

Chapter 9

Seeing the polarisation

From all that has been discussed in the earlier chapters, it seems that nearly all the natural daylight we see is at least partially polarised. Polarisation is unavoidable because we never look directly at the sun and all the light that actually enters our eyes has been either reflected or scattered by something. It turns out that many animals are able to detect both the degree of linear polarisation and its direction, and they exploit this information in several ways. Such creatures include insects, crustacea, octopus and cuttlefish and some vertebrates but not, except in an insignificant way, ourselves and other mammals. Having already seen in this book what we are missing, it is pertinent to consider how other eyes respond to polarisation and why ours do not.

It has long been suspected that some animals are sensitive to the direction of polarisation because that would explain some of the things they do. But early tests proved negative until some experiments were published by Irene Verkhovskaya in Moscow in 1940. She studied *Daphnia*, the small freshwater crustaceans popularly called ‘water fleas’, which migrate vertically over several metres in the water each day. She found that they are attracted to light and gather together where it is strongest. In several experimental arrangements, linearly polarised light was found to be two to three times more effective than unpolarised light in attracting the animals. At dawn, when they move towards the surface, the sky overhead is maximally polarised unless it is overcast, so this might increase the stimulus to migrate upwards. It was more than a decade later, however, before others showed that *Daphnia* are able to detect the actual direction of polarisation, since they align their bodies, and so direct their paths, at right angles to it.

Very recently the preference of *Daphnia* for polarised light has been confirmed and has been linked to the tendency of these and other small invertebrates to avoid the vicinity of the shore. Light penetrating into deeper water is scattered (see chapter 6) and, so becomes horizontally polarised, much more than light falling onto shallows near the beach. So the animals are attracted away from the dangerous shallow regions until they are surrounded by safer deeper water. The two basic compound eyes of *Daphnia* are fused together to form a single median eye, with a total of 22 facets, that swivels rapidly around its axis within the head. The rotating eye presumably scans all possible directions of polarisation, perhaps to ensure that it detects the predominantly horizontal polarisation of its environment, as the animal swims along in varying attitudes. This would account for the apparently equal attractiveness of different directions of polarisation first seen in the original experiments.

The early experiments on *Daphnia* showed they are sensitive to the existence of polarisation but they were not the first animals shown to be able to detect the actual direction of polarisation. This was first demonstrated in bees by the great pioneer of animal behaviour studies and Nobel Laureate Karl von Frisch in 1948. He had already found that worker bees can communicate to other bees the direction and distance of a source of food, either nectar or pollen, by an excited dance performed repeatedly on the surface of the comb in the hive (figure 9.1). The direction is indicated by the 'waggle run' element of the dance in which the bee runs forward wagging her abdomen before turning alternately left and right to return to the start. The inside of most hives is completely dark, the combs are vertical and 'upwards' is regarded by the bees as representing the direction of the sun at the time; the waggle run then deviates left or right from the vertical according to the bearing of the food source to left or right of the sun itself (figure 9.1). As the sun moves across the sky through the day, so the waggle run for a particular direction gradually rotates appropriately, at 15° per hour or half the rate of the hour hand on a clock face.

When von Frisch experimentally abolished the vertical reference by arranging the combs horizontally, the waggle runs then pointed in the actual direction of the food source itself, but only if the bees could see the sun or part of the sky through a window in the roof of their hive. The bees could just cope when only 10–15% of the sky was visible to them, provided it was blue; when their field of view was covered by a cloud, or when their window was covered over, the dances immediately became

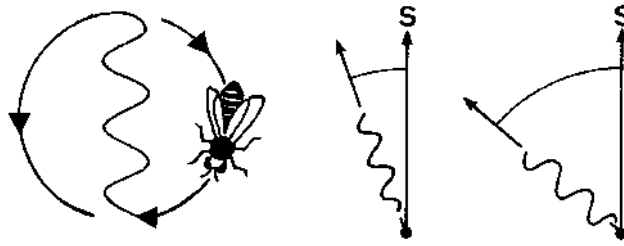


Figure 9.1. The waggle dance of the honey bee. Left: the pattern of the dance, turning alternately left and right with the waggle run up the middle. The angle of the waggle run from the vertical indicates the bearing of the food source with respect to the sun and the number of waggles gives the distance to the food. Right: the waggle run for a source 20° to the east (left) of the sun and the same two hours later when the sun has moved 30° westwards.

disorientated and random. The fact that a portion of blue sky provided a sufficient reference when the sun itself could not be seen was a major surprise but von Frisch suspected that the bees might be able to detect the sky polarisation pattern that is itself determined by the sun, as described in chapter 6. To test this he covered the window in the hive with a large piece of polaroid. When he turned the polaroid so that the polarisation of a patch of sky was altered in a controlled way, the bees' dances rotated accordingly. The story has been vividly told in several popular books by von Frisch himself, translated into English, and it is well worth reading in greater detail.

