

THE RESPONSES OF SNAILS TO POLARIZED LIGHT*†

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The purpose of this paper is to call attention to the use of extra-ocular polarization analysis in the polarized light behaviour of a snail and to suggest that an extra-ocular polarization analyser could be employed by a number of organisms reported to orient to polarized light. Behaviour responses to polarized light have been reported for a number of arthropods: Verkhovskaya (1940), von Frisch (1949), Pardi & Papi (1953), Kerz (1950), Wellington, Sullivan & Green (1951), Wellington (1953, 1955), Stevens, Fingerman & Brown (1953), Baylor & Smith (1953, 1957*a, b*), and Vowles (1954*a, b*). The behaviour responses of a marine snail, *Littorina littorea*, to polarized light have been reported by Burdon-Jones & Charles (1958). The diversity of dioptric systems suggests that more than one mechanism of polarization analysis may be involved or that some ubiquitous polarizing analyser not directly associated with the dioptric system may exist.

Intra-ocular polarizing analysers suggested so far depend on the existence of 'Polaroid'-like (dichroic) structures as proposed by Autrum & Stumpf (1950); or they depend on a single reflexion-refraction at the air-corneal interface at the polarizing angle according to Stevens *et al.* (1953); or they depend on two separate double reflexion-refraction events at the corneal surface as suggested by Baylor & Smith (1953).

One extra-ocular polarizing analyser suggested by Baylor & Smith (1957*b*) for the honey bee proposes a non-uniform distribution of intensities in the pattern of light reflected from a substratum illuminated by polarized light. Vertical parallel rays of polarized light illuminating a substratum give rise to reflexions with minimum intensities in a direction parallel to the plane of polarization and maximum intensities perpendicular to the plane of polarization. But vertical parallel rays of non-polarized light illuminating a substratum give rise to reflexions of uniform intensities in all directions. In the escape reaction of the bee, orientation to polarized light occurs only if the bee is permitted to see the substratum and it occurs whether or not the bee is permitted to see the overhead source of polarized light illuminating the substratum. It remains to be seen whether the communication dances of bees described by von Frisch are mediated by extra-ocular polarization analysis or by some intra-ocular device. Indeed, in view of the non-uniform distribution of intensities reflected from appropriate substrata illuminated by polarized light it is possible that any positive phototaxis or even a light-directed klinokinesis can appear to be an ability to discriminate the plane of polarization.

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Additionally, two other extra-ocular polarizing analysers may be available to organisms orienting to polarized light under water. Clay particles, yeast, bacteria, or phytoplankton suspended in water scatter light with greater intensity at right angles to the plane of polarization thereby providing an asymmetric intensity stimulus. The importance of using carefully filtered water for polarized light experiments is obvious. Compounds such as toluidine blue, tryptophane, riboflavine, and chlorophyll A fluoresce strongly. When these compounds are excited by polarized light fluorescence is emitted perpendicular to the plane of polarization. Such asymmetric fields of intensity produce orientation to polarized light in snails on non-analysing substrata.

METHODS AND RESULTS

The marine snail, *Nassa obsoleta*, employed in these experiments possesses a simple positive phototaxis like that of *Littorina littorea*. Both bearing and distance travelled are easily measured and provide an adequate description of the behaviour.

We did the following experiments to test whether *Nassa obsoleta* has a polarizing analyser in the eye or utilizes the pattern of intensity gradients reflected from the substratum. The snails were allowed to crawl on a substratum of black 'Lucite' illuminated by a vertical beam of light which also projected a Cartesian co-ordinate grid upon the substratum. The lines of the grid were extremely thin and did not interfere with the behaviour to be measured. Each time the snail crossed a line the event was counted. Thus the pathway of the animal is measured as the sum of all the *X* vectors and the sum of all the *Y* vectors. If orientation is random, the path lengths in the *X* and *Y* directions should be approximately equal to each other. In control experiments the light source was non-polarized. In experiments with polarized light the plane of polarization was used alternatively parallel to the *X* axis and to the *Y* axis so as to obviate any inherent bias in the system. The polished black 'Lucite' substratum showed no differential reflected intensity in non-polarized light but showed a slight differential reflected intensity in polarized light.

