Light as an Ecological Factor: II

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Polarized light as a visual cue

The human eye cannot perceive all aspects of light in the visual world—we cannot detect polarized light. Natural light is not always equally polarized in all directions. For example, reflected light differs from incident light in that certain directions of polarization are suppressed after reflection. If we could see the polarization pattern, as well as being able to discriminate intensity and wavelength, the visual world would be full of additional impressions.

A specially impressive pattern of linearly polarized light that occurs regularly in our environment is that in blue sky. This polarization pattern results from the scattering of light by small particles (Tyndall's effect) as well as by refraction in the sky. Plate 12.1 (facing p. 292) is an attempt to show with colours how the polarization pattern looks to an eye which can perceive polarized light. Here we have assumed that polarization detectors are similar to colour receptors. We have presumed that there are polarization detectors for 3 angles of polarized light, with preferred sensitivity axes to the E-vector 60° apart, similar to the three colour receptors blue, green and red. Directions of polarized light between these three main classes are illustrated by mixtures of the corresponding colours. The different amount of light polarized in any direction is shown by altering the intensity of the colour in the diagram.

There are four points in the sky, apart from the sun, where there is no polarized light: Babinet's point (20° above the sun), Brewster's (20° below the sun), the point directly opposite the sun (opposite point) and Arago's point (20° above the opposite point). Only three of these points are visible at any time. Polarization is maximal at 90° to the sun. The direction of polarization is vertical to the plane containing the observer, the observed point in the sky and the sun. As this pattern has a fixed relationship to the sun, animals with polarization detectors can orient towards it even when the sun is not actually visible. If only a small part of the sky is visible the animal cannot interpret the pattern unambiguously, for there are two or three
points with the same polarization pattern at each altitude (see Plate 12.1). However, when a large part of the sky can be seen the animal is able to use the asymmetry of the overall pattern to orient correctly. There are only two occasions when the pattern is not asymmetric: (1) shortly before sunrise (sun at 10°) when Babinet's and Arago's points are equally distant from the horizon and (2) when the sun lies at the zenith.

Behavioural experiments with arthropods have shown without doubt that arthropods orient towards the polarization pattern of the sky. This orientation was discovered in bees (v. Frisch 1967), and has also been studied in ants (Formica rufa, F. fusca, Lasius niger—Carthy 1951, Jander 1957,

Figure 12.1. Polarization orientation of the Isopod Ligia italic.

a. Individual runs by Ligia in the natural environment (near Umag, Yugoslavia). The animals were transferred from the shore to a flat field unknown to them. With sun and blue sky, their paths (run 1+2) are oriented exactly towards the shore (the arrow points in the direction of the shore). In cloudy conditions, when less than one-third of the sky is visible, the runs are still well oriented (runs 3, 4, 5). When the sky is completely covered with clouds, the runs are disoriented (runs 6, 7, 8, 9). □ indicates that the animal paused.

b. Runs in the arena under partially blue sky (half to two-thirds visible), without view of the sun. The tracks are mainly directed towards the west, the direction towards the shore in the former habitat is shown by the arrow. Then experiments were carried out at different times of day.

c. Runs in the arena under a sky wholly covered with clouds. The animals are disoriented.

These experiments show that Ligia italic orients astromonotactically to the polarization pattern of the sky.
Jacobs-Jessen 1959); bumble-bees (Bombus hypnorum, Jacobs-Jessen 1959),
dung beetle (Geotrupes, Birukow 1953), water-strider (Velia currens, Birukow
1956) and other insects. Also crustacea and spiders orient with respect to
polarized light (for example the crustaceans: Daphnia, Jander & Waterman
1960; Idotea, Pardi 1962, 1963, Talitrus, Pardi & Papi 1952, 1953; and the
spiders Arctosa, Papi 1955, 1959, Agelesa, Görner 1958, 1962; for review see
Waterman 1969).

An example of a crustacean orienting to polarized light is shown in Figs.
12.1a, b, c. The Isopod Ligia italica lives on the Mediterranean shores.
Ligia always runs back to the shore if it is taken away and achieves this by
orientating astromonactically. With sun and blue sky visible (Fig. 12.1a)
their paths are exactly directed towards the shore. In cloudy conditions when
only a small part of sky is visible (< 1/3) the runs are still well oriented.
However, when the sky is completely covered with clouds the runs are disoriented.