In order to understand how the bees distinguish the direction of polarisation, it is necessary to know something about how their eyes work. The principal paired eyes of insects are of the type known as compound eyes and have a quite different action from the familiar simple or 'camera' eyes of vertebrates such as ourselves. In the latter, as in a camera, a single lens (generally combined with refraction by the curved cornea) focuses an image on the retina, which is a screen of light sensitive cells. Nerve fibres connect each point of the retina with the brain and thus transmit a detailed representation of the image. By contrast a compound eye consists of a convex array of separate facets or optically independent units, about 5500 in each eye of a worker honey bee, all pointing in different directions. Each unit, called an ommatidium, has its own lens which is hexagonal in outline so that they pack together to collect all the available light (figure 9.2). Behind

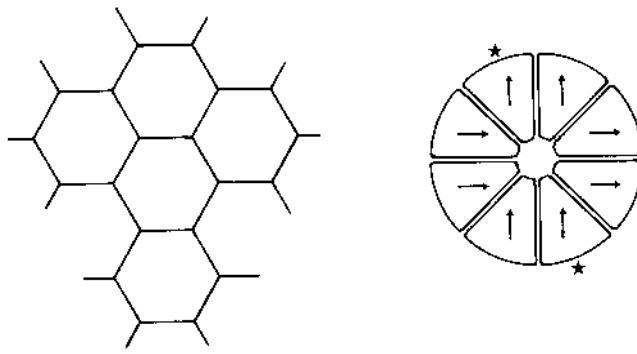


Figure 9.2. The compound eye of the honey bee. Left: the outer surface showing part of the array of hexagonal lenses, each of which faces outwards in a slightly different direction. Right: below one lens (at greater enlargement) showing the arrangement of the eight main light sensitive cells in cross section. The arrow within each cell shows the polarisation direction to which it is most sensitive. The two cells marked by stars respond best to ultraviolet light and the rest to either blue or green light.

each lens there are essentially eight light-sensitive cells (figure 9.2) in an octagonal pattern, each connected to the brain by a nerve fibre. This little set of cells does not qualify for the term retina and is called a *retinula* or 'little retina'. Clearly with such limited attributes one ommatidium cannot form and analyse an effective image and the visual field is only represented by the combined action of the whole array of such units.

Now von Frisch imagined that each of the eight light sensitive retinula cells might somehow be sensitive to one direction of polarisation so that one ommatidium would be able to analyse polarisation in terms of four components 45° apart (figure 9.3). This idea was correct in principle although the details turned out to be slightly different. Actually four of the eight cells are potentially most sensitive to one direction of polarisation while the other four are most sensitive to light polarised at right angles to this, giving simultaneous analysis into two orthogonal components (figure 9.2). The position is complicated, however, by the fact that the same cells also serve for colour vision which, as in our eyes is achieved by comparing the excitation of three kinds of cells with different spectral responses: in the bee retinula four of the eight cells are most sensitive to green, two to blue and two to ultraviolet (figure 9.2).

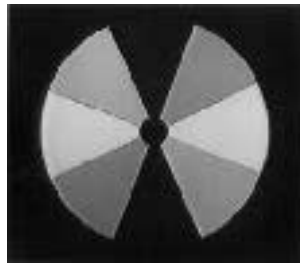


Figure 9.3. Karl von Frisch imagined the main eight sensitive cells of a bee's ommatidium might be sensitive to four directions of polarisation. He made a model from pieces of polaroid which makes a very good polariscope as shown in this replica. The actual polarisation sensitivities as determined by later, physiological studies, are shown in figure 9.2.

In common with most other insects, bees have no red-sensitive cells. It is the ultraviolet cells that are most responsive to the direction of polarisation although an additional short ninth cell, also an ultraviolet unit and tucked in among the bases of the other eight, may be the most polarisation sensitive of all in most ommatidia.

