Visual control of navigation in insects and its relevance for robotics

Mandyam V Srinivasan[1,2]

Flying insects display remarkable agility, despite their diminutive eyes and brains. This review describes our growing understanding of how these creatures use visual information to stabilize flight, avoid collisions with objects, regulate flight speed, detect and intercept other flying insects such as mates or prey, navigate to a distant food source, and orchestrate flawless landings. It also outlines the ways in which these insights are now being used to develop novel, biologically inspired strategies for the guidance of autonomous, airborne vehicles.

Addresses
[1] Queensland Brain Institute and School of Information Technology and Electrical Engineering, University of Queensland, St. Lucia, QLD 4072, Australia
[2] ARC Center of Excellence in Vision Science, Australia

Corresponding author: Srinivasan, Mandyam V
(m.srinivasasan@uq.edu.au)

Introduction

A glance at a fly evading a fly-swatter, a dragonfly catching an insect on the wing, or a honeybee returning home unerringly after a 10-kilometer search for food, would convince even the most hard-nosed skeptic that insects possess extraordinary co-ordination and surprisingly accurate navigation. Clearly, in insects, Nature has evolved vision and navigation systems that are scarcely compromised because of their diminutive size. Indeed, it would seem that the constraints on size and weight have forced these creatures to evolve eye designs and nervous systems that perform the required computations using strategies that are simple, elegant, and often unexpectedly novel.

The compound eyes of insects are obviously very different in appearance from the so-called 'simple' eyes of vertebrates. While a vertebrate eye is composed of a single lens that focuses light from the outside world on to a sheet of photoreceptive neurons in the retina – rather like a camera – the compound eye of an insect comprises a large number of 'little eyes', so-called 'ommatidia', arranged on an approximately spherical surface (e.g. [1,2]). Each ommatidium comprises a small lens, which captures light coming in from a small patch of the environment, typically a few degrees in diameter, and focuses it onto a small group of 8 or 9 photoreceptors. In a honeybee, the two compound eyes together carry an array of 11,000 ommatidia *in toto*, enabling the insect to command a nearly all-round view of the environment in which each ommatidium collects information about the intensity, colour (and possibly other properties) of light arriving from a small patch of the environment that is about $2°$ in diameter (ref [3]). Thus, one might say that the compound eyes capture and represent the world as a panoramic, pointillistic image, with an optical system that is difficult to match, in terms of size and weight, using a vertebrate-style eye design.

While compound eyes confer distinct advantages, they also impose challenges. Unlike vertebrates, insects have immobile eyes with fixed-focus optics. Therefore, they cannot infer the distance of an object from the extent to which the directions of gaze must converge to view the object, or by monitoring the refractive power that is required to bring the image of the object into focus on the retina. Furthermore, compared with human eyes, the eyes of insects are positioned much closer together, and possess inferior spatial acuity. Therefore, even if an insect possessed the neural apparatus required for binocular stereopsis, such a mechanism would be relatively imprecise and restricted to measuring ranges of only a few centimetres [4]. Not surprisingly, insects have evolved alternative visual strategies for guiding locomotion and for 'seeing' the world in three dimensions. Many of these strategies rely on using cues derived from the image motion that the animal experiences in its eyes when it moves in its environment. Here we review the ways in which insects exploit these motion cues to glean information about the environment, and to fly safely through it.

Visual guidance of flight
Stabilization of flight direction and attitude

If an insect flying along a straight line is blown to the left by a gust of wind, the image on its frontal retina moves to the right. This causes the flight motor system to generate a corrective turning response – the so-called 'optomotor response' – that brings the insect back on course. By evaluating the direction of motion of the panoramic image of the world in the eye, the flying insect is able to stabilize unwanted rotations not only in yaw, but also in roll and pitch. Indeed, the lobula plate, which represents the fourth stage of processing in the visual pathway of the fly, carries a

number of large-field, motion sensitive neurons that are selectively responsive to rotations of the head about the yaw, pitch and roll axes, as well as other axes [2,5●●,6,7,8●●]. Thus, the ensemble of responses across these neurons provides accurate information about the direction of head rotation, and drives downstream motorneurons, involved in flight control, to generate appropriate corrective rotations of the head and body.

