each translatory step in an eye-centred frame of reference. This map is also defined in relation to the current heading direction of the vehicle because the com-

pound eye is mounted integral with the steering and rotates at one with the wheels.

The architecture of the visuomotor control system is reminiscent of the layered structure called subsumption architecture (Brooks 1986*b*). It differs in one major respect, however. There is no 'arbitration' process in terms of a switch that might decide which of the two 'behaviours', target pursuit or obstacle avoidance, is taking over the control at any given time. Instead, at any time a graded fusion occurs between the spatial information concerning the angular bearings of the goal and the angular bearings of the obstacles. This multisensory fusion, which takes place on a local and short-lived motor map, ensures that the next heading direction will be the closest possible to the target direction while remaining outside the forbidden zone created by all the obstacles detected.

No permanent world model, or symbolic representation of obstacles, is required in this system where the speed of the drive and steering motors is constantly

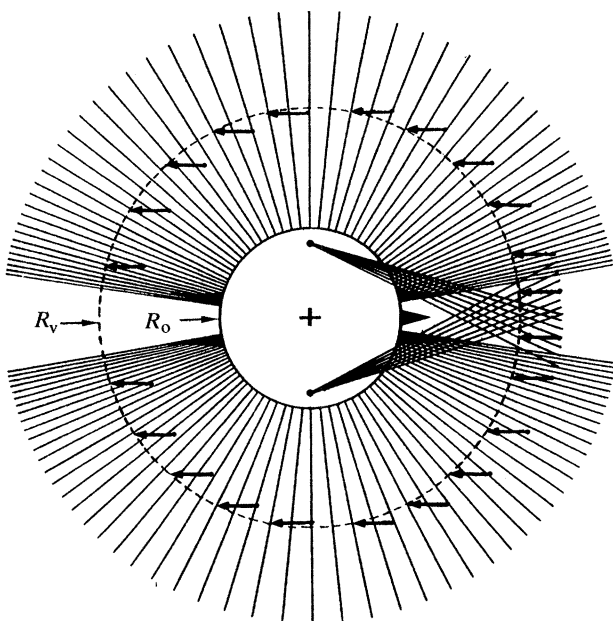


Figure 8. Complete set of visual axes of the robot's compound eye. Sampling of the visual environment is carried out in a non-uniform way, with a sine-law gradient in interommatidial angles from the anterior (and posterior) to the lateral part of the eye (see text). Two separate sets of EMDs (off centre, on each side of the vehicle) take care of a $\pm 10^\circ$ 'deadzone' around the frontal pole of the optic flow field (after Pichon *et al.* 1989).

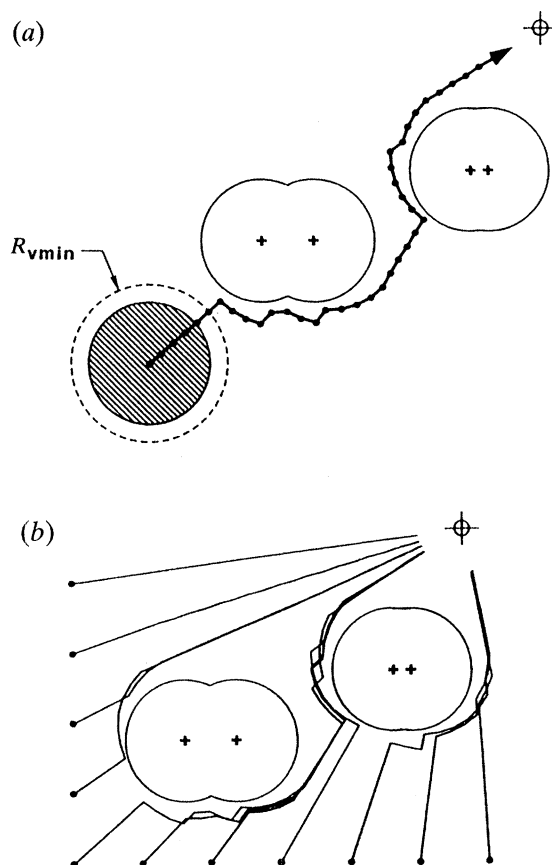


Figure 9. Simulation of the robot's behaviour in a simple world. (a) The circular robot (hatched) finds a safe path to the goal by moving amidst obstacles (consisting of contrast points at various depths). Circles drawn around these contrast points with the same radius as the robot itself define the 'configuration space', a kind of no man's land which the robot's centre is not allowed to enter. The elementary translational steps imposed upon the robot are basic to the data acquisition process and are used by the array of EMDs to build a 'snap map' of the environment. (b) A pattern of streamlines is generated by having the robot start at various locations. Note that obstacle avoidance is achieved in all cases (after Pichon *et al.* 1989).

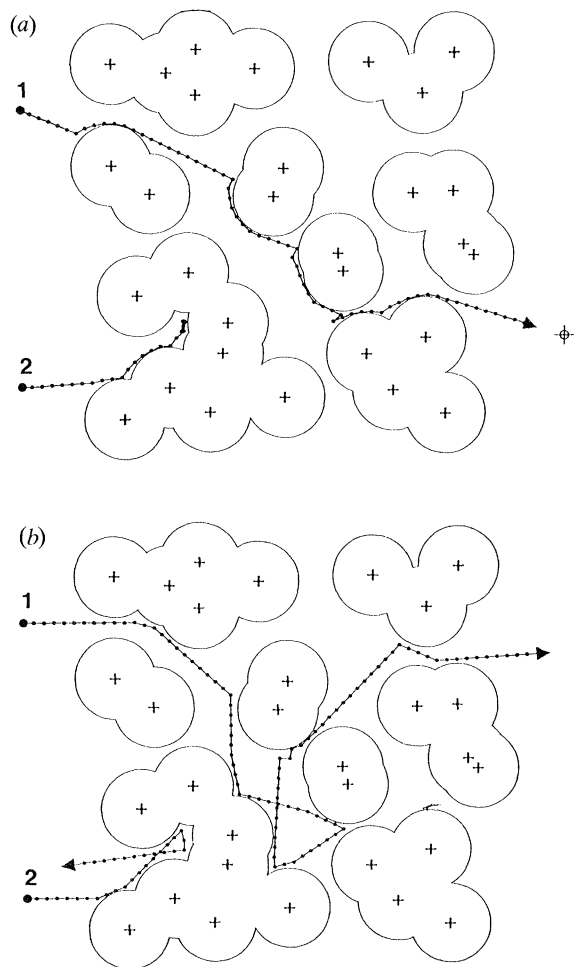


Figure 10. Simulated behaviour of the robot in a complex, forestlike environment (configuration space obtained as in figure 9). In (a) the robot has a target and finds a path through the forest when starting at point 1 but not when starting at point 2. In the latter case it is trapped forever in a 'potential well' (but survives by moving in this tight spot). In (b) the robot has no target and is roving aimlessly through the forest. In this case starting at 2 is no more problem than starting at 1 because lack of constraint to reach a target permits escape.

readjusted via the intermittent visual feedback from the environment.

This system is fraught with the set of assets and liabilities characteristic of reactive robots, which do not rely on global reasoning on the environment (Arkin 1987). For instance, as a consequence of being constantly 'attracted' by the target and 'repelled' by the obstacles, the robot can easily become stranded in a 'local minimum' (Noborio *et al.* 1989). A higher level of competence in the subsumption-like algorithm would get him out of this situation. Being equipped with this fast visuomotor control mechanism based on local data, the robot obviously does 'plan a path' *stricto sensu*. The only thing it is able to plan is the direction of its next step, based on the reafferent data acquired during the previous step.

The advantage of dealing exclusively with local data and keeping a tight feedback loop between perception and action, however, is that it provides the robot with the ability to venture uninhibited into

unknown environments. It also endows it with a natural adaptiveness to some classes of dynamic environments, including a non stationary target. This adaptive behaviour is 'inborn' and inherent to the hardwired system. It does not rely on a learning process that might, for instance, progressively alter some 'synaptic weights' in the circuits.

