Visual function: **How spiders find the right rock to crawl under**

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Animals that go on hunting expeditions face the problem of finding the way home at the end of the day. A group of hunting spiders has now been added to the list of animals that use the celestial pattern of polarized light as a compass to navigate with, and explains an old conundrum of spider eye anatomy.

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As well as having eight legs, most spiders also have eight eyes, which provide them with panoramic coverage of their world to look for danger, food or mates. Another advantage of having so many eyes is that different eyes can be assigned different visual tasks. By a wonderfully integrated approach, using evidence from anatomy, electrophysiology and behaviour and aided by building an eye model, Dacke *et al.* [1] have recently demonstrated that the gnaphosid spider *Drassodes cupreus* uses one pair of upward pointing eyes (Figure 1) for navigation. The spiders can reliably return to the rock under which a silk nest has been made after long excursions. The key to this ability is that two eyes, the postero-median pair [2], are sensitive to polarized light and use the pattern of polarization inherent in skylight as a compass to find their way home after hunting expeditions.

Polarization sensitivity, the ability to detect the orientation — the 'E-vector' [3] — of polarized light, is remarkable to us, as humans cannot see polarized light without external aids. We use 'polaroid' sunglasses to reduce glare from reflective polarizing surfaces, such as water or glass, and polarizing filters are used in photography and microscopy, often for the same reason. Photographers also use a polarizing filter to darken blue sky for dramatic effect. Scattered light tangential to the sun is partially linearly polarized in a predictable pattern, reaching a maximum degree of polarization at 90° to the sun's position in the celestial hemisphere [3]. This band of heavily polarized light can therefore be darkened and visualized by rotating a polarizing filter in front of the camera so its axis of maximum E-vector transmission is perpendicular to that in the sky (Figure 2).

Seemingly, a trick very similar to this is employed by *D. cupreus* to examine the sky as it wanders from its home rock. Instead of using a transmission filter to analyze the E-vector of incoming light, however, this spider's postero-median eyes possess a reflective, canoe-shaped tapetum below and to the side of the photoreceptors, which selectively reflects polarized light oriented along the long axis of the canoe [1]. Interestingly, and perhaps surprisingly, this is the first time that polarization optics, aside from the photoreceptors themselves, have been noted in any eye, and as Dacke *et al.* [1] show with electrophysiological recording, this adaptation boosts polarization sensitivity considerably.

Celestial compass organs are also found in insects, such as ants and bees [3], to help them navigate to and from their anthill or hive on foraging expeditions. Here, rather than using separate eyes dedicated to the job, a skyward pointing region of the compound eye — the 'dorsal rim' area — has modified photoreceptors for the detection of polarized light. A small number of birds, reptiles [4], amphibia and fish (see references in [1] and [4]) are also thought to use the sky compass as a means of navigation, but with one exception (the anchovy — referenced in [3]), the retinal mechanism for analyzing polarized light is still a bit uncertain [5]. Navigation is not the only visual function of polarization sensitivity. It may also provide glare reduction (as with our 'polaroid' sunglasses), water-surface detection in aquatic insects [6], contrast enhancement through scatter reduction or silvery and transparent camouflage breaking [7], and may even play a part in communication [8,9].

Polarized light is made use of both above and below water. Crustaceans and cephalopods [7–10] are the masters of polarization sensitivity in the aquatic environment, and on land it is the insects and now spiders that are known to make particular use of polarized light. Common to all these groups is the way their visual pigment molecule is housed. It is found on fingers of membrane, known as microvilli, rather than on the plate-like discs from which vertebrate rods and cones are constructed. This results in an inherent direction of polarization sensitivity, parallel to the long axis of the microvilli [2,10]. Perhaps it is this predisposition to absorbing polarized light, by orderly arrays of microvilli, which has enabled these groups to be so successful at exploiting this feature of light.