### Avoiding obstacles and negotiating narrow gaps

When an insect flies in a straight line, the image of a given point in the scene will move in the eye at a speed (angular speed, measured in degrees per second) that is proportional to the speed of flight and inversely proportional to the distance to the point (Figure 1a). Thus, distant objects in the scene will induce low image speeds, whereas nearby objects will generate rapid image motion. Indeed, experiments using moving stimuli reveal that honeybees tend to avoid, or steer away from, regions of the visual field that experience rapid image motion [3], suggesting that this is a strategy for sensing dangerously close objects and avoiding collisions with them. When a bee flies through a narrow passage, such as a tunnel, it positions itself such that both eyes experience approximately the same image velocity (Figure 1b). This ensures that the two walls are at the same distance from the bee, enabling a collision-free flight through the middle of the tunnel [3,9,10]. That bees indeed use this strategy has been confirmed by moving the visual texture on one of the walls, either in or against the direction of the bee's

flight. The bees then no longer fly through the middle of the tunnel, but along a new axis positioned such that the two eyes again experience equal image velocities [3]. When an object is approached, its image expands in the eye and the rate of expansion increases as the distance to the object decreases. In the fruit fly, image expansion appears to be a potential cue for detecting nearby objects and avoiding collisions [11].

Regulating flight speed

Experiments with fruit flies and honeybees have revealed that the speed of flight is monitored and regulated by measuring and holding constant the average image velocity that is experienced the two eyes. Thus, while passing through a tunnel (as in Figure 1b), bees fly at a speed such that the speeds of the images in the lateral fields of view are held constant, at about $300°/s$ [3]. However, they fly faster when the patterns on the two walls are moved in the same direction as the bee's flight, and slower when the patterns are moved in the opposite direction, always maintaining the lateral image velocity at a value close to $300°/s$ [12]. Fruit flies appear to use the same visual cue to regulate their flight speed [13]. A consequence of using image speed to control the speed of flight is that the flight speed would automatically be reduced when negotiating a narrow passage, and increased when flying in a wide-open environment. This prediction has been confirmed by filming bees flying through a tapered tunnel (Figure 1c), as well as in tunnels of different widths [14,15]. Thus, insects appear to have a simple, elegant strategy for automatically reducing

Figure 1

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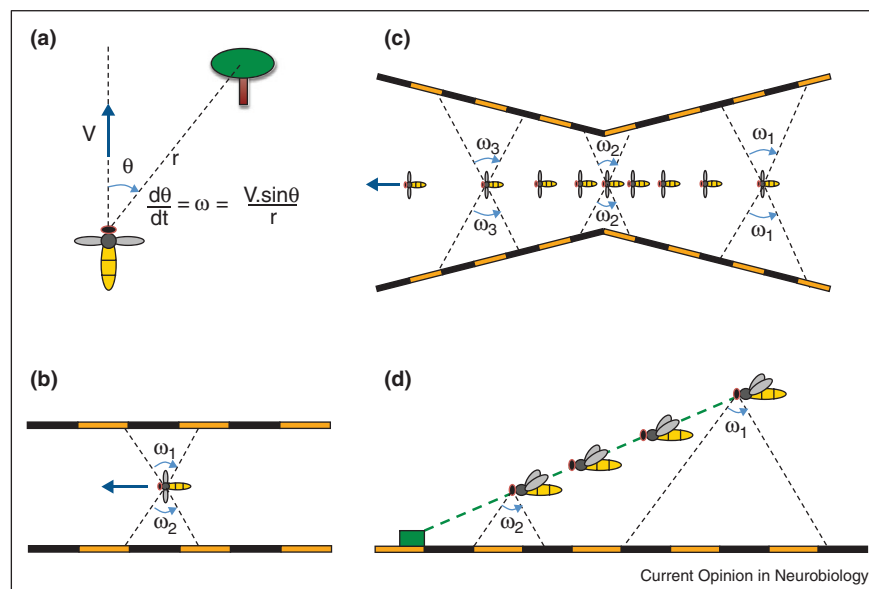
(a) Illustration of how the angular velocity (ω) of the image of an object in the eye depends upon an insect's flight speed (V), as well as the range (r) and bearing (θ) of the object. **(b)** Narrow passages are negotiated by flying a trajectory such that both eyes experience the same image velocity in the lateral fields of view ($\omega_1 = \omega_2$). **(c)** Flight speed is controlled by holding the image velocities in the lateral fields of view constant throughout the flight ($\omega_1 = \omega_2 = \omega$). **(d)** Smooth landings are executed by decreasing flight speed progressively such that the image velocity in the ventral field of view is held constant ($\omega_1 = \omega_2$).