The basis of this polarisation sensitivity is that in these eyes the light absorbing process is inherently dichroic. The visual cells of all animals detect light when it is absorbed by special receptor molecules that are thereby changed in shape by a photochemical reaction; this initiates a chain of events that culminates in messages to the brain via nerve fibres. The sensitive molecules, of substances called visual pigments, are elongated and absorb light most readily when the direction of polarisation is aligned with their long axis, or at least with a series of carbon=carbon double bonds within the molecules. In the light sensitive retinula cell of an insect compound eye these pigment molecules are all orientated in the same direction. They are held in the membranous walls of minute parallel tubular pockets called microvilli, that are tightly packed together and run from the wall of the cell across the light path (figure 9.4). Thus all the absorbing molecules lie across the light path and, with their axes all more or less parallel, the system as a whole is dichroic, like some crystals. Light polarised in one direction is strongly absorbed, leading to excitation of the cell, while light polarised at right angles is not absorbed and has no effect.

One final complication in the bee's eye concerns twisting of the

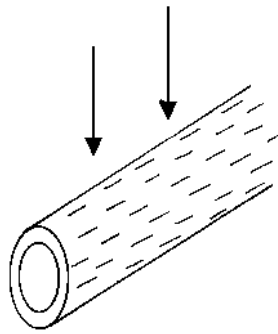


Figure 9.4. The sensitive cells of the eyes of a bee and many other invertebrate animals contain tiny tubes called microvilli that lie across the light path (arrows). The membranous walls of the microvilli contain the light sensitive pigment molecules (represented as dashes) which are all orientated in the same direction. This almost crystal-like regularity makes the light absorbing process dichroic so that the cell is inherently most sensitive to light polarised along the axes of the microvilli.

group of retinula cells. In the system described earlier, there could be an ambiguity between colour and polarisation: both are detected by the brain comparing the excitation of different cells within the ommatidium, but differences of response may equally be due to the colour of the light or to its polarisation. In order to avoid this problem, the bundles of sensitive cells in most ommatidia are twisted along their length by more than 180° , like strands of a rope, clockwise in some ommatidia and anticlockwise in others. Thus the axis of dichroicity rotates so that light not absorbed in the outer part of a cell may well be absorbed when it passes further down. This improves sensitivity because the total light capture is increased, but although the membranes with their visual pigment molecules are actually dichroic, the twisted cell as a whole is not, or it has greatly reduced susceptibility to polarisation. This may explain why the short ninth cell is often the most sensitive to polarisation, because its very shortness means it is never twisted enough to destroy its inherent dichroicity. The non-dichroic cells, however, are ideal for unambiguous colour analysis because differences in their excitation can only be due to differences in their spectral responses.

However, there is a band of about 150 specialised ommatidia that lie in the dorsal region of the eye and so face upwards. They are called the

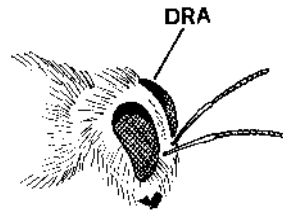


Figure 9.5. The eye of the honey bee showing the dorsal rim area (DRA in black) where about 150 upward-facing ommatidia contain polarisation-sensitive ultraviolet-sensitive cells, responsible for analysing the polarisation pattern of the sky.

dorsal rim units (figure 9.5) and they have no twist to their retinula cells. The cells are therefore highly dichroic as a whole and are thus ideally adapted to perform rapid assessment of the polarisation pattern of the sky (see chapter 6). It is this band of dorsal rim ommatidia that is responsible for the sky compass navigational abilities of the bee. Because they point upwards they are unlikely ever to be used for discriminating colours, of flowers for example, and the possible ambiguity described previously is therefore irrelevant. In some of these ommatidia the ninth cell is not short but runs up the bundle with the others, while the microvilli, with their dichroic pigment molecules, may be arranged not in just two orthogonal directions in different cells but in three or even more directions within the retinula of one ommatidium.

