06 PROCESSING AND COLOUR VISION[1]

As we look deeper in the optic lobes, we find progressively altered maps of the visual panorama. Behind the retina there are three successive neural regions, crowded with dendrites and synapses, called respectively the lamina, medulla and lobula (Figures 6.1–3). The neuron cell bodies, with no electrical activity, form a thick coat around them. The regions are separated by tracts of axons and are the result of the growth of the eye at the edges, so that groups of local circuits are reduplicated side by side in columns to form successive arrays of dendrites in layers. From the retina at least as far as the lobula, each successive layer is a retinotopic array with a different function in processing the parallel inputs, so the layers are successive stages of processing. Tracts from the lobula continue to the optic tubercle, the calyces of the mushroom bodies (Figure 6.4) and to motor centres of the neck, and finally in descending tracts to the segmented groups of neurons and motor centres of the ventral ganglia.

The basic unit of the inward pathways is the column of neurons corresponding with each ommatidium, with at least 10 synaptic relays between the visual input and the motor output. We now have neuron recordings at about eight different levels, plus some associated visual behaviour, though not all in the same system or in any one species. Functionally separate types of neurons are found side by side at every level, but few of these relate to clearly distinguishable behaviour patterns. Latencies and temporal properties are also important aspects of visual processing. The mechanisms and neurons that code decisions, long-term behaviour and learning are still obscure.

Processing in the lamina

The lamina of the bee is essentially the pre-processing neuron layer immediately below the retina. The exact 1:1 projection from each ommatidium to each cartridge of the lamina is continued through the lamina to each column of the medulla. The lamina cartridges are packed side by side. Each consists of eight to

10 neurons of which about five are lamina monopolar cells (LMCs), at least three of which have no spikes. Each LMC has a distal cell body, local dendrites in the lamina and an axon crossing in the first chiasma to the medulla (Figure 6.3).

The insect lamina is an excellent example of reasonably complex neural processing that is understood from many points of view, and is best known in the locust, fly and dragonfly. It illustrates how to investigate the central nervous system and what kind of conclusions we are likely to find with existing techniques, but analysis is difficult and our knowledge is incomplete.

Figure 6.1 General arrangement of the parts of the optic lobes and other nervous system of the bee.

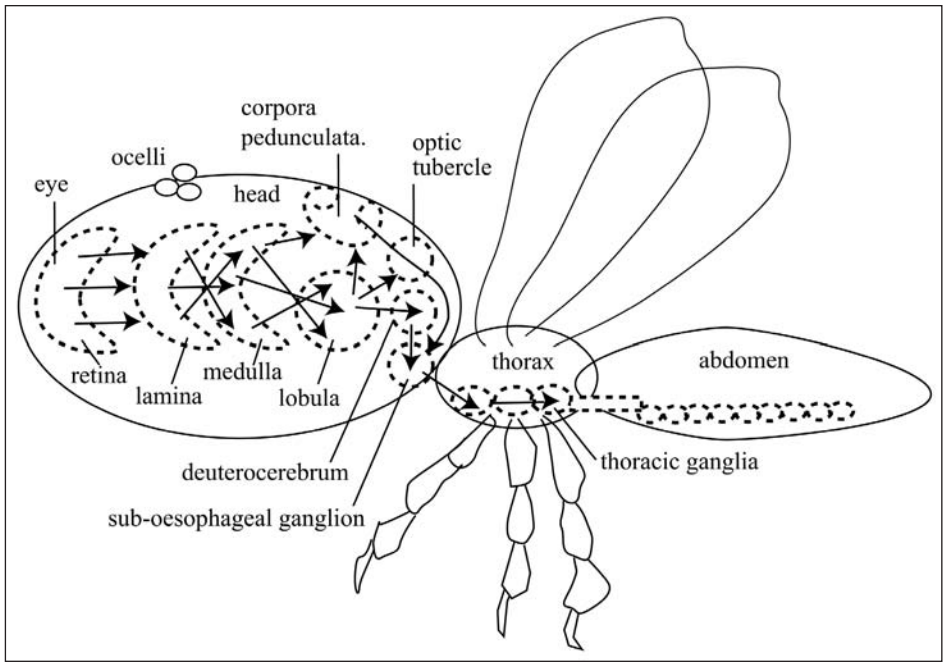


Figure 6.2 General arrangement of the successive regions of the optic lobes, leading into the brain, ventral ganglia and muscles, with the visual feedback loop.

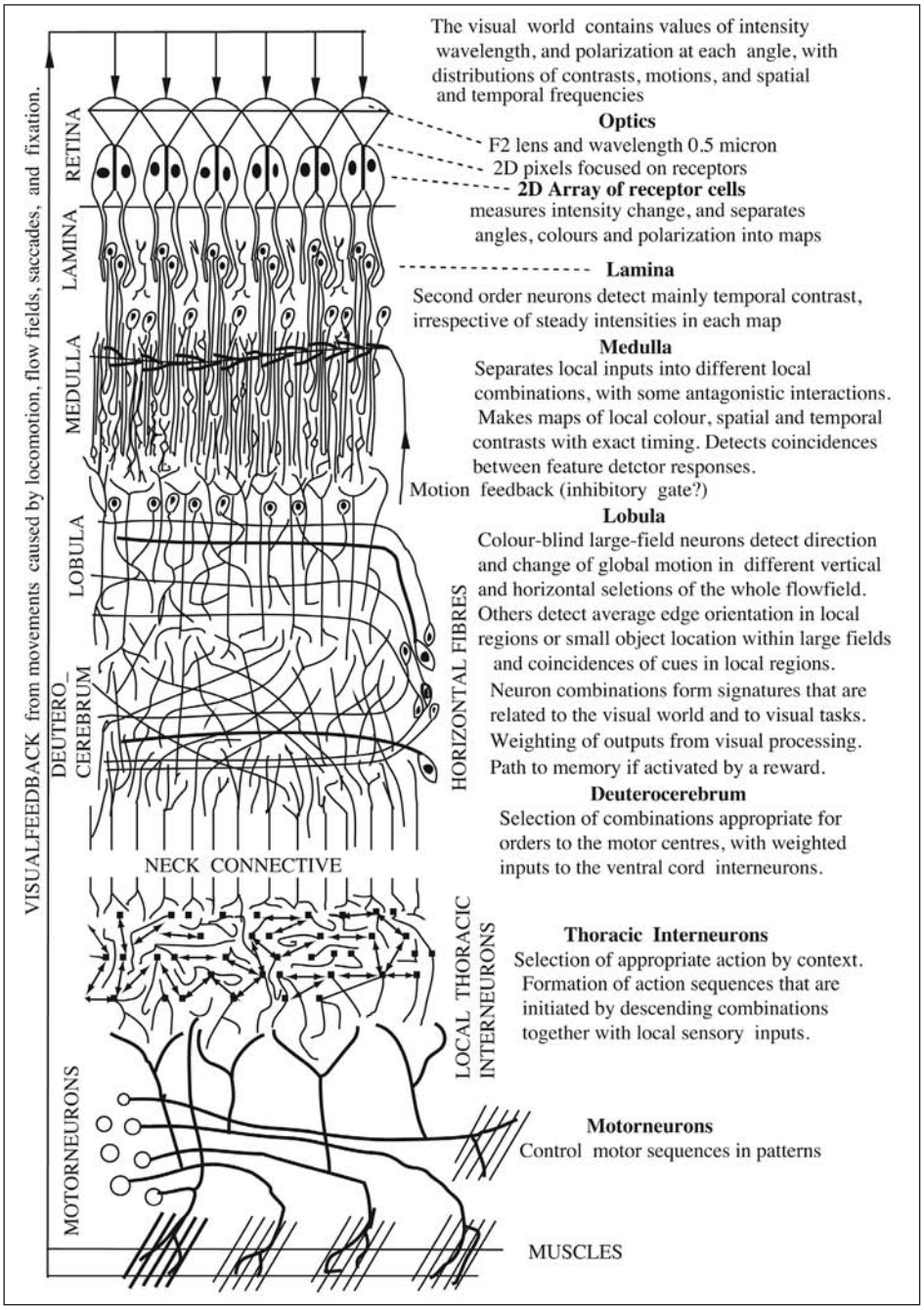


Figure 6.3 A small selection of the neurons forming the columns in the optic lobes of the bee, as described by Cajal and Sanchez (1915).

