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What can Engineers Learn from Insect Vision? [and Discussion]

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What can engineers learn from insect vision?

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SUMMARY

The mechanisms of insect vision contrast sharply with those of contemporary artificial visual systems and yet present a compelling example of what is possible with a stripped-down system of minimal weight. The first step is to describe the components with the aid of behaviour and identification of neurons. Electrophysiology has shown that numerous parallel pathways and superimposed maps, with both local and global mechanisms, are essential for the visual processing. Groups of neurons characteristically have partially overlapping fields when plotted in the dimension where they make discriminations. For example, neurons responding to motion of edges have large fields which partially overlap when the response is plotted against angular velocity, position of nodes of expansion, or inclination of moving edges. This exploitation of field overlap is one of many lessons to be learned. The advantages of 360° vision, and the ancient success story of implementing it with a compound eye, are related to the stabilization against rotation and the smooth control of locomotion. Form vision and colour vision are then improved at places on the eye where relative motion is reduced, but the 360° vision makes local gain control essential.

The analysis of honeybee vision demonstrates that local spatial resolution is excellent but the spatial layout of a pattern, region by region, is not so well discriminated. This result suggests that responses of numerous local templates are lumped together to give an aggregate quality of each local region, just as ratios of responses of different receptor types make colour discrimination independent of pattern intensity and rate of flicker. Extending this ratio mechanism to form vision works in the opposite direction from the combinatorial explosion of exact spatial distributions of pixels in pattern analysis. Insect vision works with groups of neurons which respond simultaneously, and this activity of neuron groups is able to fit the combination of visual features, although each neuron alone is inadequate for a discrimination.

1. INTRODUCTION

Insects provide us with a readily accessible existence theorem showing that low-level natural vision can function in minimal circuits. A serious problem is to discover what kind of a system insect vision actually is, and how the neuronal mechanisms implement the performance of the whole animal. Here mathematical models are of little help, because they do not even reveal the components. Insects fly expertly among obstacles in a three-dimensional cluttered world, chase mates or prey, or land and take off to escape capture. The lesson for robot vision is obvious: considering how underdeveloped is our technology for visual processing, almost anything we can learn from insect vision is likely to be of use. Their performance shows us what to attempt but not how to do it; for that, they have many clever mechanisms for us to discover.

There is no single methodology in this task but one thing is certain; neural systems do not work by moving around exact algorithms and logical instructions, as computers do. Recent useful insights into insect visual performance have come from studying whole animals in their visual tasks, such as the use of landmarks and discrimination of their form by bees, estimation of range by peering locusts and by bees in flight, and from observations of rotation and translation by hovering or floating insects. The electrophysiology of neurons of the optic lobe is particularly instructive because the properties of neurons in parallel turn out to be unexpected, often difficult to describe and always challenging to interpret. We would like to separate the key mechanisms inside the processing system, but it is hard to discern from neuron recordings how vision is actually achieved, because the neurons work in groups with overlapping fields. Modeling helps, but so far no-one has actually constructed a visual processing system based upon models of higher-order visual neurons. This delay is due to our lack of truly parallel hardware. More effort goes to copy human vision and to rely upon the video-camera, frame grabber and serial computer which operates by heavy computation looking at pixels step by step across the screen. Insect vision brings us back to the basic mechanisms of neurons.

2. VISUAL PROCESSING

We regret that we have no technology like the nervous system and lack analogies to assist our understanding.

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Humans tend to look at one thing at a time, think of space geometrically and to attribute one effect to one cause. We think of vision as a kind of repeated topological mapping that somehow reconstructs an image like our own. Our computers require long trains of exact numbers whereas nervous systems rely on the choice of lines and their combinations. Real nervous mechanisms force us to think in new ways, notably to consider how neurons in parallel divide the work between them in time as well as space and generate unexpected properties by their combinations. Nervous systems can easily add a new pathway or take over old neurons to separate off a new function, and the recombination of nonlinear pathways rapidly generates complex properties from simple components.

The electrophysiology of insects in general reveals that the vast sensory inflow causes graded excitations and inhibitions of numerous local interneurons in

