

Within the body, individual cells are subsumed into larger fields of hundreds or thousands of cells that communicate to each other when to proliferate, differentiate or die. When the molecular mechanisms by which these conversations take place are elucidated, this will greatly advance our understanding of human disease, I think.

Another big question is how the antero-posterior, dorsal-ventral and left-right embryonic axes are seamlessly integrated to produce something as perfect as a human baby time after time. This might be considered as too broad a question to ask productively, but the early amphibian embryo starts as a single field of cells that is very amenable to experimental manipulation. One can deplete or overexpress gene products and then challenge these cells by transplanting them into new surroundings. Three principal techniques are available to biologists: genetics, biochemistry and cell transplantation. Of these, transplantation is the least appreciated. Therefore, I expect to continue grafting bits of embryos for as long as my eyes and hands permit.

What are the key questions for 'Evo-Devo'? One is to reconstruct the genetic tool-kit present in Urbilateria, the last common ancestor of invertebrates and vertebrates. It turns out this is a very difficult undertaking because present computer technology is not sufficiently developed yet. Two research groups are nevertheless making steady progress at reconstructing the genome of the common ancestor of all mammals. This is a good start. Another important question is whether segmentation in invertebrates presents the gene cycling behavior observed in the vertebrate embryo tailbud. I suspect this has not been documented yet because of technical difficulties. If invertebrate segmentation cycling were documented, it would imply that the urbilaterian ancestor was a segmented, burrowing animal. This would have important implications for the evolution of segmented body plans. Finally, there is presently a great opportunity to investigate the role of gene duplications and gene losses in the evolution of animal

phyla. Here 'big biology', through the sequencing of many complete genomes, is having an impact. The mere fact that we know that the entire ancestral chordate genome (for example, that of amphioxus) has been duplicated twice in mammals and three times in teleost fishes provides enough food for thought for the present. In the medium-term it will be important to have at least one complete genome from each animal phylum, and in the long-term to reconstruct the archetypal genome of Urbilateria. As we approach the 150th anniversary of *The Origin of Species*, these are very exciting times for the burgeoning field of Evo-Devo.

What advice would you give someone starting a career in biology? Jump into it both feet forward. Get yourself admitted into the best lab possible. Wash dishes, plead, volunteer, or do whatever you need to do to secure an experienced advisor whose published work you found the most interesting read. Scientific training is like an apprenticeship in the medieval guilds, you have to learn the trade from a master. Before starting any new project read the textbooks in the field — physiology textbooks are always a good choice — and preferably old ones, which provide a fountain of unsolved questions. For cell biology, always start with E.B. Wilson, 1928. Be fearless. Do not take into consideration which areas offer best future employment opportunities, just get into the lab you find most exciting. Move to anywhere in the world where the best possible advisor is located. The world is your oyster twice: first as a graduate student and then as a postdoc. As a young man I was driven by the ambition of making something out of my life. As the years passed this morphed gradually into an unquenchable curiosity to discover the principles by which animals are constructed. This passion for cells and embryos has now become all-consuming. Believe me, the pursuit of scientific knowledge offers a wonderful life.

Howard Hughes Medical Institute
and Dept. of Biological Chemistry,
University of California, Los Angeles,
California 90095-1662, USA.
E-mail: ederobertis@mednet.ucla.edu

Essay

Vision and the organization of behaviour

Jochen Zeil, Norbert Boeddeker
and Jan M. Hemmi

What do visual neurons compute? A recent review [1] states that current models of the primary visual cortex (V1) of mammals explain less than 50% of neuron response variance and that "as much as 85% of V1 function has yet to be accounted for". In this essay, we shall consider some of the essential facts of natural vision and argue that the organization of behaviour plays a crucial role in shaping the design of visual neurons. We conclude that the specific movements and perspectives of animals need to be taken into account when using natural images or image sequences in the analysis of visual processing in neurons.

Under natural conditions, vision operates in a closed loop — the distribution of light across the retina constantly changes as we move. This intimate coupling between vision and behaviour has profound consequences for the design of visual processing mechanisms, the organization of behaviour and for the way we study both. Nervous systems have evolved under natural conditions to compute behaviourally relevant information and certain aspects of vision, especially motion vision, therefore need to be studied from the perspective of freely behaving animals. Yet, in most cases, our neurobiological knowledge is gathered in open loop experiments, with visual systems being disconnected from behavioural feedback. Most of what we know about the mechanisms of visual information processing has been gathered in abnormal situations where an animal's visual system does not experience its normal input stream. The consequences of this basic limitation are slowly becoming clear: the responses of neurons differ, depending on whether they are confronted with abstract or with naturalistic stimuli (for example

[2,3]); neuron coding properties depend on behavioural state, with the activity of motion-sensitive neurons, for instance, conveying information on either self-motion or on nearby objects depending on whether the animal currently rotates or translates (for example [3]); and as a consequence, the requirements of visual processing are reflected in the organization of behaviour (for example [4]).