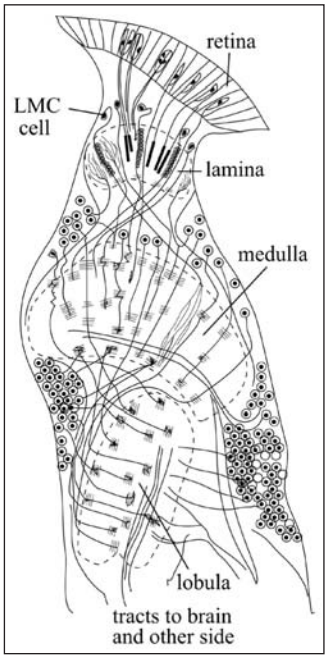
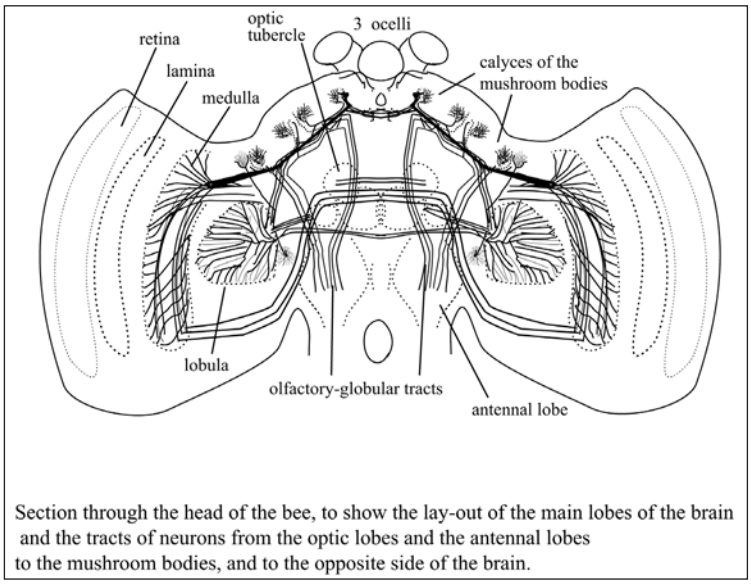
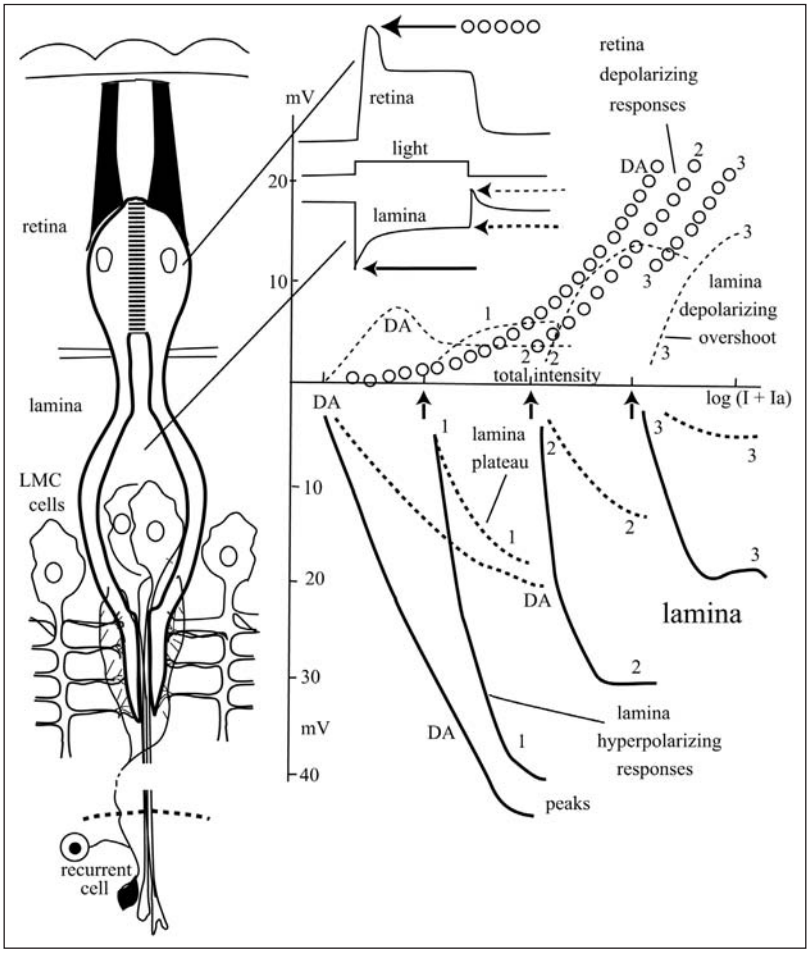


Figure 6.4 Section through the head of the bee to show the layout of the main lobes of the brain and the tracts of ('horizontal') neurons from the optic lobes and the antennal lobes to the mushroom bodies and to the opposite side of the brain.



Source: After Jawlowski (1958) and Hertel et al. (1987).

Figure 6.5 The transformation at the first synaptic layer, the lamina: data for the dragonfly. On the left are the retinula cells and the corresponding lamina ganglion cells, L1 and L2. On the right are the stimulus/response curves of the ret and lam cells at three different states of adaptation. The three background intensities are shown by vertical arrows. The points measured are indicated by the horizontal arrows, with the character of the curve. Absolute values of photon flux (524nm equivalent) are plotted against the membrane potential in millivolts. The curves are numbered with the corresponding background intensity.



Source: After Laughlin (1975).

Responses of large second-order cells (LMC 1–3)

The lamina cells detect spatial contrasts. As a bright spot passes, the retinula cells give a depolarising response (Figure 6.5 ret) and the large lamina neurons give a hyperpolarising graded response to an increase in intensity, but ignore the background intensity (Figure 6.5 lam). The height of the peak of the lamina response and its duration depend on the intensity in an approximately

logarithmic relation over about a tenfold range. In contrast, the retinal cells track intensity or photon flux and respond with a graded depolarisation in an approximately logarithmic relation that spreads across about a 1000-fold range of intensity (Figure 6.5). The lamina response is therefore more sensitive. The appropriate measure of sensitivity is the slope of the relation between the intensity of a flash and the voltage response, because at this level the system is interested in measuring the rate of change of the stimulus.

The multiple synapses in parallel that connect each retinula axon terminal to its corresponding LMC (about 200 synapses for each axon in the fly) illustrate several principles. The transmitter is histamine, which opens numerous post-synaptic chloride channels (Hardie 1987, 1988a). There is a very high gain around the midpoint in the response amplitude caused by requiring about three histamine molecules per chloride channel. Apparently, the LMC membrane is a passive integrator with no local voltage-sensitive channels and the post-synaptic gain is independent of light adaptation. The hyperpolarisation of the LMC is opposed by the large inward currents, presumably of potassium ions, which cause the overshoot at 'off'. The high bandwidth of the propagation of graded potentials is achieved by abnormally high LMC membrane resistance.

There is a substantial body of information about the anatomy and physiology of the lamina—notably, the types of neurons in flies and bees, the electron microscopy of synaptic connections and the fields of the large lamina monopolar neurons LMC1 and 2, but the functions of the smaller neurons are obscure. Most of the neurons, but not all, are monopolar with axons to the distal layers of the medulla (Figure 6.3). In insects with colour vision, there is a well-developed colour coding among the lamina ganglion cells, sometimes with antagonistic effects of different wavelengths. Where it has been measured (in dragonflies and butterflies), light adaptation alters the LMC spectral sensitivities. Except for colour processing, the lamina in the light-adapted state is mainly a high-pass, high-gain filter.

When the responses to changes of intensity on a background level of illumination are plotted for retina receptors and their corresponding LMCs (Figure 6.5), we notice several important differences. The 'on' responses in millivolts plotted against the log of the light intensity to base 10 (called V/log I curves) for the lamina are steeper (higher gain) than for the retina, but their slopes change less with adaptation. Simon Laughlin proposed that the shape of the V/log I curve of the large LMCs was the optimum to transmit the typical distribution of contrasts in the visual world, transmitting best the commonest contrasts between 30 per cent and 70 per cent, but transmitting very small and very large contrasts less precisely. The standing potentials of the receptors are largely ignored in the lamina cells (Figure 6.5 inset). The depolarising response of LMCs to 'light off' could also be an effective signal downstream. The LMC responses to common

contrasts are rather sharp because the response is brief and low frequencies are cut out. The thick LMC axons and rapid graded responses are suited to the accurate timing of responses, as required for the processing of motion.

The shapes of the LMC fields change with background intensity, from a narrow deep surround in bright light to a broader centre and shallow surround in dim light. Together with the floating zero, the fast response would optimise the number of contrasts at borders that could be detected in a natural scene. Insects seem to ignore real contrast amplitudes, however, and look for contrast frequency in their visual behaviour. Bees use a measure of the modulation in local areas as a cue for the recognition of a place—for example, in discrimination between a vertical and a horizontal grating. Colour vision appears to depend more on the photon flux in local areas than on chromatic contrast at edges.

The large LMCs behave as though their visual world consists of rapidly repeated moving contrasts. Their small circular fields provide the best compromise of high spatial and high temporal resolution for detecting moving sharp edges when light adapted and contrasting blobs when dark adapted. They teach us that for early visual neurons, the main requirement is spatial and temporal resolution in the detection and timing of contrasts on each visual axis. Their axons end in terminal bulbs at different specific layers of the next neuropile, the medulla. Their outputs are seen downstream in the medulla transient cells.

