

Going Wild: Toward an Ecology of Visual Information Processing

Jochen Zeil, Norbert Boeddeker,
Jan M. Hemmi, and Wolfgang Stürzl

ARC Centre of Excellence in Vision Science
and Centre for Visual Sciences
Research School of Biological Sciences
The Australian National University
Canberra ACT 2601, Australia

WITH ALL OUR EXTENSIVE KNOWLEDGE OF SENSORY CODING, sensory-motor feedback loops, and motor control, we are still largely ignorant about what enables animals to be such successful autonomous agents. Even in arthropods with their tiny brains, we do not fully understand how behaviorally relevant information is acquired, filtered, and processed to guide behavior. This poses a fundamental challenge to neurobiology (e.g., see Pflüger and Menzel 1999): Most of what we know about the neural basis of visual processing, for instance, comes from experiments using well-defined simple patterns, such as black and white stripes or random dots, which were chosen to facilitate our interpretation of the neuronal responses. In addition, in most cases, we have no alternative but to study neurons out of context, in stripped-down organisms and in isolated or sliced-up brain preparations, in order to be able to measure their response properties.

Neurophysiological studies have revealed a wealth of information on neurons and many of their interesting properties, but these properties are not necessarily the only ones that are relevant under natural operating conditions. Nervous systems are not general information transmission and processing devices, but they have evolved to solve specific computational tasks that are relevant to the survival and the fitness of an animal in a given environment. Visual processing mechanisms are adapted to the properties of the signals they encounter under these natural situations

(e.g., see Simoncelli and Ohlshausen 2001; Burton and Laughlin 2003), as recent studies using natural visual stimuli have demonstrated (e.g., see Reinagel 2001; Felsen and Dan 2005). But in only a very few cases has it been possible to observe the activity of visual neurons in their natural habitat, even in vertebrates (but see McNaughton et al. 2006). Passaglia et al. (1997) have recorded from single sensory fibers in freely moving horseshoe crabs under water, and Egelhaaf et al. (2001) and Lewen et al. (2001) have studied the coding properties of motion-sensitive interneurons in the blowfly as the fly and the recording setup was oscillated outdoors. An alternative approach has recently been developed for both vertebrates and invertebrates in which image sequences are recorded from the perspective of an animal and replayed to visual interneurons in an experimental animal (e.g., see Kayser et al. 2004; Körding et al. 2004 in cats). From these studies, it becomes increasingly clear, as we detail below, that the activity patterns elicited by simple stimuli such as drifting gratings are qualitatively and quantitatively different from those elicited by naturalistic ones.

There is thus a need for neurobiology to “go wild” and to consider what is biologically relevant in vision across the full inventory of visual tasks, not just with respect to an isolated feature or a specific computation. In addition, the different ways in which animals move have consequences on what they see, so that behavior itself has a major role in visual information processing (e.g., see Land and Collett 1997; Eckert and Zeil 2001). A number of important questions need to be addressed, including, What information do neurons actually extract from the varying visual input stream? What are the visual signatures relevant to important events? What are the conditions and constraints under which the visual system operates and under which it has evolved? What do animals do and what are the consequences of their natural behavior for visual information processing?

In this chapter, we outline why we see “going wild” in visual neuroethology as one of the promising future avenues of neurobiology. The systematic analysis of visual environments and visual tasks should help us identify the visual information available to animals under natural conditions and allow us to study how behavior and visual information processing interact. We aim to demonstrate that invertebrates have a number of advantages as subjects for research to understand visual processing under natural conditions. Not the least important of these is that their active space is often limited, so that their behavior can be monitored in great spatial and temporal detail. We review examples of invertebrate systems where one can monitor or manipulate behavior on a moment-to-moment basis in the natural setting together with what animals actually see (as in fiddler crabs) or where one can record natural

activity in great detail and reconstruct what they have seen (as in flies and wasps). We point out in what way we believe “going wild” has provided crucial insights into the ecology of visual information processing.

FLY VISUAL INTERNEURONS AND NATURAL OPTIC FLOW

Optic flow processing in the fly is carried out by about 40–60 so-called tangential cells in the third visual neuropil, the lobula, which all have relatively large receptive fields and are tuned to different patterns of optic flow (for reviews, see Hausen and Egelhaaf 1989; Krapp 2000; Borst and Haag 2002; Egelhaaf et al. 2002). Tangential cells respond in a directionally selective manner to visual motion, as it occurs during rotations about the three body axes, and therefore are considered to form the neuronal substrate for compensatory optomotor reflexes that maintain stability during flight (see Chapter 5).

The conclusions that we reach about the coding properties of these visual interneurons depend, however, on the details of the stimuli used to investigate them, and these conclusions had to be revised radically after it became possible to investigate how the neurons respond to natural scenes and optic flow generated by the insects themselves in free flight. The reconstruction of naturalistic optic flow was first done in indoor flight cages, where the visual effects of insect movements can be accurately determined and modeled, because the geometry of the environment is simple and its visual texture is known (Schilstra and van Hateren 1998). Natural habitats, however, contain objects distributed in complicated patterns in depth and across the visual field, causing natural motion signal distributions to be patchy, sparse, and unpredictable (Eckert and Zeil 2001; Zanker and Zeil 2005). To reconstruct optic flow outdoors, it is thus necessary to move a camera along the flight paths of insects (Boeddeker et al. 2005).

When such natural optic flow was replayed to tangential cells, their responses were seen to convey information not only about the rotational movements of the fly, as thought previously, but also about close objects seen during straight segments of flight, and thus, implicitly, on the spatial relation of the insect to its environment (Boeddeker et al. 2005; Kern et al. 2005, 2006; van Hateren et al. 2005; Karmeier et al. 2006).

The relative contributions that rotational and translational flow components make to the response of these neurons can be quantified in two ways. The first uses flight arenas, where the optic flow of a given flight path can be reproduced not only for the original space, but also for virtual spaces of increasingly larger size (Kern et al. 2005). When such modified optic flow is replayed to visual interneurons, their overall

response profiles were found to change dramatically, because the translational flow field practically disappears with increasing arena size and neurons respond primarily to the rotational components of the optic flow (Fig. 1). At the flight speed of flies in the original 40-cm flight cage, all objects further than about 1 meter away are effectively at infinity and only contribute flow vectors during rotations.