A different and rather more ‘extravagant’ solution to this problem of colour/polarisation ambiguity is found in the remarkable eyes of mantis shrimps, *Squilla*. Most crustacea, like insects, have compound eyes. Those of mantis shrimps contain as many as ten different sensitive pigments so their colour vision must be quite outstanding. Perhaps because of this variety, in the mid-band of the eye there are horizontal rows of ommatidia that ‘look at’ the same regions of the visual field, instead of all pointing in different directions. Two rows of these mid-band ommatidia are sensitive to polarisation in the broad range from blue to yellow light. So in these animals colour vision and polarisation analysis are served by different specialised ommatidia that face in the same direction. The function of polarisation sensitivity in mantis shrimps is as yet unknown.

Ants also show discrimination of sky polarisation. Some especially revealing studies have been made on desert ants, *Cataglyphis*, of North

Africa and the Middle East. These insects must forage across open spaces, often with no visible landmarks to guide them. Even if their outward path is quite tortuous they can still take a direct line back to their nest over as much as 200 m. Furthermore, unlike bees, they can be followed by experimenters who can manipulate their visual environment all the way by devices held over the walking ants. For instance the sun can be obscured by a shadowing card, leaving most of the sky clearly visible, or conversely the sky polarisation can be changed by a large sheet of polaroid while leaving the sun visible through it. It has been known since 1911 that some ants, such as the garden ant *Lasius*, rely predominantly on the sun—using so-called sun compass orientation. Shielding them from the sun, and at the same time showing them a reflection of the sun in a mirror, makes them change or even reverse their direction of travel accordingly. But the desert ant relies more on the pattern of sky polarisation than on the sun itself. In this case each eye has about a thousand ommatidia of which about 80 dorsal rim units are specialised polarisation-sensitive, ultraviolet units. Reliable navigation back to the nest without delay is essential in the desert where long exposure to the hot sand can be lethal. Perhaps a small cloud over the sun could impose a dangerous delay if only the sun compass were used.

Polarisation sensitivity of this kind now seems to be very common among the insects and examples of a different kind of application by dragonflies and water boatman bugs have been given in chapter 7. As in the bees and ants, it is generally especially associated with the ultraviolet-sensitive cells. An exception is seen in crickets where the dorsal rim cells are all blue sensitive dichroic units although ultraviolet- and green-sensitive cells occur elsewhere in the eye. The probable explanation is that whereas bees and ants are active by day, crickets tend to be nocturnal, when levels of ultraviolet light are low. It has been suggested that this may be common in other nocturnal insects although some diurnal flies also seem to be most sensitive to polarisation at blue wavelengths. Strangely, a few insects, such as certain water beetles, show best polarisation analysis at the (to them) very long wavelengths of yellow-green light and this has not yet been very convincingly explained. In general, the main significance of polarisation analysis seems to be the ability it confers of using the sky pattern for orientation, not just for homing as in bees and ants but also for keeping to a straight track. Many different insects, including butterflies, flies and mosquitoes, appear to be reluctant to fly across open spaces when the sky is heavily overcast. Even on a sunny day, it is not possible to keep the sun in sight

when moving through a wood whereas patches of sky can nearly always be seen here and there through the canopy.

The presence of microvilli with aligned receptor molecules, and their orthogonal orientation in different cells of the ommatidium is common to insects, crustacea (including *Daphnia*) and many other arthropods in general. There are some variations, for instance bunches of microvilli of different cells may actually interdigitate in an orthogonal 'dovetailed' arrangement so that light passes through each in turn along the axis of the cells. But the basic arrangement is ubiquitous. In a number of cases it has been possible to observe dichroicity within individual receptor cells by measuring light absorption for different directions of polarisation. It is tempting, therefore, to suppose that all these animals are able to detect the direction of polarisation. But this may not always be so. Twisting of the bundle of receptor cells has already been mentioned as a reason why the basic dichroicity may be lost—and twisting is not easy to observe as it requires cell orientation to be followed through a lengthy series of electron microscope sections. In many compound eyes the retinula cells within an ommatidium may also be coupled together electrically so that their excitation is shared. This increases the overall sensitivity to light but it destroys any individual dichroicity. Any such coupling through the membranes of adjacent cells cannot be seen under the electron microscope and is only revealed by electrophysiological recording of the responses of cells to light.