5. CONCLUSION

We have built a terrestrial creature equipped with a compound eye largely inspired by that of the fly (figure 11). This 10 kg demonstrator with its 1 kg visual system can now slalom to its target lamp at 50 cm s^{-1} through a random array of posts (forestlike environment, as in figure 10) using exclusively visual cues. The creature is only partially sighted: it sees only motion and depends on its own bodily movement to evaluate the hazards in its environment. It becomes completely blind if there are no photons, or no contrasts or no relative motion.

The visual system consists of an orderly array of miniature hardwired analogue circuits performing specific tasks. Although the optronic hardware is not meant to be a rigorous model of the natural system, it does borrow its main features from the fly. In particular, each one of the 100 EMDS is a slightly approximated version of its physiological counterpart (Franceschini *et al.* 1985). These circuits cannot be 'reprogrammed' for another application but the 'surface mount devices' (SMD) technology allows for some parameter adjustments via miniature potentiometers. Even though the lack of flexibility is nearly as unpleasant as in dedicated analogue integrated circuits (where a single mistake in the design is fatal), pursuing this reverse-engineering exercise beyond the conceptual level and beyond the simulation phase, up to a physical implementation on an actual robot, was worth the trouble for many reasons.

1. It forced us to an ultimate level of concreteness in specifying the design of the complete optomotor loop.

2. It circumvented the need to measure and then introduce into the computer simulations all the parameters (electronic, optical, mechanical) involved in the visuomotor loop, including the dynamics, noise lighting, reflectance of each single object, etc.

3. Developing parallel and analogue, biologically inspired signal-processing circuits was a major part of the project. The philosophy of this approach precluded the use of conventional computers from the outset and placed severe – but natural – constraints on the overall visuomotor control loop. Figure 12 shows an example of the odd pattern of projection between the thousands of analogue devices that make up the retinotopic columnar elements of the visuomotor system.

4. The fact that the undertaking ended up with a tangible creature operating swiftly and autonomously in a real world and in real time may be taken to constitute non negligible evidence that the approach is feasible and the embodied principles viable.

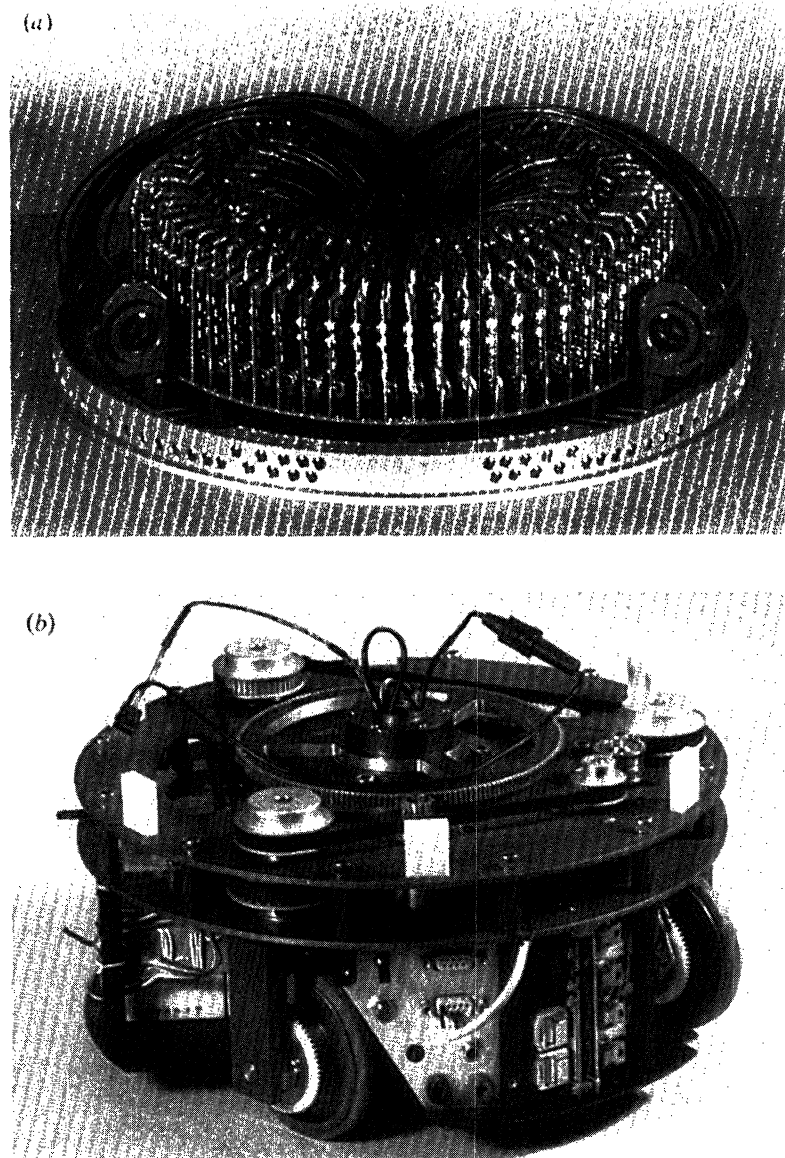


Figure 11. (a) Compound eye with facets, 'rhabdomeres', photosensors and elementary motion detectors (EMDs) copied from those of the housefly. Despite its small number of pixels (118), this artificial visual system is able to control the steering of the mobile platform shown in (b). The creature can slalom amidst a field of obstacles (posts) at 50 cm s^{-1} .

5. It was expected – and verified beyond all expectation – that the construction step itself would provide us with deeper insights into the real problems faced by any sighted vehicle, living or non-living, which dares make a move forward in a complex environment.

Our endeavour showed that an array of smallfield retinotopic visual motion sensors suffices to steer a vehicle amidst obstacles. We proposed one solution to the problem of how motion sensors can be interfaced to a motor system for the sake of survival in cluttered environments. The observed survival of the creature validates the notion that some of the motion sensitive neurons to be found in the visual system of so many creatures, including insects, fish, amphibians, reptiles, birds or mammals may well be used for the visual steering of their hosts in a three-dimensional environment. Using visual motion detectors as smart sensors

for avoiding obstacles is quite an appropriate strategy for both living and non-living creatures because the very concept of 'obstacle' makes sense only in the context of relative motion between an agent and its threatening environment.

In trying to explore the fuzzy links between perception and action (cf. Warren 1990), we actually addressed a ubiquitous problem in sensory-motor control, which is how to make a multitude of sensory input signals (here a hundred, but there could just as well be thousands of millions) coalesce into a few motor commands (here a single one: the steering angle) in a survival-related task. By adding a target seeker, we went beyond the obvious analogy with the chasing behaviour of the male fly (§ 2), and were able to make an incursion into the field of real-time 'multi-sensory fusion' with parallel, analogue neural networks. Signals from two different visual systems