Other lamina neurons

Small spiking units were recorded below the lamina of the fly, with a centre 'on' and an inhibitory zone on either side (Arnett 1972), suggesting an early stage of motion detection there. Recently, lamina tangential dendrites sensitive to flicker but not motion were found, while another efferent neuron, C2, was sensitive to motion in either horizontal direction (Douglass and Strausfeld 1995–96). Small-field retinotopic directional responses have not been found peripheral to the lowest layer of the medulla.

As well as these and the LMCs, there are several other neuron types in the lamina: a) local amacrine cells with no axon; b) presumed efferent neurons with an axon from the medulla and arborisations in the form of a basket around one or several columns of the lamina (Figure 6.5); and c) presumed efferent neurons with widespread arborisations, which stain with antibodies for polypeptides and are probably neuroendocrine neurons. Apart from the largest LMC cells, and their responses, and colour coding in dragonflies and a caterpillar, little is known about the physiology of lamina neurons.

Compression of the image in the lamina neurons

The array of retinal receptors captures the image but it contains far more information than the nervous system is able to process in real time. For a start, the light at each receptor covers a range of about 10^{14} in intensity and varies rapidly in colour and angular velocity. The motion of the image can range from zero to several thousand degrees per second in any direction in fast turns. The compression of the image into a smaller number of neurons is one of the best examples we have of processing in neuron pathways—due mainly to the work of Laughlin and his colleagues. At least five separate principles are shared between retina and lamina; let us list them.

1. Intensity compression

First, the huge range of intensities is reduced by two factors in the retina: the approximately logarithmic response of the receptors over eight orders of magnitude, and their changes in sensitivity by four to six orders of magnitude as they adapt to light by movement of absorbing pigments and other effects. As a result of backing off the background intensity, and because natural contrasts are relatively small, the responses of the receptors are up to 15mV or so, riding on a background potential that depends on the scene. As a result of the adaptation, the calibration of intensity is lost and LMC cells operate with contrast.

2. Line labelling

Second, single receptors respond to changes in colour, polarisation plane and angle of incidence of the incident light without distinction, but, by having differently tuned receptors in each ommatidium, these aspects of the stimulus are separated into different lines in parallel. Having several receptor types means more division of the signal, so there must be an economy of types. Usually in each ommatidium of large day-flying insects there are three or four types of colour receptors and three preferred orientations of polarisation plane among the cells with peak in the green. The green receptors feed the perception of motion, which is therefore colourblind. There is commonly a basal or distal cell with a small rhabdom that must be less sensitive, providing for a higher range of intensity but with different colour processing. Commonly, receptors for ultraviolet mediate a colour-specific escape response. In flies, six of the receptor cells in each ommatidium are green sensitive and sum on the second-order cells, so polarisation sensitivity is reduced in the motion-detection system. Colour and possibly polarisation are detected in flies by comparisons between receptor cells seven and eight and the other six. The way the different aspects of the stimulus are line labelled potentially tells us the priorities, but we are only just beginning to understand the details.

3. Noise limitation

Third, noise must be minimised relative to the signal by an assortment of optical tricks that increase the signal, including long rhabdoms that catch a large proportion of the incident light. The signal is amplified as early as possible in the transmission line before synaptic noise is added to the photon and transduction noise. Between each receptor terminal and its large second-order neurons, LMC 1 and 2, there are many synapses in parallel that smooth out the transmission, but even so the synaptic noise is about equal to the receptor noise. Additional noise caused by conversion to impulses is avoided by using graded potentials as far as the third-order neurons. Effort is concentrated on the high frequencies where the signal is weak relative to the noise, because where the signal/noise ratio is high, extra signal produces little extra information.

4. Redundancy removal

The fourth principle is the neglect of the redundant part of the signal. One kind of redundancy is when two parts of the signal amount to the same thing. Having started at the receptor level to respond to change of intensity rather than intensity itself, at the second-order cells the background intensity has even less effect. The large lamina ganglion cells respond almost as though to the temporal derivative of the intensity on their visual axis, with maximum slope of the response curve at the most common level of contrast. This self-inhibition removes the temporal correlation introduced by the duration and shape of the impulse response of the photoreceptor.

In the spatial domain, the resemblance between neighbouring points in an image is a form of redundancy or predictability that is reduced by lateral inhibition, which has the effect of amplifying edges and spots relative to areas of constant intensity. Both of these effects partially compensate for the smoothing of the response as a result of convolution of the signal with a filter as the eye moves. The retina introduces much of the redundancy in the lamina. Everywhere in the nervous system, filters are adapted to the predictable pass bands of previous stages, rather than to the signal, which is less predictable.

5. Under-sampling

As illustrated in Chapter 3, the blur circles behind adjacent facets never overlap sufficiently for complete sampling of the outside world, mainly because there is not room on the eye for enough facets. Reverse-motion perception due to aliasing (Figures 3.3d and 3.3e) seems never to be a problem, perhaps because adjacent ommatidia collaborate in motion perception and regular gratings are unnatural. The under-sampling improves the efficiency of the eye because it removes some of the redundancy in the adjacent regions of the image. In retinas with open rhabdomeres, under-sampling is a consequence of the separation that prevents cross-talk between rhabdomeres.

6. Speed of response

Increasing the bandwidth is the most effective way to increase information carrying capacity. It used to be thought that the response must be rapid and must decay rapidly to be useful when images move. Flying insects respond to contrasts moving at angular velocities up to 2000° per second and some detect flicker up to 200Hz when warm. Speed, however, is costly in energy terms and often not necessary. Because it takes time to collect photons in small receptors, a high speed of response is not compatible with high sensitivity and there are many examples of slow sensitive vision restricted to large objects in dim light.

7. Information transfer

In a splendid fit of collaboration, Snyder et al. (1977) showed that the design of the retina yielded the maximum transfer of information at the ambient intensity in which the insect was active. By including the distribution of spatial frequencies in the visual world, and the expected angular velocities, van Hateren (1992) carried these ideas into the temporal domain and found that the required filter at the front end of the visual system agreed with the known properties of the LMC cells—that is, temporally low passes in dim light to make use of the high power in low spatial frequencies, but faster and biphasic in bright light to increase the bandwidth, with reduced gain at low frequencies where noise was relatively small. In contrast with the theories of de-blurring, also based on lateral inhibition, predictive coding gave a similar picture and predicted that LMC cells were adapted to the detection of blobs and edges (Srinivasan et al. 1982).

8. Resolution

As will be seen, bees detect features, not the image on the retina, and therefore vision is adapted to detect features optimally. The simplest feature—contrast modulation and its position on the retina—can be the response of a single receptor, narrowed by lateral inhibition (Figure 9.2e) and is used, for example, for the detection of a small moving prey or queen bee in flight. Detection of edge orientation requires simultaneous responses of at least seven ommatidia (Figure 9.2) and motion detection requires successive responses of at least two, so the minimum detectable signal is also related to the precision in timing and the interommatidial angle. Colour, polarisation and position of black are detected by larger groups of neighbouring ommatidia, so resolution is poorer. In each case, the post-lamina processing must be related to its corresponding feature detector, as well as to the maximum signal/noise ratio.

Colour in the lamina

Discovering the above principles has dominated the study of the lamina, but the processing of colour might be quite different in that spatial and temporal resolution matter less. To discriminate colour requires that the receptor types have

parallel, or at least predictable, intensity/response curves. The first stage of colour processing always involves convergence of two colour types with an antagonistic interaction on a post-synaptic neuron. Except in *Diptera*, this process starts in the lamina and continues with greater numbers of neurons in the medulla.

In the lamina of the bee, recording is difficult, but there is some evidence of spectral opponent cells, UV-sensitive cells, depolarising cells and spiking cells, while most recorded cells are green sensitive.

The dragonfly *Hemicordulia* has five types of retinula cell with spectral peaks near 330, 430, 490, 520 and 620nm. From each ommatidium there are six retinula cells ending in the lamina, two with peaks at 520nm, two at 490nm and one each at 620 and 330nm. Five types of hyperpolarising monopolar lamina cells have been found (Yang and Osorio 1996), three of them driven directly by short retinula axons and one by collaterals of a long visual fibre. The first (m1) sums several receptor types. The second (m2) has a peak in the green and also in the ultraviolet and a surround that peaks at 360nm. Adaptation by green light reduces its sensitivity in the green. The third (m3) has a peak similar to that of the 430nm receptor; m4 has a peak in the green and also in the ultraviolet. Adaptation by ultraviolet enhances the UV sensitivity and by green abolishes UV sensitivity. In both cases, the sensitivity to green is unchanged. Finally, m5 has a peak similar to the 525nm receptor. Adaptation to 430nm narrows the spectral sensitivity. At least two other colour types run directly to the medulla. Since we do not know whether dragonflies have colour discrimination, only colour-specific responses or both, sorting out the destinations and functions of these neurons will be a difficult task.

In all insects studied, the usual responses in motion perception, edge detection and several behavioural responses, except colour discrimination itself, all turn out to be colourblind, with inputs only from green receptors. So far, the neural processing of colour has not been correlated with behaviour.