the speed of flight to lower and safer levels when flying through densely cluttered environments. Recent work [15] suggests that the measurement of image velocity includes regions in the fronto-lateral part visual field, which introduces an 'anticipatory' component into the regulation of flight speed.

Regulating flight height

When an insect flies at a fixed speed, the speed of image motion in the ventral field of view provides an indication of the height of flight above the ground – the higher the image speed, the lower the altitude. In principle, this cue can be used to control the altitude of flight. Observations of bees flying in a tunnel in which the image speed generated by the floor is artificially manipulated, suggest that bees indeed use this cue [16]. Movement of the floor pattern in the direction of flight causes the bees to lower their altitude, while maintaining the same air speed [17]. In this study the bees maintained a ventral image velocity of about 265°/s, a value not very different from that used to regulate flight speed (ca. 300°/s, see above). Therefore, it is possible that both the speed and the height of flight are regulated by the same kind of movement-detecting system. Under certain conditions, flight speed may be regulated by maintaining a prescribed image velocity in the lateral fields of view, and height by maintaining a prescribed image velocity in the ventral field [17]. When flying through relatively wide tunnels, honeybees no longer fly down the middle, but closer to one wall, at a constant distance from it [9]. This 'wall-following' strategy appears to be achieved by holding constant the speed of the image of the closer wall, as when regulating height. In *Drosphila*, there is evidence that height regulation is achieved by sensing expansions or contractions of the image of the ground to detect and respond to decreases or increases of height [18••].

Orchestrating smooth landings

As every aircraft pilot knows, performing a safe landing is not an easy task. How do insects achieve this? Video films of bees performing grazing landings on visually textured surfaces have revealed that the speed of flight is progressively reduced as the surface is approached, in such a way as to hold constant the angular speed of the image of the ground in the eye [19]. This strategy automatically ensures that the speed of flight decreases as the ground is approached, leading to a perfectly smooth touchdown (Figure 1d). The simplicity and elegance of this landing strategy lies in the fact that it does not require knowledge of the instantaneous height above the ground, or the instantaneous speed of flight – all that is required is the measurement (and regulation) of the speed of the image in the eye. A mathematical model of this landing strategy successfully predicts all of the observed characteristics of the landing trajectories [19]. During landing, bees maintain image velocities of about 500°/s in the ventral field of view [19].

The importance of measuring and regulating image velocity

The observation that bees strive to balance the image velocities in the two eyes while negotiating narrow gaps, as well as maintain a constant image velocity while regulating flight speed, controlling flight height and guiding landing, suggests that measuring and controlling the speed of the image in the eye may be a fundamental and overarching principle of visual guidance in insects. That the regulated image speed is in the vicinity of 300–500°/s in all of these behaviours suggests the involvement of the same, or very similar movement-detecting circuitry in each case, and a parsimonious, yet effective utilization of the restricted computational capacity in these miniature brains to deal with a number of tasks. Interneurons in the ventral nerve cord of honeybees, which respond to large field motion stimuli [20], and other neurons in the optic lobe that appear to encode image velocity [21] may be components of the neural circuits that are involved in control of the speed and height of flight, the guidance of flight through narrow passages, and landing.

Gauging distance travelled

Insects that make repeated foraging excursions and return home safely each time – the so-called 'central place foragers' – must possess competent navigation systems that include a reliable method of estimating the distances that they have travelled. A reliable 'odometer' would help them navigate back home, as well as return to a food source if necessary. Behavioural experiments have revealed that bees estimate distance flown by summing (integrating) the optic flow, over time, that is generated by the movement of the image of the environment in their eyes as they fly from the hive to the food source (ref [3]). The advantages and disadvantages of measuring distance flown by using visual signals in this way – rather than by measuring energy consumption or time of flight, or by counting wing beats, for example – are reviewed in [3]. Desert ants, on the contrary, assess distance travelled by monitoring the motion of the legs, in a process analogous to counting footsteps [22••].