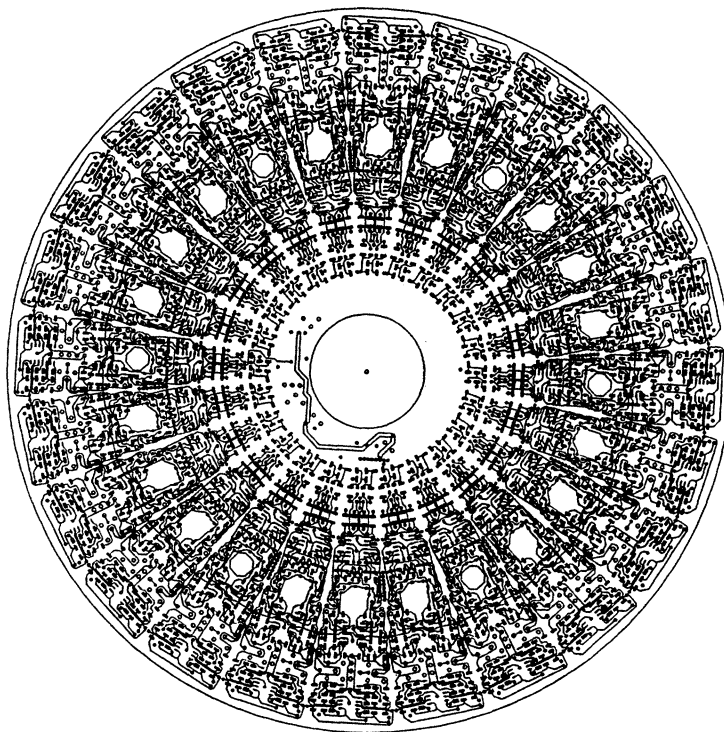


Figure 12. Routing of one face of the six-layered printed circuit board implementing the anticollision algorithm in a fully parallel way. The rose-window-like pattern is due to the repeat units of the analogue circuits and to their retinotopic projections. This board receives analogue components of only four kinds: resistors, capacitors, diodes and operational amplifiers. The surface mounted devices (SMD) technology used throughout to construct the visual systems has some ability to carry out complex information processing in a relatively small volume.

were fused together on the local motor map, with the stringent constraint that obstacle avoidance should at all times keep a tight rein on target pursuit.

In this attempt to link real-time vision with real-time action, specific emphasis has been given to completing the sensory-motor control loop that allows the creature to dynamically interact with its environment. Yet the creature we have produced only partly meets the challenge provided by the fly, whose efficient dodging manoeuvres in tight situations is likely to put man-made robots in the shade for many years to come.

The retinal front-end of 'simple animals' such as insects (Strausfeld 1976) seems to display about the same complexity-per-pixel as the vertebrate retina (Dowling, 1989). The apparent simplicity of the insect eye may be mainly due to its having a much lower number of pixels. Likewise, visuomotor neural circuits may be of the same essence in both arthropods and vertebrates. If so, those interested in 'visual perception for immediate action', such as the creators of artificial seeing systems for visually handicapped people and automatically guided vehicles ought perhaps to pay heed to the visuomotor control system of skilled however humble creatures such as insects, in addition to contemplating the higher level cognitive processes mediated by the cortex of less humble creatures such as mammals (cf. Horridge 1987; Cliff 1990).

This research was supported by C.N.R.S., M.R.T., Conseil Régional P.A.C.A. and Commission of the European Commu-

nities (ESPRIT, basic Research Action). We acknowledge A. Le Nestour and L. Oufar for assistance during the early phases of this project. We thank J. Blanc, A. Totin and J. Creuzet and J. Roumieu for expert technical assistance. J.M.P. was supported by C.N.R.S. (Life Sciences and Engineering Sciences), I.I.R.I.A.M. and I.M.T. C.B. was supported by C.N.R.S. (Life Sciences and Engineering Sciences) and Conseil Régional P.A.C.A.

REFERENCES

- Arkin, R.C. 1987 Reactive/reflexive navigation for an autonomous vehicle. *Proc. Am. Inst. Aeron. and Astron. Comp. Aerospace*, pp. 298–306. Washington: AIAA.
- Beer, R.D., Chiel, H.J. & Sterling, L.S. 1990 A biological perspective on autonomous agent design. *Robot. Autonom. Syst.* **6**, 169–186.
- Beersma, D.G.M., Stavenga, D.G. & Kuiper, J. 1975 Organization of visual axes in the compound eye of the fly *Musca domestica* L. and behavioural consequences. *J. comp. Physiol.* **102**, 305–320.
- Braitenberg, V. & Strausfeld, N.J. 1973 Principles of the mosaic organization in the visual system's neuropil of *Musca domestica*. In *Handbook of sensory physiology*, vol. 7, 3A (ed. R. Jung), pp. 631–659. Berlin: Springer.
- Braitenberg, V. 1984 *Vehicles, experiments in synthetic psychology*. Cambridge, Massachusetts: M.I.T. Press.
- Brooks, R. 1986a Achieving artificial intelligence through building robots. A.I. Memo 899, M.I.T.
- Brooks, R. 1986b A robust layered control system for a mobile robot. *IEEE J. Robot. Autom.* vol. RA2 No. 1, 14–23.
- Buchner, E. 1984 Behavioral analysis of spatial vision in