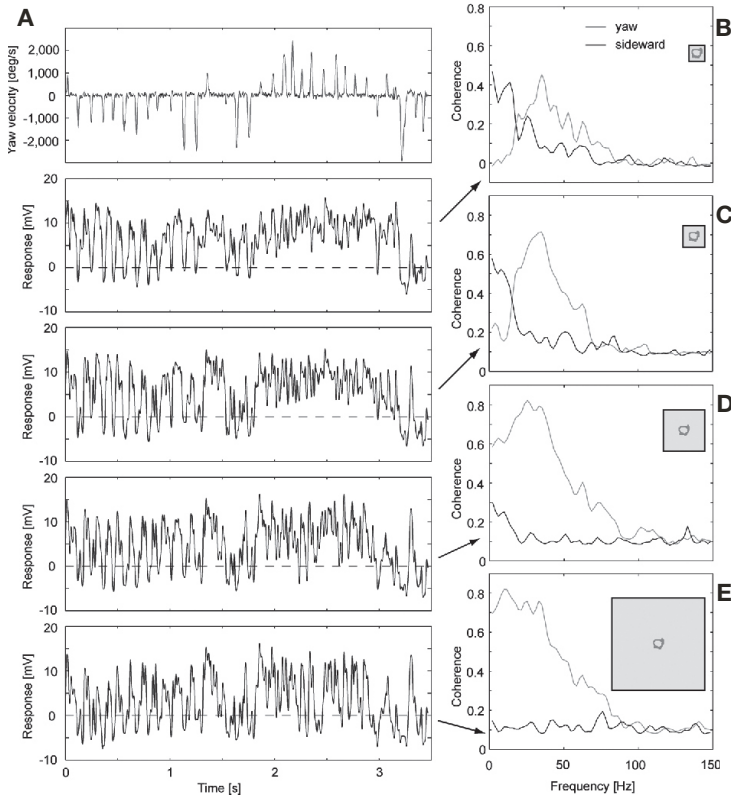


Figure 1. Influence of arena size on the neural activity of fly lobula plate neurons in response to behaviorally generated optic flow. (A) Horizontal angular velocity (yaw) and the average responses of neurons ($n = 4$, low-pass-filtered with a Gaussian standard deviation of 3 msec) to optic flow reconstructed for a given flight path in the original flight arena and in virtual flight arenas with increasingly larger size. (B–E). Coherence of yaw velocity (gray) and sideways angular velocity (black) for different cage sizes: 40-cm side length (original cage; B), 55 cm (C), 105 cm (D), and 235 cm (E). For C through E, the flight was centered in the virtual space. (Insets in B–E) Original and virtual arenas as seen from above. The coherence quantifies the similarity of self-motion parameters predicted from the neuronal response by the optimal linear filter with the actual motion parameters as a function of frequency. (Modified, with permission, from Kern et al. 2005.)

The second approach is similar, but done outdoors: By moving a camera along different paths, outdoor optic flow can be reconstructed along the original flight path of a fly, and also along the same path shifted in space, away from close objects. When the same neurons are presented with optic flow along a flight path that, for instance, was shifted 40 cm further away from vegetation that the fly had originally approached, their responses again mainly reflect the rotational components of optic flow, because the strength of translational optic flow decreases with the distance of objects (Fig. 2) (Boeddeker et al. 2005).

When in flight, the fly makes finely coordinated movements of its head and body that are essential for its visual system to extract behaviorally relevant information (van Hateren et al. 2005; Kern et al. 2006); these are analogous to the eye movement saccades that we make to investigate the visual scene. The flight path of a fly consists of straight segments—translations—separated by fast changes in orientation (Wagner 1986; Zeil 1986; van Hateren and Schilstra 1999; Tammero and Dickinson 2002). Saccadic changes of flight direction are performed as banked turns, which require a succession of thorax rotations about all rotational axes, occurring in a fixed order, while gaze is stabilized and rotational flow components are minimized (Hengstenberg 1993; van Hateren and Schilstra 1999). Gaze changes are performed by head saccades, which are faster and shorter than body saccades (Fig. 2E,F) and thus aid the behavioral elimination of rotational components from the optical flow pattern on the retina (Land 1973; van Hateren and Schilstra 1999).

The inferred coding properties of fly visual interneurons depend not only on the particular dynamics of optic flow, but also on the visual pattern. When tested with drifting sinusoidal gratings, the fly's movement-detecting mechanism is seen to be sensitive to the contrast frequency of visual stimuli, confounding the angular velocity of a striped pattern with its spatial period (see Borst and Egelhaaf 1993). It therefore appears to be ill suited for measuring image velocity (Srinivasan et al. 1996; see, however, Zanker et al. 1999; Higgins et al. 2004). Yet, electrophysiological experiments and model simulations have shown that the responses of these neurons become less dependent on texture when they are stimulated with broadband natural scene patterns (Dror et al. 2001; Shoemaker et al. 2005). In fact, when presented with natural optic flow dynamics, motion detector model output is very similar in response to natural scene or random dot textures (Lindemann et al. 2005). From a functional point of view, the invariance of these biological motion detectors to changes in texture has the big advantage that it makes motion estimates robust against variations in scene properties.

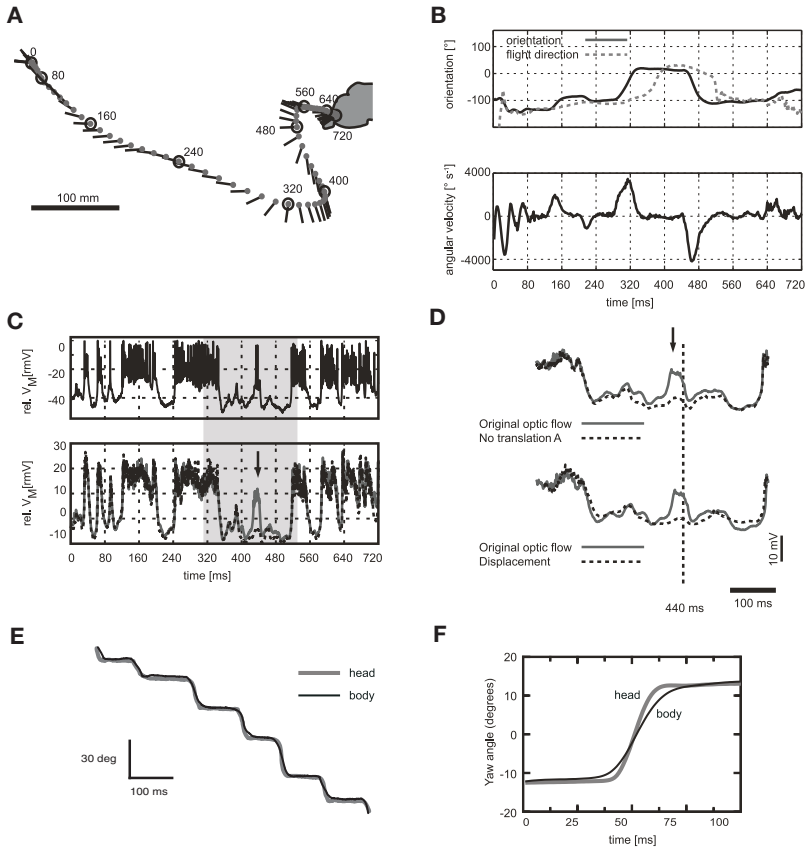


Figure 2. Responses of visual interneurons to optic flow reconstructed along outdoor flight paths. (A) Flight path of a blowfly landing on a leaf outdoors. Positions and orientation of the fly are shown every 10 msec, with the head marked by a dot and the orientation of the body axis by a line attached to it. (B) Orientation of the fly's longitudinal body axis (*solid line*) and flight direction (*dashed line*) in the external coordinate system (*top*) and yaw angular velocity (*bottom*). (C) Individual (*top*) and average (*bottom*) response of a visual interneuron (right HSE-cell) to optic flow experienced during the flight shown in A. (*Gray lines* in the bottom panel) Response of HS cells to the optic flow generated during the original flight sequence; (*dashed lines*) response to optic flow from which the translational components had been removed. (D) Detailed comparison of responses to original optic flow with responses to modified optic flow. (*Top*) Optic flow from which the translational components had been removed (*gray area* in C). (*Bottom*) Optic flow generated on a path that had been displaced by 40 cm away from the landing site. (E) Saccadic changes in yaw body orientation (*black*) and gaze (*gray*) of flies flying in a cubic flight arena (40 × 40 × 40 cm). (F) Mean time course of 620 saccades to the right, with amplitudes between 20° and 30°. (A–D: Modified, with permission of Springer Science and Business Media, from Boeddeker et al. 2005.) (E–F: Modified, with permission of The Company of Biologists Ltd., from van Hateren and Schilstra 1999).

In the “real life” of a fly, then, the activity of motion-sensitive neurons during straight segments of flight represents the image flow generated both by nearby objects and by residual rotations. The challenging question now is whether and how downstream neuronal circuits decode the rotational and translational response components of these motion-sensitive cells. They might be extracted in a computationally parsimonious way by temporal frequency filtering, because translational image flow is confined to low frequencies and thus could be segregated from the rotational flow that dominates the higher frequencies (Fig. 1B) (Kern et al. 2005, 2006; van Hateren et al. 2005; Karmeier et al. 2006). The neuronal responses may thus be used not only for the stabilization of gaze, but also for detecting obstacles, gaps, landmarks, or landing sites and to adapt flight speed to the spatial layout of the environment. Bees, for instance, slow down when they fly through a narrowing passage and speed up again when it becomes wider (Srinivasan et al. 1996).