Actual evidence for polarisation analysis can take a number of forms, either behavioural or physiological. Examples of spontaneous behaviour in response to polarised light, and of changes of behaviour when the direction of polarisation is manipulated experimentally, have been described already. A number of investigators have also trained animals to respond to the direction of polarisation in an artificial visual stimulus. For instance an animal may be rewarded for pressing a pedal when shown vertically polarised light but not when shown horizontally polarised light. Such experiments, however, may be misleading even when the responses appear to be completely reliable. The problem is that an animal working for a reward will identify any clue as to which is the 'correct' signal and it may not be the clue the experimenter has in mind. This is especially true of polarised light stimuli. For instance, the light is sure to be reflected from some part of the enclosure or from objects within it. But light polarised in one direction is often (indeed generally, to some extent) reflected more strongly than light polarised at right angles (chapter 7). So an animal that is completely insensitive

to polarisation might nevertheless spot differences in the brightness of a reflection and learn to respond quite consistently to achieve a highly 'correct' score.

A more direct way of demonstrating sensitivity to the direction of polarisation is to record the excitation of individual receptor cells or their messages to the brain in single nerve fibres. A very fine electrode is inserted into a receptor cell or nerve fibre and is used to record the electrical changes brought about by light stimuli. When polarised light is used, the direction of polarisation is varied to give the strongest response, and this is compared with the response to light of equal intensity polarised at right angles to the first. A large difference means that the response is greatly dependent on polarisation and therefore the animal as a whole could be affected; a small difference of response naturally means the unit is only weakly sensitive to the direction of polarisation. Then if two responses with orthogonal directions can be found in different units, the animal should be able to analyse the direction of polarisation. This approach has now been used successfully to study bees, ants, crustaceans and a range of other creatures.

Incidentally, it seems to be commonly assumed that two orthogonal sensitivities are necessary to analyse the direction of polarisation but of course one strongly sensitive direction will do provided that the animal is able to rotate its head, or at least its eye, and make successive observations. Conversely, even two orthogonal sensitivities can give ambiguous answers if no movement is made—vertically and horizontally sensitive cells will be equally stimulated by oblique polarisation at 45° . The problems are exactly the same as with the polariscopes described in chapters 1 and 2. In the case of reflections from water, which is always horizontal, no such ambiguity need arise and two orthogonal sensitivities will do for the water boatman bug or the dragonfly (chapter 7). But the sky compass analyser of the dorsal rim of the bee's eye has a more difficult task that justifies a greater complexity, with more than two sensitive directions.

Octopus, squid and cuttlefish are very highly developed molluscs. Their eyes are not multifaceted compound eyes but simple or 'camera' eyes, optically very like our own although they have evolved quite independently. The receptor cells of the retina contain their receptor molecules within microvilli and half the cells have their microvilli running horizontally while the other half have them vertically. Two cells of each kind form tetrads throughout the retina, suggesting the presence of polarisation sensitivity. Recently, behavioural tests have shown that an

octopus can indeed analyse the direction of polarisation. They have been trained to respond to lamps that have a polarisation contrast pattern, say a vertical polarisation in the centre with a horizontal polarisation in the surround, or *vice versa*. They can even respond when the difference of direction is as small as 20° instead of 90° . The risk of 'false' cues being involved here can be made very small. Moreover, octopuses are also able to distinguish between a clear piece of Pyrex glass with no strains and an otherwise identical piece that has been subjected to heat stress to create internal strains. These produce birefringence that is only made visible by polarisation analysis (see chapter 2 and figure 2.10)—both glasses look identical to our eyes.

The significance of all this for vision in their environment is not yet clear but perhaps it enhances their ability to detect the shiny fishes on which they prey. Silvery scales reflect the colour of their surroundings, which is perfect camouflage underwater, but the reflections can be strongly polarised in ways that do not match the polarisation produced by scattering in the surrounding water. So polarisation analysis can be used to 'break' the camouflage. Quite apart from this, some cuttlefish apparently use polarisation to communicate with each other. As well as signalling by their well-known transient patterns of light, shade and colour, they can also produce patterns of light polarisation in their skin by means of iridophores: cells that are iridescent because they produce multiple internal reflections which interfere and polarise the light they reflect (see chapter 7). Like all iridophores, these cells are not themselves changeable but in cuttlefish they can be quickly concealed or exposed by tiny overlying sacs of black pigment controlled by radial muscle fibres. It has been suggested that these cuttlefish are thus able to communicate 'secretly' with each other without disturbing their general camouflage patterns of shade and colour that alone would be seen by any predator that lacks polarisation sensitivity.