The results of control experiments using non-polarized light on black 'Lucite' show random orientation. In Fig. 1 the path lengths in the *X* and *Y* directions are plotted against each other. The points are distributed on both sides of the diagonal line which indicates randomness of orientation.

In contrast, results of experiments using polarized light on polished black 'Lucite' show definite orientation perpendicular to the plane of polarization. In Fig. 2, the path length perpendicular to the plate of polarization is plotted against the path length parallel to the plane of polarization. With few exceptions all the points lie above the diagonal.

In order to determine whether the organism could respond to substratum reflectivity, scratched 'Lucite' was used. The scratches on the black 'Lucite' were all parallel and threw the surface into tiny ridges and valleys. Non-polarized light striking the sides of the ridges is reflected predominantly at right angles to the direction of the scratches. Polarized light vibrating parallel to the direction of the scratches is well reflected at right angles but poorly reflected parallel to the

direction of the scratches. Polarized light vibrating perpendicular to the direction of the scratches is poorly reflected perpendicular to the direction of the scratches, but is even more poorly reflected in the direction of the scratches.

Regardless of the plane of polarization of light the snails uniformly oriented perpendicular to the scratches. The data in Fig. 3 show that orientation was most pronounced when the plane of polarization was parallel to the scratches.

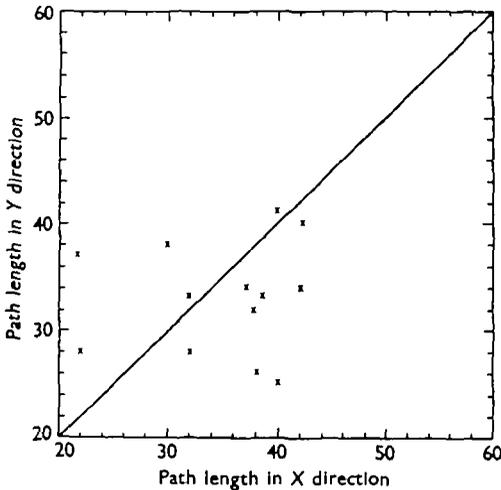


Fig. 1

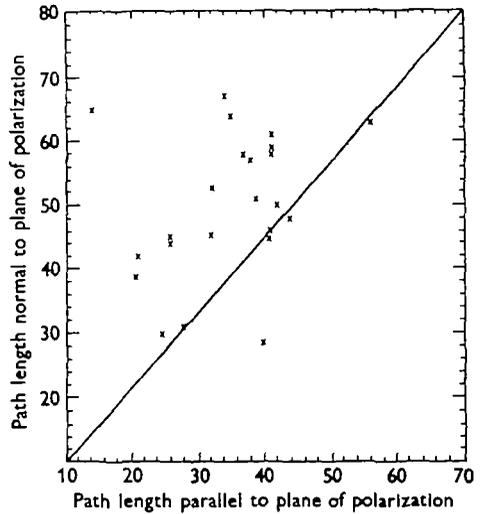


Fig. 2

Fig. 1. Orientation to non-polarized light by snails crawling on polished black 'Lucite'. Path lengths of the snails were measured and plotted on a Cartesian co-ordinate grid. When points fall equally on both sides of the diagonal line orientation is random.

Fig. 2. Orientation to polarized light by snails crawling on polished black 'Lucite'. The diagonal line represents random orientation. Orientation is predominantly at right angles to the plane of polarization.

To eliminate the possibility of snails seeing the overhead source of polarized light we attached black 'umbrellas' to the shell. The 'umbrella' was a circle of 'Scotch' photographic masking tape 10 to 20 mm. in diameter completely shading the tentacles bearing the eyes. A small area of the shell was scraped clean for attachment of the 'umbrella'. It is important that the attached 'umbrella' does not seriously alter the centre of gravity of the snail.