Using the sky as a celestial compass

If a foraging insect is to find its way back home safely, it needs to know not only how far it has travelled from home, but also the direction in which it has moved. Bees and desert ants estimate their heading direction and set their course by using the sun as a compass (ref [23]). When the sun is hidden by a cloud, but a patch of open sky is still visible, then the pattern of polarized light that is created in the sky by the sun, and is visible in this patch, is used as a compass in lieu of the sun [24,25]. As the sun moves across the sky during the course of the day, the polarization pattern moves with it, and can be used to infer the position of the sun, even when it is obscured by a cloud. The sun and the pattern of polarized light that it creates in the sky constitute a 'celestial compass' [26]. Behavioural

experiments have revealed that, in using the celestial compass to set a course to a known food location, bees and desert ants take into account the sun's movement across the sky during the day. Evidently, this is done by using information from an internal clock to continuously re-calibrate the compass [23] [27]. In many insects, including bees, ants, crickets and locusts, the ommatidia in the uppermost dorsal parts of the compound eyes (the so-called dorsal rim area) carry photoreceptors that are highly sensitive to the orientation of polarized light [26,28,29]. Each photoreceptor responds maximally when the light is polarized in a particular orientation (the 'preferred' orien-tation), and minimally when it is polarized in the orthog-onal orientation. Information from these polarization-sensitive photoreceptors is fed to interneurons in the medulla and eventually to the central complex region of the brain. Recordings from the medulla reveal three classes of polarization-sensitive (PS) neurons, with broad orientation tuning curves and preferred orientations sep-arated by about 120° [28]. Recordings from the central complex, on the contrary, reveal PS neurons that are individually much more sharply tuned. Their preferred directions are distributed more or less uniformly in all compass directions [30••]. Recent work has revealed that the preferred orientations of these neurons change during the course of the day, indicating that they are being continually recalibrated by signals from an internal cir-cadian clock to compensate for the movement of the polarization pattern across the sky [31•].

Tracking and pursuing other flying objects

There is, of course, more to the life of a flying insect than just avoiding collisions with obstacles, executing flawless landings, or even finding a food source. For many insects, the ability to detect and pursue airborne mates or prey, or to ward off intruders, is crucial to survival of the individual as well as the species. In two pioneering studies, Land and Collett [32••,33] obtained high-speed films of male flies pursuing other flies, and developed a mathematical model to characterize this behaviour. They found that the chasing fly tracks the leading fly by means of a control system in which the turning (yaw) rate of the chaser is proportional to (i) the angle between the pursuer's long axis and the angular bearing of the target (the so-called 'error angle') and (ii) the rate of change of this error angle (Figure 2a). This feedback control system causes the pursuer to (almost) always point towards the target [34]. While this kind of strategy will eventually to lead to capture if the target continues to move in a straight line and the pursuer is flying faster than the target, it is not necessarily the quickest way to intercept the target. This is because, even if the target is moving in a straight line at a constant speed, the pursuer's resulting trajectory will be a curve (Figure 2b). There is evidence that hoverflies overcome