- insects. In *Photoreception and vision in invertebrates* (ed. M. A. Ali), pp. 561–621. New York: Plenum.
- Cajal, S.R. & Sánchez, D. 1915 Contribución al conocimiento de los centros nerviosos de los insectos. Parte I Retina y centros opticos. *Trab. Lab. Invest. Biol. Univ. Madrid* **13**, 1–168.
- Cliff, D. 1990 Computational neuroethology: a provisional manifesto. In *From animals to animats* (ed. J. A. Meyer & S. W. Wilson), pp. 29–39. Cambridge, Massachusetts: M.I.T. Press.
- Collett, T.S. 1978 Peering: a locust behavior pattern for obtaining motion parallax information. *J. exp. Biol.* **76**, 237–241.
- Collett, T. & Land, M. 1975 Visual control of flight behaviour in the hoverfly, *Syriffa pipiens*. *J. comp. Physiol.* **99**, 1–66.
- Dowling, J. 1989 *The retina*. Cambridge, Massachusetts: Belknap Press.
- Exner, S. 1891 *Die Physiologie der facettierten Augen von Krebsen und Insekten*. Leipzig: Deuticke.
- Franceschini, N. 1972 Pupil and pseudopupil in the compound eye of *Drosophila*. In *Information processing in the visual system of arthropods* (ed. R. Wehner), pp. 75–82. Berlin: Springer.
- Franceschini, N. 1975 Sampling of the visual environment by the compound eye of the fly: fundamentals and applications. In *Photoreceptor optics* (ed. A. Snyder & R. Menzel), pp. 98–125. Berlin & New York: Springer.
- Franceschini, N. 1984 Chromatic organization and sexual dimorphism of the fly, retinal mosaic. In *Photoreceptors* (ed. A. Borsellino & L. Cervetto), pp. 319–350. Plenum Publ. Corp.
- Franceschini, N. 1985 Early processing of colour and motion in a mosaic visual system. *Neurosci. Res.* (Suppl.) **2**, 17–49.
- Franceschini, N. 1992 Sequence discriminating neural network in the eye of the fly. In *Analysis and modeling of neural systems* (ed. F. H. Eckman), pp. 189–197. Boston: Kluwer Acad. Publ.
- Franceschini, N., Blanes, C. & Oufar, L. 1985 Appareil de mesure passif et sans contact de la vitesse d'un objet. Patent ANVAR (France) No. 51549, Paris.
- Franceschini, N., Chagneux, R., Kirschfeld, K. & Mücke, A. 1991 Binocular vergence eye movements in flies. In *Synapse, transmission, modulation* (ed. N. Elsner & H. Penzlin), p. 276. Stuttgart: Thieme.
- Franceschini, N., Hardie, R.C., Ribi, W. & Kirschfeld, K. 1981b Sexual dimorphism in a photoreceptor. *Nature, Lond.* **291**, 241–244.
- Franceschini, N., Kirschfeld, K. & Minke, B. 1981a Fluorescence of photoreceptor cells observed in vivo. *Science, Wash.* **213**, 1264–1267.
- Franceschini, N., Pichon, J.M. & Blanes, C. 1991 Real time visuo-motor control: from flies to robots. *IEEE Proc. Intern. Cong. Advanced Robotics, Pisa*, pp. 931–935.
- Franceschini, N., Riehle, A. & Le Nestour, A. 1989 Directionally selective motion detection by insect neurons. In *Facets of vision* (ed. D. G. Stavenga & R. Hardie), pp. 360–390. Berlin & New York: Springer.
- Gibson, J.J. 1958 Visually controlled locomotion and visual orientation in animals. *Brit. J. Psychol.* **49**, 182–194.
- Götz, K.G. 1968 Flight control in *Drosophila* by visual perception of motion. *Kybernetik* **4**, 199–208.
- Götz, K.G. 1972 Principles of optomotor reactions in insects. *Bibl. Ophthalmol.* **82**, 251–259.
- Götz, K.G. 1983 Bewegungssehen und Flugsteuerung bei der Fliege *Drosophila*. In *BIONA report 2* (ed. W. Nachtigall), pp. 21–34. Stuttgart: Fischer.
- Goodale, M.A. & Milner, A.D. 1992 Separate visual pathways for perception and action. *TINS* **15**, 20–25.
- Hardie, R.C. 1986 The photoreceptor array of the dipteran retina. *TINS* **9**, 419–423.
- Hausen, K. 1976 Functional characterization and anatomical identification of motion sensitive neurons in the lobula plate of the blowfly *Calliphora erythrocephala*. *Z. Naturforsch.* **31c**, 629–633.
- Hausen, K. & Egelhaaf, M. 1989 Neural mechanisms of visual course control in insects. In *Facets of vision* (ed. D. G. Stavenga & R. C. Hardie), Chap. 18, pp. 391–424. Berlin: Springer.
- Hausen, K. & Strausfeld, N.J. 1980 Sexually dimorphic interneuron arrangements in the fly visual system. *Proc. R. Soc. Lond. B* **208**, 57–71.
- Heide, G. 1983 Neural mechanisms of flight control in *Diptera*. In *BIONA report 2* (ed. W. Nachtigall), pp. 34–52. Stuttgart: Fischer.
- Helmholtz, von H. 1867 *Handbuch der physiologischen optik*. Leipzig: Voss. (Translated by Southall, J.P.C. (ed.) 1925 *Helmholtz's treatise on physiological optics*, Reprinted edition 1962. London: Dover Publications.)
- Hengstenberg, R. 1991 Gaze control in the blowfly *Calliphora*: a multisensory, two-stage integration process. *Sem. Neurosci.* **3**, 19–29.
- Horridge, G.A. 1987 The evolution of visual processing and the construction of seeing systems. *Proc. R. Soc. Lond. B* **230**, 279–292.
- Horridge, G.A., Scholes, J.H., Shaw, S. & Tunstall, J. 1965 Extracellular recording from single neurons in the optic lobe and brain of the locust. In *The Physiology of the insect central nervous system* (ed. J. E. Treherne & W. L. Beament), pp. 165–202. New-York: Academic Press.
- Howard, J., Blakeslee, B. & Laughlin, S. 1987 The intracellular pupil mechanism and the maintenance of signal-to-noise ratios in the blowfly *Lucilia cuprina*. *Proc. R. Soc. Lond. B* **231**, 415–435.
- Hubel, D. & Wiesel, T. 1959 Receptive fields of single neurons in the cat's striate cortex. *J. Physiol., Lond.* **148**, 574–591.
- Johansson, G. (1982) Visual space perception through motion. In *Tutorials on motion perception* (ed. A. H. Wertheim, W. A. Wagenaar & H. W. Leibowitz), pp. 19–39. New-York: Plenum Press.