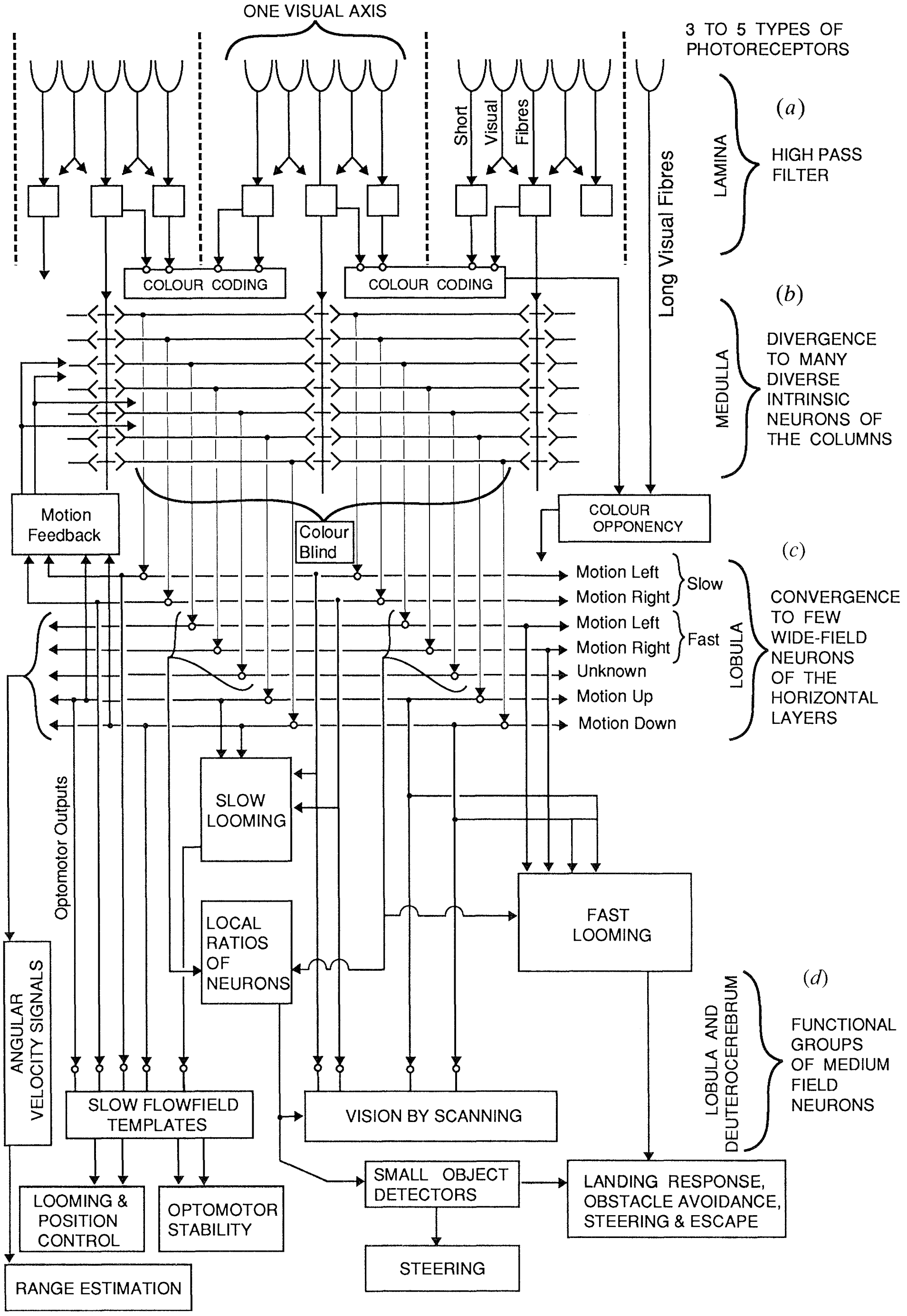

Figure 1. Summary of insect visual processing channels. (*a*) Angular sampling at retinal level by 3 to 5 spectral types of receptor on each visual axis (which are separated by dashed lines). The lamina monopolar cells act as a high pass filter at lamina level. (*b*) Divergence at the medulla to many small neurons on each visual axis. (*c*) Convergence upon neurons which gather data of different types from different combinations of medulla neurons. Neurons act in overlapping groups, and they do not each recover the individual features of the image. Combinations of local groups generate a variety of specific task-oriented responses.

parallel arrays which interact among themselves in multidimensional networks. When a temporary threshold is reached by a local group of interneurons, they set off impulses in patterned groups of premotor interneurons, and eventually control organized responses of groups of muscles. These are all parallel arrays from start to finish. We find this basic plan also in vision. The array of local interneurons expands in the medulla and then converges again in the lobula (figure 1). We find simple thresholds of features such as direction, darkening, expansion, or their ratios, which set off the optomotor responses to flowfields, the escape response to shadow, the landing response to expansion or the steering response to avoid or catch objects in flight. The advantages of numerous neurons with simple thresholds are their short latency and the endless possibility of modifying and adding more modules in parallel.

Parallel processing

Behind each facet lies a small group of eight or so receptor cells of two main types, six with short axons that end upon second-order neurons of the lamina and two with axons that run to the next layer, the medulla (figure 1*a*). These receptors are usually of three colour types, ultraviolet, blue, and green. The principal second-order neurons of the lamina (the LMC cells) act as a high-pass filter and preserve the maximum spatial and temporal contrast (getting brighter or darker, or no change). The next layer, the medulla, has a column of about 50 small neurons on each visual axis. Here the signal simultaneously diverges (figure 1*b*) into what must be a large number of detectors of local features formed by combinations of neighbouring pixels at successive instants (Horridge 1991). This array then converges in several different ways in the next region, the lobula (figure 1*c*). The large-field directional motion-detector neurons collect the local detection of horizontal and vertical motion; other large-field object detector neurons collect non-directional motion of a small contrast anywhere in their field, often irrespective of background motion.

At all levels, right through to the motor neurons, there are numbers of neurons in parallel, besides the extraordinary divergence in the medulla. The elementary reason is that the projection of the retina necessarily breaks up the visual world by simultaneous sampling. A better reason is that at each point in the image there may be a local feature which cannot be identified by a single visual axis because inputs on one axis respond only to the total light absorbed and cannot relate that temporal modulation to a particular direction, pattern or colour. The general explanation of why visual processing is done by groups of neurons can be seen from figure 2, where a neuron field detects a figure embedded in noise. It is intuitively apparent that the best signal-to-noise ratio is given by a field that exactly matches the shape that is to be detected, no matter how many dimensions it occupies, but a specific field for each possible target soon becomes unwieldy. Images are so diverse that the only way that different combinations of pixels can be detected is to have different combinations of neurons that each respond to simple local features.

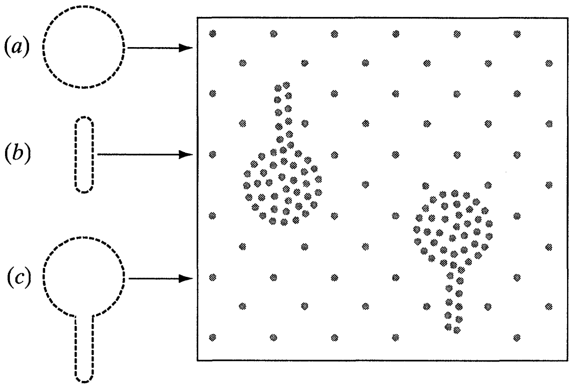

Figure 2. For optimum performance, a feature detector neuron should have a field that matches in shape and size the object sought against a noisy background. However, a combination of fields as in (*a*) and (*b*) would be more suitable to detect the racket-shaped object than the matched field (*c*). This result holds irrespective of the number of dimensions in the stimulus, and helps explain why visual features excite specific combinations of visual processing neurons.

3. HOW DO NEURONS RELATE WITHIN GROUPS

We quickly discern a common plan in the mutual relations between neurons with similar fields in parallel: they overlap in a special way.

(*a*) *Angular overlap of receptor fields*

Vision is essentially spatial sampling in eye-centred radial coordinates by an array of receptors. The special arrangement of a compound eye allows the projections of adjacent receptors in the outside world to overlap, unlike the situation in a camera-type eye, where the receptors must lie side by side. Sensitivity to a diffuse source is thereby increased. In practice we find that the angular sensitivity curves of adjacent receptors cross at about the 50% level of sensitivity. The ideal overlap that combines maximum spatial resolution of the array with maximum lens resolution of the apertures would have more overlap (figure 3*a*) with two receptor fields for each period of the narrowest regular striped pattern that the lens can resolve. Having facets that alternate in parallel rows, however, makes it possible to dispense with half of the visual axes in any one row, because motion is detected between pairs of receptors in different rows at six inclinations on the array (figure 3*c* and see figure 5). The detection of least motion, not most pixel combinations, appears to be the basis of insect vision.

(*b*) *The colour vision model*

With only three types of photoreceptors with peak sensitivities in the green, blue and ultraviolet, many insects, notably bees, have excellent discrimination of