Processing in the medulla

The medulla, as shown by painstaking work in a few preparations, is where the first real work of vision is done, making combinations of inputs and detecting their coincidences. There is a column of small neurons corresponding exactly with each ommatidial axis, with a sudden and early expansion of the numbers of neurons in each column (Figures 6.2 and 6.3). The principle is that the map of the visual world on the retina is reduplicated at an early stage into numerous and different successive maps, each of which is composed of its own type of feature detector. There are about 50 types of diverse small-field feature detectors in each column, even in a small fly. These arrays receive the same inputs from the retina but process them differently, in distinct layers in some cases. All complex visual

systems have such stages, after which they introduce large-field collector and feedback neurons. Each of the medulla columns has several projections to the next neuropile, the lobula.

Six or more lamina neuron types, and the terminals of receptor cells seven and eight, project directly to the medulla. The neurons of the medulla columns are mainly:

1. Narrowly arborising, 'on–off' or sustaining units as described below, but superimposed on these maps are at least three other systems.
2. Layers or strata of horizontal axons with widespread arborisations at right angles to the columns (Figure 6.4). At least some of these are whole-eye motion detectors, which are efferent to the medulla from the deeper optic lobe—some ipsilateral, some contralateral. They could be rapidly acting gates, for example, for cutting out background motion to show up relative motion.
3. Efferent neurons to the lamina.
4. Numerous types of medium-field neurons, only a few of which have been described.

The neurons of the medulla are mainly small, with numerous similar anatomical and physiological types, which are difficult to record from and characterise in terms of appropriate stimuli. Only two species have yielded useful data: the larval eye of the butterfly *Papilio* and the locust. The locust medulla has been studied with a stimulus that is sufficiently sophisticated to classify the spatio-temporal fields of the neurons in a non-arbitrary way.

Locust medulla neurons

Analysis of locust medulla neurons by James and Osorio (1996) omitted colour, which the locust appears not to use much, but concentrated on the spatio-temporal properties of the column neurons measured by a rapid method. The local neurons are diversified in their polarity, latency, time course, adaptation properties and sensitivity to motion. There is a huge diversification of small and medium-sized fields providing the higher-order neurons with plenty of combinations of inputs. This conclusion presumably holds for all insect groups.

To identify the unknown properties of its field quickly while the neuron was held on a microelectrode, a method of white noise analysis was introduced. As a first step, an oscilloscope screen is divided into 64 squares in an 8 x 8 array. Each square can be bright or dark in random sequence (or a calibrated grey level if required for greater accuracy). Care must be taken to get the right spatio-temporal scales, as seen by the insect eye. This two-dimensional randomly flickering distributed stimulus is moved to cover the field of a newly penetrated small neuron and the graded responses of the neuron are correlated online by computer with the exact previous occurrences of the stimulus in two spatial

and one time dimensions. Another way to say this is that the summed response seen in the neuron is divided into the constituent parts arising from each of the 8 x 8 squares on the screen for all previous combinations in space and all latency periods. The result is that the multidimensional spatio-temporal field of the neuron can then be examined in any of a number of ways, called kernels. For example, the spatial field can be plotted for any time after the onset of a flash or the response can be plotted as a function of time for any point in the field. The first-order kernels show some linear temporal or spatial responses to intensity changes or modulation. These can be subtracted from the total to give the non-linear parts. The second-order cross-kernel shows the responses plotted against various delays in one spatial direction and against delays in the other direction. It indicates directional motion irrespective of edge polarity, like a motion detector. The third-order kernel indicates contrast gain control and the fourth-order kernel indicates the non-directional motion, like an edge detector.

The square array of flickering stimuli classifies the field but is not appropriate for many neurons. At one extreme, the spatio-temporal responses of photoreceptors, and even of the lamina monopolar cells, are too simple to justify an extensive white noise analysis. At the other extreme, dedicated neurons respond to a very small part of the white noise mixture. They might respond to bars of certain orientation or small spots, so that their responses are lost in the noise caused by the large stimulus array. Those with peculiar spatial/colour antagonism are not suitable because they are not excited. Another problem is to avoid trends caused by adaptation to intensity, flicker or motion.

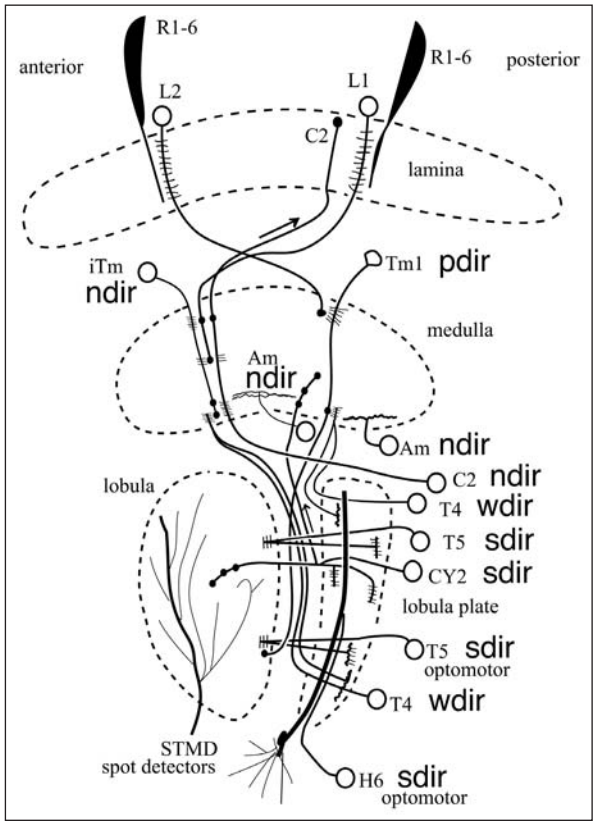
To find the fields of complex dedicated neurons, a combination of a dedicated stimulus and white noise is used. If the neuron responds to the motion of a bar, random bars can be presented in different orientations in random parts of the visual field and moved at random speed for a random distance. By correlating the responses with the various inputs, the whole field can be plotted in the selected ways. Another method for a neuron that responds to bar motion is to project two bars alternately on the screen, separated by about the angle between visual axes, and modulate them by two independent white noise signals. The bars appear to move in either direction at a range of speeds and the responses are correlated with the stimulus changes over all latencies. For a neuron with a spatial field with a centre and surround, a spot on the centre and a large patch covering the surround are similarly modulated at random, so that all possible interactions are measured as a function of time. As recorded by these methods, the common small-field neurons in the locust medulla are of three main types.

- Linear sustaining cells that respond with graded potentials in opposite directions to ‘on’ and ‘off’, like LMC cells; they could be the inputs to many later systems. Some show spectral or spatial opponency. They encode local intensity with various adaptation rates so that some are effectively transient, but still give opposite responses to ‘on’ and ‘off’ and show spatial summation

within small fields. They are commonly tuned to flicker frequencies about 15Hz in the dark-adapted locust and do not respond to motion within their field.

- Non-linear transient cells that respond with spikes equally to 'on' and 'off' and are sensitive to motion in any direction rather than flicker. They have a long but remarkably constant latency as though important in timing events. Some have fields corresponding with a single ommatidium.
- Directional motion-detector neurons with a variety of temporal and spatial constants are revealed by second-order kernels. Some are sensitive to either black/white or white/black edges (as shown by their first-order linear kernels), but only one with a small field has been recorded in the medulla (or anywhere else) in the locust.

Figure 6.6 A tentative circuit for part of the motion-detection pathway in the medulla and lobula columns of the fly, based on recording from neurons dyed through the electrode. Note the feedback to the lamina and to the medulla (arrows). The labelled cells have the following properties: ndir = directional; pdir = partly directional; sdir = strongly directional; wdir = weakly directional. The outputs to the brain are all of horizontal fibres.



Source: Composed from work by Douglass and Strausfeld (1995–96).

Medulla transient cells

These abundant cells fire with one or two spikes only, with a remarkably constant latency of 25–35ms in response to intensity increment or decrement. This is rather slow for inputs to a motion-detecting mechanism. Some have fields of 2–5°, others 7–20°, corresponding with their dendritic spread. The motion of a contrast within the field in any direction causes a steady stream of spikes by successive stimulation in an array of presynaptic small cells of the medulla columns (Figure 6.6). Successive stimuli, even at a single visual axis, cause strong localised self-inhibition, which decays after about 100ms, but stimuli of one polarity do not suppress responses to the opposite polarity, suggesting separate inputs for 'on' and 'off'. The interesting feature is that the response returns when the contrast is increased after adaptation to contrast. An increase of 20 per cent contrast is sufficient to bring back a full response. The result is a rapid habituation to the background contrast level, so that the visual system could ignore a constant modulation at every point, but respond to a novel contrast. Their non-directional response to motion is at the highest spatio-temporal resolution achievable by the retina, so the inputs are single columns. They have fields of different sizes with a range of time constants. Therefore, at all points in the visual field, the medulla contains a large number of non-directional motion detectors forming overlapping maps with different scales in space and time (compare Am cells in Figure 6.6).