Snails carrying black 'umbrellas' in polarized light on polished black 'Lucite' oriented perpendicular to the plane of polarization although they could not see the incident radiation. The data from Fig. 4 show that this response was obtained in all but three experiments.

To eliminate the possibility of snails seeing the substratum and to assure their seeing only the overhead source of polarized light we caused them to crawl upside down underneath a plate of clear glass. The plate of glass was 25 mm. above the substratum. The snails carried their 'umbrellas' beneath them. It was necessary

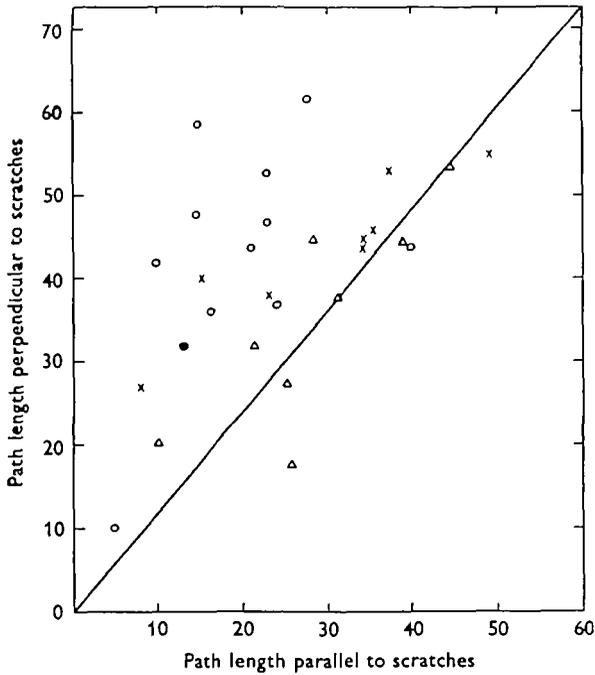


Fig. 3. Orientation of snails on scratched black 'Lucite'. Orientation to polarized light appears maximal when the plane of polarization is parallel to the scratches on the substratum. This combination of plane of polarization and direction of scratches produces maximum reflected intensity perpendicular to the scratches. The triangles are the path length in non-polarized light. Circles are path length when the plane of polarization is parallel to the scratches. Crosses are path lengths when the plane of polarization is perpendicular to the scratches.

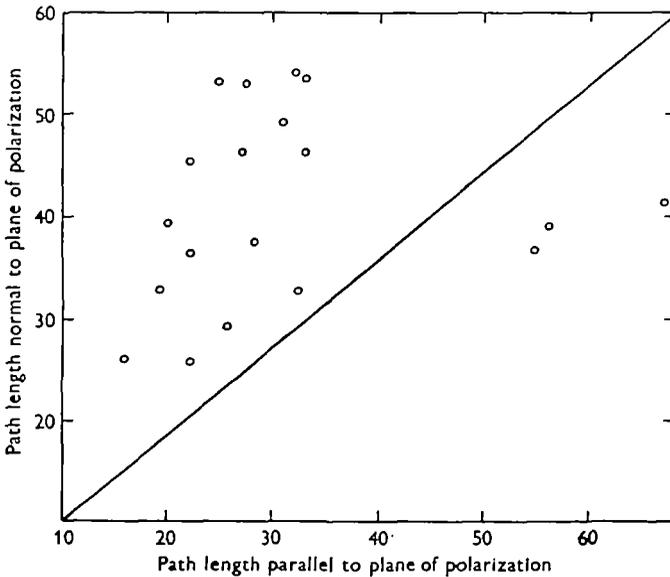


Fig. 4. Orientation to polarized light by snails carrying black 'umbrellas' while crawling upright on polished black 'Lucite'.