These preliminary experiments were repeated under better controlled
conditions in Darmstadt (Germany). A circular arena (diam. 2 m) was placed
on the flat roof of the laboratory building. The arena was surrounded by a
white band which hid any landmarks on the horizon. The animals were
placed in the centre of the arena facing in different directions and the runs
were quantified as shown in Fig. 12.1a, b and c. When at least 1/4 of the sky
is visible the tracks are mainly directed towards the west. The coastline of
their former habitat runs approximately from north to south. However, when
the whole sky is covered with clouds the runs are evenly distributed in all
directions. (Menzel unpublished experiments.)

Bees direct their dances with respect to a polarization pattern but only
when the polarized light is in the UV. (v. Frisch 1967, v. Helversen &
Edrich 1974). Similarly the desert ant Cataglyphis bicolor orients only to
polarized light of short wavelengths (< 410 nm, Duelli & Wehner 1973). It is
important to note that although the skylight throughout the spectrum is
polarized these animals use only the short wavelengths. It was found that
atmospheric disturbances affect the long wavelength light 10 times more than
UV light (v. Frisch 1967). The greater stability of the UV light may be an
important reason for long wavelengths not being used for polarization detec-
tion. Furthermore after Rayleigh’s law the intensity of scattered light is
inversely proportional to the fourth power of the wavelength (I ∝ 1/λ^4).

Therefore direct sunlight appears redder than scattered light. This is clearly
seen when one considers the chromatic distribution of sky light at different
distances from the sun (Plate 12.2). The columns in Plate 12.2 show the relative
stimulation received by the 3 known colour receptors of the bee eye (Autrum
& v. Zwehl 1964, Menzel unpublished), when the bee looks at different
points in the sky. It is clear that the long wavelength receptors are more

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Plate 12.1. (opposite) An attempt to demonstrate the polarization pattern of the blue
sky by using different colours for different directions of the E-vector. The three main
E-vector directions 210°/90°, 90°/170° and 150°/330° relative to the orbit of the sun are
represented by three colours: blue, green and red (see upper left corner); other E-vector
angles are given by intermediate colours. The amount of light polarized is illustrated by the
colours’ saturation. The light is not polarized when it comes directly from the sun (★, here
20° above horizon), from Babinet’s point (B, 20° above the sun), Brewster’s point (Br, 20°
below the sun), the point directly opposite the sun (not seen here) and Arago’s point (A,
20° above the opposite point). Polarization is maximal at 90° to the sun (79% of the light,
see values along the lower side) and decreases in both directions. See text for further
explanation.

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facing p. 292
Plate 12.2. Demonstration of the spectral distribution of light coming from different parts of the blue sky. The diagram is based on measurements by Hess (1939), cited in Rosenberg (1966) and were carried out along the sun's orbit with the sun 20° above horizon. Spectral energy is normalized to 300 nm for each point of measurement.

Figure 12.2. Electronmicrograph of a cross section through the rhabdom of the Australian bulldog ant, Myrmecia gulosa. The rhabdom is composed of the rhabdomeres of the 8 retinula cells. Four rhabdomeres contain microvilli lying in the same direction, the four others have their microvilli at ±60° to this group. The black dots within the retinula cells are screening pigment granules which move close to the rhabdom during light adaptation.

Polarized light sensitivity in arthropods

strongly stimulated by the light near the sun, which is weakly polarized. However, at 90° from the sun, where polarization is maximum (Fig. 12.1), the UV receptors clearly dominate. Therefore UV receptors are most reliable as polarization detectors, both because UV light is least influenced by atmospheric disturbances and because the area of maximal polarization has the maximal relative intensity of UV light.

Functional basis of polarized light detection

For an animal to perceive the plane of linearly polarized light (the E-vector) it is necessary that the photo-receptors have polarization sensitivity (PS). The structure containing the photopigment molecules in the insect eye (e.g. the rhabdom of the ant eye in Fig. 12.2) consists of sectors of microvilli
polarization sensitive. However, to my great surprise, my intracellular recordings from single retinula cells in the worker bee revealed that these cells were either nor only slightly sensitive to the direction of the E-vector (Fig. 12.3a). The intensity, spectral and polarization sensitivities were measured in over 250 cells in the eye of the worker bee. Fig. 12.4 shows the polarization sensitivity from all cells which maintained a stable resting potential for at least 30 minutes. The green cells which one finds most frequently have either no PS (group 1) or a very small PS (group 2). The blue receptors too, as in the drone eye (compare Shaw 1969), have only a small PS. There are two types of UV-receptors, with a low PS and some with a high PS. Those UV receptors with the low PS respond not only to UV light, but also to light of longer wavelength (> 420 nm). On the other hand the group with the high PS is much less sensitive to longer wavelengths (below 5% relative sensitivity for λ > 420 nm). These UV cells were