Clearly, such properties of neurons would be very difficult to detect and to study without some way of working with unrestrained animals in their normal environment or some way of recreating this environment in a realistic and interactive way (e.g., see Schuster et al. 2002). Although visual environments are self-similar on a certain level of image statistics (e.g., see Simoncelli and Ohlshausen 2001), in any specific case, the ecological context helps us to ask neurons the relevant questions. As our examples of fly motion-sensitive neurons illustrate, it is becoming increasingly clear that the particular spatial structure of natural scenes and the specific properties of behaviorally generated, and in that sense natural, optic flow are important aspects of what makes a relevant stimulus for these cells (Egelhaaf et al. 2002).

LEARNING FLIGHTS AND VIEW-BASED HOMING

In many cases, like the one we just described for flies, eye movements are organized in such a way as to aid visual information processing by generating a particularly structured visual input (for review, see Land and Collett 1997; Land 1999a). Some insects use structured movements that are tailored to produce relative movement of objects at different distances (motion parallax) to aid range discrimination. They employ this active vision strategy because the range in which stereoscopic vision can be used to gain depth information is very limited because most insects have close-set eyes (e.g., see Srinivasan 1993). Bees have been shown to actively acquire range information to detect raised edges between textured surfaces by adopting a flight strategy that provides them with motion parallax cues (Lehrer and Srinivasan 1994). Other examples of active vision

strategies are the peering movements made by locusts and praying mantids (for review, see Kral and Poteser 1997), or the zigzag flights by wasps when encountering novel landmarks (Voss and Zeil 1998). In some cases, we know how animals use the information they have actively gained. We discuss here an example where this is far from clear.

A wealth of evidence suggests that insects find their way back to places of significance using remembered views (Collett and Zeil 1997, 1998). However, the acquisition of visual memories in this context does not appear to be straightforward and simple. For instance, when a ground-nesting wasp or bee departs for a foraging trip in the morning, it goes through an elaborate procedure, which serves to acquire a visual representation of the nest environment that will later guide it safely home. These learning flights or “turn-back-and-look” procedures (Lehrer 1993) have a distinct organization that is astonishingly similar across different species of wasps and bees (for review, see Zeil et al. 1996). Ground-nesting wasps, for instance, upon leaving their nest entrance, turn back to face it and then begin to pivot around the nest in a series of arcs (Fig. 3A). During these pivoting movements, they steadily gain height above ground at about the same rate as their distance to the goal increases, so that the nest entrance is seen at about 45° below the horizon in the ventral visual field. The wasps also turn against the pivoting direction in such a way that the nest entrance is held in the frontolateral visual field (Fig. 3A). While they back away, the wasps’ speed above ground increases proportionally with distance from the goal.

Why do insects move in this way during learning flights, and how does this elaborate acquisition procedure relate to their ability to find their way back home? A number of suggestions have been made to explain the computational significance of these learning flights (see Collett 1995; Zeil et al. 1996), including (1) they serve to systematically link a series of snapshots taken at different spatial locations relative to the nest; (2) they generate motion parallax information that could be used to filter out shadow contours, to distinguish close from distant landmarks, or even to gain information on their absolute distance; and (3) they act as a return flight simulation in which the animal continuously checks how views change close to the goal and whether the visual representation it already has acquired is sufficiently robust for successfully guiding the subsequent return.

There is a need then to find out what visual information the insects extract during such learning flights. We know that ground-nesting wasps do learn the location of their nest relative to landmarks throughout these flights, because shifting them during such a flight leads to an equivalent

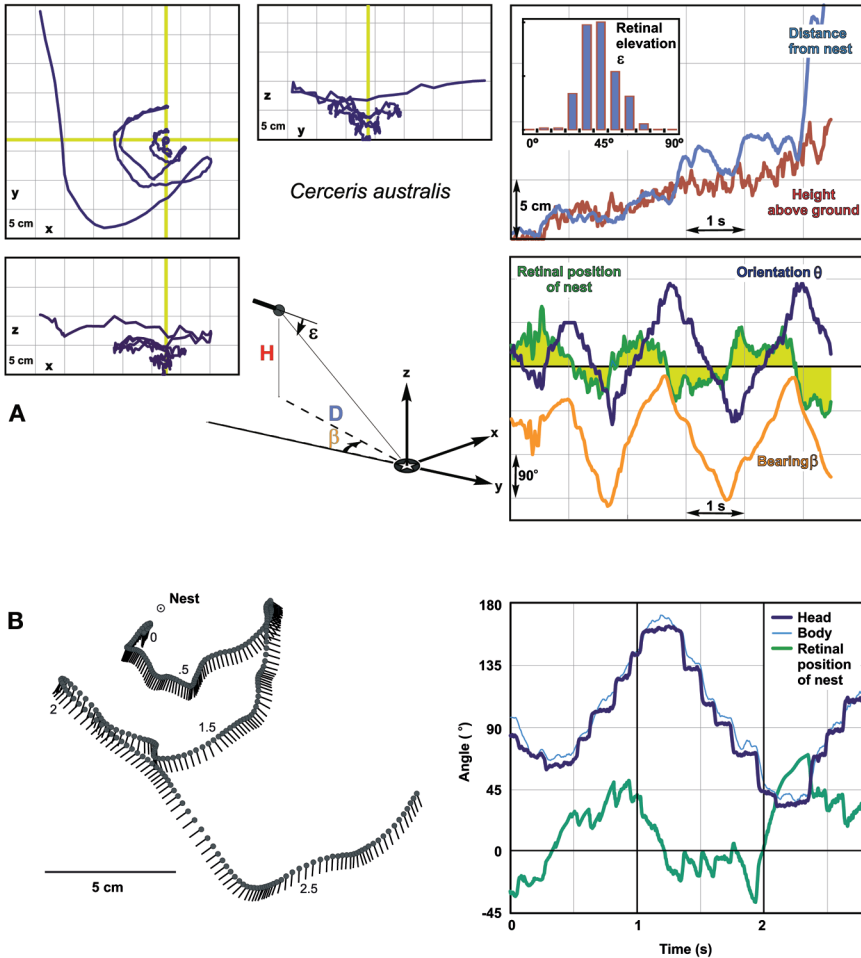


Figure 3. Organization of learning flights in ground-nesting wasps (*Cerceris australis*). (A, Left) Three-dimensional flight path; (top right) time course of distance from burrow and height above ground (see schematic diagram for definitions of parameters). (Inset) Histogram of retinal elevation of nest entrance for the same flight; (bottom right) time course of body axis orientation, bearing, and retinal azimuth position of the nest entrance. Gaze direction was estimated from body axis orientation at 50 fps. (B) Head and gaze orientation for a learning flight (horizontal positions [dots] and true gaze directions of a wasp [lines] are shown on the left) as determined at high resolution and at 500 fps. Positions are labeled every 0.5 second. Note the saccadic changes in true gaze direction (light blue trace on the right) and the resulting retinal position changes of the nest entrance (green trace).

shift of their subsequent search distribution (Zeil 1993a). Ground-nesting wasps, solitary bees, and honeybees are able to judge the distance between a goal and close landmarks, independently of their apparent size (Zeil 1993b; Brännert et al. 1994; Lehrer and Collett 1994), although in many situations, insects locate places by matching the apparent size of landmarks, an observation that has led to the so-called “snapshot memory” hypothesis (e.g., see Collett and Land 1975; Wehner and Rüber 1979; Cartwright and Collett 1983, 1987).