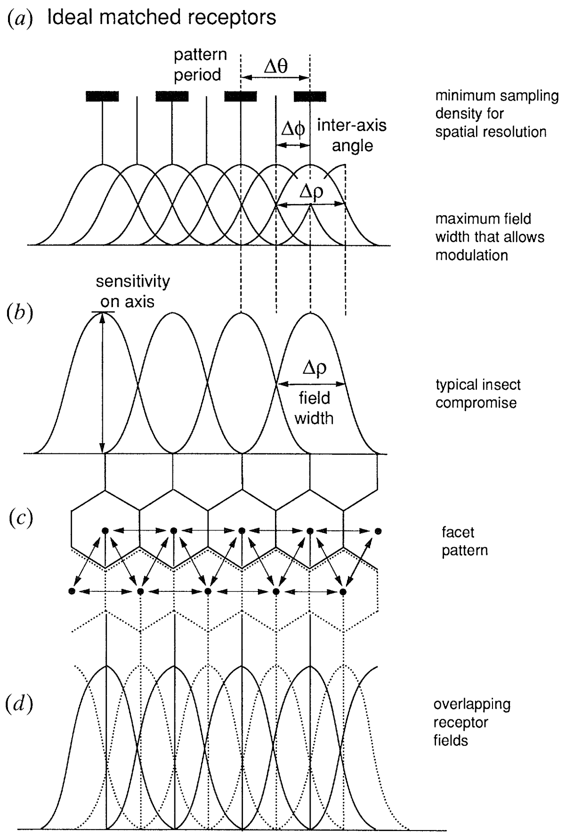

Figure 3. Matching the sampling density of visual axes to the width of the fields of individual receptors. (*a*) With an ideal match, the spacing of the receptor axes just enables the pattern to be resolved spatially, and at the same time the width of the receptor field allows just sufficient modulation from the pattern to reach the receptor. (*b*) Insects frequently have receptor fields which overlap at the 50% level of sensitivity. As a result the facets are fewer and so larger than in (*a*) and the sensitivity on axis is increased. (*c*) Interactions for motion detection spread between rows of facets. (*d*) The partial overlap between horizontal rows brings back the full sampling of vertical edges.

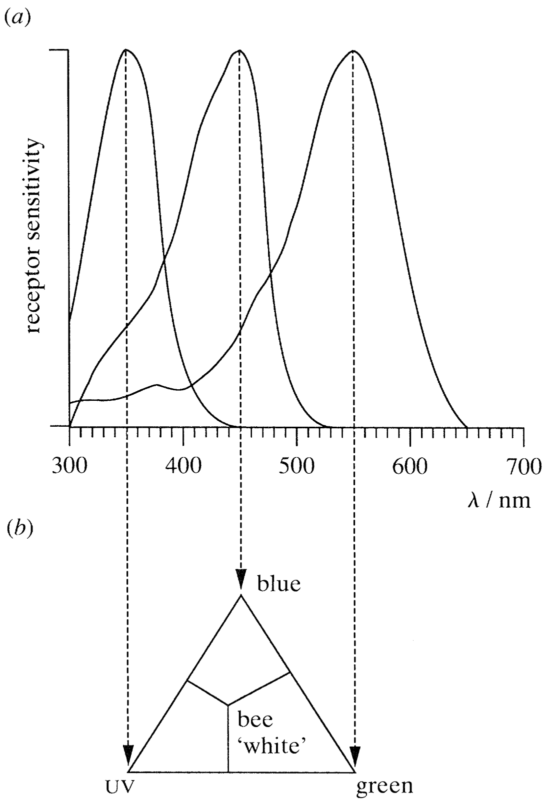

Figure 4. The principle of taking ratios to discriminate colour irrespective of contrast, intensity, pattern or flicker. Relative counts of photons absorbed by three receptor types (*a*) can be represented as a point in a colour triangle (*b*), with white near the middle. The spectral sensitivity curves of the three receptors cross at about their 50% level, and must overlap broadly to make discrimination possible. Even two partially overlapping curves as in figure 6, are sufficient for discrimination over the region of overlap. Compare overlapping sensitivity curves in figures 3, 5*d*, 6 and 8.

spectral colours that differ by only about 15 µm in wavelength. This ability is attributed to a mechanism equivalent to the measurement of the ratios of the responses of the different receptor types, so cancelling out differences in intensity, pattern or frequency of presentation. Bees have difficulty in discriminating intensity and contrast frequency. For this mechanism to function effectively, the receptor spectral sensitivity curves must be broad and must cross at about their 50% level of sensitivity with large areas of overlap to provide a range of ratios as a function of the wavelength mix in the stimulus (figure 4). The ratios of responses should not depend on other variables, a property called univariance. The mechanism allows discrimination of colour but does not allow the wavelength mixture to be recovered from the ratios of the receptor responses. I think this model is also useful for form vision (Horridge 1991).

(*c*) *Sampling of motion direction*

Motion detection in insects is done locally, with high gain for detection of contrast and full use of the spatial resolution available from the overlapping fields of the receptors which are projected exactly to the second-order neurons of the lamina and to columns of the medulla (figure 1*a*,*b*), but motion detection is restricted to adjacent and sub-adjacent visual axes. The electrophysiology of the actual directional mechanism still eludes us because recording from the motion detectors is too late, and the input pathways into the motion detectors do not identify themselves. Motion detection along the three rows of facets at different angles in the hexagonal facet array (figure 3*c*) has to be integrated with different weights into four sets of horizontal and vertical wide-field directional motion-detector neurons (figure 5).

It is essential to have local high-gain motion detection repeated for every visual axis, but this design has several disadvantages. First, the directionality of a bi-local motion detector (one with two adjacent inputs) means that when an edge passes, the interval between the two inputs is a function of the direction of the edge (van Hateren 1990). Secondly, local motion detection tends to be noisy because adjacent receptors inevitably have similar responses, but the detection of motion depends on the timing of the small differences