Spiders are much more closely related to insects and crustacea, since all three belong to the Arthropoda, or joint-limbed animals with external skeletons. Yet their eyes are of the simple or 'camera' type (actually most insects also have three simple eyes called ocelli, but they are quite crude). The eyes of spiders vary considerably but most have four pairs of eyes looking in somewhat different directions. In the hunting or 'wolf' spiders, *Arctosa* (figure 9.6), the two 'principal', or anterior median eyes have large lenses and form good images. They are used for orientation and respond to the polarisation pattern of the 'sky compass'. Both they and the upward-looking posterior median

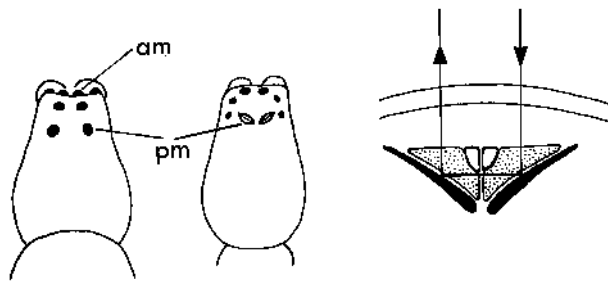


Figure 9.6. Left: the eyes of a wolf spider, *Arctosa* species, as seen from above; the forward-facing anterior median or 'principal' eyes (am) and upward facing posterior median (pm) eyes have been shown to be sensitive to the direction of polarisation. Centre: the 'squinty' boat-shaped polarisation sensitive posterior median (pm) eyes of the spider *Drassodes* as seen from above. Right: a section across a pm eye of *Drassodes*, with two reflecting layers (shown black) that lie obliquely below the masses of light-sensitive cells (dotted). The arrows show how light that is not absorbed on its first passage through one group of receptor cells is reflected back through them, across the eye and then through the other group of cells. Polarisation by reflection (chapter 7) acts together with the dichroicity of the receptor cells to enhance their polarisation sensitivity. There is no lens and no image is formed in these eyes but the two set at right angles are well adapted to detect the polarisation of sky light.

eyes have microvilli which, in parts of the retina, are arranged in orthogonal groupings. Electrical recordings have confirmed the presence of polarisation sensitivity in both wolf spiders and jumping spiders.

In 1999 a new kind of eye was discovered in another spider called *Drassodes*. Here again the two posterior median eyes are on top of the head, looking vertically upwards (figure 9.6). They are boat shaped and orientated at right angles to each other in a way that is aptly described as 'squinty'. In common with many other spider eyes, the retina is backed by a reflective layer which, as in the eyes of cats and many other nocturnal creatures, directs any unabsorbed light back through the retina. Such reflections from spiders' eyes can often be seen at night if one holds a torch close to one's face and looks around a garden lawn for instance. In *Drassodes* the reflection is bright blue and is polarised along the axis of the eye so that a rotating polariser extinguishes the reflection from each eye in turn. As shown in figure 9.6, the reflective

layer is folded into two flat plates forming a V-shaped trench along the sides of the 'boat'. Light therefore reaches the retinal cells either directly or after reflection by one or both reflectors. Even an isolated piece of a reflector is found to polarise light and this clearly enhances the inherent dichroicity of the 60 or so main retinal cells whose microvilli run along the longer axis of the eye. The electrical responses of the cells peak in the ultraviolet and show an unusually high dependence on the direction of polarisation. These eyes have no lenses so they can form no image and they receive light from a wide angle, about 125° . The spiders are active around dawn and dusk when the sky overhead is polarised in a rather simple north-south band (figure 6.3 and chapter 6). Behavioural tests support the suggestion that the two eyes act together as a polarising sky compass to enable the spiders to return to their lairs after hunting forays. The structure of the polarising reflector layers is not yet known but it probably involves multiple layers and a Brewster-type reflection (chapter 7).

In the retinas of vertebrate eyes, the receptor cells, rods and cones, are quite different in structure from any of the foregoing. Instead of having microvilli, they have a stack of transverse disclike membranes that lie across the light path and contain their receptor molecules in random orientation (figure 9.7) in their walls. Indeed within the rather fluid membranes the individual molecules are free to rotate around the optical axis so that they all point randomly in different directions and fluctuate continuously. This arrangement would not be expected to be dichroic and optical measurements have confirmed this. In fact, when light is shone experimentally *across* the cell, there is marked dichroicity since all the receptor molecules are at least parallel with the planes of their holding membranes and strongly absorb when the direction of polarisation is in this plane. But in life and a whole eye, light never shines across the cells, only down their length.