On the one hand, behaviour is organized in such a way that it subserves visual information processing, creating favourable conditions for image analysis. Visual and non-visual control systems stabilize the position and orientation of the eyes in space (reviewed in [6]). The importance of these controls for image interpretation can be appreciated by considering the efforts we make to keep cameras horizontally oriented and still. On the other hand, movement itself produces visual information that would not exist without it: in fact, movement is a prerequisite for vision, because photoreceptors rapidly adapt to similar activity levels. Moreover, the apparent movement of objects as seen from the perspective of a translating observer carries information on their relative distances, as can best be appreciated when looking out through the window of a travelling train.

But mobile vision generates problems. Photoreceptors do not respond infinitely quickly to changes in light intensity, and fast movements of the visual system, as every photographer knows, lead to motion blur, a reduction of contrast in the image and a loss of resolution [7]. One way of counteracting blur is to adjust the dynamics of photoreceptors to the speed of locomotion. Fast-flying animals do indeed have faster photoreceptors than slowly flying ones, demonstrating that the interdependence of vision and behaviour starts at the level of photoreceptors [8]. A second strategy is to keep the visual system still for most of the time: in birds on a moving perch, the neck, hip and leg muscles all cooperate in keeping the head (and the eyes) fixed in space between rapid changes in position [9] (Figure 1). The effect is similar to what many hovering insects achieve. Their superb manoeuvrability allows them to move

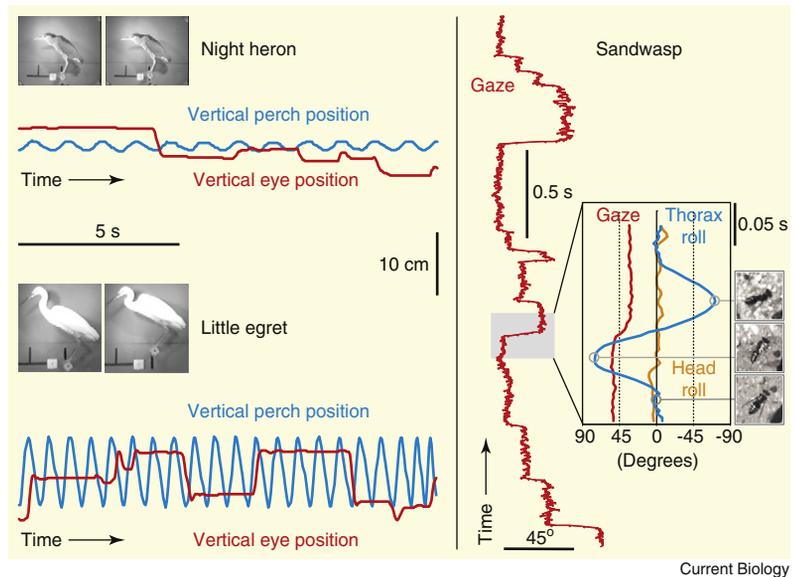


Figure 1. Gaze stabilization in birds and insects.

Left: A night heron, *Nycticorax nycticorax* (top) and a little egret, *Egretta garzetta* (bottom) standing on an oscillating perch. Time series show vertical eye position (red) and vertical perch position (blue). Note long periods of perfectly stable eye position, interrupted by brief re-positioning movements of the head. Data extracted with permission from video clips kindly provided by Gadi Katzir and Danny Weihs (Department of Biology, Oranim-University of Haifa, Tivon, Israel). For further information see [9]. Right: Horizontal gaze direction and head roll stabilization in a sandwasp (*Bembix* sp). Inset on right shows thorax and head roll movements during a fast sideways translation to the left (see pictures) and a concurrent saccadic gaze change to the right.

fast in any of the translational degrees of freedom — forward, backward, sideways, up and down — enabling them to maintain a position in space even in the presence of wind.

Even when moving about, many birds use their flexible necks to keep head position fixed in space for most of the time, thus truly stabilizing the retinal image while in motion. They advance the head in a rapid forward movement to reach a position ahead of the body where it is then fixed in space again while the body catches up [10]. Animals without long flexible necks, but with mobile eyes can only stabilize the image of an individual object on the retina during locomotion by smooth pursuit eye movements. The resulting image stabilization is local, however, not global, because tracking eye movements create a pivoting parallax field, in which the foreground and the background move in opposite directions (for example, [11]).