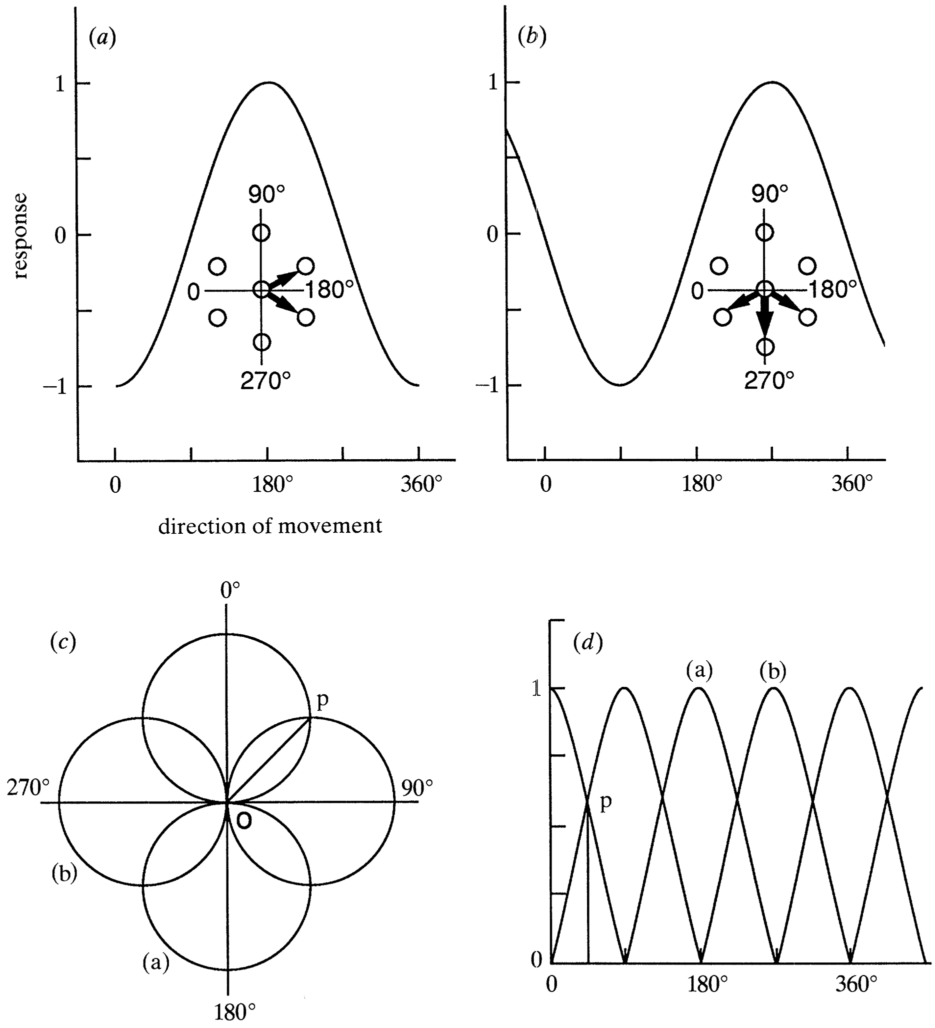

Figure 5. Postulated one-way interactions between adjacent visual axes in the hexagonal array of facets to produce the directional sensitivity of the four sets of motion-detector neurons, which are known to follow closely the sine and cosine of the direction of motion. (*a*) The directional sensitivity curve produced by summing interactions towards the right at 150° and 210° to the horizontal is almost a sine curve. (*b*) That produced by summing interactions at 210°, 270° and 330° is almost a cosine curve. (*c*) The four large-field orthogonal directional sensitivities plotted in radial coordinates. (*d*) As in (*c*) but plotted to emphasize the partial overlap of fields. Compare figures 3, 4 and 8. (Redrawn after van Hateren (1990).)

between them. Thirdly, unit motion detectors respond to every edge that passes and therefore their summed responses are dependent on the pattern, and give a measure of contrast frequency, not pattern velocity. For detection of motion in artificial vision, almost any local nonlinear directional algorithm behaves as described above.

A single algorithm for detecting directional motion by integration of the inputs on adjacent visual axes is not necessarily realistic when there are large numbers of neurons in parallel, each responding to what passes its own field of view. Also, there is no time for taking averages over time, and the response depends on choice of neuron. There is some evidence that the process is not pure algebraic multiplication and that black–white and white–black edges are processed separately (Horridge & Marcelja 1990, 1991).

(*d*) *Velocity sampling*

Many responses of insects in flight seem to rely on measurements of range which depend on an immediate estimation of angular velocity irrespective of pattern, number of repetitions, contrast, intensity, colour, edge polarity or inclination, or period over which a measurement can be averaged (Srinivasan, this symposium). Again, the trick available to insects is very instructive; different neurons have partially overlapping fields when their responses are plotted against velocity (figure 6). We found 'fast' and 'slow' types in four groups of insects (Horridge & Marcelja 1992). We already have colour vision as a model for the immediate on-line discrimination of colour irrespective of other factors, by taking running ratios of the responses of receptors with different spectral peaks, provided that the same ratios are maintained even though other factors change. In the case of motion detection, the ratio of the fast and slow responses, over the middle part of the range, is a measure of the velocity irrespective of any other factor that we have tested.

As described below, the main function of directional

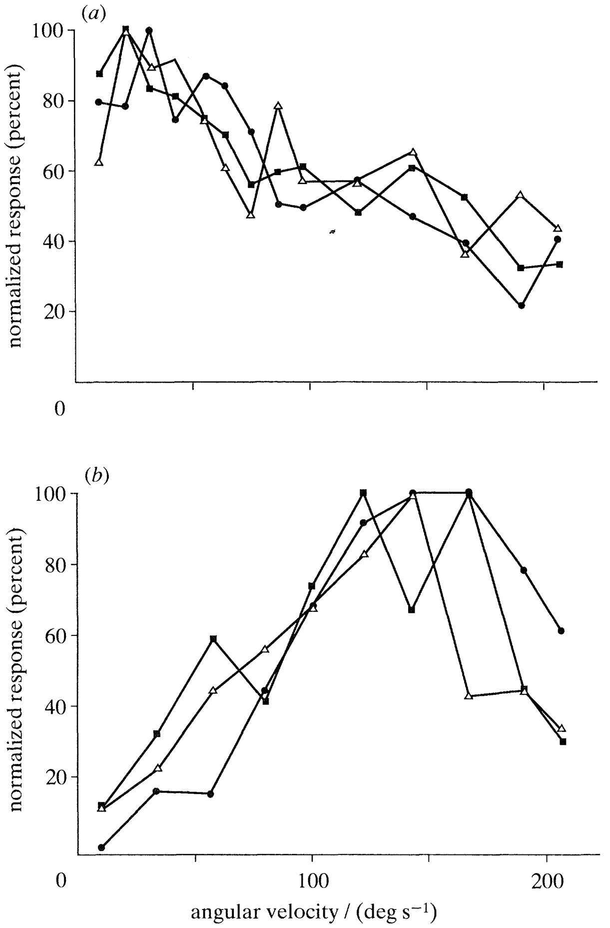

Figure 6. Responses of three (*a*) slow and (*b*) fast neurons of the common Australian dragonfly (*Hemicordulia tau*) to different velocities of a regular striped pattern of period 11·5°. The neurons are recorded in the deuterocerebrum just lateral to the oesophageal canal. They descend the ventral cord to the thorax as part of a group carrying information about directional large-field motion.

motion detectors may be to respond only to direction, so that the qualities of the flowfield, and especially the positions of nodes of expansion, can be immediately signalled by overlapping groups of ventral cord neurons. Local neuron groups would then have outputs in five states, leftwards, upwards, stationary, downwards and rightwards, and two polarities of edge. The separation of slow and fast neurons then enables the nodes of expansion to be classified as slow or fast, the first indicating approach of distant objects, the latter having more urgency because indicating nearer objects. These ideas fit well into the general design which supports 360° vision and short latency response by choice of neuron group.

(*e*) *Figure–ground sampling*

Another set of large-field neurons in the deep optic lobe, mainly in the lobula (figure 1*c*,*d*) respond to small dark objects moving in any direction but not to motion of the whole background. Groups of neurons continuing in the ventral cord have rather similar properties and large overlapping fields (Olberg 1981). They do not obviously divide the visual world into regions, and they respond in different ratios and different combinations to particular features of interest in the insect's repertoire. Stabilization being catered for elsewhere, these are the neurons which see objects irrespective of motion. They must have inputs from groups of local feature-detector neurons of the columns of the medulla (figure 1*c*) but they are inhibited by high spatial frequency flowfields and large objects. Many of them habituate to a repeated stimulus. The more objects to be seen separately, the more of these neurons would be required. Similar neurons in groups carry the information down the ventral cord to the motor centres. This object-detector system presumably combines with detectors of nodes and shadows and controls rapid steering towards or away from targets or obstacles (Land & Collett 1974; Gilbert & Strausfeld 1991). To do this it has to override the optomotor stabilization system by acting faster (Wolf & Heisenberg 1990), but it does not inhibit the optomotor system because stabilization is still essential while steering. This dual system for steering and for keeping straight on an even keel is probably essential in any control of a moving vehicle.