Individual landmarks can dominate the search distribution of homing insects, provided they are close to the goal and salient. Landmark removal experiments, however, show that the insects also memorize more than the appearance of individual objects (e.g., see Zeil 1993b; Graham et al. 2003). Indeed, panoramic snapshots uniquely define a location in space, especially outdoors (Zeil et al. 2003) and therefore are also increasingly being used in robotics (e.g., see Franz et al. 1998; Vardy and Möller 2005). It is interesting in this context that wasps look in the same directions during learning flights and return flights and some of their flight dynamics are also similar (Collett and Lehrer 1993; Zeil 1993b; Collett 1995), a prerequisite for accurate image matching.

To investigate the problems involved in view-based homing under natural conditions, where it is hard to predict how salient landmarks are and how views change, we reconstructed what ground-nesting wasps see during learning and homing by recording the three-dimensional flight paths of the insects together with the orientation of their heads, using two high-resolution and high-speed digital video cameras. We then moved a panoramic imaging device along the same paths with a robotic gantry, recording image sequences from the perspective of the wasp during learning and homing flight maneuvers (see Zeil et al. 2003; Boeddeker et al. 2005; W. Stürzl et al., in prep.).

This method of reconstruction now allows us to determine the image transformations that the wasps create by their particular flight pattern, and how the views correlate with those the wasps see during their return. We discovered a number of properties of learning and return flights that had been difficult to recognize before and that challenge some of our current ideas. First, like flies, wasps change their gaze in a saccadic manner and move by a rapid series of translations, during both their learning (Fig. 4A) and their homing flights (Fig. 4C). Each translation is followed by a fast, saccadic head movement, which during learning, seems to correct for the shift of the retinal position of the nest entrance caused by the previous translation (Figs. 3B and 4A). Second, during the return flight, the insects experience varying patterns of small and large image differences, relative to what they had seen during learning (Fig. 4B). Small

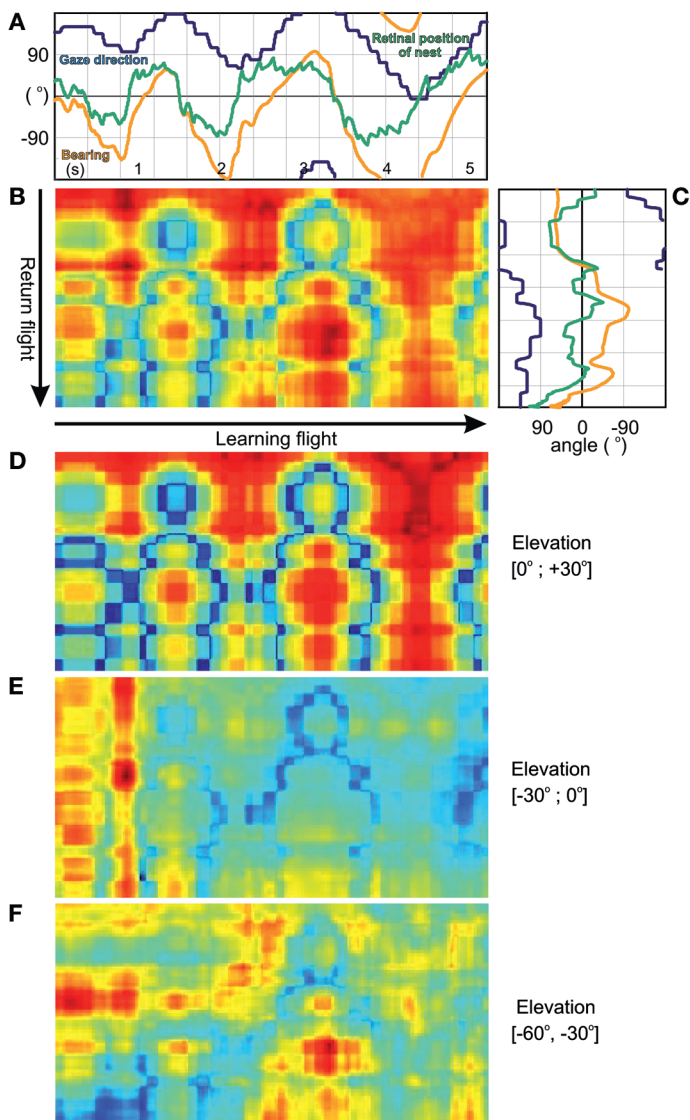


Figure 4. (A) Wasp's orientation, bearing, and the retinal position of the nest entrance over time during a learning flight. Same time axis as the matrix of image differences (ID) in B. (B) ID matrix between each position along a return flight (vertical axis) and the previous learning flight (horizontal axis). Panoramic images were taken at each position and at the appropriate orientation of the wasp during its learning flight, and IDs were calculated between the image experienced at that point of time and the images experienced at all other locations during the learning flight. Each color-coded element of the ID matrix corresponds to the sum of squared pixel differences between two images, with small image difference values marked in blue and large difference values marked in red. (C) The wasp's orientation, bearing, and the retinal position of the nest entrance over time during the return flight. (D–F) ID matrices for different 30°-wide elevation ranges above the horizon (D) and below the horizon (E, F).

image differences (blue areas in Fig. 4B) occur when the orientation of the returning wasp is similar to the orientation it had while fixating the nest entrance laterally during learning. Third, areas of small image differences are linked in time during a return flight, and some form “valleys” that lead toward the goal (bottom left corner in Fig. 4B), for image differences both above the horizon (Fig. 4D), which are mainly affected by differences in orientation, and below the horizon (Fig. 4C, D), which are in addition strongly affected by differences in position.

We do not yet know whether and how these patterns of image differences guide homing wasps. We also caution that our technique does not at this stage deliver a truly veridical reconstruction of the visual input experienced by the insects: It takes time to reconstruct flight paths, the gantry cannot be moved at the flight speed of wasps, and the imaging device is much larger than the insect, so that we cannot reconstruct views close to the ground. However, we believe that developing these techniques is a step in the right direction: They allow us to systematically investigate the natural conditions in which homing insects operate and the way in which behaviorally guided vision and visually guided behavior interact. Insects offer us unique opportunities to study view-based homing in their natural habitats, because they repeatedly perform this task at a defined location, thus allowing us to monitor them closely, and because we can record their gaze direction, while they behave freely. The latter condition is particularly difficult to achieve in vertebrate animals (but see Land and Hayhoe 2001; Körding et al. 2004; Hayhoe and Ballard 2005). We next discuss a third example of an information processing task that is crucial for many animals, but that is very hard to comprehensively describe in terms of visual processing without the help of yet another invertebrate animal.

ORGANIZATION OF PREDATOR AVOIDANCE AND THE QUALITY OF INFORMATION

Many animals respond to an approaching predator with a distinct sequence of behaviors that serve to minimize risk and at the same time appear to maximize information on the actual threat (Hemmi 2005a,b; Hemmi and Zeil 2005). The problem prey animals face is that the sensory cues they have on the presence and movements of predators do not necessarily correlate well with the actual threat. This information deficit is one of the reasons that animals employ a staged sequence of behaviors in response to predators, such as freezing, running for cover, and vigilance behavior. In prey animals that rely on vision to detect and identify predators, we know

little about the kind of visual information they have available in making these decisions (e.g., see Cronin 2005; Hemmi and Zeil 2005), and in most cases, we are not in the position to characterize the detailed flow of visual information available to an animal during the different stages of its predator evasion response. The main problem is that it is usually very difficult to monitor in the natural setting both an animal's behavior and what it actually sees. One exception, where this is possible, involves an invertebrate with an unusually complex, but transparent lifestyle—which is in most aspects continuously open to observation—and which therefore allows us to begin to reconstruct how this animal perceives and responds to its bird predators on a moment-to-moment basis.