In the natural visual world, large areas of background can have a texture at about the same contrast level. As the eye scans across this background, numerous transient cells respond only when they come to a boundary at a greater contrast. A near object will often have a sharp boundary when seen against a distant background, even if only because of different illumination and shadow; and this detection of an outstanding boundary by medulla transient cells is independent of contrast polarity and average background contrast. The precise timing of their spike responses suggests that they participate in coincidences with others. Also, to distinguish a spot requires a precise timing to discount coincidences of responses from a moving background.

At several levels in the insect medulla there are strata of horizontal fibres at right angles to the columns. One type of transient cell of the locust, called the tangential medulla amacrines, with fields of about 20°, spreads over a wider region of the medulla, synapsing on many medulla columns. In the butterfly, most of the large medulla neurons appear to be wide-field directional detectors, similar to the detectors of flow-field patterns in the lobula plate of flies. Some of these come from the lobula, and all eventually adapt to a continued motion, so that they detect velocity changes, not steady motion. Some cross from the other eye, others terminate with the directional lobula neurons in the deuterocerebrum and make synapses with descending interneurons to the motor centres of the thorax.

Neurons with fields of 10–20° are possibly the regional detectors of the cues that are inferred in trained bees (see Figure 10.8). In the bee, there are tracts from the medulla and the lobula to the calyces of the mushroom bodies (Figure 6.4).

Directional motion detection

Elementary motion detectors

The elementary motion detector (EMD) is a convenient hypothetical circuit, a kind of reduplicated miniature black box, first introduced by Reichardt about 1956 as the mechanism of the optomotor response, and subsequently of the large-field directional motion-detector neurons that fit so well with the optomotor responses. They measure the rate of passing of edges—that is, the temporal frequency, not the angular velocity—and are very slow, with peak response near 10Hz, but the motion detection occurs at the maximum spatial resolution of the eye, down to very low contrasts and low intensities, with a low ratio of noise to signal. The maximum response occurs when the jump of an edge is the angle between adjacent visual axes, falling off rapidly over a few visual axes. This local limitation of the interaction was confirmed by stimulating single photoreceptors of the fly retina. For some, the Reichardt EMD is the behavioural unit of motion detection, but any algorithm that extracts the direction of a shift in the square of the contrast is sensitive to directional motion.

The detection of directional motion at first assumed that the lateral interaction was between adjacent ommatidia (Hassenstein 1951; Götz 1965) and the true situation was never properly published (see Figure 3.4). Experimental analysis eventually showed that explanations of the response were complicated by receptor and regional diversity, by sub-adjacent interactions and by pooling of channels in low light. Moreover, under-sampling is the rule, so the true direction of motion is not detected in the finest patterns that the insects can detect by temporal modulation.

Directional motion perception of all kinds at neuronal or behavioural level is consistently colourblind in insects and does not measure angular velocity. The mechanism saturates at low contrast and low velocity and adapts, so that the feature that is detected consistently is the local direction of velocity change over a huge range of light intensity. At the lowest intensity threshold for motion detection in the fly each photoreceptor averages 6 photons (two to three bumps) per second.

Despite extensive work by Buchner and his colleagues showing that the metabolism of desoxy-glucose during motion perception implicates some layers of the medulla but not others, we have no firm anatomical or electrophysiological indication of where the directional motion detectors are. The medulla is certainly not stuffed with EMD neurons.

Mechanisms of motion detection

Electrophysiology with one electrode cannot find the locus of motion detection because there is no suitable place to probe and motion detection is not a single process. Douglass and Strausfeld (1995–96, 2005) recorded from a few types of small-field neurons in the fly and proposed a circuit for motion detection, based partly on latency measurements and anatomy (Figure 6.6). Axons L1 and L2 connect to short iTm fibres of the medulla that are sensitive to non-directional motion. The iTm fibres connect with T4 cells of the lobula that are weakly directional. Long Tm1 fibres also connect with T5 fibres of the lobula that are strongly directional. T4 and T5 fibres connect with the large directional lobula neurons that run to motor centres of the neck muscles and the thorax. In later work, they also found differences between the angular velocities at which these and other neurons gave peak responses. The conclusion was that local directional motion detectors had inputs from non-directional ones. These circuits alone, however, would not provide a suitable substrate for the measurement of angular velocity and control of flight speed by non-directional inputs in bees flying in a tunnel (Chapter 7).

The bee probably resembles the locust rather than the fly. Directional motion detectors with retinotopic medium-sized fields, but not small fields, are abundant in the medulla of the locust. The directional mechanism appears to be a directional delayed lateral inhibition with the same time constants as the self-inhibition of the transient cells, acting over 30–100ms, with inputs from many columns.

Some details fail to agree with the rest of the account. Curiously, direct stimulation of the two large lamina monopolar cells, L1 and L2, in the fly failed to excite directional motion detectors. The directional response to a single 1° jump of a single edge and the memory of a stationary pattern both suggest that a DC component is essential as one or both of the inputs to a directional motion detector, but evidence that L1 or L2 can carry a DC signal for long is doubtful. In bees, dragonflies and butterflies, the motion perception has inputs only from green receptors, but L1 and L2 are not so restricted in these insects.

In conclusion, the medulla is an expansion of the visual input into local combinations of features in space, time and colour, with some wide-field neural input from other visual centres. The medulla contains many maps of local features and passes on coincidences of combinations of the inputs. There is range fractionation (that is, division of the total range into parts) for motion detection, angular velocity, spectral sensitivity, edge orientation, latency, direction of motion, adaptation rate and more, so there could easily be 50 types of neuron in each medullary column.

The lobula and lobula plate

The third optic neuropile, the lobula, contains retinotopic projections of small fibres but is usually considered as the terminus where the spatial representation is converted to local sums and coincidences of feature detector responses in large fields.

Large directional motion detectors

Large neurons that detect directional motion were first discovered in the lobula in the 1960s. They have large fields in different parts of the eye with different optimum directions of motion (Figure 3.5). The directional sensitivity curves are very wide, with angular widths near 90º at the 50 per cent level. As described in Chapter 3, their properties match the optomotor response, but it is not yet clear how they act during normal flight because they adapt to the visual feedback from the moving surroundings.

In the fly, butterfly, dragonfly and locust, there are at least two types of direction-selective motion-detector neurons—one slow and matching the optomotor response in time constants, the other fast, with responses increasing up to angular velocities of 1000º/s or 100Hz or more. Both respond to contrast frequency irrespective of velocity. They terminate lateral to the oesophageal canal. In the bee, the fast fibres respond more constantly to velocity irrespective of contrast frequency and so are of interest for possible relations to the flight speed, either as sensory input or feedback control. As in many arthropods, the bee has tonic and phasic muscle fibres, corresponding motor neurons and probably slow and fast pre-motor interneurons of the ventral cord.

Other movement and small-object detectors of the lobula

Abundant behavioural studies have shown that dragonflies, pond skaters, hoverflies, mantids and others detect small moving spots against a moving cluttered background. In the lobula of hoverflies, Barnett, Guerten, Nordström, O'Carrol and co-workers in various combinations find large numbers of interesting neurons lateral to the oesophageal canal, which are thought to be detectors of small moving objects or complex features. The field sizes range from 10º to 30º at the front of the eye, which is all that is required to home in on a prey or potential mate, or even 40–50º in female hoverflies, which is sufficient for escape. The range of sensitivity to angular velocity corresponds with detection of a similar insect flying at a typical speed at a range of 1 metre. Some neurons detect a small object moving over a patterned background. When presented with several small targets simultaneously, the whole animal is confused and two small targets close together inhibit the response (for example, Meyer 1974). The neurons behave similarly (Guerten et al. 2007). Recordings from the dragonfly lobula reveal large neurons that detect small black or bright spots down to the minimum allowed by the

width of the acceptance angle as sharpened by lateral inhibition—about 1°. These detectors of small spots are usually non-directional and are not restricted to green-sensitive receptors. The response soon fades on repetition.

Similar neurons have been found in the lobula of the bumblebee, which seems more suitable for recording than the honeybee (Paulk et al. 2008). Responses of different types are segregated into at least six different layers—some are precise in the timing of the first spike; others are more erratic. Obviously, there is much more to come from this animal.

Neurons that detect non-directional motion and directional motion in various proportions can be found running between the lobula and the midbrain in the bee. Similar neurons in the locust measure angular velocity irrespective of the stimulating pattern.

Neurons that are sensitive to the edge orientation have been recorded in worker bee lobula after a long search (Yang and Maddess 1997). The plot of the response against the angle of a thin bar has two opposite lobes because the feature detector is symmetrical about one axis (Figure 9.2). They could be non-directional motion detectors. The required length of edge is small and the orientation tuning is very coarse, mirroring the behavioural tests. They run from the lobula to the deuterocerebrum on the opposite midbrain, where they connect with descending neurons of the ventral cord. A tract of axons from the lobula to the calyces of the mushroom bodies of the bee deserves examination.