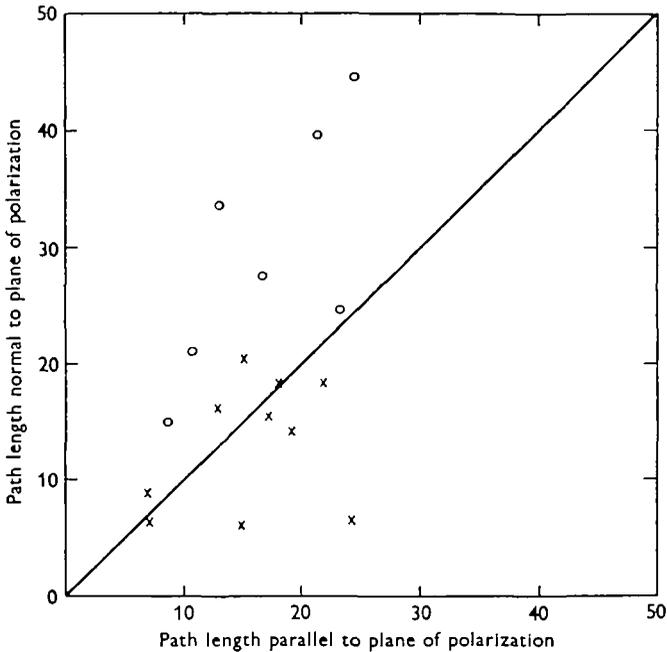


Fig. 5. Orientation to polarized light by snails crawling upside down with and without 'umbrellas' beneath them. Crosses show path lengths of snails with 'umbrellas' beneath them permitting no view of the polished black 'Lucite' substratum underneath but permitting a direct view of the polarized light source above. Circles show path lengths of snails without 'umbrellas' beneath them, permitting a view of both the substratum underneath and the polarized light source above. Orientation to polarized light appears best in snails permitted to see the substratum.

to attach a small float to prevent the snail from falling off the glass plate. No orientation was apparent in these experiments, shown in Fig. 5, although the overhead source of polarized light is fully visible to the snails. Control snails, in polarized light, crawling upside down and without 'umbrellas' orient almost as well as the snails crawling upright.

DISCUSSION

The conclusion from these experiments is that *Nassa obsoleta* under polarized light with all spurious reflexions reduced to a minimum is oriented by the intensity of substratum reflexions and not by a polarizing analyser within the eye. Also it follows from these experiments that the mere exhibition of an oriented response to polarized light does not inevitably imply the possession of a polarizing analyser within the eye.

An organism using extra-ocular polarization analysis orients to asymmetric directions of intensity or patterns of intensity which arise by: (1) preferential reflexion from the substratum; or by (2) preferential scatter from suspended particles such as yeast, algae, bacteria, clay, etc.; or by (3) preferential emission of fluorescence perpendicular to the plane of polarization of the exciting light in compounds like chlorophyll *a*, riboflavin, and chlorophyll degradation products.

So far extra-ocular polarization analysis appears to be principally a laboratory phenomenon. Its use by animals in the natural habitat is probably limited to situations where the sun but not all the sky is obscured from view, as for example in the shadow of a cliff, under trees, or in other conditions obscuring the sun. As a rule the normal intensity of light in the terrestrial environment is so much greater than the reflected intensity from polarized light that extra-ocular polarization analysis is not anticipated.

Three different mechanisms have been proposed as possible intra-ocular polarizing analysers. Autrum & Stumpf (1950) have suggested that the rhabdomeres of the honey bee are dichroic like 'Polaroid' and that they constitute more efficient receptors of polarized light than of non-polarized light. Stephens *et al.* (1953) have proposed that in accordance with the Fresnel laws a single reflexion-refraction at the corneal surface of the *Drosophila* eye serves as a polarization analyser. Baylor & Smith (1953) independently advanced a reflexion-refraction mechanism for the cladoceran and acarid eye which involves a somewhat unusual light path having two reflexions and refractions.