- Kirschfeld, K. 1972 The visual system of *Musca*: studies on optics, structure and function. In *Information processing in the visual system of arthropods* (ed. R. Wehner), pp. 61–74. Berlin: Springer.
- Kirschfeld, K. 1979 The visual system of the fly: physiological optics and functional anatomy as related to behavior. In *The neurosciences IV* (ed. F. O. Schmitt & F. G. Worden), pp. 297–310. Cambridge, Massachusetts: M.I.T. Press.
- Kirschfeld, K. & Franceschini, N. 1969 Ein Mechanismus zur Steuerung des Lichtflusses in den Rhabdomeren des Komplexauges von *Musca*. *Kybernetik* **6**, 13–22.
- Kirschner, W.H. & Srinivasan, M. 1989 Freely flying honeybees use image motion to estimate object distance. *Naturwiss.* **76**, 281–282.
- Koenderink, J.J. & van Doorn, A.J. 1976 Local structure of movement parallax in the plane. *JOSA* **66**, 717–723.
- Labhardt, T. 1988 Polarization-opponent interneurons in the insect visual system. *Nature, Lond.* **331**, 435–437.
- Land, M.F. 1975 Head movement and fly vision. In *The compound eye and vision of insects* (ed. G. A. Horridge) pp. 469–489. Oxford: Clarendon.
- Land, M.F. & Collett, T.S. 1974 Chasing behaviour of houseflies (*Fannia canicularis*). *J. comp. Physiol.* **89**, 331–357.

- Laughlin, S. 1989 Coding efficiency and design in visual processing. In *Facets of vision* (ed. D. G. Stavenga & R. C. Hardie), Chap. 11, pp. 213–234. Berlin: Springer.
- Lee, D.N. 1974 Visual information during locomotion. In *Perception: Essays in honor of J. J. Gibson* (ed. R. B. MacLeod & H. Pick), pp. 250–267. Ithaca: Cornell University Press.
- Lehrer, M., Srinivasan, M.V., Zhang, S.W. & Horridge, G.A. 1988 Motion cues provide the bee's visual world with a third dimension. *Nature, Lond.* **332**, 356–357.
- Lettvin, J.Y., Maturana, H.R., McCulloch, W.S. & Pitts, W.H. 1959 What the frog's eye tells the frog's brain. *P.I.R.E. New York* **47**, 1940–1951.
- Longuet-Higgins, H.C. & Prazdny, K. 1980 The interpretation of a moving retinal image. *Proc. R. Soc. Lond. B* **208**, 385–397.
- Maes, P. 1991 Designing autonomous agents: theory and practice from biology to engineering and back. Cambridge, Massachusetts: M.I.T. Press.
- Milde, J.J. & Strausfeld, N.J. 1986 Visuo-motor pathways in arthropods: giant motion-sensitive neurons connect compound eyes directly to neck-muscles in blowflies (*Calliphora erythrocephala*). *Naturwissenschaften* **73**, 151–154.
- Nachtigall, W. & Wilson, D.M. 1967 Neuro-muscular control of dipteran flight. *J. exp. Biol.* **47**, 77–97.
- Nachtigall, W. & Roth, W. 1983 Correlations between stationary measurable parameters of wing movement and aerodynamic force production in the blowfly (*Calliphora vicina*). *J. comp. Physiol.* **150**, 251–260.
- Noborio, H., Wazumi, S., Fukuda, S. & Arimoto, S. 1989 A potential approach for a point mobile robot on an implicit potential field without the generation of local minima. *IEEE/RSJ Intern. worksh. IROS*, pp. 70–77.
- Pérez, J. 1911 Sur quelques particularités curieuses du rapprochement des sexes chez certains diptères. *Bull. scient. Fr. Belg.* T.45, 1–14.
- Pichon, J.M., Blanes, C. & Franceschini, N. 1989 Visual guidance of a mobile robot equipped with a network of self-motion sensors. In *Mobile Robots IV* (ed. W. J. Wolfe & W. H. Chun) (*Proc. S.P.I.E.* **1195**), pp. 44–53.
- Prazny, K. 1980 Egomotion and relative depth map from optic flow. *Biol. Cybern.* **57**, 1–9.
- Reichardt, W., Poggio, T. 1976 Visual control of orientation behaviour in the fly. Part I, A quantitative analysis. *Q. Rev. Biophys.* **9**, 311–375.
- Riehle, A. & Franceschini, N. 1984 Motion detection in flies: parametric control over ON-OFF pathways. *Expl Brain Res.* **54**, 390–394.
- Rossel, S. 1989 Polarization sensitivity in compound eyes. In *Facets of vision* (ed. D. G. Stavenga & R. C. Hardie), Chap. 15, pp. 298–316. Berlin: Pringer.
- Strausfeld, N.J. 1976 *Atlas of an insect brain*. Berlin: Springer.
- Strausfeld, N.J. 1989 Beneath the compound eye: neuro-anatomical analysis and physiological correlates in the study on insect vision. In *Facets of Vision* (ed. D. G. Stavenga & R. C. Hardie), Chap. 16, pp. 317–359. Berlin: Springer.
- Strausfeld, N.J. & Lee, J.K. 1991 Neural basis for parallel visual processing in the fly. *Vis. Neurosci.* **7**, 13–33.
- Warren, W.H. 1990 The perception-action coupling. In *Sensory-motor organization and development in infancy and early childhood* (ed. H. Bloch & B. I. Bertenthal), pp. 23–37. Holland: Kluwer.
- Warren, R. & Wertheim, A.H. 1990 *Perception and control of self-motion*. Hillsdale: L. Erlbaum Ass.
- Waterman, T.H., Wiersma, G. & Bush, B.M.H. 1964 Afferent visual responses in the optic nerve of the crab *Podophthalmus*. *J. cell. comp. Physiol.* **63**, 135–155.
- Wehner, R. 1981 Spatial vision in arthropods. in *Hdbk of Sensory Physiology*, VII/6c (ed. H. Autrum), pp. 288–616. Berlin: Springer.
- Wehrhahn, C. 1979 Sex-specific differences in the chasing behaviour of houseflies (*Musca*). *Biol. Cybern.* **32**, 239–241.
- Weiskrantz, L. 1990 Outlooks for blindsight: explicit methodologies for implicit processes. *Proc. R. Soc. Lond. B* **239**, 247–278.
- Whiteside, T.C.D. & Samuel, G.D. 1970 Blur zone. *Nature, Lond.* **225**, 94–95.
- Zanker, J.M. 1990 The wing beat of *Drosophila melanogaster*. III. Control *Phil. Trans. R. Soc. Lond. B* **327**, 43–63.