A large neuron in the lobula of the locust, the DCMD, sensitive to ultrasound and very small non-directional movements of edges and spots but not large targets, was originally thought to be an alert mechanism, but turned out later to be a detector of impending collision. Again, it soon adapts on repetition and the first neuron to fire on the left or right side inhibits the other. Analysis suggests that the inputs to this neuron are the small-field transient cells of the medulla.

All who have recorded from the lobula of large insects remark on the great diversity of responses that are not understood, and it is quite likely that some of these neurons will reveal to be large-field summation of feature detectors of edges, spots or orientation, or even parallax, when the proper tests are made. For example, there are different motion detectors that show range fractionation of contrast frequency, but it is not known whether these relate to the measurement of optic flow.

For some reason, the mechanisms of learning and the location of memories have not appeared among the neuron studies, yet presumably they are initiated in the optic lobes. The traditional sites—the four mushroom bodies at the top of the brain—are essential for learning odours but extensive work shows that they are not required for tactile, visual or motor learning in *Drosophila* (Wolf et al. 1998). It is still possible that the layout of the sensory input is somehow coded in the calyces of the mushroom bodies.

It is pertinent to note, however, that there is no sign among the neuron responses of the rapid learning of muscle control and flight posture that is demonstrated in flies when the visual feedback loop is reversed (see Chapter 7). There is also no sign of a separate pre-motor control from non-directional motion detectors, which might control the flight speed or measure the distance flown. Just asking these questions is a reminder that, despite 30 years of effort, theories that are based on curve fitting to whole-animal or single-neuron performance tell us little about the underlying interactions, and they avoid the hard work of unravelling the circuitry. It is of some consolation that in the vertebrate retina, which has been explored far more intensively, we still lack all the neuronal mechanisms.

Colour in insect vision

Colour vision has to be recognised by a test and therefore is defined by performance. Possession of two or more receptor types with different spectral peaks is suggestive, but insufficient. Some responses, such as food appraisal, might show colour vision while others, such as motion vision, are colourblind in the same animal. Third-class colour vision passes the test of discriminating at least one wavelength from all shades of grey or separating two colours irrespective of intensity. Second-class colour vision discriminates different colours from one another irrespective of saturation and intensity. First-class colour vision recognises a colour even when the wavelength mixture in the illumination changes, irrespective of saturation or intensity, as in humans and bees, but confuses some mixtures of wavelengths that combine to make the same colour, just as green for humans can be made from various mixtures of blue and yellow. Few animals have been tested for colour vision. Insects also have receptor-specific vision, in which the outputs of different colour-coded receptors are used separately for different responses. All of these kinds of colour vision can exist side by side, together with colourblindness of the same responses in dim light. The performance gives us little information about the number or types of receptors or the neuronal mechanisms of processing—or vice versa. Even if we understood our own colour vision, it would not be a model for insects.

Colour cues

Confusion surrounds the question of specificity of insects' visual responses to colour because there are numerous observations but very few critical tests. A sharp distinction between colour-specific responses and colour vision based on inadequate data probably adds to the confusion. Certainly, there are responses that are tied to one type of retinula cell, so the response is monochromatic but responds to quite a broad band of wavelength. For example, all insects tested detect motion via the receptors with a peak in the green and some make their escape towards UV light or detect the polarisation plane with a single type of UV receptor.

Colour cues suggest colour vision, but each must be analysed and usually the colour is effective only in context. Receptors with a peak in the ultraviolet occur in the eyes of all insects—male and female—and there is sufficient ultraviolet in daylight for it to be a useful colour. Some insect sexes and white flowers are discriminated by their UV reflectivity. There are many examples where trigger cues depend on special receptors, but the question of colour vision remains open. Butterflies are at the centre of the confusion. For example, the white butterfly *Pieris* has at least four receptor types with peaks at 360, 450, 540 and 620nm and several behavioural responses that depend on the colour and intensity of the illumination. Feeding is triggered by red (600nm) and especially by blue (447nm), egg laying by discrimination of green (542nm) and yellow induces a tactile test with the feet. The same butterfly is attracted to blue or yellow flowers and ignores green when feeding. Male butterflies in flight will turn and chase another suitably coloured butterfly as a potential female or territorial intruder. An unexpected finding is that *Pieris* females reflect more of the ultraviolet than the males, but in lycaenid butterflies it is the other way round. In each case, the males easily discriminate the sexes visually. Some butterflies—for example, the satyrid *Pararge*—distinguish some colours from all shades of grey. The diurnal hawkmoth *Macroglossum* prefers blue flowers but is easily trained to reverse its preference. The butterfly *Papilio demoleus* prefers blue flowers with few petals, and models that resemble them, rather than other colours or models with more rays.

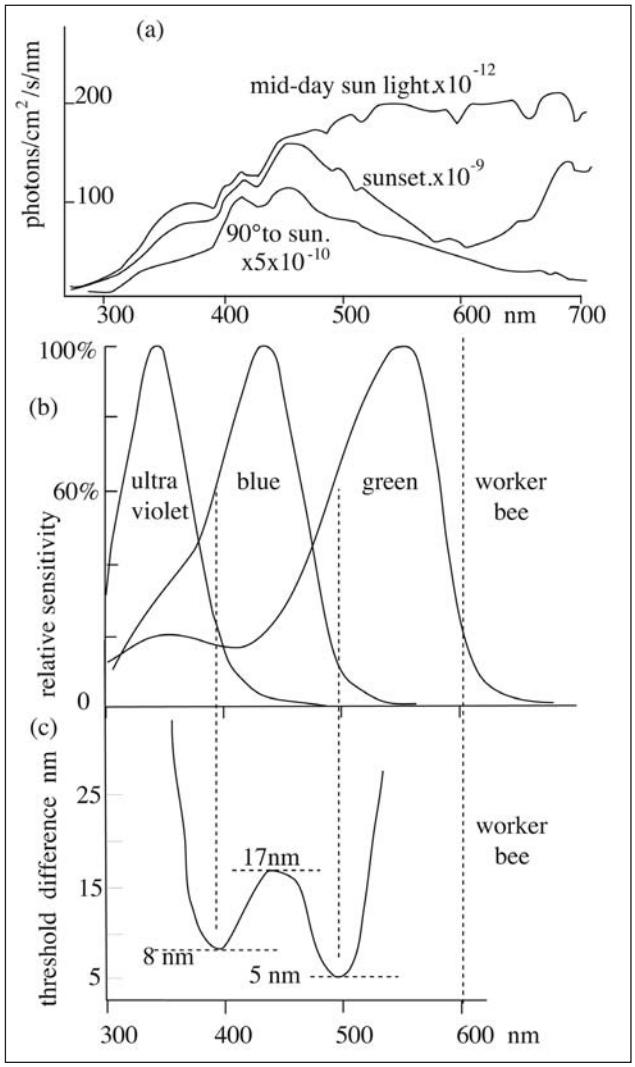
Red is little used by insects except by dragonflies, some wasps and butterflies with red markings. Butterflies of the family Papilionidae, when hungry, select red from all shades of grey in mistake for flowers. The large black *Papilio aegeus* has red spots on the wings and both sexes have red receptors in the eyes—presumably to recognise their own species.

Some insects, such as the cockroach, have only two types of receptors, with peaks in the ultraviolet and green. Whether they have some form of dichromatic colour vision is unknown. Some dragonflies, butterflies and wasps have four types among the six large retinula cells, with peaks in the ultraviolet, blue, green and red, together with one or two types of small cells, one at least of which is UV sensitive. Each receptor type could be the input for a monochromatic response and two or more of them might collaborate in behaviour that passes as one of the forms of colour vision. Narrow-band wavelength-specific responses are rare. A well-known example is the bee, where the dorsal light response, escape to the light and the sky compass depend only on UV receptors; landing, scanning, landmarks and behaviour that depends on motion, only on the green receptors; dim light vision is colourblind, with ultraviolet, blue and green simply summed together; and finally all three receptor types collaborate in antagonistic interactions in first-class colour vision. In the dragonfly, ultraviolet participates in the antagonistic responses of lamina monopolar cells, and in the

bee the UV cells of the retina have long axons to the medulla, with side branches in the lamina, perhaps to allow them to participate in two different activities.

Electrophysiology of the optic lobes reveals far more neuron types than needed for a minimal model of colour vision. The neurons, with multiple inputs and alternative outputs, deserve careful analysis because in fact they, not the model, are the mechanism.

Figure 6.7 Physical background to colour vision of the bee. a) Photon flux of sunlight at different wavelengths. b) Spectral sensitivity curves of the three types of retinula cells of the worker bee. c) The threshold minimum difference in wavelength that is discriminated by the bee at different wavelengths.



Sources: (b) from Autrum and von Zwehl (1962); (c) from von Helversen (1972).

Colour discrimination

An enormous literature on colour vision in bees tells us much about performance but nothing about mechanisms of discrimination. Bees have three types of large retinula cells with broad spectral peaks in the green, blue and ultraviolet, with uneven distribution over the eye. In the honeybee, unlike other insects, colour vision has been studied in sufficient detail to show that bees discriminate colour from all shades of grey in their selection of food targets and at the hive entrance. Certain mixtures of colours interact together to produce 'bee white', which is close to human green. Colours are discriminated irrespective of the amount of bee white (called saturation) in the mixture. Data on trained bees strongly suggest that they detect the relative positions of at least two neighbouring patches of different colours.