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Example: The bee retina

The first model for the mechanism of polarization detection was designed for the bee, the first animal found to orient towards polarized light. Von Frisch (for summary v. Frisch 1967) devised a model in which the starlike arrangement of the 8 retinula cells produced 8 polarization sensitive inputs. Later he adapted his model to Goldsmith's (1962) finding that the microvilli are arranged only in two directions. The new model consisted of a 'four branched polarizer' in each ommatidium.

This model requires that all 8 long retinula cells in each ommatidium are arranged in different directions. In the example given here there are three groups of microvilli directions arranged at 60° to each other. Obviously one can postulate that these three microvilli directions are the basis for the three assumed receptor types in Plate 12.1. Indeed microspectrophotometry (MSP) both, in the fly (Langer & Thorell 1966, Kirschfeld 1969) and the crayfish (Waterman et al. 1969, Waterman & Fernandez 1970) has shown that the absorption of polarized light is higher when the E-vector lies parallel to the long axis of the microvilli. (An exception is receptor 7 in the fly ommatidium, which absorbs most strongly when the E-vector lies perpendicular to the microvilli, Kirschfeld 1969). However, these absorption changes have been found to be small, the dichroic ratio is only 1:2 and this result has been taken to indicate a random distribution of photopigment molecules on the microvillembranes (Moody & Parriss 1961).

The recordings from single receptors in the almost intact eye (unlike the eye treated for MSP measurement) have revealed a high PS, up to 1:12, in the crustaceans Carcinus (Shaw 1969) and Procambarus (Waterman & Fernandez 1970). In the fly, although a low PS of 1:2 was found in most cases (Burkhardt & Wendler 1960, Autrum & v. Zwehl 1972), a PS of 1:5 was found occasionally. The occurrence of cells with a high PS suggests that the low values of dichroic absorption ratios found using MSP are due to artefacts arising during preparation and measurement (see discussion in Goldsmith 1975).

Dichroic absorption is obviously a prerequisite for PS in receptors, but other factors add to and are maybe more important than the initial dichroic ratio. The gross morphology of the light absorbing structure (e.g. length and diameter of the rhabdom) and its fine structure (e.g. microvilli orientation, number of microvilli directions) have a strong influence on the retinula cells' PS (Snyder 1973). Also electrical coupling between retinula cells can alter the PS (Snyder et al. 1973). The example given below demonstrates how important these factors are in determining the PS of each receptor cell.

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Figure 12.3. Intracellular recorded response of retinula cells in the worker bee eye to light flashes through a polarization filter. The polarization filter has moved by 10° between each light flash.

a. An example typical of most of the retinula cells which show no PS.

b. An example of a retinula cell which is highly sensitive to the rotation of the E-vector.

This cell was recorded in the proximal third of the ommatidium and had a spectral sensitivity function with a maximum at 348 nm and no sensitivity above 420 nm.
only found when the electrode was positioned in the proximal third of the ommatidium near the basement membrane.

The bee's ommatidium contains 8 long and one short proximal retinula cell (Fig. 12.5). This short cell, the 9th cell, appears in the basal quarter of the ommatidium and it has a total length of about 50–80 μm. It replaces the 7th cell which withdraws from the rhabdom as an axon. When the 9th cell appears the two directions of microvilli within the rhabdom are not changed. We know from Gribakin's (1969) spectral adaptation experiments that cell Nos. 1 and 4 (his group I) are UV cells. It is of great importance for the PS of the 9th cell that the microvilli of these 2 UV cells are oriented perpendicular to those of the 9th cell. The arrangement of the colour receptors in the bee ommatidium given in Fig. 12.5 was deduced from a comparison of Gribakin's data of the distal part of the ommatidium with our own electron microscope study of the proximal part, and is based on the assumption that the ommatidium does not twist around its long axis. Meanwhile we have found that ommatidia in hymenopteran eyes do twist (see also Gründler 1974). The total twist angle between the distal end of the ommatidium and the appearance of the 9th cell is about 90°. In addition we found that the 9th cell does not replace retinula cell No. 7 (as shown in Fig. 12.5) but one of the two UV cells (No. 1 or 4). Therefore, the 9th cell microvilli are oriented perpendicular to the distal part of the UV cells. This means that our general conclusion on the crossed polarizer effect of the UV cells and the 9th cell holds with this different arrangement of the colour receptors.

