AUSTRALIAN ALMANAC Vol.2 No 15

The Extended Sensorium

Polarisation Sensitivity: a Strong and Weak Sense

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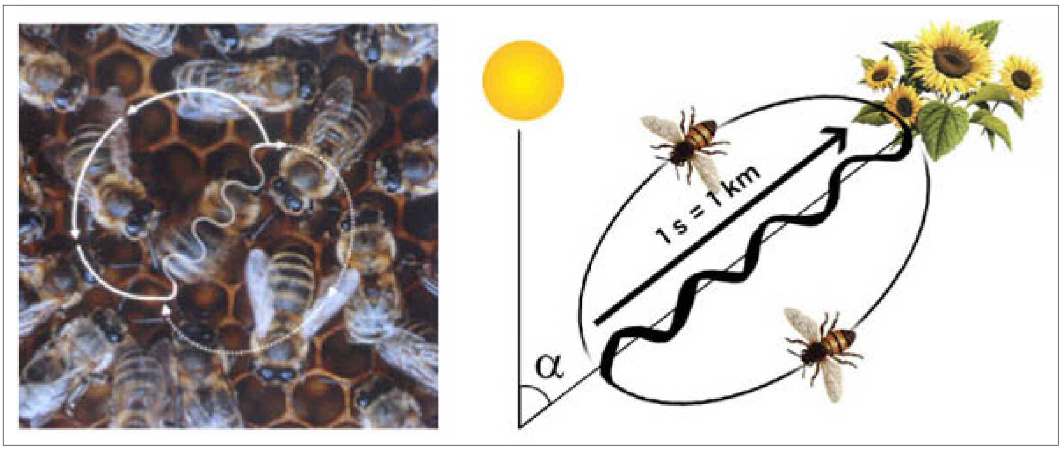
Part 1 of 2

Bows and bees

Our eyes are able to distinguish polarized from non-polarized light [1] only very faintly without the aid of other visual devices—when visible, this appears as a small yellow and blue bowtie image in the center of the visual field, called Haidinger's Brush—try staring at the white screen of your laptop, while tilting your head slowly to the side, to see it. Otherwise, our eyes require polarized filters to distinguish it. That is not to say that we don't see polarized light without them, we just typically don't see it as something which stands out against light which is not polarized. We will return to the human biological polarisation sense later, but for now, let us compare the first known cases of human and animal navigation using polarized light.



The honeybees' waggle waggle dance. "S" indicates the time during which the "waggle" part of the dance takes place, and the distance to the food source. The angle alpha, an angle on the honeycombs between the vertical direction and the waggle part of the dance, indicates the angle between the sun's position and the direction of flight to be taken. Another variation of the dance occurs when done on a horizontal plane, but the orientation towards the Sun is still necessary. Image Credits: (left) J. Tautz and M. Kleinhenz, Beegroup Würzburg, (right) Chris Jadatz.

Many years ago, it is thought that Vikings used a crystalline "sunstone" to determine the location of the sun on very cloudy days for navigational purposes. Crystals are known to polarize light, and to produced polarized light of different colours. Surely this could have been used to infer the position of a light source, but it is thought that certain kinds of crystals, such as quartz, tourmaline, or cordeirite, which could have served the purpose of a sunstone, could also have indicated the angle of incoming sunlight through changing colour and brightness, to perhaps indicate the position of the sun, even indirectly, through polarized sunlight patterns in the sky.[2] Animals have been found to operate based on a similar principle, though, of course, they do not use crystals as supplemental instruments. The capability to distinguish polarized light by some birds, insects [3], and a few sea creatures, is more developed than our own. Early on in this study, the polarisation sense was surmised to be used by bees, who can additionally sense the earth's magnetic field, and are known to dance based on gravitational cues, and the position of the sun.[4]

The sun sense and the polarisation sense were found to be closely related. Their dance, based on knowing the location of the sun, is used to give directions to other bees to indicate where a distant food source may lie, and they have been found to use this dance when a food source is 100 or more meters away from the hive. In this dance, the sun's position is the key reference point. This dance is called the "waggle waggle dance" (by humans, of course.)