Fiddler crabs live on open mudflats and within mangroves in the tropical and subtropical intertidal zone. They graze on the surface during low tide, for the most time less than 1 meter from their individual burrows, which serve as a refuge against a variety of predatory birds (Land 1999b; Ribeiro et al. 2003). Because the crabs normally do not venture far from their burrows, are fast runners, and are able to locate their burrows with great precision, flying birds cannot intercept them. Instead, birds have to either find crabs without a burrow or wait for burrow owners to come back to the surface. The behavior of the crabs can be monitored continuously throughout their daily activity together with the position of their eyes, which do not make directed eye movements. Their compound eyes have a panoramic visual field and a peak resolving power of about $0.5\text{--}1^\circ$, so that simple bird dummies can be used to elicit the predator avoidance responses of the crabs (for review, see Hemmi and Zeil 2005; Zeil and Hemmi 2006).

In this natural situation, when a crab becomes aware of a predator, it first freezes, which makes it less detectable, but also improves its own visual signal because its eyes are not moving. It then runs back to its burrow where it stops again, continuing to gather information. Next, it may enter its refuge, minimizing risk at the cost of losing visual information about the state of the world. It stays for a variable length of time in the refuge, before resurfacing and reassessing the situation from a position of relative safety, before deciding to continue its normal activities.

We know that soon after a crab sees a bird dummy moving parallel to the mudflat, it responds by running home (Hemmi 2005b). At this stage, the visual signal is nonspecific and its information content is very low, being restricted to ambiguous cues such as angular size and angular speed: It does not allow a crab to identify the predator, nor its direction of movement (Fig. 5B). Despite this information deficit, the initial hair-trigger response is context-dependent; a crab responds earlier, the

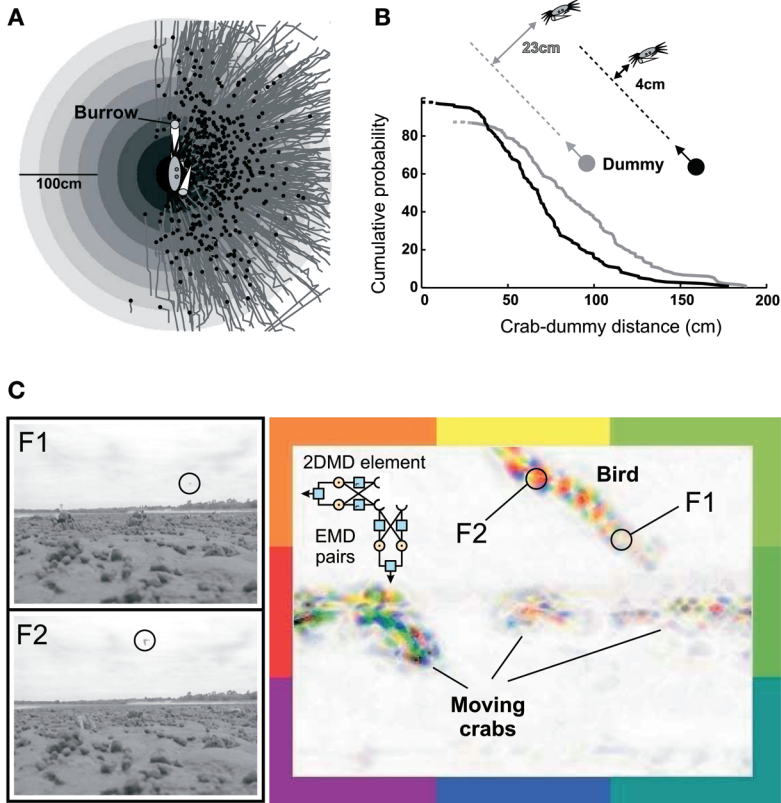


Figure 5. How fiddler crabs respond to predators. Fiddler crabs respond to approaching dummy predators within an egocentric frame of reference. (A) Repeated approaches of a black spherical bird dummy (*gray lines*) toward the central crab. The coordinate system has been rotated such that the burrow–crab vector always points upward, and the crab has been fixed at the center. All trials where the dummy moved from left to right have been flipped over for clarity. (*Black dots*) Positions of the dummy at the moment the crabs responded form an annulus around the crabs’ positions. The concentric gray rings around the burrow position are 25 cm in width. (B) The cumulative response probability, i.e., the probability that a crab responds to an approaching dummy before it reaches a given distance to the crab, shows that the crabs respond later to dummies that approach more directly. (C) The output of a two-dimensional network of elementary motion detectors (EMDs) (see Zanker and Zeil 2005) in response to an image sequence showing the approach of a tern as seen from a crab’s perspective. Two frames of the sequence are shown on the left bird. The location of the bird has been marked by a black circle. The image on the right shows the network output for the whole sequence. Motion direction has been color-coded. The output is given for an EMD network with a sampling base of 1° and a time constant of 80 msec. (A and B modified, with permission from Elsevier, from Hemmi 2005a,b.)

further away it is from its burrow (Hemmi 2005a), and it also takes note of what other crabs are doing (Wong et al. 2005). A crab normally stops at the entrance of its burrow; it can now afford to wait and gather more robust visual information on the direction of approach and the distance of a bird.

The change in apparent size (looming) and the changes in retinal elevation of the approaching bird are potential visual cues, which have a high information content regarding the direct risk of predation. The image of a bird on a collision course does not shift position in the visual field, but simply increases in apparent size. A bird on a path passing directly overhead, on the other hand, would be seen at constant azimuth as it approaches from a distance, but at higher and higher elevations in the visual field, in addition to growing in apparent size. The image of a predator approaching along a trajectory that is offset from a direct approach would shift position in azimuth and less so in elevation on the crab's eye. Looming, however, is the most reliable indication of approach, and neurons in the crab brain that are sensitive to such looming stimuli may perform computations very similar to the so-called lobula giant movement detector of locusts (Gabbiani et al. 1999; Rind and Simmons 1999), discriminating between objects approaching on a collision course and objects that fly by (Gray et al. 2001).

These cues determine not only whether and when crabs decide to descend into their burrows, but also how long they will stay underground (Jennions et al. 2003; Hugie 2004). Furthermore, at some stage of their response sequence, the crabs seem to decide whether a given visual signal can in the future be ignored or not: After a while, crabs become less responsive to the dummies they continue to see, but their response does not habituate when the same dummy keeps approaching from a distance (Zeil and Hemmi 2006). We do not yet know what the rules are for this elementary form of learning and what visual signatures provide robust and reliable predictors for bird behavior. So far, we have used dummies, which move in straight lines and have no flapping wings. Real birds, however, provide potentially much richer visual signals, which need to be identified. The wing beats of an approaching bird, for example, are clearly visible in the output of a two-dimensional elementary motion detector network (see Zanker and Zeil 2005) when it is stimulated with an image sequence recorded from the perspective of a fiddler crab (Fig. 5C).

The visual signatures of predatory birds and how they affect decision making in fiddler crabs thus still await a full description and analysis. What we can say, however, is that visual information processing in this example is context-dependent in several ways: The responses of crabs

depend on the state of their path integrator, which provides them with information on how far away the burrow is (multimodal context); they may respond to the antipredator behavior of other crabs (social context); they appear to respond to different cues at the different stages of their predator avoidance strategy (behavioral context); and they habituate to specific aspects of predator-related visual information (historical context).

Clearly, these crucial components of information processing can only be uncovered and analyzed *in situ*; that is to say with the animal's functional, social, and ecological integrity intact and in the space in which they occur. Like ants and bees, whose motivation to forage and ability to learn have helped us understand, for instance, the computational structure and the ecology of navigational abilities (e.g., see Srinivasan et al. 1996; Giurfa and Capaldi 1999) and of learning and memory dynamics (e.g., see Menzel 1999), fiddler crabs are another invertebrate example with unique potential for neurobiology: Because they play out their lives so openly and in such a simple visual environment, they allow us to monitor under natural conditions the visual input stream together with all aspects of their behavior. They thus enable us to generate testable predictions about the underlying information-processing strategies that must be implemented in the crabs' neural systems to perform such tasks, as the discussion below shows.