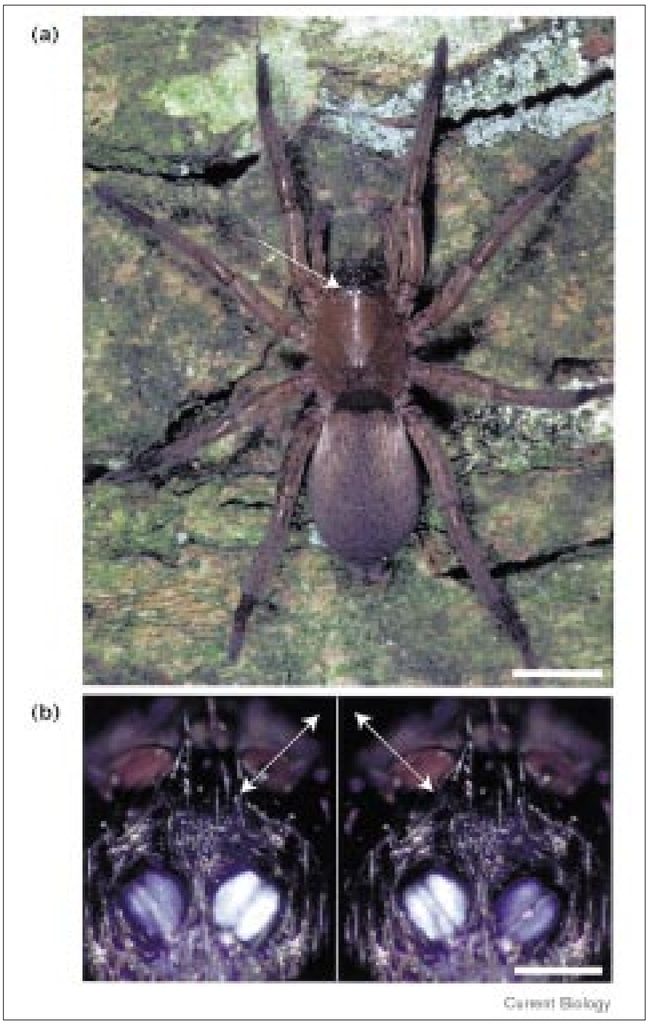
Common to many polarization sensitivity systems, whether constructed from microvilli or not, is that they are sensitive to ultra-violet or short wavelength light. The photoreceptors of the postero-median eyes of *D. cupreus* are maximally sensitive at 350 nm, and it is likely that the blue tapetum (Figure 1) is an efficient reflector for these wavelengths, but this has yet to be measured. The polarization of scattered light in the atmosphere is maximal in this spectral region, explaining why many polarization sensitivity photoreceptors are tuned to this waveband. The twinkling blue reflectors on the postero-median eyes of *D. cupreus* (Figure 1) literally reflect the blue of the sky.

One feature that is critical for the analysis of polarized light is the possession of at least two sets of polarization sensitivity photoreceptors with optimal E-vector sensitivities at different angles. This can be likened to colour vision, where the output of at least two different colour channels, say red and green, are compared for dichromatic vision [11]. Nearly all invertebrates with polarization sensitivity have two sets of photoreceptors with optimal E-vector orientations at 90° to each other, and it is comforting to find the same orthogonal arrangement in these spiders [1]. *D. cupreus* apparently compares the output of the whole left postero-median eye to the right postero-median eye, as the canoe-shaped tapeta and all the microvilli in the two eyes are arranged perpendicular to each other (Figure 1b). In other systems, the outputs of locally orthogonal photoreceptors in the same eye are compared [10–12]. Having left the home rock, *D. cupreus* must somehow keep track of its direction by comparing the output of the two eyes relative to the sky pattern and using this information to retain a 'home vector' as it wanders in search of food. Insects are known to be capable of this feat also, and the details of the system in ants have been uncovered by the ingenious experiments of Wehner and colleagues [3].

A few arthropods have polarization-sensitive systems with microvilli arrayed in three directions. When the angles between these are right and the correct comparisons made, this makes an ideal polarization sensitivity system as it eliminates the 180° ambiguities found in systems in which only two orthogonal arrays are present [3,4,11]. This is analogous to the advantages of trichromacy over dichromacy in colour vision [10,11]. As *D. cupreus* only has two polarization-sensitive receptors at an angle of 90°, it must rely on other cues to distinguish a polar direction having found, using polarization sensitivity, the axis on which the sun lies. One possible way the spider could do this would be to look for a brightness gradient in the sky, and it is interesting that such a gradient — provided by a window at one end of the lab — was essential for the success of the elegant behavioural experiments conducted in the new study [1]. Furthermore, a second set of photoreceptors are present in the postero-median eyes of *D. cupreus* which, because of their disorderly microvilli, are not polarization sensitive, and these may be the ones that process this luminance cue.

Why not just rely on the sun's position and brightness in the sky for navigation, and dispense with polarization

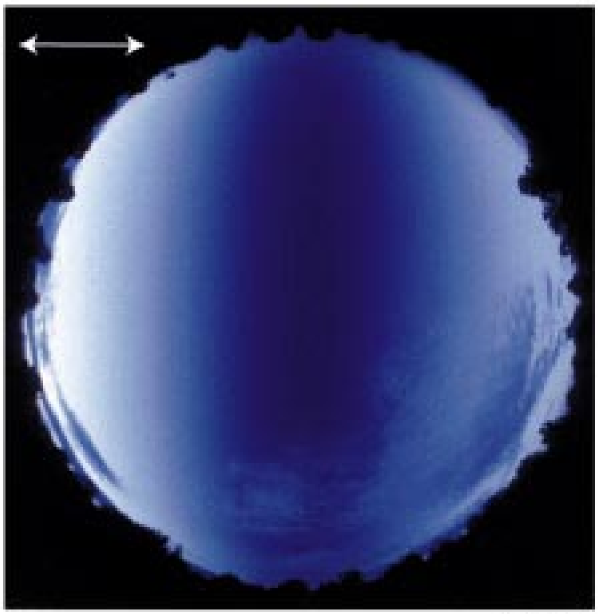
Figure 1



(a) *Drassodes cupreus* illuminated to show the eye-shine that results from the tapetal reflection in the postero-median eyes (arrowed). For an explanation of spider eye nomenclature and morphology see [2] and references therein, especially those by Homman. The scale bar represents 2 mm. (Photograph courtesy of Pär Brännström.)
(b) Enlargement of the postero-median eyes. Blue reflection from the tapeta is photographed through a polarizing filter whose axis of E-vector transmission is shown by the arrows in each photograph. The tapetum reflects polarised light back out of the eye and this is partially extinguished by the filter held at 90° to its principle axis of reflection. The canoe-shaped tapeta within the eyes are visible, as no lens exists above the retina. The scale bar represents 0.2 mm. (Photograph courtesy of Marie Dacke.)