These dances were studied by an Austrian ethologist (studier of animal behavior) named Karl von Frisch. He says his main discoveries were made in 1944, but were not accepted until decades later. He noticed that when he prevented the bees from seeing the sun's light, or when they were exposed to diffuse light, their dance became disoriented, but when exposed to even only a very small portion of the blue sky, they would resume the dance as though the sun were in view. This led him to assume that the bees were responding to the polarisation of light from the sun in the sky.[5]

"There can be no doubt that the sun's position is decisive for the direction of their dancing... But there was one big puzzle. To prevent excessive heating during most of the experiments, a protective roof was installed over the observation hive. The dancers were unable to see the sun. Nevertheless their dance was usually correct. Orientation by heat rays, by penetrating radiation, as well as other explanations seemed possible had to be discarded- until I noticed that a view of the blue sky is the same as a view of the Sun. When clouds passed over the section of the sky visible to the bees, disoriented dances immediately resulted. Therefore they must have been able to read the sun's position from the blue sky. The direction of vibration of polarized blue light,[7] differs in relation to the sun's position across the entire vault of the sky, thus, to one that is able to perceive the direction of vibration, even a spot of blue sky can disclose the sun's position by its polarisation patterns. Are bees endowed with this capacity?"

To give further weight to the hypothesis that they were responding to polarisation, Frisch performed an additional experiment :

"The following test furnished an answer. The observation hive was set horizontally in a dark tent from which the dancers had a lateral view of a small area of blue sky. They danced correctly toward the west where their feeding place was located 200m away. When a round, rotatable polarising foil was placed over the comb in a way as not to change the direction of the vibration of the polarized light from that part of the sky, they continued to dance correctly. If, however, I turned the foil right or left, the direction of the bees' dance changed to the right of the left by corresponding angle values."

Von Frisch went on to conclude that for the bees, the sky revealed a pattern of polarized light from the sun. He acknowledged that other creatures were known to see it, but that human beings and other vertebrates remained unendowed with this sense. We will revisit the admittedly more weak, but interesting case of the human ability to detect polarized light after exploring the visual world of some of polarisation sensitive sea creatures, where this sense appears to be the most honed.

Cephalopods

The cephalopods seem to share a relatively unique capability to respond to, and to reflect, patterns of polarized light. Cephalopods, with only one kind of squid as an exception, are colourblind, but their eyes serve them well through an enhanced ability to selectively perceive linearly polarized light. The cephalopod eye has photoreceptors and corresponding hair-like microvilli which expand their surface area, which appear to be oriented orthogonally to adjacent ones, as seen here:

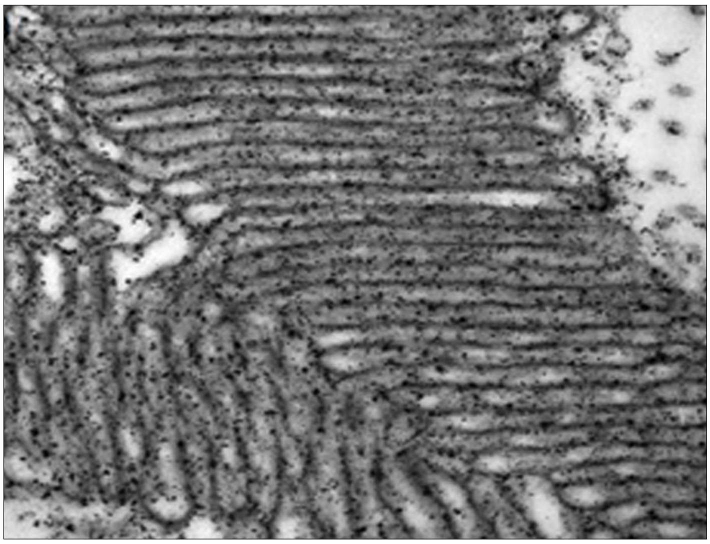
The common explanation for the polarisation perception in cephalopods is that, since it's said that a specific population of retinal cells would be activated by polarized light in a specific plane, it is due to the orthogonal orientation of photoreceptors in the cephalopod, as in this case there would be a high population of retinal cells oriented in two different directions. Our photoreceptors are said to be less organized, and that we humans barely perceive polarized light because the orientation of our visual pigment cells is "semi-random." In the arthropods, and also the stomatopods which we will look at next, their visual pigments have a radial arrangement. Here is a common description of how polarized light interacts with visual pigments, which we will show to be rather too simple:

"Visual pigment molecules are based on a single type of chromophore, whose highest absorption occurs when the molecule's dipole is aligned with the e-vector axis of the light, making visual pigment molecules naturally polarisation sensitive. In vertebrate rods and cones the visual pigment is arranged in a semi-random array of axes, which makes the photoreceptor equally sensitive to any e-vector orientation when the light arrives parallel to the photoreceptor's long axis." [8]

In this statement, there are a few problems which we should keep in mind. One, is that we don't know exactly what causes the highest absorption of the light polarized in a given plane when aligned with the pigment, let alone how phototransduction occurs in eye, converting light into electrical signals. We know of the association, but polarisation is a tricky phenomena, because light itself is. But two, it would appear that it is the *macro-organisation* of the pigments which matter, contrary to what this statement implies.

The so-called randomly organized pigments of the human eye do not appear to be as highly organized as they are in the eyes of these other creatures, if we consider the macro-organisation of these pigments— but wouldn't the same polarized light activate a portion of our retinal cells oriented in a parallel fashion, just not close-packed together, if the orientation of the pigments is the simple requirement? Perhaps the sheer number of pigments oriented in the same plane is simply not comparable to what the cephalopods have.

The fact that we do perceive some polarized light should mean that their organisation is not in fact random, assuming this has something to do with polarisation sensitivity. This is besides the fact that claiming that any feature of human anatomy is semi-random, usually means something more like, "we don't know how they are organized." Accounts of the polarisation sensitivity of humans, arthropods, stomatopods, and cephalopods, all hinge on a particular kind of arrangement of the visual pigments, but, as we have indicated, in each of these cases, each class represents a different arrangement.



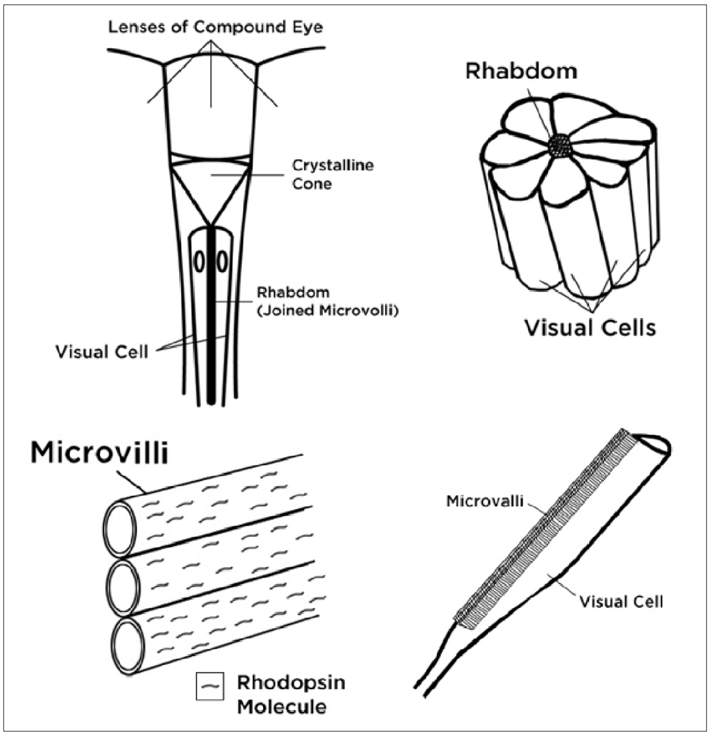
Close-up of Cuttlefish eye(top) and orthogonal microvilli(bottom). Bottom image courtesy of Nadav Shashar

Another paradox: the polarisation sensitive bees can perceive the colours white, yellow, blue, violet, and ultra-violet, but the polarisation sensitivity of bees and other insects seems to correspond only to the ultra violet wavelengths of light. But if the bees see five different colours, why would they only see polarized light in one of them? The simple radial arrangement of all visual pigments, as is typically presented, however, does not account for this.