KEEPING TRACK OF MULTIPLE OBJECTS: BURROW SURVEILLANCE IN FIDDLER CRABS

Animals need to move around in order to forage, mate, and maintain a territory. A fundamental problem they face is that they cannot be everywhere at the same time and need to allocate their presence in such a way as to assure the ownership of their assets. They are particularly challenged to protect their nests or shelters while being absent. Even in situations in which the world is unobstructed and assets can be monitored from far away, the problem remains how to identify threats effectively, by recognizing when another animal is approaching the resource.

Fiddler crabs live in such an unobstructed world and the asset they care most about is their burrow. They cannot see their burrows from even a short distance away, because of perspective foreshortening and visual clutter (Zeil and Layne 2002; Ribeiro et al. 2006). Yet the crabs are exquisitely sensitive to other crabs approaching their (invisible) burrow (Hemmi and Zeil 2003a,b,c). They are able to be so because the world they inhabit has a predictable geometry, allowing them to combine information from the path integration system with visual information

to solve the task of measuring the spatial relationship between their invisible asset and a moving conspecific. Foraging crabs respond to another crab approaching their burrow whenever that animal approaches to within a certain distance of the burrow, irrespective of its direction of approach and therefore irrespective of the distance between the owner and the intruder (Fig. 6A,B).

This judgment of allocentric, not egocentric, relations is possible because in the flat world in which fiddler crabs live, the visual projection of the burrow environment changes predictably as a crab moves away from it. The crab “knows” about this transformation, because its path integration system monitors its movements relative to the burrow and informs the visual system about the transformations necessary to survey a constant area around the burrow. Crabs show us that they know, because they respond earlier if they themselves are further away from their burrow.

Burrow surveillance in fiddler crabs is thus a further example that justifies the need for “going wild.” As in predator avoidance, visual information processing in burrow surveillance is dependent on the behavioral context, which determines the state of path integration. However, even though the visual detection task is almost identical in both contexts, the information the crabs use to make a decision is actually very different. Although the crabs should respond when either predator or conspecific has reached a certain distance from the burrow (e.g., see Ydenberg and Dill 1986), in the predation context, they do not have the necessary information and are forced to respond in an egocentric fashion. In burrow surveillance, they can respond in an allocentric fashion, because the geometry of the task offers them more direct information about the threat. This ability of fiddler crabs to combine visual and non-visual information and to make use of the predictable geometry of their visual world would have remained undetected if these animals were taken out of the natural context in which they normally operate.

Going wild again helps us to ask animals (and neurons) the right questions and to design appropriate experiments. For instance, the burrow surveillance task can be explained by the use of a small number of matched retinal filters, which take into account how a circular area around the burrow is mapped onto the retina at different distances from the burrow (Fig. 6C) (Hemmi and Zeil 2003a,b,c). Because crabs are always aligned sideways toward their burrow, this matched filter bank can be hardwired with a constant azimuth orientation in the lateral visual field, but stacked at different elevations. It should be possible to test at least some aspects of this prediction in electrophysiological experiments.

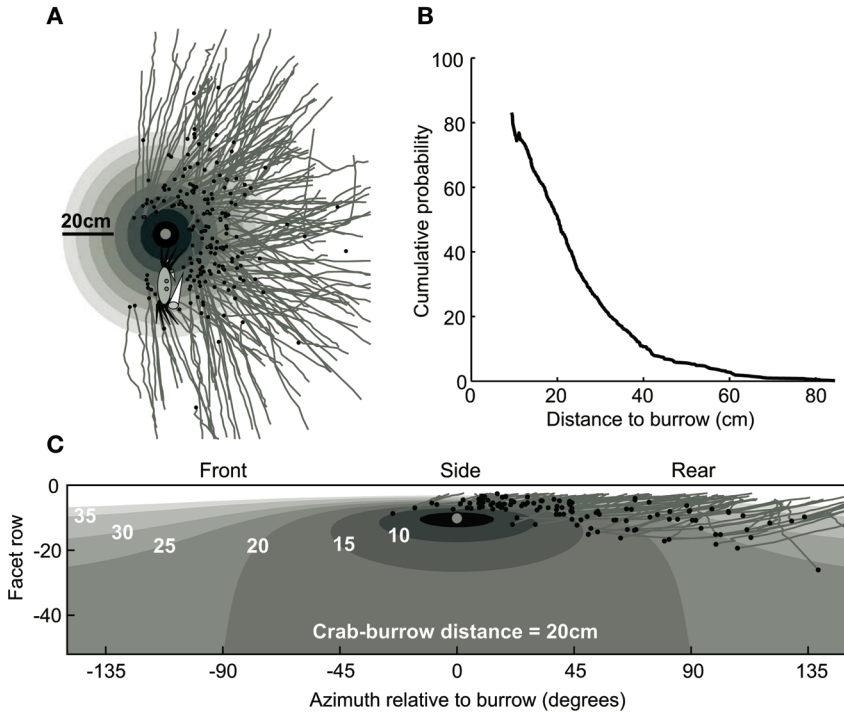


Figure 6. Burrow surveillance in fiddler crabs. The crabs respond to approaching dummy crabs within an allocentric, burrow-centered frame of reference. (A) Repeated approaches of the dummy (gray lines) toward the burrow (central gray circle) of crabs. The coordinate system has been rotated such that the burrow-crab vector always points upward and the burrow has been fixed at the center. All trials where the dummy moved from left to right have been flipped over for clarity. The black dots, which form an annulus around the crabs' burrows and not around the crabs themselves, mark the position of the dummy at the moment the crabs responded. The concentric gray rings around the burrow position are 5 cm in width. Only experiments where the crab was between 20 and 25 cm away from its burrows are included. Note the difference in scale compared to Fig. 5A. (B) The estimated cumulative response probability, i.e., the probability that a crab responds to an approaching dummy before it reaches a given distance to the burrow. (C) A proposed matched filter for burrow surveillance. Because crabs align their longitudinal body axis with the direction to their burrow, there exists a simple retinal mapping of the distance of any point on the mudflat to the crab's burrow (central gray circle). (Gray lines and black dots) Dummies' approach trajectories and position at the moment of response as in A. The concentric gray rings shown in A are also remapped into retinal coordinates. The retinal mapping of burrow distance depends on the crab's distance from its burrow and is shown here for a distance of 20 cm. Only experiments where the crab was between 15 and 25 cm away from its burrow are included. (Modified, with permission of the Company of Biologists Ltd., from Hemmi and Zeil 2003b,c.)

OUTLOOK

There is still a huge gap between what we know about information processing in the real life of animals and what we know about how these abilities are implemented at the neural level. The gap exists for good and technical reasons: With rare exceptions, neurobiological analysis has to work with restrained animals, which are removed from their normal operating conditions. When we study the properties of neurons in these situations, we constantly face the problem that we may ask them the wrong questions. We cannot be sure that our stimulus regimes address their normal operating range and mimic the normal context in which they have evolved. Behavioral ecology and ethological analysis in turn have no access to operating neurons and thus, in most cases, cannot by themselves identify the pattern of ongoing neural activity and information-processing constraints. In the end, however, information processing has to be understood in the ethological and ecological context. Behavioral analysis is needed to identify the necessary computations, and the challenge for vision scientists is to do so in terms of the image-processing problems these computations pose under real-life conditions. As far as invertebrate vision is concerned, there are many successful examples where such an analysis has led to specific hypotheses that have been or can in principle be tested in electrophysiological experiments.

In many cases, however, we do not know what the information-processing problems are under natural conditions, especially because vision works in a closed loop and can strictly only be studied in the freely behaving animal. For the time being, natural vision in invertebrates has to be studied by reconstruction and by carefully tailored ethological studies that produce specific and testable hypotheses. We have introduced a number of examples and discussed the methodological difficulties involved, but also the novel and crucial insights that can be gained by attempting to “go wild” with neurobiology. We hope that they motivate more neuroscientists to venture outside their laboratories and become neurocomputational naturalists.