(*f*) *Separation of channels and their organization*

As in lower vertebrate vision, the separation of motion and colour pathways is instructive for engineers. Insects have colour-blind motion-detector neurons and colour is channelled separately. In primates a comparable separation is found at the level of the visual cortex. The method of processing colour television is totally different because the three colours alternate in a single channel, and motion and colour are inferred by the observer. The examples discussed show that groups of neurons have partially overlapping fields, often with neighbouring fields crossing each other at about the 50% level of sensitivity, when they are plotted along the dimension in which they make discriminations. The model of ratios of responses of three colour types of receptors (figure 4), can be extended to sampling of space, direction of motion, object quality, velocity, and probably more. These groups then become known as separate neuron types; each type is a parallel array forming a kind of map of the outside world in its own domain.

4. MOBILE EYES AND 360° VISION

We ourselves cannot imagine what it would be like to have a fixed eye with vision all round in the horizontal plane, as well as upwards and downwards, because we have a relatively narrow field of view, a very small area for object recognition in and around our fovea, and mobile eyes which fixate. The earliest ancestors of the arthropods, 400 million years ago had 360° vision in the horizontal plane, which could have had three main functions, to detect danger or prey, to detect the ultraviolet pattern of the sky and the horizon for navigation, and, during swimming, to separate translation from rotation by making use of the poles in the visual flow field. These are all good reasons, and 360°

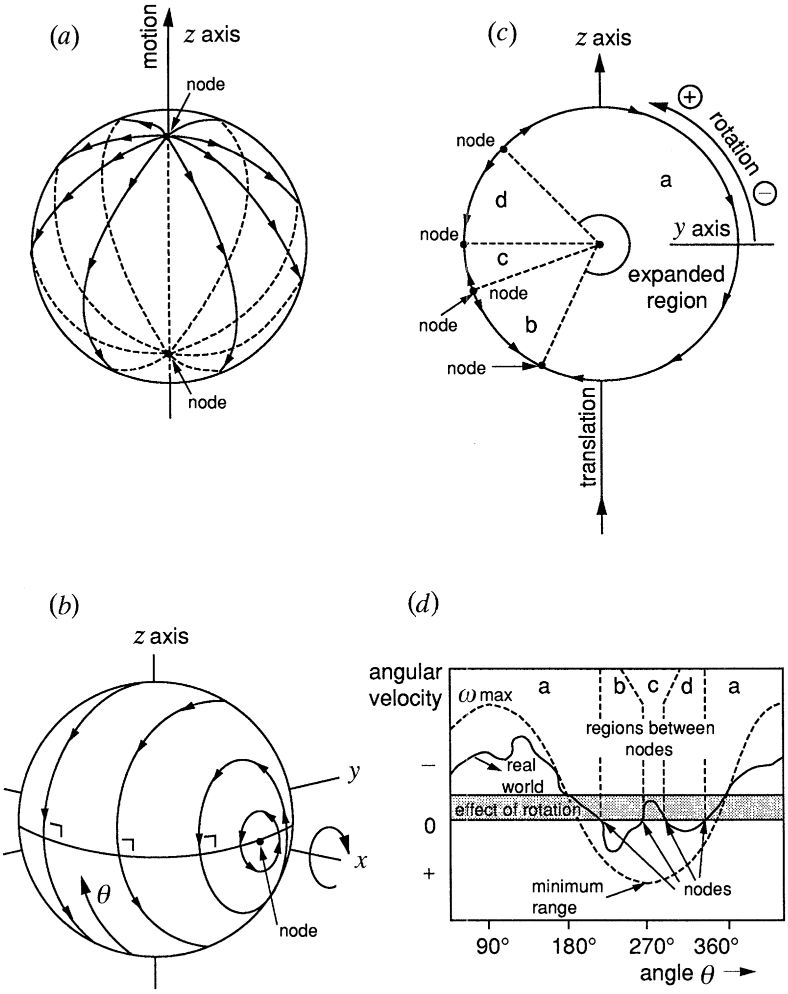

Figure 7. Rotation and translation of the flowfield in angular coordinates centred on the eye. (*a*) Pure translation produces a node of expansion and one of contraction 180° apart. (*b*) Pure rotation about the *x*-axis generates continuous flow in the *y*–*z* plane. (*c*) in the *y*–*z* plane, rotation causes the translation nodes to move closer together (on the left side). The presence of a nearby object causes two other nodes. (*d*) The angular velocities along the equator in the *y*–*z* plane are shown as the solid line. The dashed line is the flow in (*a*) but normalized for the nearest object. The shaded area shows the shift of the coordinates caused by rotation. (Redrawn from Nelson & Aloimonos (1989).)

vision has persisted in many groups of crustaceans and (especially flying) insects. Mobile eyes and 360° vision are not mutually exclusive, as shown by their occurrence together, e.g. in crabs.

In the horizontal plane, 360° vision is desirable for a robot which moves along the ground. A similar functional brief has been implemented in the eye of the water strider, *Ranatra*, which is a predatory insect living on the surface of streams. Each eye has a diameter of 0·5 mm, with a total of 920 facets. There are about 80 facets 2·3° apart in the row around the equator, with a concentration of visual axes in the horizontal visual streak. Dorsally and ventrally the interommatidial angles are up to 10°, so that off the horizon the visual world is not fully sampled (Dahmen 1991). Waterstriders illustrate how many visual axes are needed for the kind of life they lead, keeping station on a flat surface and using their eyes to detect predators, prey or other waterstriders.

(*a*) *Poles of the flowfield in 360° vision*

If locomotion is predictable and the visual world reasonably rich in contrasts, the primary advantage of 360° vision for a freely moving animal is the ease of separating rotation from translation (figure 7). Rotation generates the same angular motion all round the equator of the motion, and can be eliminated by subtraction of apparent motion until the residual poles of expansion and contraction are 180° apart. Translation generates opposite angular motion on the two sides and usually along the line joining the pole of contraction to the pole of expansion (Nelson & Aloimonos 1988). Groups of appropriately located directionally-sensitive neurons form templates that extract rotation and direction of translation from expected flowfields irrespective of pattern (figure 8).