The Autrum & Stumpf (1950) hypothesis of intra-ocular polarization analysis is intuitively appealing and suggests a model which is consistent with the experimental observations of von Frisch (1950) on the communication dances of bees. But actual proof of the model as a valid analogue to the eye is lacking. Menzer & Stockhammer (1951) reported birefringence of bee rhabdomeres, but they used fixed material for their observations. Using unfixed material, de Vries *et al.* (1953) finds that the birefringence, if it exists, of the bee rhabdomere is less than 1%. The principal experimental evidence advanced by Autrum & Stumpf (1950) in favour of their model was a contention that the insect compound eye is a more efficient receptor of polarized light. This contention was based on a slightly greater magnitude electroretinogram voltage associated with polarized light stimulation than with non-polarized light stimulation. They employed a 50% neutral density filter to give non-polarized light of the same intensity as polarized light. Thus the increased electroretinogram voltage with polarized light in their experiments can be anticipated from the fact that most 'Polaroids' are not good neutral density filters. On the contrary, depending on the conditions of manufacture, they leak at one end of the visible spectrum or at both ends. When a light source is viewed through such polaroids crossed exactly at 90 degrees to each other the light source appears blue, red, or purple. Baylor & Kennedy (1958) using better intensity and wavelength control failed to corroborate the results of Autrum & Stumpf (1950) and adduced other evidence against a dichroic model of the bee eye. Further, extra-ocular polarization analysis has been demonstrated in the escape reaction of the honey bee by Baylor & Smith (1957*b*). Their findings, which are consistent with the experimental observations of von Frisch (1950), suggests that the communication dances of the bee are 'cued' by extra-ocular polarization analysis. Although their interpretation remains to be proved, it provides a more parsimonious explanation of von Frisch's observations than the Autrum & Stumpf model.

It is quite feasible for such organisms as *Cladocera*, having both an intra-ocular

polarizing analyser and a positive phototaxis, to utilize both intra- and extra-ocular polarization analysis simultaneously. It is not clear at this time how much substratum reflexion contributes to the polarized light responses of *Cladocera* but the polarized light response persists when substratum reflexions, fluorescence, and suspended particle scatter are eliminated.

In addition to substratum reflexion, *Cladocera* utilize the asymmetric intensity of scattered light found when a suspension of yeast or algae is illuminated by polarized light. Similarly, the asymmetric intensity of fluorescence of riboflavin, toluidine blue, chlorophyll degradation products, etc., excited by polarized light appears to enhance the response of daphnids.

There is no good evidence available at this time for cladoceran orientation to the polarized light of the sky.

It is unfortunate that some papers in the literature strongly imply that because there is a response to polarized light, it therefore must have evolutionary adaptive value as a navigational aid. Any timidity in pressing this classical fallacy of teleology is understandable. The invocation of polarized light as a navigational aid is probably unnecessary because usually when the sky is strongly polarized the sun is visible and inference of solar azimuth by polarized light becomes redundant. Pre-sunrise and post-sunset skies may constitute important exceptions and although both starlight and 'Gegenschein' are polarized there is as yet no necessity to invoke the polarization of either as an explanation of animal behaviour.

In concluding this discussion it seems worth while to suggest that most instances of polarized light response reported in the literature should be re-examined to determine whether they are 'cued' by intra-ocular or extra-ocular polarization analysis.

SUMMARY

1. Experiments were performed to test whether the polarized light responses of the marine snail, *Nassa obsoleta*, are mediated by a polarizing analyser within the eye or by the pattern of intensities reflected from the substratum.
2. Snails able to see only the substratum orient at right angles to the plane of vibration of vertically incident polarized light.
3. Snails unable to see the substratum but able to see the overhead source of polarized light fail to orient to the polarized light.
4. Implications regarding the rare occurrence of intra-ocular polarizing analysers and the improbability of extensive animal use of polarized light as a navigational aid are discussed.

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