ACKNOWLEDGMENTS

We are grateful to M.V. Srinivasan for the generous loan of high-speed cameras. We acknowledge financial support from the Australian Research Council-ARC (J.M.H., J.Z.), the ARC Centre of Excellence in Vision Science (N.B., J.M.H., J.Z.), the German Science Foundation (N.B., W.S.), and the Centre for Visual Sciences at The Australian National University (J.M.H., W.S., J.Z.).

REFERENCES

- Boeddeker N., Lindemann J.P., Egelhaaf M., and Zeil J. 2005. Responses of blowfly motion-sensitive neurons to reconstructed optic flow along outdoor flight paths. *J. Comp. Physiol. A* **191**: 1143–1155.
- Borst A. and Egelhaaf M. 1993. In *Visual motion and its role in the stabilization of gaze* (ed. F.A. Miles and J. Wallman), pp. 3–27. Elsevier, Amsterdam.
- Borst A. and Haag J. 2002. Neural networks in the cockpit of the fly. *J. Comp. Physiol. A* **188**: 419–437.
- Brünnert U., Kelber A., and Zeil J. 1994. Ground-nesting bees determine the distance of their nest from a landmark by other than angular size cues. *J. Comp. Physiol. A* **175**: 363–369.
- Burton B.G. and Laughlin S.B. 2003. Neural images of pursuit targets in the photoreceptor arrays of male and female houseflies *Musca domestica*. *J. Exp. Biol.* **206**: 3963–3977.
- Cartwright B.A. and Collett T.S. 1983. Landmark learning in bees. Experiments and models. *J. Comp. Physiol.* **151**: 521–543.
- . 1987. Landmark maps for honeybees. *Biol. Cybern.* **57**: 85–93.
- Collett T.S. 1995. Making learning easy: The acquisition of visual information during the orientation flights of social wasps. *J. Comp. Physiol. A* **177**: 737–747.
- Collett T.S. and Land M.F. 1975. Visual spatial memory in a hoverfly. *J. Comp. Physiol.* **100**: 59–84.
- Collett T.S. and Lehrer M. 1993. Looking and learning: A spatial pattern in the orientation flight of the wasp *Vespa vulgaris*. *Proc. R. Soc. Lond. B* **252**: 129–134.
- Collett T.S. and Zeil J. 1997. Selection and use of landmarks by insects. In *Orientation and communication in arthropods* (ed. M. Lehrer), pp. 41–65. Birkhäuser Verlag, Basel.
- . 1998. Places and landmarks: An arthropod perspective. In *Spatial representation in animals* (ed. S. Healy), pp. 18–53. Oxford University Press, United Kingdom.
- Cronin T.W. 2005. The visual ecology of predator-prey interactions. In *Ecology of predator-prey interactions* (ed. P. Barbosa and I. Castellanow), pp. 105–138. Oxford University Press, United Kingdom.
- Dror R.O., O'Carroll D.C., and Laughlin S.B. 2001. Accuracy of velocity estimation by Reichardt correlators. *J. Opt. Soc. Am. A* **18**: 241–252.
- Eckert M.P. and Zeil J. 2001. Towards an ecology of motion vision. In *Motion vision: Computational, neural, and ecological constraints* (ed. J.M. Zanker and J. Zeil), pp. 333–369. Springer, Berlin.
- Egelhaaf M., Grewe J., Kern R., and Warzecha A.K. 2001. Outdoor performance of a motion-sensitive neuron in the blowfly. *Vision Res.* **41**: 3627–3637.
- Egelhaaf M., Kern R., Krapp H.G., Kretzberg J., Kurtz R., and Warzecha A.K. 2002. Neural encoding of behaviourally relevant visual motion information in the fly. *Trends Neurosci.* **25**: 96–102.
- Franz M.O., Schölkopf B., Mallot H.A., and Bühlhoff H.H. 1998. Where did I take that snapshot? Scene-based homing by image matching. *Biol. Cybern.* **79**: 191–202.
- Felsen G. and Dan Y. 2005. A natural approach to studying vision. *Nature Neurosci.* **8**: 1643–1646.
- Gabbiani F., Krapp H.G., and Laurent G. 1999. Computation of object approach by a wide-field, motion-sensitive neuron. *J. Neurosci.* **19**: 1122–1141.
- Giurfa M. and Capaldi E.A. 1999. Vectors, routes and maps: New discoveries about navigation in insects. *Trends Neurosci.* **22**: 237–242.

- Graham P., Fauria K., and Collett T.S. 2003. The influence of beacon-aiming on the routes of wood ants. *J. Exp. Biol.* **206**: 535–541.
- Gray J.R., Lee J.K., and Robertson R.M. 2001. Activity of descending contralateral movement detector neurons and collision avoidance behavior in response to head-on visual stimuli in locusts. *J. Comp. Physiol. A* **187**: 115–129.
- Hausen K. and Egelhaaf M. 1989. Neural mechanisms of visual course control in insects. In *Facets of vision* (ed. D.G. Stavenga and R. Hardie), pp. 391–424. Springer-Verlag, Berlin.
- Hayhoe M. and Ballard D. 2005. Eye movements and natural behavior. *Trends Cog. Sci.* **9**: 187–194.
- Hemmi J.M. 2005a. Predator avoidance in fiddler crabs: 1. Escape decisions in relation to the risk of predation. *Anim. Behav.* **69**: 603–614.
- . 2005b. Predator avoidance in fiddler crabs: 2. The visual cues. *Anim. Behav.* **69**: 615–625.
- Hemmi J.M. and Zeil J. 2003a. Robust judgement of inter-object distance by an arthropod. *Nature* **421**: 160–103.
- . 2003b. Burrow surveillance in fiddler crabs. I. Description of behavior. *J. Exp. Biol.* **206**: 3935–3950.
- . 2003c. Burrow surveillance in fiddler crabs. II. The sensory cues. *J. Exp. Biol.* **206**: 3951–3961.
- . 2005. Animals as prey: Sensory-motor abilities and flexibility of behavior in an arthropod. *Marine Ecol. Progr. Series* **287**: 274–278.
- Hengstenberg R. 1993. Multisensory control in insect oculomotor systems. In *Visual motion and its role in the stabilization of gaze* (ed. F.A. Miles and J. Wallman), pp. 285–298. Elsevier, Amsterdam.
- Higgins C.M. 2004. Nondirectional motion may underlie insect behavioral dependence on image speed. *Biol. Cybern.* **91**: 326–332.
- Hugie D.M. 2004. A waiting game between the black-bellied plover and its fiddler crab prey. *Anim. Behav.* **67**: 823–831.
- Jennions M.D., Backwell P.R.Y., Murai M., and Christy J.H. 2003. Hiding behavior in fiddler crabs: How long should prey hide in response to a potential predator? *Anim. Behav.* **66**: 251–257.
- Karmeier K., van Hateren J.H., Kern R., and Egelhaaf M. 2006. Encoding of naturalistic optic flow by a population of blowfly motion sensitive neurons. *J. Neurophysiol.* **96**: 1602–1614.
- Kayser C., Körding K.P., and König P. 2004. Processing of complex stimuli and natural scenes in the visual cortex. *Curr. Opin. Neurobiol.* **14**: 468–473.
- Kern R., van Hateren J.H., and Egelhaaf M. 2006. Representation of behaviourally relevant information by blowfly motion-sensitive visual interneurons requires precise compensatory head movements. *J. Exp. Biol.* **209**: 1251–1260.
- Kern R., van Hateren J.H., Michaelis C., Lindemann J.P., and Egelhaaf M. 2005. Function of a fly motion-sensitive neuron matches eye movements during free flight. *PLoS Biol.* **3**: 1130–1138.
- Körding K.P., Kayser C., Einhäuser W., and König P. 2004. How are complex cell properties adapted to the statistics of natural stimuli? *J. Neurophysiol.* **91**: 206–212.
- Kral K. and Poteser M. 1997. Motion parallax as a source of distance information in locusts and mantids. *J. Insect Behav.* **10**: 145–163.
- Krapp H.G. 2000. Neuronal matched filters for optic flow processing in flying insects. *Int. Rev. Neurobiol.* **44**: 93–120.