Discussion

J. M. BRADY (*Department of Engineering Science, University of Oxford, U.K.*). What assumptions is Dr Franceschini making about the visual characteristics of the environment his robot operates in? Does he, for example, ensure that the obstacles are clearly distinguishable from the background and from each other by high contrast boundaries?

N. FRANCESCHINI. Our experimental robot is a terrestrial creature adapted to a flat world. It is designed to operate in a simplified environment in which objects are textured with vertical stripes having random widths (in the range 5 cm to 25 cm) and random contrast (in the range 0.15 to 0.75). It can, however, navigate safely in an environment composed of randomly arranged posts as long as these contrast strongly enough with the background. The retinal front-end is designed to operate in an environment where the illuminance can vary by up to two decades.

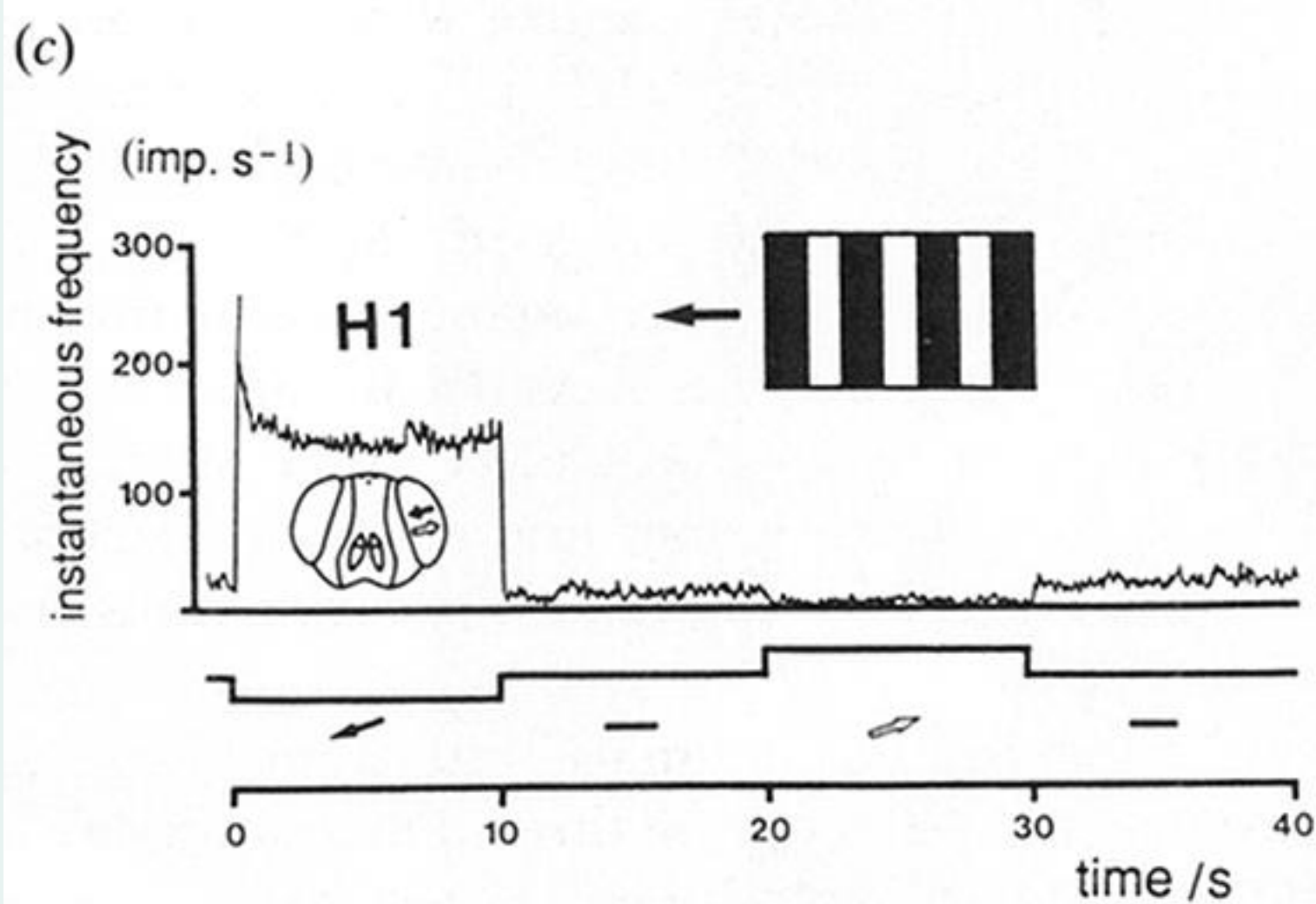
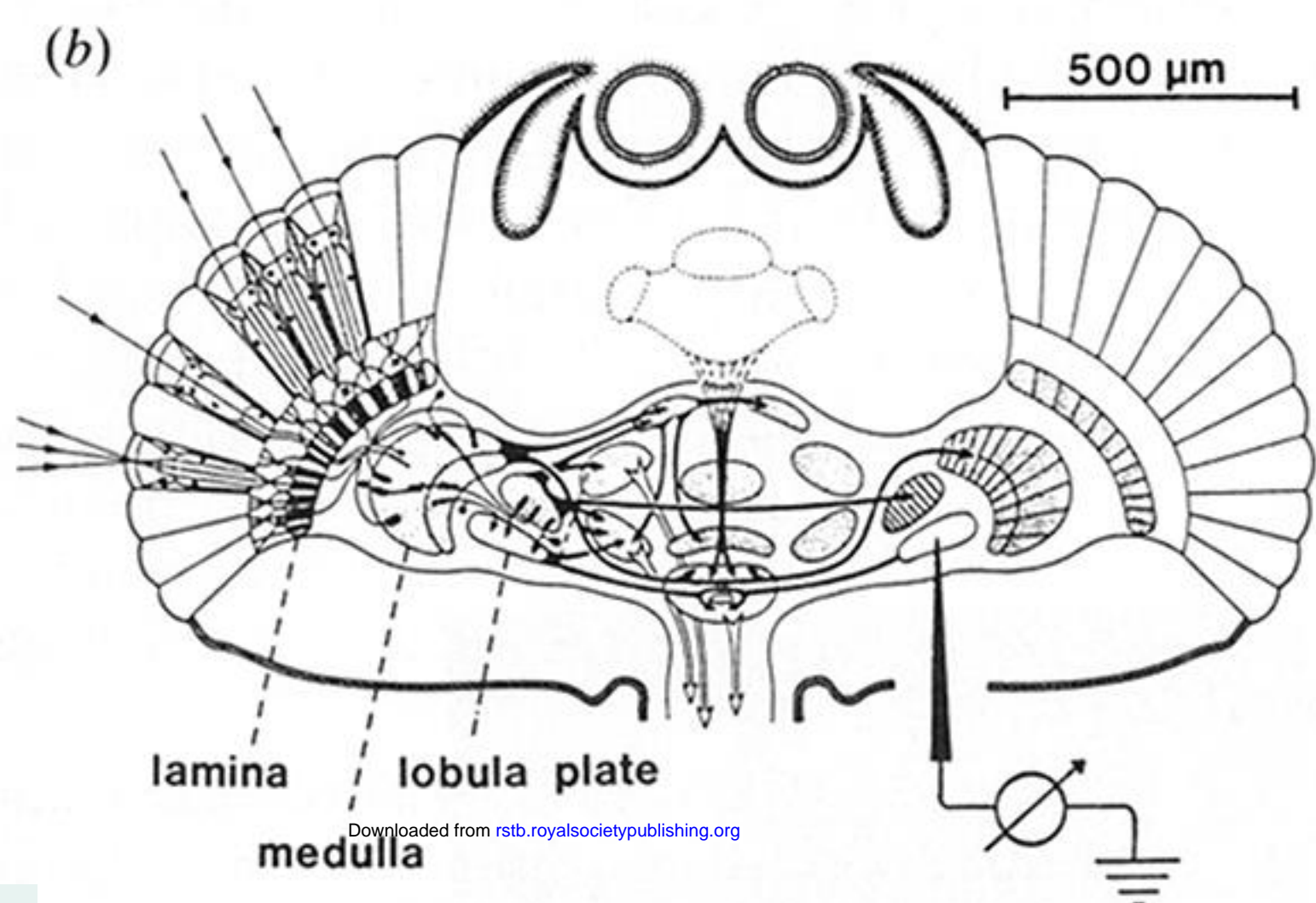
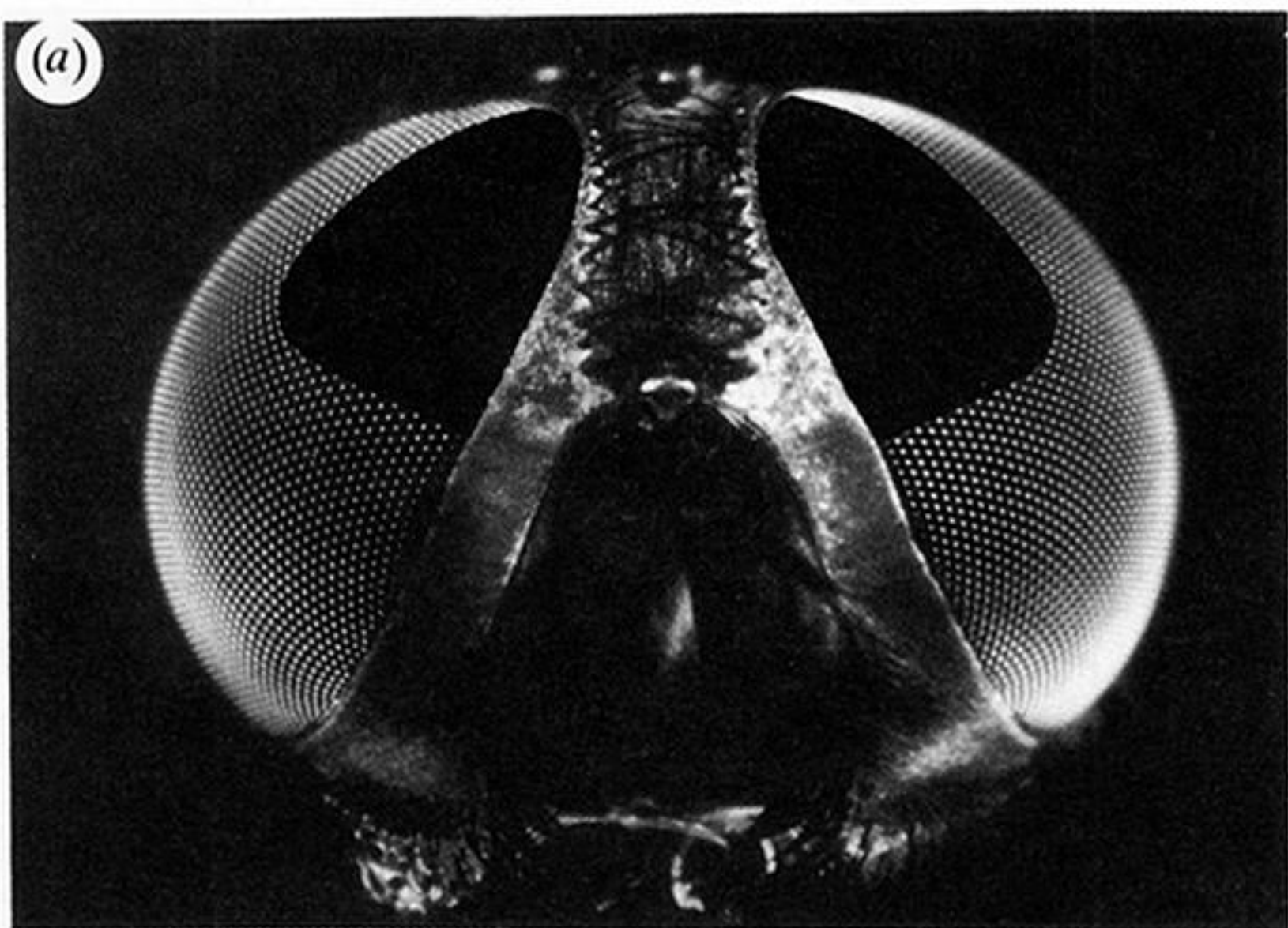


Figure 1. (a) Head of a male housefly observed with a Lieberkühn microscope. The shaded area delineates approximately the 'love spot', i.e. the upward looking region of the eye which is invested by male-specific photoreceptor cells that are likely to be involved in female chasing (after Franceschini 1984). (b) Schematic horizontal section through the head of a fly and principle of microelectrode recording from the motion sensitive neurons of the lobula plate, which play an essential role in visuomotor course control (after Kirschfeld 1979). (c) Response of the motion sensitive H1-neuron of the lobula plate to horizontal motion of a striped pattern presented to the ipsilateral eye in the preferred (back to front) and non-preferred (front to back) directions (after Riehle & Franceschini 1984).