Figure 2
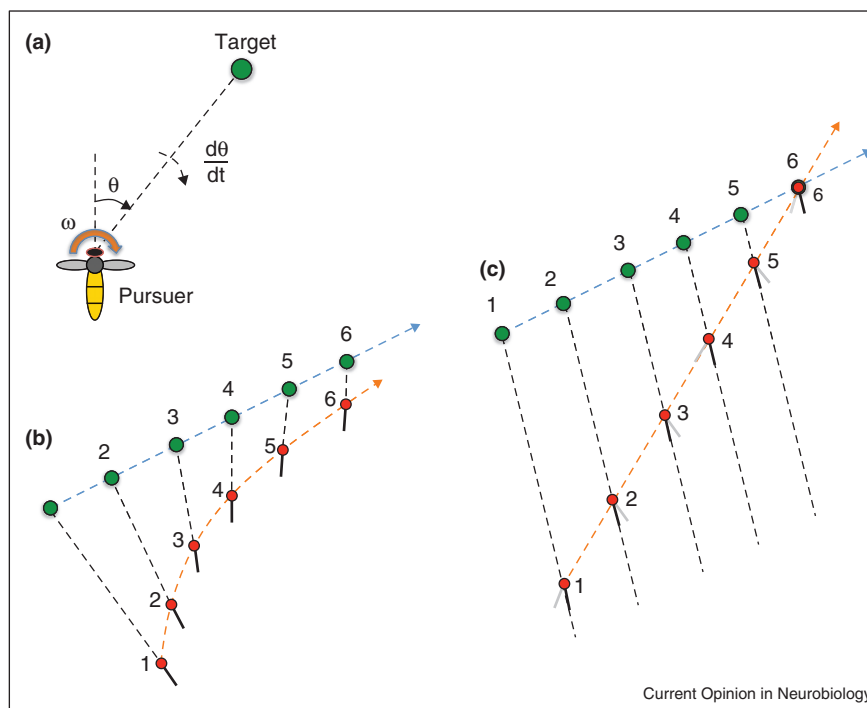
Models characterizing pursuit and interception of a moving target. **(a)** Model of pursuit in which the rate of yaw of the pursuer is proportional to the error angle (θ), and to the rate of change of the error angle (dθ/dt). **(b)** Example of a trajectory in which pursuit is steered according to the model in **(a)**. **(c)** Example of an interception strategy in which the pursuer maintains the target at a constant absolute bearing. Numbers in **(b)** and **(c)** represent successive (and corresponding) positions of the target (green) and the pursuer (red).

this problem by pre-computing a direct course of interception, based on information about the angular velocity of the image of the target in the eye at the time the target is initially sighted [35]. Dragonflies seem to use a different, and perhaps more elegant interception strategy [36••], in which they move in such a way that the absolute bearing of the target is held constant, as shown by the dashed lines in Figure 2c. If the target is moving in a straight line at a constant speed, then the pursuer's trajectory (assuming that it is also moving at a constant speed) will also be a straight line (Figure 2c), which ensures interception in the quickest possible time. Note that this strategy of interception only requires preservation of the absolute bearing of the target. The orientation of the pursuer's body during the chase does not matter, as shown by the grey lines in Figure 2c. If the target changes its direction or speed mid-stream, it will cause the pursuer to change its flight direction automatically, and set a new interception course that is optimal for the new conditions. There is an intriguing potential for application of motion-camouflage strategies in the defence arena, yet to be explored.
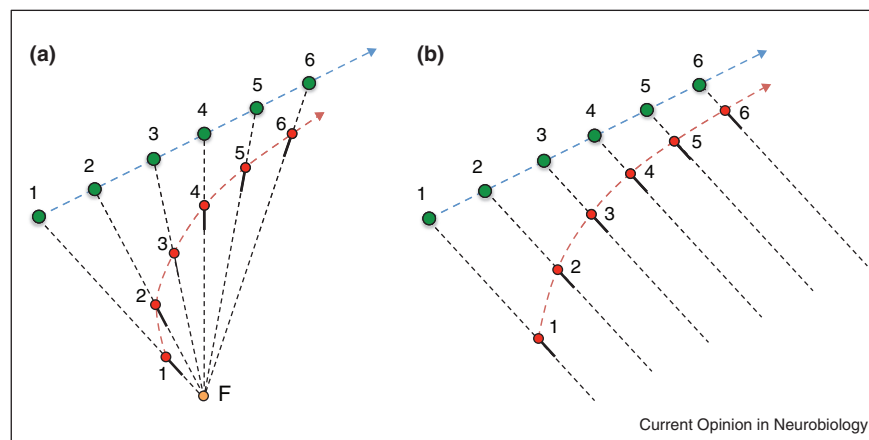
Motion camouflage