We have seen that motion detection is local but noisy, and the only feature detected quantitatively

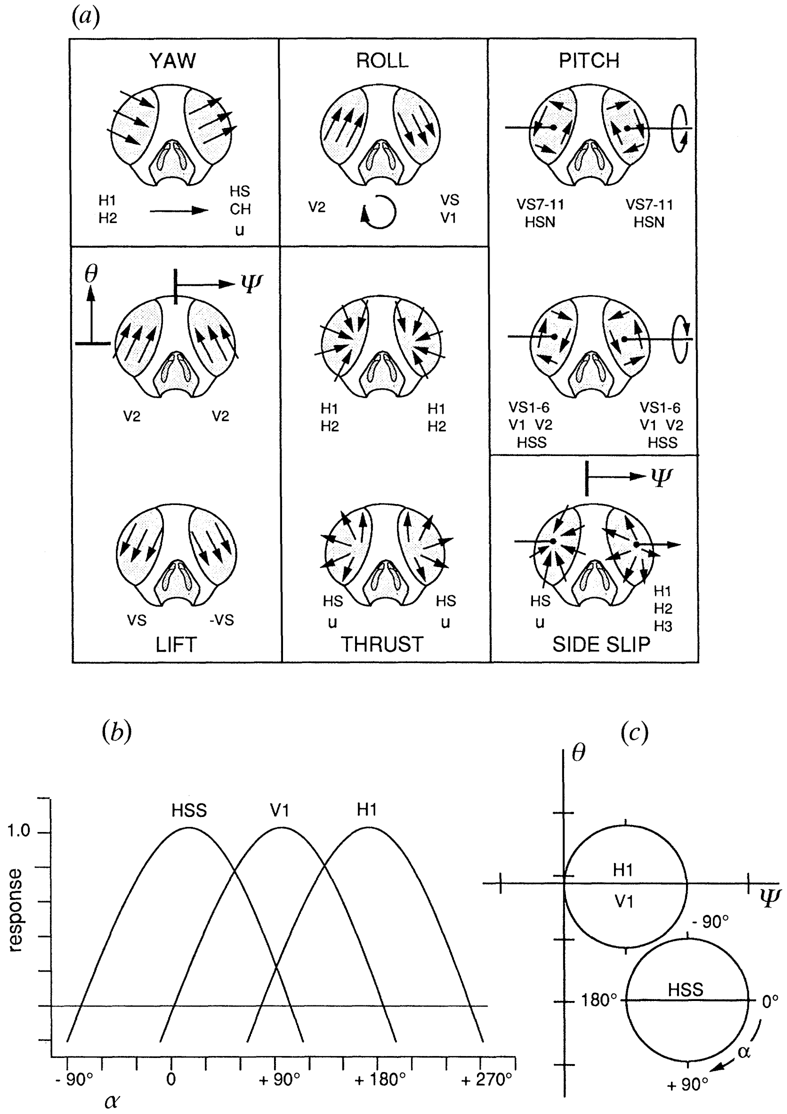

Figure 8. The directional sensitivities of some of the large-field motion detector-neurons of the lobula plate of the fly. (*a*) The principal types of flowfield across both eyes excite different combinations of these neurons. The letters which identify the neurons are placed on the side where that stimulus direction is effective. H, horizontal; V; vertical; U, unknown; HSS, horizontal system, south. (*b*) The overlap of directional fields of three of the above neurons. Compare overlapping fields in figures 3, 4, 5*d* and 6. (*c*) The regions on the eye where the plots in (*b*) were measured. (Redrawn after Hausen (1981).)

and instantly is local direction. For the optomotor stabilization of hovering insects it was proposed that each local region on the eye generates a component of thrust at right angles to the local visual axes and in the direction of the motion (Collett 1980; Kelber & Zeil 1990). We can now add the separation of fast and slow motion, so that nodes of expansion can signal whether a crash is to be expected. This stripped-down data is perhaps sufficient to prevent collisions in flight, provided it has a short enough latency (which the separate optomotor system for control of rotation, yaw, pitch and roll does not). The DCMD neurons of the locust (Rowell 1971) are an excellent example of a pair of neurons which detect fast expansion, and trigger a signal to flight steering motoneurons (Simmons 1980) when the expansion reaches a critical threshold, and which act in opposition on the two sides so that the flying animals turn away from an impending collision (D. Reye, unpublished results). The adequate signal is surprisingly simple. Similarly, the escape response of the fly is triggered simply by a threshold of motion coupled with darkening (Holmqvist & Srinivasan 1991) and there is no need to invoke a computation of even the time to contact.

(*b*) *The optomotor system of large-field directional neurons*

The most obvious neurons recorded in the deep optic lobe of insects respond qualitatively to direction and quantitatively to contrast frequency not velocity, have large fields and a response to either vertical or horizontal or to expansion or contraction of the flowfield. This is the slow system that is associated with the optomotor stabilization of locomotion. As illustrated (figure 8), different combinations of these

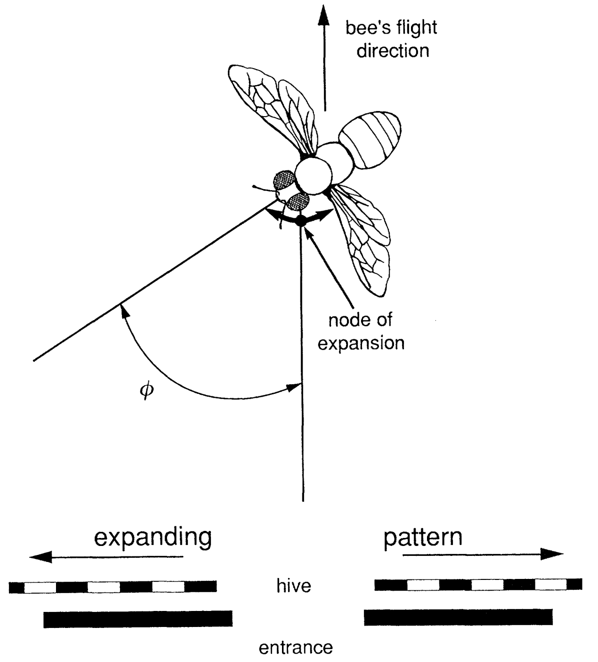

Figure 9. A guard bee hovering in front of its nest entrance. A striped pattern, placed on each side of the entrance, is made to expand causing a node of expansion on the eye of the bee, which responds by moving directly away from the node. This, together with similar experiments, suggests that the node is an indicator for approach or impending collision. Compare figures 7 and 8. (Redrawn after Kelber & Zeil 1990).)

neurons in the deep optic lobe respond to the flowfield along the axes for roll, pitch or yaw in flight, and others respond to expanding or contracting nodes. As a group these neurons provide 'precise information on the actual movement of the visual world with respect to the head in all six degrees of freedom' (Hausen 1981). The information they provide best is not the local motion in each region, and not a mixture of information about objects moving over backgrounds. Groups of neurons act as templates for the expected global flowfield, sufficient to separate rotation of the whole animal from sideways or forward translation (figure 9), and identify the positions of any poles of expansion and contraction. They continue into further groups in the ventral cord (Borst 1991). These neurons should not be considered in isolation as movement detectors but as groups in different combinations.

(*c*) ***Steering, stabilization and saccadic eye movements***

The function of the optomotor response is to reduce rotation so that vision can be processed more easily. At the same time, some motion is essential for vision. Small saccades of the eyes, up to only 2°, cause edges to excite local motion detectors which can then signal the directions of contrasts or measure local spatial frequency. Something like this is necessary to explain many aspects of arthropod vision. In crabs, we observed long ago that the amplitude of continual small eye movements is influenced by feedback from contrasting edges (Horridge & Sandeman 1964). Numerous observations show that freely moving animals respond as if to angular velocity but individual neurons respond only to contrast frequency. A measure of spatial frequency is needed if single neuron responses are to be calibrated in terms of angular velocity. A single saccade of the eye can initiate the appropriate spatial input. Of course, having fast and slow systems also helps (figure 6).