One explanation, is that in the region which is not sensitive to polarized light, there is a 180 degree rotation of the pigments along the length of the photoreceptor, canceling out the polarisation. But even in the area receptive to UV light, there is a 40 degree rotation of the pigment. [9] This account does not quite match up with the descriptions of how polarized light interacts with visual pigments based on their perfect alignment, since high sensitivity to polarized light is apparently otherwise achieved with a 40 degree rotation of pigments through a twisting of the rhabdoms. It seems like the pigments in our human eye, though they be randomly arranged, should have an array of pigments spanning at least 40 degrees in their orientation with respect to one another. But out polarized vision is clearly less acute, which means this simple explanation of how "polarized vision" works doesn't quite make.

In discussion of the polarisation sensitivity of animals, there is heavy emphasis on the orientation of visual pigments, but this alone does not account for the phenomenon of polarisation perception. It is not simply the organisation of a substance which allows it to be sensitive to polarized light; the material itself determines the interaction with polarized light; it can also polarize light itself, in addition to simply being sensitive to it. In the human eye, it is thought that our ability to weakly perceive polarized light is additionally influenced by a crystal-like property of the cornea itself which has its own slight polarising effect on light. For the mantis shrimp, as we will see, the crystalline structure of their microvilli is said to effect the polarisation. All we know is that the material and organisation together seem to correspond to the ability to polarize light, and to selectively perceive it. The mechanism remains unclear, although it may have seemed somewhat intuitive at first, but it is the activity of the cephalopods and a handful of other creatures in response to the polarized light is that we *do* know.

This capability has been tested more extensively with the cuttlefish, which has a camouflage capability that includes a polarisation variable. This ability of the skin to polarize light seems to be especially prominent in the blue-green light range, a range in which it is colourblind. When placed in front of a blue, yellow, or a blue and yellow checkerboard background, the cuttlefish never changes its camouflage in response, when