Stealth can be crucial when a predator approaches its prey. Thus, a related challenge is that of concealing one's own motion while stalking a target. Prey are likely to be constantly on the lookout for other moving objects in the environment. Let us assume that the approaching pursuer (or stalker) is far away from the prey – far enough to be characterized as a point object that produces negligible looming cues in the eyes of the prey. Then the pursuer can conceal its own movement by moving along a trajectory such that it is always on a line that connects the prey's current position with a 'virtual' fixed point (F) in the environment, as shown in Figure 3a. The pursuer will then appear as a stationary object in the eyes of the prey,

because the motion of the pursuer's image in the prey's retina would be indistinguishable from that of a *stationary* object located at the virtual point [37,38]. Hoverflies and dragonflies occasionally move along such trajectories when tracking other moving objects of interest, raising that possibility that this behaviour may indeed serve to promote camouflage. In principle, the virtual fixed point can be located anywhere in the environment. It can be a physical object, or simply a virtual location. Techniques by which motion-camouflaging trajectories can be realized are described in [37] and [38]. If the virtual fixed point is positioned at infinity, then the lines connecting this point to successive prey positions will all be parallel to each other, as shown in Figure 3b. In this case, the motion-camouflage strategy (Figure 3b) turns out to be identical to the optimum-pursuit strategy (Figure 2c). This suggests that some flying insects, such as dragonflies, are capable of not only capturing their prey in the shortest possible time, but also concealing their own motion in the process!

Visual processing for the detection of small moving objects

Detecting a small object moving in the environment is a challenging task, even for a stationary observer. But if the observer is also moving (as is usually the case), the task is much more challenging because then the image of the background is also in motion. Relative motion between the images of the object and the background does not reliably signal the presence of a moving target, because such a stimulus can also be elicited by a stationary target that is being viewed against a more distant background. Male flies have been found to possess neurons that respond selectively to small moving targets in the dorsofrontal visual field [39•,40]. These neurons are likely to play a role in detecting such targets and guiding the chase. However, the nature of the underlying processing mechanisms remains

Figure 3

Motion camouflage: Illustration of strategies by which a pursuer (red) can track a target (green) while concealing its own motion. In **(a)** the pursuer emulates a stationary object at a fixed, virtual point (F). In **(b)** the pursuer emulates an object that is infinitely far away. Numbers represent successive (and corresponding) positions of the target and the camouflaged pursuer.

to be clarified. Recently, neurons have been found in the optic lobes of dragonflies and hoverflies that respond with exquisite sensitivity to small, dark, moving targets, regardless of whether or not the surrounding background is in motion [41[••],42]. Exactly how this sensitivity and selectivity are achieved remains to be discovered, but major features appear to be a high sensitivity to differential motion, coupled with appropriate processing of spatial information to enhance the detection of small, dark targets.

Applications to robotics

In recent years there has been considerable interest in implementing some of the insights gained from the study of vision and navigation in insects to the guidance of terrestrial and aerial vehicles. The reasons for doing this are twofold. First, robotic platforms offer a means of testing rigorously, under real-world conditions, our understanding of how insects see and steer their way through the environment. Second, there is the possibility that biological inspiration will provide novel solutions to difficult and persistent problems in the design of navigation systems for autonomous vehicles.

We have seen that insects rely heavily on cues derived from optic flow to gauge the distances to various obstacles and surfaces, and to manoeuvre safely in their three-dimensional environment. From the standpoint of machine vision, the use of optic flow cues for navigation is far less demanding, computationally, than is the more classical approach of using stereo vision for this purpose, making the optic-flow-based approach attractive for implementation in small, compact, and lightweight aerial vehicles [43[••]]. The following sections outline some of the ways in which the principles of insect vision and navigation have been used for the guidance of autonomously navigating robots.

Guidance of robots along corridors

The principle by which bees fly safely through narrow passages offers a simple strategy for guiding a robot along a corridor. By balancing the speeds of the images of the two side walls, one can ensure that the robot progresses along the middle of the corridor without colliding with the walls. Furthermore, the speed of the robot can be adjusted to a safe value by holding constant the average velocity of the images of the two walls. The feasibility of this technique has been demonstrated many times over the past 15 years, in simulations (e.g. [44]) as well as in real, land-based robots (e.g. [45[••]]). References to additional studies can be found in [46] and [3].