The freedom of receptor molecules to rotate within the membranes of vertebrate retinal cells has been demonstrated by some ingenious observations. First, the visual cells of a frog were treated with a chemical (glutaraldehyde) that killed the cells and 'set' the fluid membranes, so preventing further movement of their constituents. A bright flash of polarised light shining in the normal direction along the length of the cells then left them strongly dichroic for further beams of light along this axis. Any receptor molecules that had absorbed light with the direction of polarisation of the first flash were inactivated (when they are 'bleached' and no longer absorb light), so further absorption in a

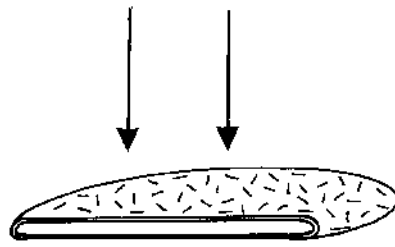


Figure 9.7. The light-sensitive cells, both rods and cones, of vertebrate eyes contain disclike double membranes that lie transversely to the light path (arrows). The light-sensitive molecules (dashes) are contained within these membranes but they point in all directions and are therefore not sensitive to the polarisation of light coming from the lens. This arrangement contrasts with the regularly orientated molecules in the eyes of bees and other invertebrates (figure 9.4).

second flash was favoured for light polarised at right angles to the first, in the molecules that were still receptive. But in living cells, where these molecules are free to rotate rapidly and randomly, such dichroicity persists for only a very brief time, around $20\ \mu\text{s}$ (millionths of a second). Restoration of sensitivity by the regeneration of bleached molecules is very slow by comparison, taking a matter of minutes, and so cannot explain the rapid loss of dichroicity in normal eyes after the first flash. In this way paired flashes of polarised light can be used to measure the rate of molecular rotation within the membranes of living visual cells.

From all this one would not expect vertebrates to be sensitive to the direction of polarisation of light, and until a few years ago this was believed to be so. One exception may be found in the anchovy fish, *Anchoa* species, where the cone cells of the retina are contorted so that the membranous discs run almost lengthways and so lie edge on to the light path (figure 9.8). The cones are arranged in the retina in vertical rows (with rods in between) and there are two kinds of cone that alternate in each row, with the two types having their discs arranged orthogonally, either vertically or horizontally. This arrangement is expected to make each cone dichroic and the two orthogonal directions could give the anchovy the ability to detect the direction of polarisation. The way in which one kind of cone fits neatly under the other may increase overall sensitivity since the horizontally polarised light that passes through the short cones may then be absorbed by the horizontally sensitive long cones and not be wasted. In this respect there is a functional resemblance

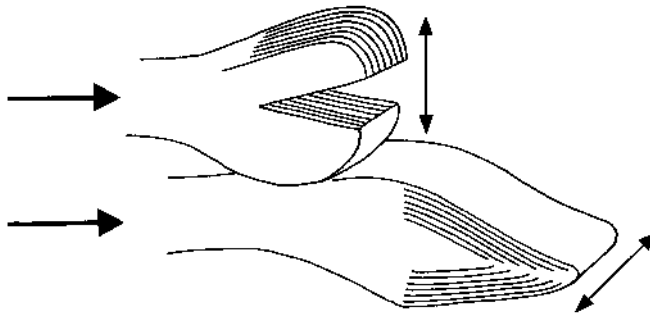


Figure 9.8. The outer, light-sensitive regions of retinal cone cells in the anchovy. The edges of the sensitive membranes are indicated by the close parallel lines (though there are very many more than shown here). The double-headed arrows show the planes of the membranes, which are tilted to lie along the normal light path and are therefore likely to be dichroic. There are two kinds of cell that alternate along the vertical rows of cones within the retina. The short forked cones have vertical membranes and should respond to vertically polarised light, while the long pointed cones have horizontal membranes and should respond to horizontally polarised light. This orthogonal arrangement is unknown among other vertebrates and probably forms a polarisation analyser. Light that has entered the eye through the lens comes from the left as shown by the larger arrows.

to the twisted arrangement of the cell bundles in insect eyes. So far this arrangement appears to be unique among vertebrates and the reason for it is unknown.