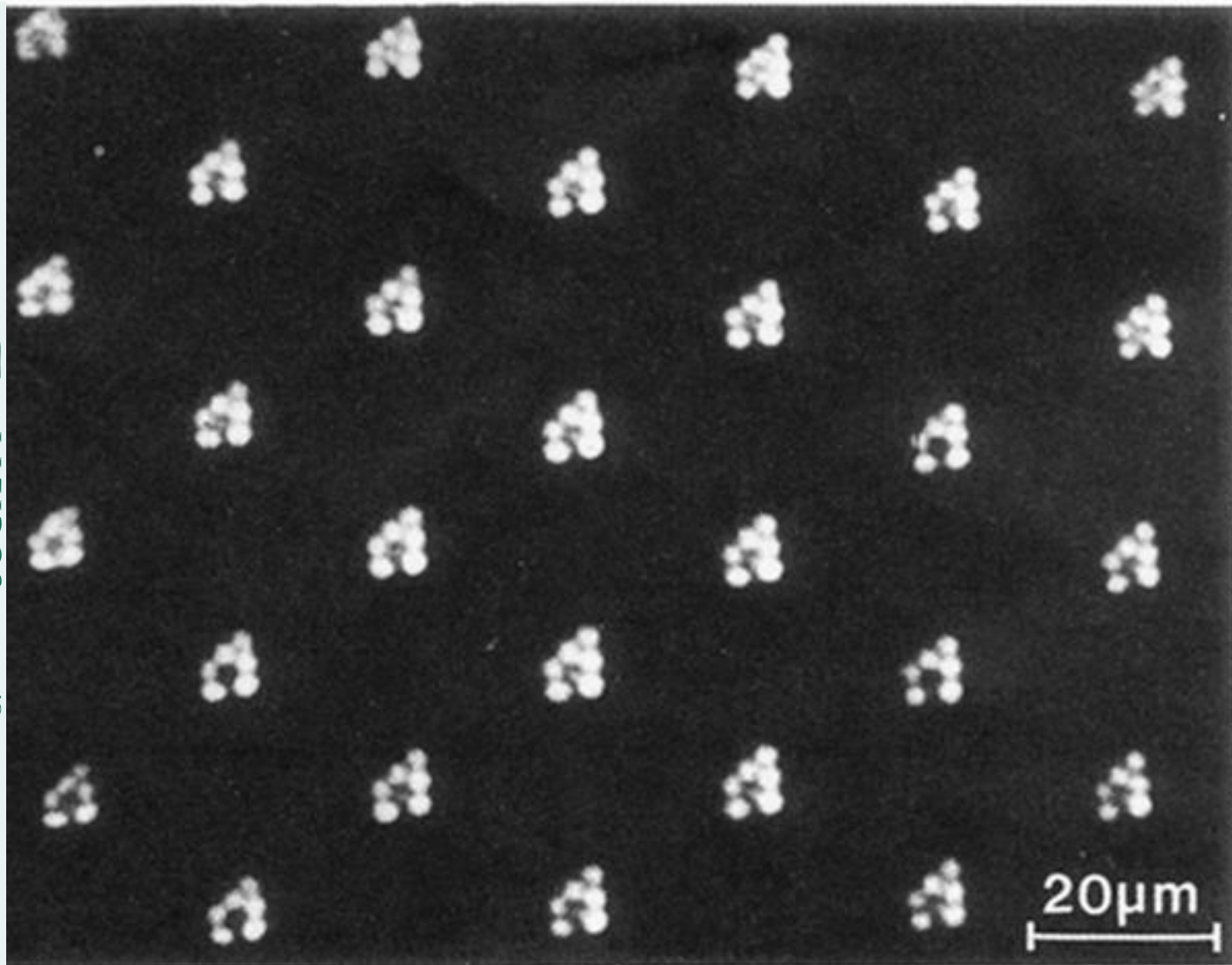
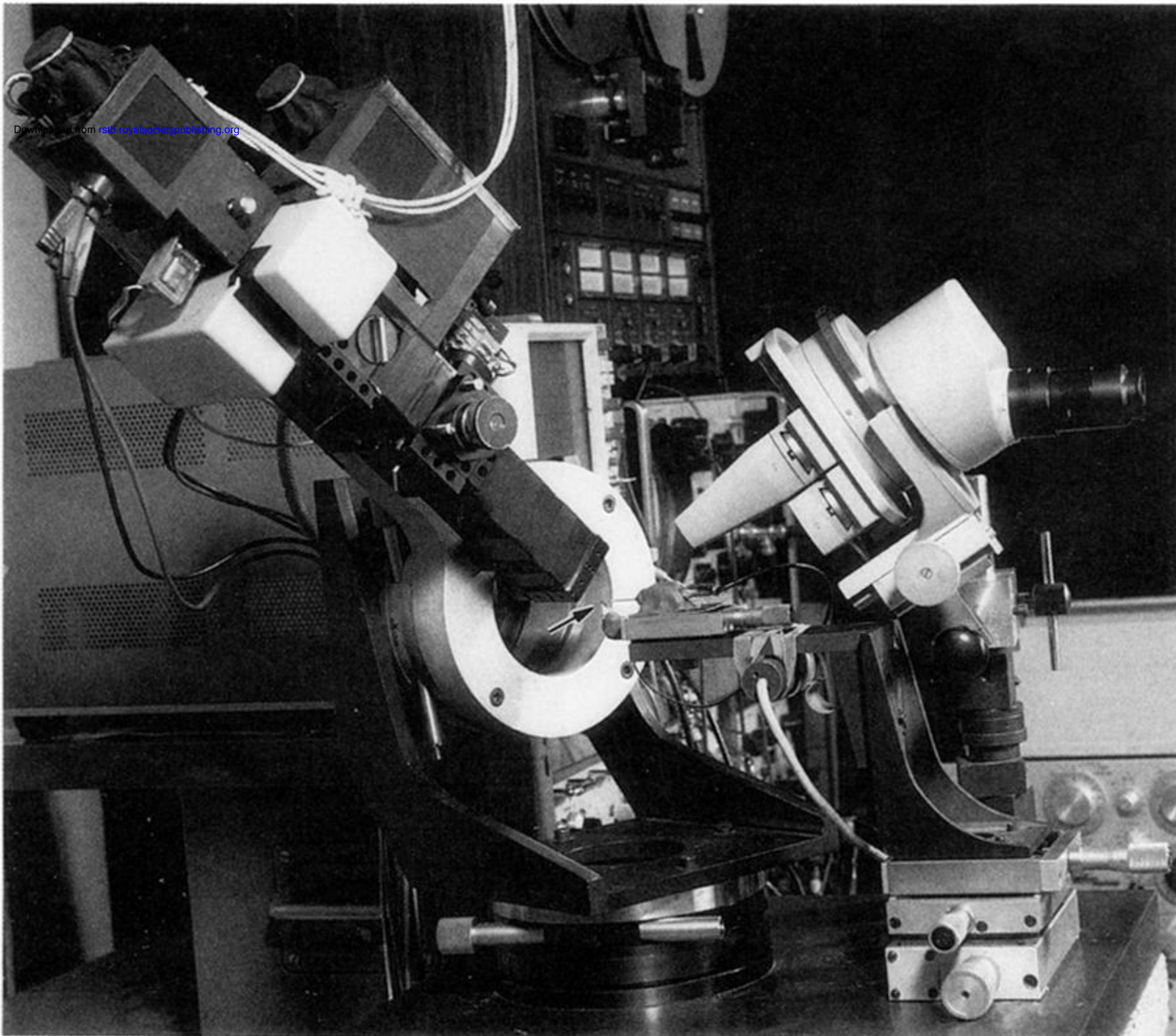


Figure 2 Photoreceptor mosaic in the compound eye of the housefly observed *in vivo* under epi-fluorescence microscopy (the corneal facets were 'optically neutralized' with a drop of water). A group of seven micrometer-sized photoreceptors (for their numbering R1–7 refer to figure 4, inset) can be seen here behind each facet lenslet. The central cell (R7) of each group usually does not display the same fluorescence colour as its six neighbours (R1–6), due to its specific visual pigments. An 8th receptor cell (R8, not seen here) lies in the prolongation of R7, with yet another spectral sensitivity. Only about 1% of the fly retinal mosaic is visible here (after Franceschini 1985).



Downloaded from rspb.royalsocietypublishing.org

Figure 3. Triple-beam incident light 'microscope-telescope' (left) pointing at the fly's eye (arrow). This instrument was used to investigate the basic neuronal mechanism underlying directional sensitivity in a motion detecting neuron. It can deliver a sequence of $1\text{ }\mu\text{m}$ spots to two different photoreceptor cells within a single facet in association with microelectrode recording from single, identifiable neurons, such as H1, in the lobula plate (cf. figure 2, c).