Terrain following guidance for aircraft

Flying at a constant, low height above the ground is important when there is a need to prevent detection by enemy radar, or to perform close-up photographic exploration of terrain. If the ground speed of the aircraft is known (for example, from measurements of airspeed, or from GPS

information) then, following the example of the honeybee, the height above the ground can be computed from the optic flow that is generated by the image of the ground. This information can be used to control the aircraft's height above the ground, and to achieve terrain following. This approach is attractive because it only requires the presence of a small, inexpensive, low-resolution video camera on board. It is thus cheaper and demands a smaller payload compared to other strategies for height measurement such radar or ultrasound. This strategy of terrain following has been implemented successfully in fixed-wing [47] as well as rotary-wing aircraft [48]. References to additional studies can be found in [46] and [3].

Control of aircraft landing

We have seen that honeybees perform grazing landings by adjusting their flight speed so as to hold the image velocity of the ground constant during the approach. Autonomous landing approaches using approximations of this strategy have been achieved with fixed wing aircraft [49,50[••]]. It is difficult to implement the honeybee landing strategy exactly on a fixed-wing aircraft, because this requires the ground speed to approach arbitrarily small values (below stall speed) as the aircraft nears the ground. Consequently, a modified landing strategy has been implemented and tested, in which the throttle is cut and the elevator setting is adjusted in closed loop to hold the magnitude of the optic flow from the ground constant as the altitude drops. The result is that altitude and forward speed decrease approximately linearly with time as the ground is approached, ensuring a smooth touchdown.

Robot navigation using a polarization compass

The efficacy of using the polarized light pattern in the sky for navigation has been tested by incorporating an insect-inspired polarization compass into autonomous robots [51]. 'Sahabot', a terrestrial robot steered by a polarization compass, was put through its paces in the arid, featureless landscapes of the Saharan desert where only the sky provided visual cues as to the robot's heading. The robot used three polarization-sensitive channels, with preferred directions separated by 120°. Each channel consisted of a polarizing filter positioned over a photodetector. The signals from the three photodetectors were analysed to compute the orientation of the polarization vector in the overhead sky, and to steer the robot successfully in any prescribed direction. In addition, the heading information was combined with information from wheel-based odometry to determine, with impressive accuracy, exactly where the robot was located at any point along its journey.

Odometry a la bee vision

Visual odometry, using the honeybee-inspired principle of integrating optic flow, has been implemented successfully in a number of terrestrial robots. In one example a robot was able to traverse a corridor repeatedly, always stopping after it had travelled a fixed distance as reported by its visually

driven odometer. The error in the stopping position was less than 2% of the traverse distance [52]. In another study [53] a robot was able to use optic flow to compute all of its translations and rotations along any arbitrary route that it took from a starting point, and was able to use this information to (a) compute where it was in relation to the starting point, at all times; and (b) return successfully to the starting location – again relying solely on optic flow information, and without knowledge of or reference to any landmarks in the environment. Visual odometry based on optic flow has also been implemented successfully in large automotive vehicles, by using a downward-facing video camera to view the road surface [54].

Conclusions and outlook

It is becoming apparent that insects are surprisingly unhampered by their miniscule brains and limited processing capacity, when it comes to tasks that require intricate visuomotor co-ordination. Instead, they seem to have evolved simple, elegant and alternative solutions to deal with many of their everyday tasks. Given their small interocular separations, many insects appear to have eschewed stereo vision to rely heavily on cues derived from optic flow. We have seen that many important behaviours, such as collision avoidance, control of flight speed, landing, odometry, and the detection and tracking of moving targets, are all mediated by cues derived from the measurement of optic flow. The continuing challenges in this field are, first, to better understand the neural processing mechanisms that underlie these remarkable faculties, and second, to explore whether these insights can provide further and better inspiration for the design of autonomously navigating vehicles. An important and related area of research, which has also seen a good deal of progress in recent years, involves exploration of the roles played by landmarks and spatial memory in the context of navigation. This topic, too extensive to address here, is the subject of many reviews, for example [55], [56] and [57].

Acknowledgements

Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.conb.2011.05.020.

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