We interpret our electrophysiological results to mean that only the 9th cell is a polarization detector. Theoretical considerations show that the 9th cell is especially suited for polarization detection:

1. Because the rhabdom is short, the absorption is smaller, and the smaller the absorption the smaller the influence of the self absorption which reduces the PS;
2. Above the 9th cell the two long UV cells work as polarization filters in the UV and thereby raise the PS of the 9th cell.

It is astonishing that the 8 long retinula cells have so little PS as the

Figure 12.4. A histogram showing the PS values (abscissa) of retinula cells in the worker bee eye. The vertically striped bars give the green sensitive cells, the black dots indicate blue sensitive drone-bee cells, the bar with a circle represents a blue sensitive cell of a worker bee eye. Those marked with black stars are UV sensitive worker bee cells, which had considerable sensitivity to long wavelength (>5% relative spectral sensitivity above 420 nm), and the white stars mark UV cells (worker bee), which were recorded in the proximal third of the ommatidium and had less than 5% relative spectral sensitivity to longer wavelengths (>420 nm).

Figure 12.5. A schematic drawing of the proximal third of the worker bee ommatidium. The ommatidium contains 8 long retinula cells (Nos. 1–8) and a proximal 9th cell. When the 9th cell appears it replaces No. 7. No. 8 withdraws from the rhabdom and is more proximal than No. 7. Also shown is the distribution of the colour receptor types in the worker bee eye, based on the findings of Gribakin (1969, 1972). UV, B and G indicate the UV, blue and green receptors. The roman numerals (I, II and III) give Gribakin's grouping of the retinula cells. The microvilli direction is shown for the UV cells and the 9th cell. Note that the 9th cell has its microvilli perpendicular to those of the long UV cells.
parallel filter effect in the fused rhabdom (Snyder et al. 1973) should raise
the PS in spite of the high absorption. The low PS of the 8 long cells may
have several causes:
(1) The dichroic absorption is much smaller in these 8 cells than in the 9th
cell;
(2) the retinula cells are electrically coupled to each other;
(3) the microvilli of each retinula cell may not lie in a constant direction
throughout the length of the rhabdom as the ommatidium may be twisted.

We can say nothing about the first possibility as there is no information
on the dichroic absorption of individual rhabdomeres in the bee eye. It is
unlikely that the 9th cell has a different dichroic absorption from the 8 long
cells (see Snyder et al. 1973 for discussion). Electrical coupling between the
retinula cells is most probable. Simultaneous recordings from 2 cells in the
drone eye by Shaw (1969b) clearly demonstrated a coupling. We find that cells
which show a low PS also have secondary peaks in their spectral sensitivity
curves. These secondary peaks are thought to be caused by electrical coupling
between the different colour receptor cells (Menzel & Snyder 1974, Menzel
unpubl.). The third possibility (twisting of the rhabdom) has been recently
verified in the bee (Grundler 1974). The ommatidia are very regularly
arranged immediately under the crystalline cone but the arrangement be-
comes less regular in the proximal portion of the ommatidia (Fig. 12.5). This
twisting and the electrical coupling would both reduce the PS of the long cells.

The separation of function between the 8 long cells and the 9th cell solves
the problem of the ambiguity which would occur if all cells simultaneously
code intensity, wavelength and polarization direction. Also the develop-
ment of a specialized polarization detector reduces the complexity of the neuronal
wiring in the optic lobe compared with that required if all cells were polariza-
tion sensitive.

One PS cell in an ommatidium is not sufficient to provide unambiguous
determination of the polarization plane. This failure can be overcome by the
interaction of neighbouring 9th cells, either through simultaneous or succes-
sive interaction. In both cases it is necessary that the neighbouring 9th cells have
different orientations of their microvilli. In order to verify this assumption
we have examined the orientation of the 9th cell's microvilli in different parts
of the eye (Fig. 12.6). The results show clearly that the ommatidial pattern
and especially the directions of the microvilli differs in the various eye regions.
The two eyes are mirror images of each other with respect to the orientation
of their ommatidia and the 9th cell. We know from v. Frisch's experiments
that the dorsal part of the eye is most important for polaro-menotactic
orientation, and only in this eye region do the 9th cells show clear groupings
of microvilli orientations. The two groups lie at 120° to each other. Fur-
more the probability of two neighbouring 9th cells having their microvilli at

120° to each other is much higher than for pairs with 2 ommatidia between
them.