Depending on the lifestyle and the needs of animals, there are thus a number of strategies to cope with these disadvantages of mobile vision [7]. Keeping still is one option; if that is impossible, keeping still for most

of the time is the next best strategy; and if the animal has to move, the resulting optic flow needs to be carefully controlled to take advantage of the opportunities of mobile vision.

A moving visual system experiences two kinds of image motion patterns, one due to the rotation of the system (rotational optic flow) and one due to its translation (translational optic flow) (reviewed in [12,13]). The two optic flow components have different information content: rotational optic flow is generated by orientation changes around the roll, yaw and pitch axes; it is depth-invariant, image displacements have uniform directions across the visual field and amplitudes are independent of the distance of objects. Rotational optic flow thus does not carry information about the world, but can only be used to estimate rotations of the visual system itself. In contrast, optic flow generated by a pure translation depends on the viewing direction relative to the direction of heading and on the distance of objects in the world. For a given linear speed close objects appear to move faster across the retina than distant objects and motion vectors appear to emanate

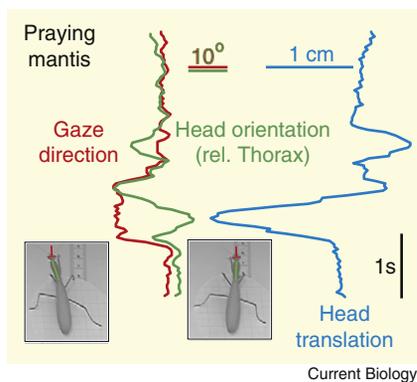


Figure 2. Peering in the praying mantis, *Mantis religiosa*.

As the animal sways from side to side (blue trace), gaze direction (red) is kept constant by counter-rotation of the head (green). Data extracted with permission from a video clip kindly provided by Karl Kral (Institute of Zoology, Karl-Franzens-University, Graz, Austria). For details see [17].

from the direction of heading [12]. The informative structure of the translational flow field, however, is degraded by any simultaneous rotation, because both flow field components superimpose.

For a number of reasons, the separation of rotational and translational components of optic flow is not trivial, and animals invest substantial sensory and computational resources for the sole purpose of minimizing rotational optic flow. Solutions for this fundamental task have evolved many times independently and can be surprisingly similar – swimming crabs, for instance, possess semi-circular canals [14] very much like the ones found in vertebrates, which serve to detect rotational acceleration. Other animals have inertial sensors that are very different from the ones in our inner ear – like the modified wings in flies and Strepsiptera [13]. These oscillating clubs (halteres) are subject to Coriolis forces within the rotating system of the body, which are registered by arrays of strain sensors at the base of the halteres and serve to stabilize flight and head orientation around the three rotational axes. Many other flying insects however lack such specialised inertial sensors and it is not entirely clear how they stabilize gaze in flight (reviewed in [13]). Depending on the mode of locomotion and on the most salient information provided by their particular environment, animals employ different

cues to different degrees for the attitude control of their bodies and eyes. Eye stabilization in swimming crabs, for instance, is mainly driven by the vestibular system, in rock crabs by statocysts and by leg receptors sensing unequal loading, and in crabs that live on mudflats, by the visual system [15].

Animals cannot always avoid generating rotational optic flow, but they confine it to short periods of time, by changing their gaze in fast, open-loop movements. These saccadic eye, head or body movements are similar across different species of animals (reviewed in [7]) and serve to compress the visual system's exposure to rotational optic flow into very brief moments in time. In the case of blowflies, these gaze changes involve coordinated head- and body movements, whereby head saccades are faster and shorter than body saccades [16]. Between these changes in gaze direction the head is stabilized around the three rotational axes of rotation (see Figure 1).

Once animals have control over the nuisances of closed-loop vision, behaviour can be recruited and adapted to generate visual information by actively shaping optic flow. Birds, lizards and some insects, for instance, perform deliberate movements that lead to particular patterns of image motion for the purpose of absolute or relative distance judgements. The most obvious of these are the peering movements performed by locusts and praying mantids when investigating a scene or just before deciding to jump (reviewed in [17]; see Figure 2). As in some birds [18], these coordinated body and head movements carry the head along a path perpendicular to the direction of gaze, leading to differential image motion that separates close objects that appear to move fast, from distant ones that appear to move more slowly.