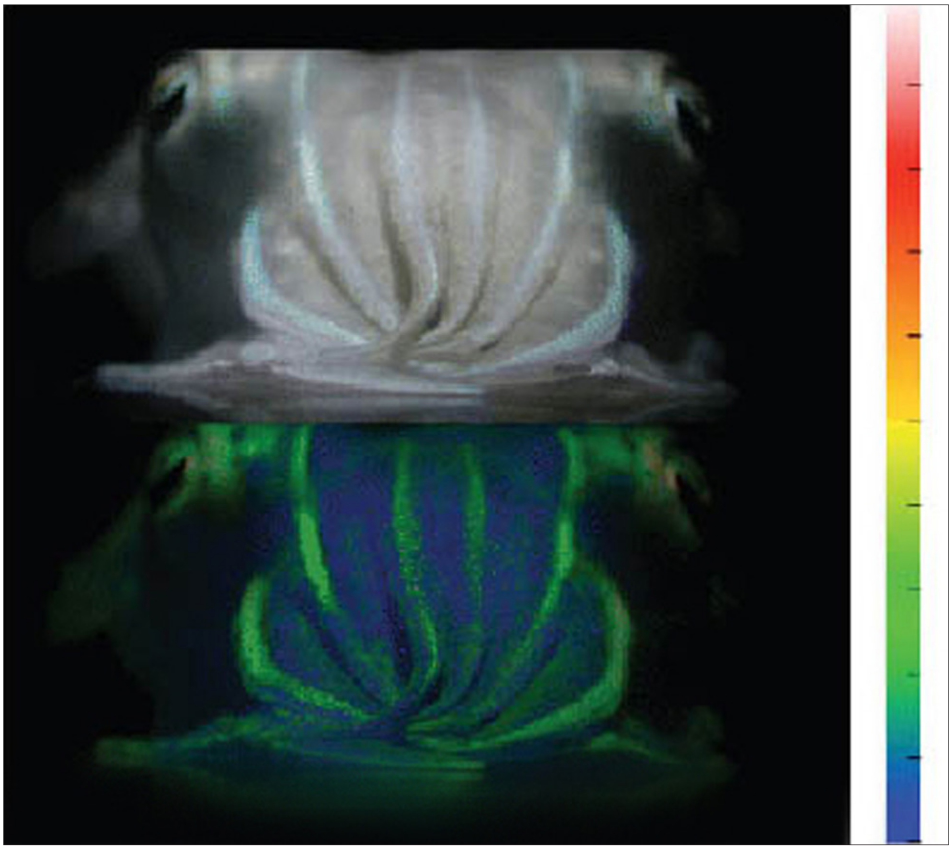


Several images of cuttlefish eye, from top left to bottom right with increasing resolution. Image Credit: Chris Jadatz.

these colours are of the same intensity. [10] Despite lacking one aspect of a visual sense, they can respond to changes in the polarisation of light much more efficiently than other creatures.

For example, a cuttlefish will respond differently to its own reflection if seen through different polarized filters, and will change polarisation patterns around other cuttlefish in displays of aggression or when attacking prey. Their skin demonstrates distinct patterns when seen though a polarized filter which are otherwise not visible, and there are indications that the polarisation of their skin is able to be physiologically controlled. In one experiment, changing the chemical environment of the skin changed the polarisation characteristic of the light reflected off of the skin. These examples indicate that the cuttlefish may communicate with each other through induced polarisation patterns in their skin, taken in addition to what it known about their orthogonal visual pigments.

The polarisation is achieved through reflective cells called iridophores, which lie underneath a layer of chromatophore skin pigments. The chromatophores have small pigment sacs which expand, contract, and change shape to create the cuttlefish's camouflage. The iridophores, or guanophores, are crystalline plates made of guanine, among other things, and are also used to produce colours in the cuttlefish's camouflage. For example, purple can be created by a red chromatophore and an iridophore. The cuttlefish can also use an iridophore and a yellow chromatophore to produce a brighter green.



Cuttlefish seen through polarized filter (bottom image). Blue=less polarisation, Red=greater. The top image shows the reflective iridophores in blue (not seen through polarizer). Image made after T. Chiou in cited paper, footnote 15.

As for using these iridophores to create the polarisation patterns, do the cuttlefish achieve this by the iridophores themselves changing in orientation with respect to the incident light, while being present over all of the skin? Or, are there special patterns of iridophores which have this induced polarisation capability? In squid, it seems that the latter may be the case. But the change in polarisation patterns is able to occur so quickly, it is thought by researchers to be neurological (as opposed to hormonal), and researchers are currently puzzled as to how the changes in polarisation can be induced within less than a second. Only very recently have nerve fibers been found in the vicinity of the iridophores. Prior to this, no squid had been known to have iridophores which are under neural control, and even this is still unproven, since the nerve fibers have only been found near the iridophores—no actual connection has yet been established. [11]

Colourful, colourbind, camouflaged cuttlefish! Image courtesy of flickr user:Jenny

Another paradox about the cuttlefish vision was communicated in a 2007 study which tested the "optomotor response" of cuttlefish in response to moving patterns of contrasting stripes, and moving patterns of polarized stripes. In the optomotor response, the cuttlefish, in a tank surrounded by one of these backgrounds, should rotate around its center to follow the moving image, which is circling around the tank. The cuttlefish did just this in response to the patterns of contrasting stripes (of different intensities), but not for polarized stripes. While this experiment was only done with one rare species of cuttlefish, it still puzzled researchers. The orthogonal structure of the eye's pigments were present. Are polarisation and intensity perceived differently by this cuttlefish, they asked? Are only certain kinds of visual cues involved in an OMR? Or is it possibly not seeing polarized light, despite having the eye structure to account for it? [12]

How can insight into the control over the biological polarisation mechanism, and the mechanism accounting for its perception, give us more insight into the still not well understood phenomenon of polarisation? Is it achieved biologically by means which do not fully reconcile with our current explanations? This will be suggested even more in the case of the mantis shrimp.