Another possibility involves the eyes of some fish such as trout, in which the retina retains a fold called the embryonic fissure into later life. In some cases this fold holds small numbers of cone cells that are therefore sideways on to the light path and would be expected to be dichroic. But no correlation has been attempted between this arrangement and the ability to detect polarisation, nor would it enable the fish to analyse more than a tiny part of the visual field.

Nevertheless evidence has steadily accumulated to suggest that many other non-mammalian vertebrates may be sensitive to polarisation and even observe its direction. For instance a variety of fish including trout and goldfish show spontaneous responses such as orientation to the direction of polarisation. Salamanders and pigeons can be trained

to respond to the direction of polarisation; hatchling turtles seem to orientate towards the sea by observing polarisation; some small migratory birds appear to use the sky compass (chapter 6) after dusk, and during development may 'set' an internal sense of the earth's magnetic field by comparison with the polarised sky compass.

The mechanism is still not clear but it seems that polarisation dependence in these vertebrates may be associated with 'double cones' in the retina. These comprise two similar cone cells in an intimate association, the combined pair having an elliptical cross section. It has been suggested that these pairs might somehow conduct light in a birefringent way and therefore may be polarisation dependent. This suggestion is supported by the layout of the double cones in the retina, where they are set in a square mosaic of tetrads with the long axes of the ellipses set in two orthogonal directions. Furthermore the polarisation sensitivity of the Green Sunfish, *Lepomis cyanellus*, has been found to be best at the same red wavelength as light absorption by the double cones, whereas in this fish no other cones have the same pigment. It also seems to be significant that double cones are found in fishes, amphibia, reptiles and birds but not in mammals, where no case of polarisation sensitivity has (yet) been discovered.

The story is far from clear, however. Electrical recordings from single cells and nerve fibres in trout and goldfish have shown that green and red double cones respond to the same direction of polarisation although they are orientated at right angles to each other. A common basis of birefringence due to asymmetry of cross section seems unlikely therefore. Also the ultraviolet cones (but not the blue ones) respond strongly to polarisation direction although they are not formed into double cone pairs.

Finally, there is one way in which humans are sometimes said to be able to detect strong polarisation directly, without reference to reflections or scattering. The effect is not strong and I myself, in common with others, have great difficulty seeing it. By gazing at an even field of strongly polarised light, especially if it is blue in colour (such as a clear sky at right angles to the sun) one is supposed to see a small faint figure, called Haidinger's brush after its discoverer who described it in 1844. It consists (figure 9.9) of two yellow, brushlike patterns back to back and with blue areas between. The whole figure is about 3° wide (the full moon is about half a degree wide) and the yellow-brown wings are aligned at right angles to the direction of polarisation. I have only seen it very faintly after staring for some time with one eye through a

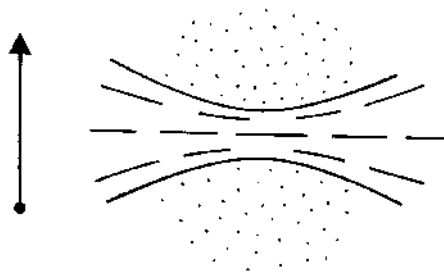


Figure 9.9. An impression of the pattern known as Haidinger's brushes that is sometimes seen when people look at a patch of polarised light (from various sources). The barlike figure (dashes) with open fuzzy ends, the 'brushes', is faintly yellow–brown while the (dotted) areas either side of its waist are bluish. The axis of the figure is at right angles to the direction of polarisation, shown by the arrow, and extends for about 3° .

polaroid film at a brightly lit sheet of white paper. Even then it only works for me when the polaroid is suddenly rotated by 90° or so and the figure appears as it rotates too. It is also said that circularly polarised light can produce brushes, aligned lower left to upper right for right-hand circular polarisation and upper left to lower right for left-hand circular polarisation. I cannot vouch for this.

There is no consensus on the explanation for these figures although they are commonly attributed rather vaguely to 'dichroism in the fovea', or that part of the retina responsible for the most detailed central vision and sometimes called the yellow spot. The usefulness of the figures is probably negligible and they are mentioned here simply because some people say that humans *can* see the effects of polarisation after all. To see a small figure, however, is not at all the same as being able to see the property of polarisation in an image. What the world might actually look like to animals which have that ability is, after all, something we can only imagine. Our knowledge of the various phenomena described in this book is only the beginning. We can only dream about its part in any whole sensory experience.