A variety of visual mechanisms are now known which participate in control of locomotion. Flying insects use closing parallax of foreground over background to land on edges (Srinivasan, this symposium). Waterstriders are able to hold a fixed position on a moving water surface by making forward jumps using a single light as a landmark, for which they use short-term spatial memory (Junger 1991). They also correct for rotation, but for that they need an extended contrasting target, especially when they have only one eye (Junger & Dahmen 1991). The fruitfly *Drosophila* is able to get a measure of angular velocity and to see the direction of contrasts, for which small head saccades seem to be essential to create a spatial input (Wolf *et al.*, this symposium). Separation of rotation from translation in insects appears to be done by use of the properties of 360° vision, as described above. Separate pathways for rotation, translation, direction of poles, specialized object detectors and spatial memory, all with different time constants, contribute to chasing or tracking (Land & Collett 1974; Gilbert & Strausfeld 1991) and help explain how an insect can head towards one target and ignore others and also be under optomotor control. These are important problems for engineers of mobile robots to consider. A robot should be able to direct its sensors without falling over, and these reflexes should be in place before it is able to recognize a pattern.

5. LOW LEVEL SPATIAL VISION

(*a*) ***Fixation and spatial memory***

If we compare our recent results on pattern discrimination by bees in flight (Zhang & Horridge 1992), with the earlier work in which the bees were allowed to fixate (Wehner 1981), we see that fixation improves the discrimination of pattern. Many bees, wasps, dragonflies and hoverflies fixate upon objects of interest and may hover for long periods using their eyes. For colour and form vision it may be essential to look through a node where the flowfield is minimized. Looking for landmarks, however, seems to be done while circling in flight. Some insects, e.g. guard bees hovering by the hive entrance (Kelber & Zeil 1990), hawk moths hovering in front of a flower (Pfaff & Varju 1991), and bees using landmarks, remember the angular size of the target to stabilize their range. A temporary spatial memory appears to be very widespread in arthropods, especially for local navigation and station-keeping (Collett, this symposium). I found, long ago, that the eyestalk of the crab *Carcinus* compensates with a movement in the appropriate

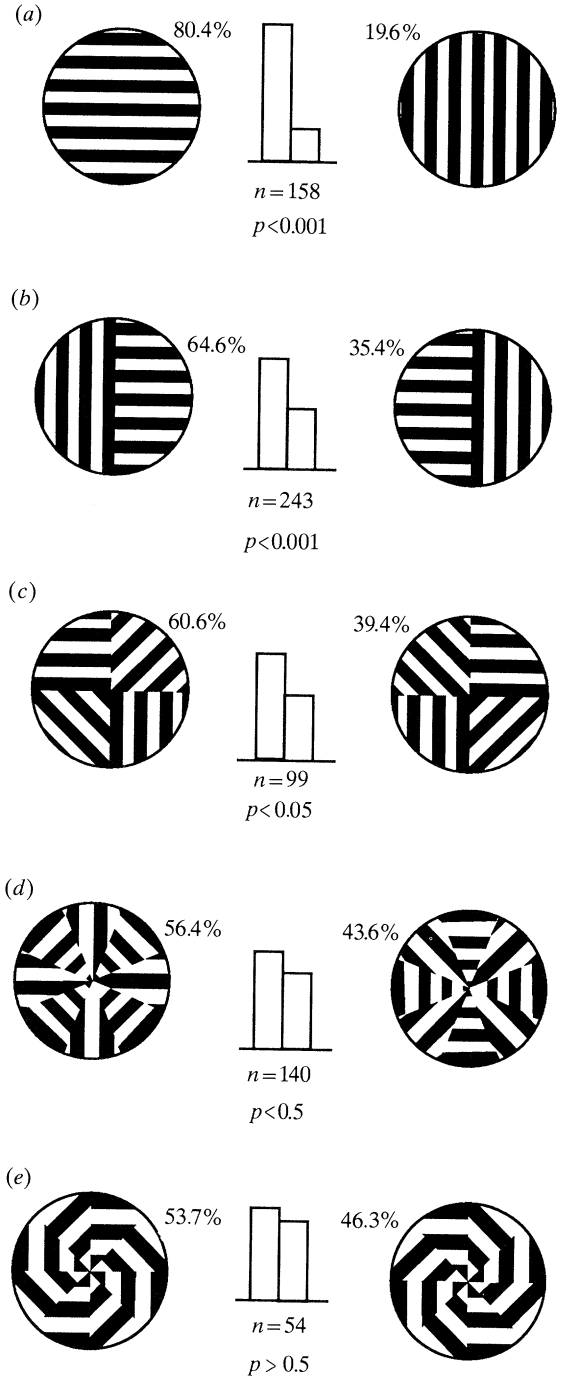

Figure 10. Patterns on a vertical surface used to test visual discrimination of spatial layout by bees, in order of increasing difficulty. Previous tests had shown that the bees resolve the regular stripes and discriminate their angles. The rewarded pattern is on the left in each case, although the side was randomized in the training and tests. The performances are shown in the histograms and percentages. The bees succeed with a wide variety of patterns up to four quadrants but find patterns of eight segments too difficult to distinguish (Zhang & Horridge 1992).

direction if surrounding contrasts are moved by only 1° during a short dark period (Horridge 1966). The response, measured as the linked movement of the other eye, occurs whether the experimental eye is free to move or clamped stationary. This absolute position sensitivity lasting several minutes in the dark, called optokinetic memory, shows that spatial memory can be considered as the basis of motion detection. After all, if a contrast in the visual world suddenly jumps to a new position nearby, its previous stationary location has to be remembered in some way, otherwise the direction it has moved cannot be inferred. Directional motion detection is sensitivity to a contrast not being where it was!

The individual templates respond to extremely simple spatiotemporal features. A single one cannot signal velocity, form or edge inclination but single templates can signal the direction of motion unambiguously, and these templates could be the unit direction indicators required for optomotor stabilization (Collett 1980; Kelber & Zeil 1990). The general idea (Horridge 1991) is that templates have the full spatial and temporal resolution of the retina for detection of motion and edges, but their responses are summed by the hundred to yield ratios for discriminations of spatial layouts (figure 10). This explains how the insect copes with spatial vision without a huge brain to sort out all the two-dimensional spatial combinations of retinal inputs.

(*b*) *Pattern perception*

Insects segment the three-dimensional world by range and parallax (Srinivasan, this symposium) and locate colours. Contrary to the usual accounts, local spatial and motion resolution of motion is quite sharp but discriminations of pattern reveal a poor representation of the spatial layout (figure 10). In some ways bees resemble brain-damaged humans with certain types of visual agnosia. Bees flying over a horizontal target seem unable to relate the coordinates of the target to the directions of local landmarks, so that with flight lines in different directions they are not able to build up a memory of the pattern or recognize it when they return, except by features that are independent of rotation such as the amount of flicker (disruption by edges) or ratio of area to perimeter. Although bees lack the processing required to see the arrangement of a complex pattern, they can recognize landmarks around a food supply or on the distant horizon. Probably this puzzle is merely an extension of the fact that to avoid excess weight they process what they normally need for their visual repertoire but ignore most of the arrangement of a pattern. Insects have diversified their vision, especially object vision, by having more kinds of insects, not new programs in a general-purpose computer.