An additional puzzling question for researchers is how the cuttlefish, who is colourblind, can match colours in their camouflage. They can perceive brightness and intensity, and patterns based on these contrasts, but how they are able to match colours, even in complete darkness, is puzzling to researchers. Using night-vision video, scientists at Woods Hole Marine Lab discovered that cuttlefish even match their background at night, when there isn't enough light for colour vision. Claims by some that this is explained by passively reflective cells called leucophores, do not seem to account for the sharp changes in patterns which they can induce. Dr. Roger Hanlon, who has written many research papers on the cuttlefish and has done a lot of field work with them, when asked how the cuttlefish's skin changes to any hue in the rainbow, despite having only one visual pigment which is sensitive to coloured light at 492 nm, said, "That's a vexing question. We don't know how it works." [13]

In the case of the cephalopods, we have a creature which discerns polarized light, and has the ability to induce changes in its skin polarisation patterns in less than a second by an unknown mechanism, which then appears to be seen by other cephalopods, a creature which is colourblind, but can clearly perceive colour in some way, as its camouflage demonstrates. Vision more generally seems to be quite perplexing!

However, even the polarized vision and communication capability of the cephalopods is not nearly as well developed as the capability of a specific kind of crustacean called the stomatopod, or Mantis Shrimp.

To be continued...

Footnotes

[1] See accompanying piece by Jason Ross on discoveries about polarized light. Also see "Louis Pasteur: the Science of Life," on www.larouchepac.com

[2] www.livescience.com/history/070302_viking_navigation.html , or www.polarisation.com, a very useful website for this and other references from this report.

[3] Polarized vision of many insects, such as dragonflies, can be deadly when they are tricked into laying their eggs on murderous solar panels, which they mistake for water because of the reflected polarized light. Let us be rid of these killers!

[4] As Karl von Frisch said of the bees, "thus the language of the bee, which was initially brought to our attention by the physiology of sense perception...led to general questions of orientation in time and space." For more on this question see Peter Martinson's report on Circadian Rhythms. Also see Ben Deniston's report on Magnetoreception, and Oyang Teng's Report on Insect Infrared Perception.

[5] The polarisation of the sun's light is greatest 90 degrees from the sun, something you can test with polarized sunglasses. If the bee can so precisely indicate the location of the food based on this kind of reading, it is not hard to imagine that the polarisation pattern seen by the bees has more resolution than this. Here we quote von Frisch's account of his discovery in his 1973 Nobel Lecture:6 www.nobelprize.org/nobel_prizes/medicine/laureates/1973/frisch-lecture.pdf

[7] Von Frisch alludes to polarisation in a particular colour of light, an indication that the eyes' pigments themselves are contributing to the polarisation sensitivity. As it turns out, bees, and many insects, perceive polarized light distinctly in the UV range. Other experiments have shown that the perception of polarized light by bees can still be somewhat efficient in a partially cloudy sky which would support this idea. There are conflicting accounts about whether or not bees see polarized blue light, to which von Frisch alluded. We will further examine what this means and how it is determined a bit later in this report.

[8] Mathger, Lydia M, Shashar Nadav, Hanlon, Roger T. (2009) "Do Cephalopods Communicate using polarized light reflections from their skin?" Journal of Experimental Biology 212, 2133-2140, Doi:10.1242/jeb.020800

[9] To what extent this is based on observation, or just a model, was not clear from the account.

[10] Mathger, Lydia m., er al, "Colour blindness and contrast perception in cuttlefish determined by a visual sensorimotor assay," Vision Research 46 (2006) 1746-1753, doi: 10.1016/j.vires.2005.09.035

[11] Shashar, Nadav, et al (2001) "Polarisation Reflecting iridophores in the arms of the squid Loligo pealeii," Biol. Bull, 201:267-268

[12] Shashar, Nadav, and Darmaillacq, Anne-Sophie, "Lack of polarisation optomotor response in the cuttlefish Sepia elongata,"Physiol Behav (2008), doi:10.1016/j.physbeh.2008.01.018

[13] www.nytimes.com/2008/02/19/science/19camo.html