These results do not distinguish between the two possibilities of either
simultaneous or successive polarization detection. The structural require-
ments of a simultaneous detection method are certainly fulfilled as the recep-
tive fields of neighbouring ommatidia in the dorsal eye region show a broad
overlap. (Baumgartner 1928, Portillo 1936), Laughlin & Horridge 1971). The
neuronal mechanisms whereby groups of neighbouring 9th cells can simulta-
nously measure the direction of the E-vector appear simpler than a
method of successive comparison. Behavioural experiments may be able to
solve this question.
Conclusion: Structure of rhabdom polarization sensitivity

An eye composed of many receptors is able to deliver information which increases in detail with narrower acceptance angles, higher temporal resolution, narrow spectral sensitivity and strong polarization sensitivity. Thus a fine receptor mosaic made up of different cell types allows the visual world to be analysed with respect to several parameters. The number of quanta reaching the receptors is strongly reduced with the sharpening of the spatial, temporal, spectral and E-vector sensitivities. Therefore the absolute sensitivity must be increased. The increase in sensitivity is of extreme importance in insects with apposition eyes as the aperture of the ommatidia is approximately 20 μm. This is much smaller than the aperture in superposition eyes (ca 500 μm) or in lens eyes (some mm's).

The mechanisms for increasing absolute sensitivity are a high concentration of photopigment, the dense packing of the photopigment carrying membranes into microvilli, the formation of the rhabdom into a light guide and the length of the rhabdom. Asymmetric photopigment molecules can be packed most tightly when their axes lie parallel to one another. Also the most efficient way to pack membranes into a confined space, while still allowing diffusion of metabolites, is in a hexagonal lattice. Absorption of light is most efficient if the dichroic axis of the pigment molecules is at right angles to the light path (Wald et al. 1963). If the rhabdom contains several directions of microvilli it is a more efficient light gatherer than if it contains only one direction of microvilli (Staw 1969).

As a consequence of the strategy to increase absolute sensitivity the rhabdomees become polarization sensitive. This PS is maintained in the fused rhabdom by means of optical coupling. Similarly optical coupling sharpens the spectral sensitivities if rhabdomees with different photopigments are combined in a light guide structure. (Snyder et al. 1973). The great functional advantage of the fusion of several rhabdomees with different photopigments and different microvilli orientations is that a high absolute sensitivity can be maintained simultaneously with high spectral and polarization sensitivity.

It is not then astonishing that the PS is destroyed by electrical coupling between cells whose microvilli lie in different directions and twisting of the rhabdom. Possibly partial electrical coupling is a consequence of the dense packing of membranes in a fused rhabdom. However, electrical coupling has also several functional advantages. PS depends on the wavelength of the incident light, and this effect is very pronounced (Menzel 1975). There could be an ambiguity between differences in receptor outputs due to polarization and colour. Although this could be corrected by integration in the optic ganglion it might be considerably easier for the system to abolish the PS by electrical coupling and twisting and leave the detection of polarized light to a single specialized cell.

Snyder (1973) has shown that the tiered rhabdom of crustaceans is a special adaptation to maximize polarization sensitivity. The functional consequence of these mechanisms is a high PS at low intensities in the crustacean type of rhabdom. Since each receptor is highly sensitive to polarized light the rhabdom has high PS over a broad wavelength region if more than one colour receptor type exists in each ommatidium. The presence of more than one colour receptor type per ommatidium has been verified by Eguchi et al. (1973) who found two violet and five yellow receptors in each ommatidium of Procambarus. Underwater light is strongly polarized in a definite pattern related to the sun's position (Waterman 1972). Because of the strong attenuation of light with depth and the chromatic light climate under water there are distinct adaptive advantages in having a high PS at low intensities throughout a broad spectral region. In contrast, as insects use the polarization pattern of the blue sky light, intensity is high enough and PS at low intensity is of less importance. Their fused rhabdom seems to have evolved to combine high sensitivity with fine grain colour vision, while polarization sensitivity is restricted to a special receptor type and exists only in a small spectral range.

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References

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Questions and discussion

In answer to a question from the Chairman Dr. Menzel dismissed any importance of the differential reflection of polarized light from the surface of the cornea on the basis that the polarization sensitivity in different ommatidia differs in its plane of maximal response and any effect of dichroic activity in the lens system can have no influence.