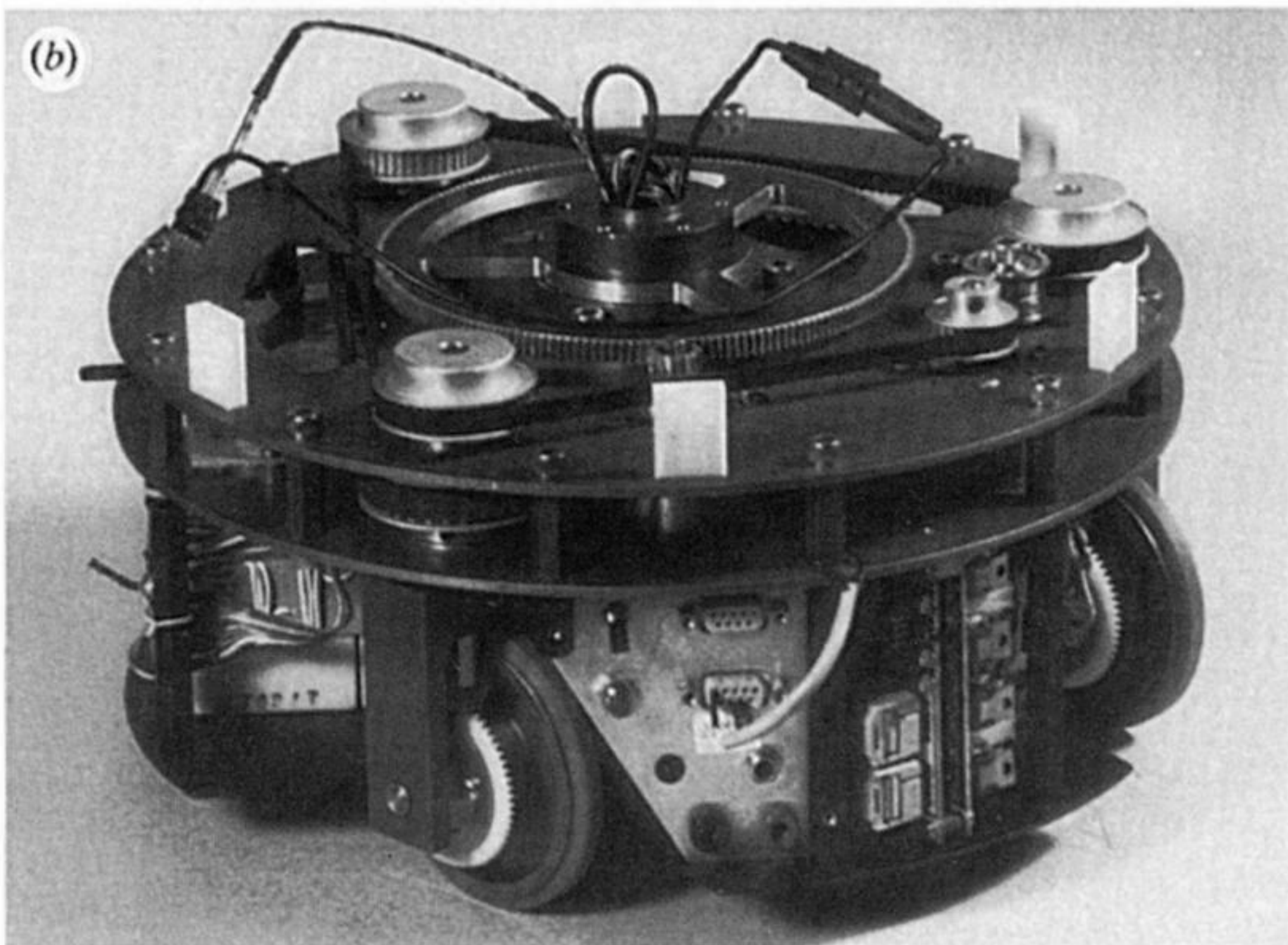
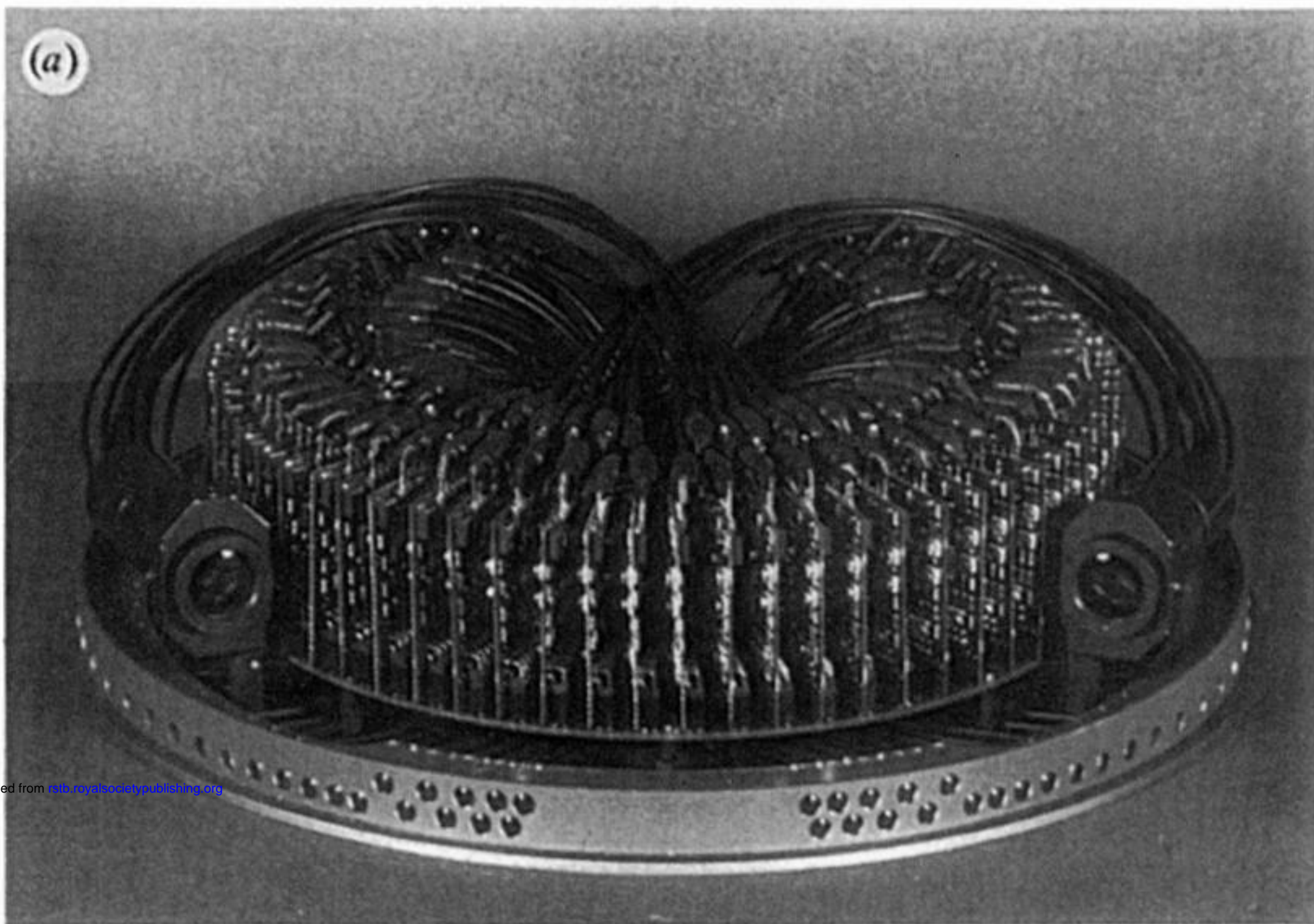


Figure 11. (a) Compound eye with facets, 'rhabdomeres', photosensors and elementary motion detectors (EMDs) copied from those of the housefly. Despite its small number of pixels (118), this artificial visual system is able to control the steering of the mobile platform shown in (b). The creature can slalom amidst a field of obstacles (posts) at 50 cm s^{-1} .