6. CONCLUSION

The main difference between natural and video-computer vision is that the former has truly parallel channels with partially overlapping fields all the way to the muscle groups, while the latter requires a frame-grabber to reconstitute just one picture from a serial sequence of digits. Insect visual processing, in the later stages, is done by groups of large-field neurons looking at the same regions of the flow-field with partially overlapping fields, and the final outcome depends on the balance of neuron responses. The neurons are not all mixed up, however, and do not form a continuum of variety: there are a number of major types which apparently are concerned with either motion direction, nodes of expansion, object detection, colour, polarization plane of ultraviolet light and estimation of range. Each item of relevant information is not processed in a special neuron: rather, the only way that the visual processing neurons can bring themselves to match the immense variety of visual images is to respond by different combinations within functionally distinct groups of neurons with partially overlapping fields. Each neuron carries a signal that cannot be interpreted by higher level neurons except in the context of the group. We observe combinations of colour-blind neurons that respond to directions of flowfields of various kinds irrespective of contrast, pattern, colour or temporal frequency; there is another direction-blind group that respond to small object motion, irrespective of background, intensity, or shape, and another group with colour opponency irrespective of anything else. These groups tend to become the categorized types of neurons for our present state of knowledge. The visual behaviour has been used to interpret the neuron properties, unfortunately not the other way round, and we are far from being able to trace synaptic circuits or record neuron properties and predict how they function. Modeling so far has been of limited parts of the system and if we are about to build robot vision along insect lines, we had better restrict the Mark I version to very simple tasks.

REFERENCES

Borst, A. 1991 Fly visual interneurons responsive to image expansion. *Zool. Jahrb. Physiol.* **95**, 305–313.

Collett, T.S. 1980 Some operating rules for the optomotor system of a hoverfly during voluntary flight. *J. comp. Physiol.* **138**, 271–282.

Dahmen, H. 1991 Eye specialisation in waterstriders: an adaptation to life in a flat world. *J. comp. Physiol.* A **169**, 623–632.

Gilbert, C. & Strausfeld, N.J. 1991 The functional organisation of male-specific visual neurons in flies. *J. comp. Physiol.* A **169**, 395–411.

Hausen, K. 1981 Monocular and binocular computation of motion in the lobula plate of the fly. *Verl. Dtsch. Zool. Ges.* **1981**, 49–70.

Holmqvist, M.H. & Srinivasan, M.V. 1991 A visually evoked escape response of the housefly. *J. comp. Physiol.* A **169**, 451–459.

Horridge, G.A. 1966 Optokinetic memory in the crab *Carcinus. J. exp. Biol.* **44**, 233–245.

Horridge, G.A. 1978 The separation of visual axes in apposition compound eyes. *Phil. Trans. R. Soc. Lond.* B **285**, 1–59.

Horridge, G.A. 1980 Apposition eyes of large diurnal insects as organs adapted to seeing. *Proc. R. Soc. Lond.* B **207**, 287–309.

Horridge, G.A. 1991 Ratios of template responses as the basis of semivision. *Phil. Trans. R. Soc. Lond.* B **331**, 189–198.

Horridge, G.A. & Marcelja, L. 1990 Responses of the H1 neuron to jumped edges. *Phil. Trans. R. Soc. Lond.* B **329**, 65–73.

Horridge, G.A. & Marcelja, L. 1991 A test for multiplication in insect directional motion-detectors. *Phil. Trans. R. Soc. Lond.* B **331**, 199–204.

Horridge, G.A. & Marcelja, L. 1992 On the existence of 'fast' and 'slow' directionally sensitive motion detector neurons in insects. *Proc. R. Soc. Lond.* B **248**, 47–54.

Horridge, G.A. & Sandeman, D.C. 1964 Nervous control of optokinetic responses in the crab *Carcinus. Proc. R. Soc. Lond.* B **161**, 216–246.

Junger, W. 1991 Waterstriders (*Gerris paludum F.*) compensate for drift with a discontinuously working visual position servo. *J. comp. Physiol.* A **169**, 633–639.

Junger, W. & Dahmen, H.J. 1991 Response to self-motion in waterstriders: visual discrimination between rotation and translation. *J. comp. Physiol.* A **169**, 641–646.

Kelber, A. & Zeil, J. 1990 A robust procedure for visual stabilisation of hovering flight position in guard bees. *J. comp. Physiol.* A **167**, 569–577.

Land, M.F. & Collett, T.S. 1974 Chasing behaviour of houseflies (*Fannia canicularis*). *J. comp. Physiol.* **89**, 331–357.

Nelson, R.C. & Aloimonos, J. 1988 Finding motion parameters from spherical motion fields (or the advantages of having eyes in the back of your head). *Biol. Cybern.* **58**, 261–273.

Olberg, R.M. 1981 Object and self-movement detectors in the ventral nerve cord of the dragonfly. *J. comp. Physiol.* **141**, 327–334.

Pfaff, M. & Varju, D. 1991 Mechanisms of visual distance perception in the hawk moth. *Zool. Jb. Physiol.* **95**, 315–321.

Rowell, C.H.F. 1971 The orthopteran descending movement detector (DMD) neurons: a characterization and review. *Zeit. vergl. Physiol.* **73**, 167–194.

Simmons, P. 1980 Connexions between a movement-detecting visual interneurone and flight motorneurones of a locust. *J. exp. Biol.* **86**, 87–97.

van Hateren, J.H. 1990 Directional tuning curves, elementary movement detectors and the estimation of the direction of visual movement. *Vision Res.* **30**, 603–614.

Wehner, R. 1981 Spatial vision in arthropods. In *Handbook of sensory physiology*, vol. VII/6C (*Vision in invertebrates*) (ed. H. Autrum), pp. 287–616. Heidelberg: Springer Verlag.

Wolf, R. & Heisenberg, M. 1990 Visual control of straight flight in *Drosophila melanogaster. J. comp. Physiol.* A **167**, 269–283.

Zhang, S-W. & Horridge, G.A. 1992 Pattern recognition in bees: size of regions in spatial layout. *Phil. Trans. R. Soc. Lond.* B **337**, 65–71.

Discussion

H. C. Longuet-Higgins (*Laboratory of Experimental Psychology, University of Sussex, U.K.*). I was not altogether clear what Professor Horridge meant by the 'nodes' of the optic flowfield in the case where the insect's eye is rotating as well as translating, and consequently there is no focus of expansion (or focus of contraction). Perhaps he could elucidate this point.

G. A. Horridge. Besides what is said in the paper, perhaps four types of answer are helpful.

1. The facts have not been carefully documented but the nodes must be wandering over the eye during normal locomotion, when rotation is reduced by the strong optomotor reflex.

2. Vision of colour and form are important and improved by the strong stabilization of the eyes.

3. There can be an internal subtraction of the rotation component, at least along the equator during the normal repertoire of locomotion.

4. Specific combinations of neurons, such as those illustrated in figure 8, can perform this on-line elimination of rotation for the expected motions. The general case is irrelevant.