Over the region of the spectrum where the spectral sensitivities of the receptors overlap (Figure 6.7b), the honeybee can discriminate differences of about 20nm in wavelength irrespective of intensity (Figure 6.7c). In dim light, the spectral types are apparently added together, so increasing the sensitivity, but bees are poor at discrimination of brightness differences, which suggests that the colour discrimination system has only opponent neurons. Neurons with opponent wavelengths in both centre and surround, as in primates, have not been found in insects.

Electrophysiology of the bee's optic lobe (Yang et al. 2004) revealed at least 10 colour types of neuron without antagonistic responses and eight types with antagonistic responses—for example, excited by blue and inhibited by green and ultraviolet, as in the caterpillar medulla (Figure 6.9). A centre-surround organisation, as in primates, was not found. Presumably, there are many more types. Antagonistic responses help explain why the discrimination of a small change in wavelength is optimal near the wavelengths where the spectral sensitivity curves are steepest and cross (Figure 6.7b). Most importantly, the invariance of colour vision—such as independence from intensity, object size and repetition rate—is explained in principle by the opponency of neurons. In the bee, as in humans, colour discrimination is recalibrated according to the colour of the illuminating light, as though the weighting functions of the three receptors are modified so that known objects such as clouds or leaves are detected as expected. Beyond the medulla, large-field neurons involved in motion perception tend to be green sensitive and colourblind and those sensitive to spots tend to have various spectral sensitivities.

The various distributions of spectral receptor peaks, distributions of the various colour types of receptors, responses to colour and numerous details of bee responses to coloured targets are available in a large but well-reviewed literature, showing endless adaptations to the world of colour. It seems certain that, before flowers evolved, insects had receptors with a variety of spectral

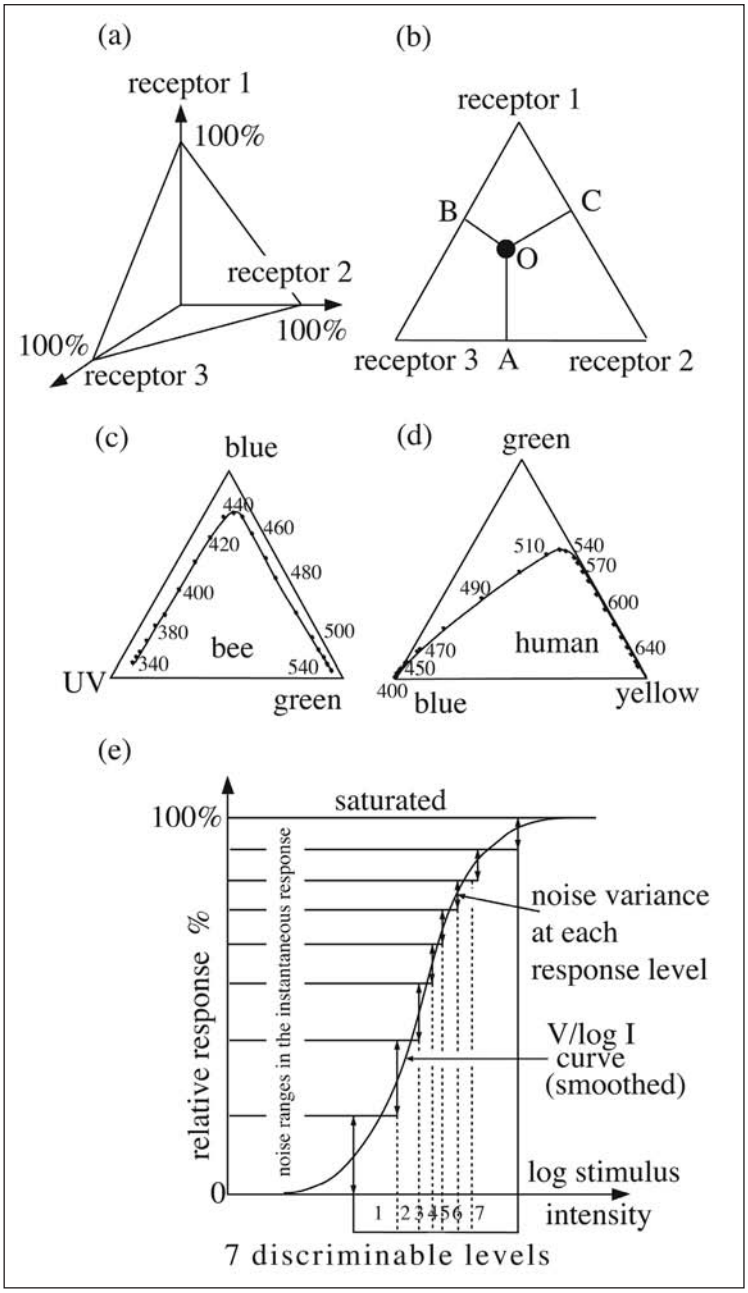
peaks and colour-specific responses. A recent finding is that flower colours have spread themselves out across the range of colour vision of the pollinating insects, just as they are spread out in time of day or in different seasons. Smaller steps in flower colour are observed at the wavelengths where pollinators discriminate smaller colour differences. Conversely, the spectral peaks of the photoreceptors are near the theoretical optimum wavelengths to discriminate the observed range of flower colours.

A superficial model of colour vision

A useful model of colour vision that necessarily fits a system of receptor types with broadly overlapping spectral sensitivities is a colour triangle for three receptor types (Figure 6.8) or a tetrahedron for four types. The equilateral triangle represents a plane that cuts across the corner of three Cartesian coordinates. Three lines drawn perpendicular to each side from any point in the triangle represent the normalised responses of the three receptor types as a fraction of the sum of all three responses. Each point in the triangle then represents the relative responses of all three types irrespective of total intensity. When the responses of the receptors to two different colours are calculated from the spectral sensitivity curves, the colours are hard to discriminate if the two points obtained lie close together in the triangle. Each pure wavelength has a position in the triangle according to its relative stimulating effect on three receptor types (Figure 6.8c). The line of the spectrum curves from the corner of the short wavelength receptor towards the corner of the middle wavelength receptor and terminates near the corner of the long wavelength receptor, but never reaches the corner of the middle wavelength because this receptor is never stimulated alone. A point on the plane near the middle is indistinguishable from grey or white. Points that are more separated on the plane (in stimulus space) are more easily discriminated. Each point on the plane is really a small patch, the size of which is a measure of the noise level (Figure 6.8e). Because there are three receptor types, the data from discriminations of colours can be related uniquely to their measured spectral sensitivities. Any point within the spectral line can be reached by a very large variety of combinations of wavelengths, so the exact mixture of wavelengths is not recoverable—for example, there are many mixtures of various blues and yellows that will match any green.

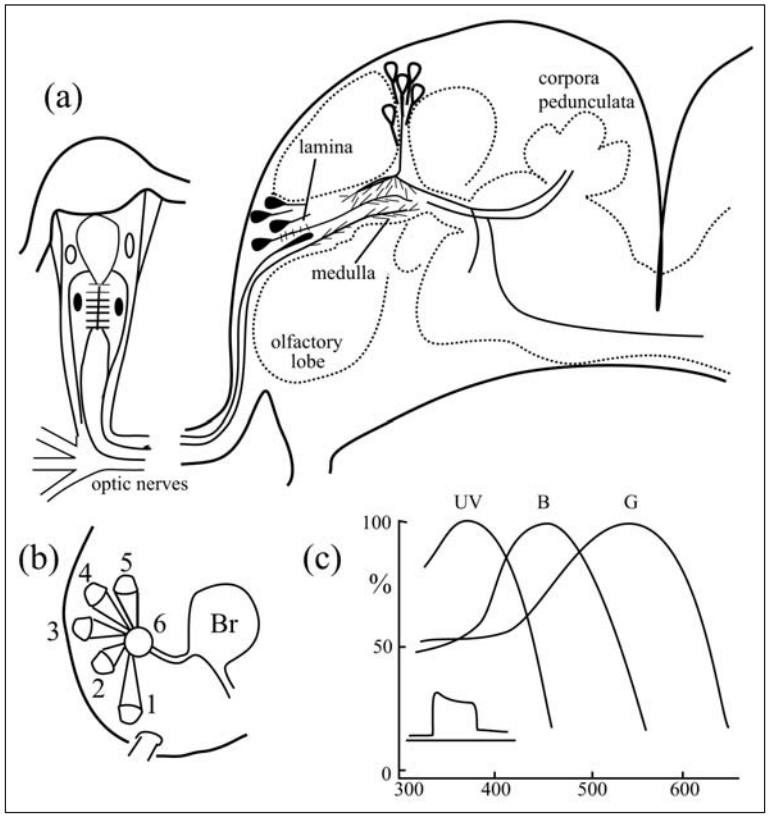
With this model, it is impossible to see two colours simultaneously at the same place because there is only one output. We know, however, from the spectral sensitivities of different responses, even in the honeybee, that receptor types can be used independently of each other. We do this ourselves with our ears when we hear separately the notes in a chord, because our cochlear is able to detect two or more simultaneous notes. Even more, we detect constituents of odours and flavours, but we cannot see two colours at the same place.