Flies do something quite equivalent in free flight: between fast saccadic changes in gaze and flight direction, they tend to move along straight lines while keeping gaze direction constant, a strategy that leads to a pure translational flow field with a constant orientation in the visual field (reviewed in [19]). Why is it important to control the orientation of the optic flow field? One possibility is that it facilitates

the computation of depth from optic flow, allowing for instance image expansion to serve as a trigger for the rapid turns [20]. The saccadic gaze strategy also helps with distinguishing self-generated image motion from that generated by moving objects and enables motion-sensitive visual neurons to extract information on the spatial layout of the environment [3,4].

A different pattern of image motion is generated by animals like ground-nesting wasps pivoting around novel objects [19] or by a human observer fixating objects away from the direction of heading [11]. These movements produce shearing parallax fields on the retina in which the point of fixation is stationary, objects beyond this point appear to move with the direction of pivoting and objects between the observer and the fixation point appear to move against that direction.

Arguably the most elaborate sequence of insect behaviours in the service of visual information processing are the learning flights performed by foraging wasps and bees when leaving their nest for the first time or when leaving a newly discovered food source (reviewed in [21]). The initial sections of these flights have the insects facing the goal while backing away from it, pivoting around it in ever increasing arcs and gaining height and distance at about the same rate. They move along these arcs in short straight flight paths during which gaze direction is kept constant, but which are linked by saccadic head movements against the direction of pivoting that change gaze direction and lead to subsequent changes in flight direction [22]. During the straight segments of flight, the insects thus experience a translational optic flow field, much like the peering locusts do, which may allow them to judge the distance of landmarks relative to the goal.

The examples considered so far illustrate how behaviour generates visual information that relies on patterns of image motion. There are likely to be many other cases, however, in which the organization of behaviour is driven by visual information processing needs. One such example is vigilance in birds, where ground-feeding birds have a need to 'look up' from time to time, in order to update their knowledge about the world and to scan for

predators (for example [23]). Vigilance requires a behavioural switch from viewing the ground and pecking to an upright stance that clears the head of vegetation and frees it for scanning movements. It also improves perspective by increasing the area of ground plane that can be seen and aligns the visual field so that the celestial and the terrestrial hemispheres are mapped onto the retina in a defined way [24].

A second example is the organisation of anti-predator responses in refuge-using animals, like fiddler crabs, which can be understood as a result of an optimization, balancing risk and costs while increasing the reliability of information [5]: the crabs first 'freeze' when becoming aware of a predator, then run towards the refuge ('home run'), where they may remain at the surface to continue observing the approach ('burrow vigilance'), before deciding to enter the refuge ('burrow entry') or to continue activity on the surface. In the first case, the crabs remain underground for variable amounts of time ('burrow time') and upon surfacing again survey the scene ('resurfacing vigilance') before eventually deciding to continue activities.

Beside risk-reduction, each of these stages also has distinct consequences for visual information processing: 'freeze' reduces blur; the 'home-run' may allow distance judgement by motion parallax; 'burrow vigilance' allows the crabs to collect information that is more robustly correlated with risk, like the direction of approach of a predator; 'burrow entry' and 'burrow time' are associated with nearly complete loss of information about predator activities on the surface; and 'resurfacing vigilance' serves to update that information. This interdependence of visual information processing and behaviour is likely to be ubiquitous in the context of predator avoidance and challenges us to not only consider such behavioural sequences as being visually guided, but also as behaviourally guided information processing events.

Behaviour thus plays an important and active role in visual information processing, making it difficult to extrapolate the response properties of visual neurons in restrained 'preparations' to their coding

properties in the freely behaving animal. For instance, although the distribution of local directional sensitivities throughout the receptive field of an optic flow processing interneuron in the fly is fairly robust, its global response properties may depend on the current flight manoeuvre and on concurrent signals from other modalities [13]. Recent insect work shows that it is crucial to know how animals actually move under natural conditions and what visual input they receive. Because vision is behaviourally guided, the organization of behaviour has fundamental implications for what neural activity actually represents: depending on behavioural state, the activity in the same motion-sensitive neuron, for instance, may signal the direction of turns or the presence of a close object (for example [4]). The design of photoreceptors [8] and of visual interneurons [25] reflects the way in which the signals they receive are shaped by behaviour and the way in which the information they extract is used in coordinating behaviour in turn [26]. In order to understand the intimate relationship between vision and behaviour, an effort needs to be made to reconstruct vision from the view-point of behaving animals in their natural environment. The future of visual neuroscience thus lies in going natural; after all, to paraphrase a famous quotation by Theodosius Dobzhansky, nothing in vision research makes sense, except in the light of behaviour, ecology and evolution.

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ARC Centre of Excellence in Vision Science and Centre for Visual Sciences, Research School of Biological Sciences, The Australian National University, PO Box 475, Biology Place, Canberra ACT2601, Australia. E-mail: jochen.zeil@anu.edu.au