- Land M.F. 1973. Head movements of flies during visually guided flight. *Nature* **243**: 299–300.
- . 1999a. Motion and vision: Why animals move their eyes. *J. Comp. Physiol. A* **185**: 341–352.
- . 1999b. The roles of head movements in the search and capture strategy of a tern (*Aves*, Laridae). *J. Comp. Physiol. A* **184**: 265–272.
- Land M.F. and Collett T.S. 1997. A survey of active vision in invertebrates. In *From living eyes to seeing machines* (ed. M.V. Srinivasan and S. Venkatesh), pp. 16–36. Oxford University Press, United Kingdom.
- Land M.F. and Hayhoe M. 2001. In what ways do eye movements contribute to everyday activities? *Vision Res.* **41**: 3559–3565.
- Lehrer M. 1993. Why do bees turn back and look? *J. Comp. Physiol. A* **172**: 549–563.
- Lehrer M. and Collett T.S. 1994. Approaching and departing bees learn different cues to the distance of a landmark. *J. Comp. Physiol. A* **175**: 171–177.
- Lehrer M. and Srinivasan M.V. 1994. Object detection by honeybees: Why do they land on edges? *J. Comp. Physiol. A* **173**: 23–32.
- Lewen G.D., Bialek W., and de Ruyter van Steveninck R.R. 2001. Neural coding of naturalistic motion stimuli. *Network* **12**: 317–329.
- Lindemann J.P., Kern R., van Hateren J.H., Ritter H., and Egelhaaf M. 2005. On the computations analyzing natural optic flow: Quantitative model analysis of the blowfly motion vision pathway. *J. Neurosci.* **25**: 6435–6448.
- McNaughton B.L., Battaglia F.P., Jensen O., Moser E.I., and Moser M.-B. 2006. Path integration and the neural basis of the “cognitive map”. *Nat. Rev. Neurosci.* **7**: 663–678.
- Menzel R. 1999. Memory dynamics in the honeybee. *J. Comp. Physiol. A* **185**: 323–340.
- Passaglia C., Dodge F., Herzog E., Jackson S., and Barlow R. 1997. Deciphering a neural code for vision. *Proc. Natl. Acad. Sci.* **94**: 12649–12654.
- Pflüger H.-J. and Menzel R. 1999. Neuroethology, its roots and future. *J. Comp. Physiol. A* **185**: 389–392.
- Reinagel P. 2001. How do visual neurons respond in the real world? *Curr. Opin. Neurobiol.* **11**: 437–442.
- Ribeiro P.D., Christy J.H., Rissanen R.J., and Kim T.W. 2006. Males are attracted by their own courtship signals. *Behav. Ecol. Sociobiol.* **7**: 1–9.
- Ribeiro P.D., Iribarne O.O., Jauregui L., Navarro D., and Bogazzi E. 2003. Variable sex-specific mortality due to shorebird predation on a fiddler crab. *Can. J. Zool.* **81**: 1209–1221.
- Rind F.C. and Simmons P.J. 1999. Seeing what is coming: Building collision-sensitive neurons. *Trends Neurosci.* **22**: 215–220.
- Schilstra C. and van Hateren J.H. 1998. Stabilizing gaze in flying blowflies. *Nature* **395**: 654.
- Schuster S., Strauss R., and Götz K.G. 2002. Virtual-reality techniques resolve the visual cues used by fruit flies to evaluate object distances. *Curr. Biol.* **12**: 1591–1594.
- Shoemaker P.A., O’Carroll D.C., and Straw A.D. 2005. Velocity constancy and models for wide-field visual motion detection in insects. *Biol. Cybern.* **93**: 275–287.
- Simoncelli E.P. and Olshausen B.A. 2001. Natural image statistics and neural representation. *Annu. Rev. Neurosci.* **24**: 1193–1216.
- Srinivasan M. 1993. How insects infer range from visual motion. In *Visual motion and its role in the stabilization of gaze* (ed. F.A. Miles and J. Wallman), pp. 139–156. Elsevier, Amsterdam.

- Srinivasan M., Zhang S., Lehrer M., and Collett T.S. 1996. Honeybee navigation en route to the goal: Visual flight control and odometry. *J. Exp. Biol.* **199**: 237–244.
- Tammero L.F. and Dickinson M.H. 2002. The influence of visual landscapes on the free flight behavior of the fruit fly, *Drosophila melanogaster*. *J. Exp. Biol.* **205**: 327–343.
- van Hateren J.H. and Schilstra C. 1999. Blowfly flight and optic flow. II. Head movements during flight. *J. Exp. Biol.* **202**: 1491–1500.
- van Hateren J.H., Kern R., Schwerdtfeger G., and Egelhaaf M. 2005. Function and coding in the blowfly H1 neuron during naturalistic optic flow. *J. Neurosci.* **25**: 4343–4352.
- Vardy A. and Möller R. 2005. Biologically plausible visual homing methods based on optical flow techniques. *Connection Sci.* **17**: 47–90.
- Voss R. and Zeil J. 1998. Active vision in insects: An analysis of object-directed zig-zag flights in a ground-nesting wasp (*Odynerus spinipes*, Eumenidae). *J. Comp. Physiol. A* **182**: 377–387.
- Wagner H. 1986. Flight performance and visual control of flight of the free-flying housefly (*Musca domestica* L.). I. Organization of the flight motor. *Phil. Trans. R. Soc. Lond. B* **312**: 527–551.
- Wehner R. and Räber F. 1979. Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Experientia* **35**: 1569–1571.
- Wong B.B.M., Bibeau C., Bishop K.A., and Rosenthal G.G. 2005. Response to perceived predation threat in fiddler crabs: Trust thy neighbor as thyself? *Behav. Ecol. Sociobiol.* **58**: 345–350.
- Ydenberg R.C. and Dill L.M. 1986. The economics of fleeing from predators. *Adv. Study Behav.* **16**: 229–249.
- Zanker J.M. and Zeil J. 2005. Movement-induced motion signal distributions in outdoor scenes. *Network: Comp. Neural Syst.* **16**: 357–376.
- Zanker J.M., Srinivasan M.V., and Egelhaaf M. 1999. Speed tuning in elementary motion detectors of the correlation type. *Biol. Cybern.* **80**: 109–116.
- Zeil J. 1986. The territorial flight of male houseflies (*Fannia canicularis*). *Behav. Ecol. Sociobiol.* **19**: 213–219.
- . 1993a. Orientation flights of solitary wasps (*Cerceris*; Sphecidae; Hymenoptera): I. Description of flight. *J. Comp. Physiol. A* **172**: 189–205.
- . 1993b. Orientation flights of solitary wasps (*Cerceris*; Sphecidae; Hymenoptera): II. Similarities between orientation and return flights and the use of motion parallax. *J. Comp. Physiol. A* **172**: 207–222.
- . 1997. The control of optic flow during learning flights. *J. Comp. Physiol. A* **180**: 25–37.
- Zeil J. and Hemmi J.M. 2006. The visual ecology of fiddler crabs. *J. Comp. Physiol. A* **192**: 1–25.
- Zeil J. and Layne J. 2002. Path integration in fiddler crabs and its relation to habitat and social life. In *Crustacean experimental systems in neurobiology* (ed. K. Wiese), pp. 227–247. Springer Verlag, Heidelberg.
- Zeil J., Hofmann M.I., and Chahl J. 2003. Catchment areas of panoramic snapshots in outdoor scenes. *J. Opt. Soc. Am. A* **20**: 450–469.
- Zeil J., Kelber A., and Voss R. 1996. Structure and function of learning flights in bees and wasps. *J. Exp. Biol.* **199**: 245–252.