Figure 6.8 The classical representation of the colour triangle for the bee and for humans. a) Three vectors representing the normalised responses of the three colour types of receptor. b) The fractional contribution of each receptor is represented on the triangle. c) and d) The position in the triangle for each pure wavelength for the bee and humans. e) The stimulus/response curve of a retinula cell, showing how the increased noise at low levels limits the possibility of discrimination of intensity and therefore of contrast and colour.



This model is much simplified for many reasons. It is really just a geometrical way of representing a summary of one part of the data. The behavioural responses are influenced by effects of summation of inputs, adaptation over time, regeneration of photo-pigments by long wavelengths, screening pigment, and so on. It illustrates how three input filters with broad overlapping tuning curves result in a great many discriminations, but is simply a consequence of the properties of the three types of receptors. There is a version of the model for the bee (Backhaus 1991) that postulates central antagonistic interactions, based on the responses to various wavelengths by just two medulla neurons, but this does an injustice to the variety of colour types of neurons that are really present.

Figure 6.9 Receptor, lamina and medulla neurons of the caterpillar of *Papilio*. a) Each eye is a single ommatidium; lamina cells are filled black; medulla cells are white on black, with a tract to the corpora pedunculata. b) The six eyes look out in different directions on each side of the head. c) Spectral sensitivity curves of the three types of retinula cells.



Source: Based on works by Ichikawa and Tateda.

Colour processing in the medulla

One would not have thought that the humble caterpillar would help us elucidate colour mechanisms, but it is a simplified version of the adult at the right level of complexity to show what we can expect in the adult insect. The medulla of the larva of *Papilio* has a wide variety of colour-coded neurons, which can be recorded with microelectrodes. There are only six separate simple eyes (stemmata), each like one ommatidium of a compound eye, each with seven photoreceptor cells of three spectral types beneath a small lens. The neuroanatomy is similar to the adult, but much simpler (Figure 6.9).

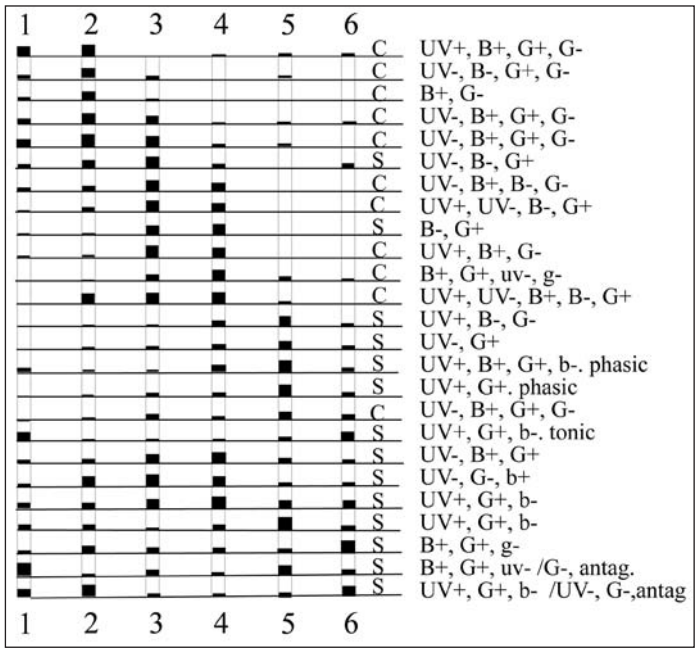
The receptors each have one spectral peak near 380, 450 or 540nm, which are typical values for many insects. The photoreceptor axons are of two types, long and short, of which the latter terminate on a monopolar cell of the lamina. The total of 24 LMC axons project to the medulla, where most of the neurons have graded potentials with small superimposed spikes. In the medulla are numerous interneurons with antagonistic interactions in all ratios that generate a large variety of neuron types in parallel (Figure 6.10). This is an example of range fractionation that is common in sensory systems.

One group of 50 or so intrinsic medulla neuron types responds to different combinations of the six stemmata (Figure 6.10). Eleven of them receive different types of *spatially opponent* colour inputs from a few stemmata, mostly all different from each other, but looking forwards. In their responses, they look like colour-pattern detectors, with areas separated from edges. Seven neurons show a relatively homogeneous spectral sensitivity over their whole receptive field and have inputs from two or three dorsally directed stemmata; three of these neurons are tonic and three phasic. Another seven neurons are spectrally homogeneous with large receptive fields covering four to six stemmata. Some of them show spatial summation, others spatial antagonism within their receptive fields. In their responses, they look as though they serve phototaxis.

The 50 or so neurons receiving inputs from single stemmata have been examined with reference to chromatic and neutral backgrounds. They look like local colour discriminators. Eight types are from stemmata with only blue and green receptors. Of these, six have specific colour opponency on different backgrounds; one has strong colour opponency on a neutral background and the other five have colour opponency only with coloured backgrounds. The most complex has excitatory responses on a black background, inhibitory responses on a white background and various colour opponency on coloured backgrounds. Two other types show simple summation of blue and green receptors. Eight types with inputs from trichromatic stemmata (ultraviolet, blue and green) have colour opponency in different combinations—some of them depending on the background colour. The neurons with inputs from several stemmata are not summations of the inputs of constituent stemmata or post-synaptic to single-

stemmata neurons: they have different colour combinations but from different stemmata. There is little sign of centre/surround organisation of fields, unlike in vertebrates. All of these medulla neurons could be third order on the visual pathway. They clearly generate many of the total possible combinations of broadly tuned inputs in colour and direction (Figure 6.10), but have not been related to visual tasks.

Figure 6.10 The distribution of 25 medulla cell colour types among the six eyes of the caterpillar *Papilio*. Capital letters mean a large contribution, small letters a small contribution. Note the phasic units for edges and the tonic units for areas, and the resemblance to the coding in olfactory systems by coincidences in diverse populations of neurons.



Sources: Based on Ichikawa (1990, 1991).

It is remarkable that such a small ganglion in such a simple visual system contains neurons with so many combinations of inputs. We must infer that the caterpillar uses colour as a source of information about its surrounding leaves, but with so many neuron types in parallel, any model relating outputs to inputs would be hard to prove uniquely.

There are strong indications that the same system occurs in other insects, and perhaps in primates. In the bee, Yang et al. (2004) recently recorded non-opponent and also opponent cells, some broadband and others fed from one type of receptor. Combinations such as (UV + B − G −), (UV − B + G +) and (UV − B + G −) were recorded—in all, 50 types—but no spatial opponency. In dim light, the opponency disappears at the same level as colour vision is

lost. Spatial fields were huge: >50°. As in the locust medulla, edges and motion are coded by varieties of related neurons. The point is that the coding of small-column neurons of the medulla is of very simple local features that are close together in feature space and that are combined in further selections by collector neurons downstream.

Each colour is represented by its own pattern of activity in many neurons: edges by phasic neurons, areas by tonic ones. Colour discrimination then involves the detection of familiar coincidences of neuron activity. Similarly, the colour system of the primates contains a great variety of colour-coded neurons that cannot be correlated individually with the behavioural data.

Conclusions

Electrophysiology of identified neurons reveals what is going on, cell by cell, and leads to many conclusions about information flow, but fails to explain or predict behaviour because that depends on the combined action and coincidences of many neurons. Sensory input is the easy part. Discovering the feature detectors is the next step. Some feature detectors are inferred from behaviour, others from the responses of the optic lobe neurons, and a few from both. One example where the feature detector has been isolated is the modulation detector, which is a lamina ganglion cell that is sharpened by lateral inhibition. Another example is the orientation detector, which has a maximum and minimum size of three facets long and three wide. A third is the elementary motion detector, where stimulation of a single optical axis with a flash, followed by the same at a neighbouring axis, shows that two adjacent or two sub-adjacent axes are effective, but we know that they are not as small or as homogeneous as is usually proposed (Figures 3.4 and 6.6).

In general, we can infer from the electrophysiology that there is a high-speed inflow of sensory information, then an expansion into combinations of inputs in the medulla and lobula, followed by a rapid integration and reduction to a relatively small number of neurons in the tracts to the brain. This reveals nothing about discrimination or about the coordination of inputs of different kinds, except that processing must depend on coincidences between different neuron responses at every level. Long-lasting modulating transmitters and neuron hormones are known to exist, but how they participate is largely a mystery. The analysis of a nervous system is a difficult, tedious and never-ending task.

Endnotes

1. There are two impediments to the understanding of neural processing. First, the work has been done in a small number of laboratories, where the techniques are nourished for decades and different conclusions emerge. Second, the study of one neuron can continue for many years and each new researcher entering the field tends to introduce a different preparation.