sensitivity altogether? The problem with such a solution is that the sun is often obscured by cloud, especially in Sweden, and an animal as small as a spider is in a world like down-town Manhattan, where tall rocks and leaves may hide the sun. It is much more reliable to examine the polarization pattern, which is readable in any part of the sky, and in ants and bees it is known that only a small patch of blue sky is necessary for successful navigation [3].

Figure 2



The pattern of polarized light in the sky at dusk. The camera is pointed directly upwards and is fitted with a fish-eye lens and polarizing filter. By rotating the filter, the E-vector axis of which is shown by the arrows, the axis of polarized light in the sky is revealed as a dark band when the filter and the sky pattern are orthogonal to each other. This pattern is present in the sky at dawn and dusk when *D. cupreus* is most active, and presents the most readable directional signal to the wide-angle postero-median eyes as the direction of polarization is uniform. (Photograph courtesy of Dan Nilsson.)

A sufficiently large bit of sky is needed for this system, however, and photoreceptors in the 'dorsal rim' of insects often have an increased photoreceptor acceptance angle. Bees are known to degrade optical quality of the lens elements of the dorsal rim by including bubbles in the cornea, effectively allowing the photoreceptor to act a bit more like a cosine collector and integrate over a larger area. *D. cupreus* has taken this to an interesting extreme and thrown away the lenses in its postero-median eyes altogether, resulting in a solid angle of collection, into which both eyes look, of around 125°. At first this may seem a good way of examining a large amount of the celestial polarized light pattern but, as identified by Dacke *et al.*, it actually causes a problem. When the sun is well off the horizon, a wide-field detector will see a mixture of different polarization planes (Figure 3 in [1]). Combined with strong direct sunlight, which inevitably strikes this wide-angle eye and which is unpolarized, the polarization signal becomes scrambled. The solution to this problem is a simple behavioural one, as *D. cupreus* sets out on foraging trips only at dawn and dusk when the sky is polarized in one direction only (Figures 2 and 3 in [1]) and the sun is below the horizon.

Hunting spiders, such as the wolf spiders (Lycosidae) and jumping spiders (Salticidae), do not have canoe-shaped tapeta, and many seem content either to wander without a home base or to set up a home and sit and wait for food to walk by. Some previous studies did indicate polarization sensitivity in lycosid spiders [1,2], but the basis for this was not fully investigated. *D. cupreus* and other gnaphosid spiders are probably eager to be able to re-find the rock under which they made their silk nest home, as the nest is a large investment of energy.

Interestingly most spiders — 22 of the 50 or so families of the classification system cited in [2] — do have secondary eyes with canoe-shaped tapeta. Dacke *et al.* [1] suggest that all these species may use such eyes as compass organs, and they have demonstrated that this is so in at least one other species, the unpleasantly venomous Australian white-tail *Lampona cylindrata*. Evidence supporting the idea comes from an old problem in spider eye anatomy. For some time it has been noted that spider eyes with canoe-shaped tapeta have lenses too close to the retina to be well focussed, and a good explanation for this was lacking [2]. It seems possible that the eyes are designed this way as sharp focus is not needed to look at polarizing sky patterns. Also, with the retina closer to the lens than expected, the resultant visual field of the eye is increased and, as we have already seen, this is an adaptation adopted by a number of polarization sensitivity systems.

If all canoe-shaped tapeta eyes are polarization-sensitive organs, we are left with another intriguing problem, as rather few of the spiders within the 22 families that have such eyes show the forage and return behaviour of *D. cupreus*. Indeed one of the families, the Araneidae, contains the orb web spiders. What possible use could such sedentary species make of a sky compass? Orientation of the web relative to the sun is known in nephilid spiders within this family: nephilid species include the bird catching spiders, whose large webs are oriented east–west in cold seasons, apparently for thermoregulation [13]. A compass of any sort would be handy for this behaviour, and as many webs are spun before and after sunrise and sunset, the canoe-tapeta eyes would do nicely. Specific orientation relative to the sun may also reduce or increase web visibility, a feature of web placement that some spiders are known to worry about to avoid birds or entrap insects [13].

This wonderful exposition of the biology of two of the eight eyes of one spider certainly points the way to many other exciting possibilities in a variety of its relatives. It is fitting that the discovery comes from Scandinavia, as centuries ago the Vikings navigated using 'magical' translucent rocks to examine the sky. The rocks contained quartz, which polarizes light and the patterns revealed in the sky helped them navigate on foraging trips also.

References

1. Dacke M, Nilsson D-E, Warrant EJ, Blest AD, Land MF, O'Carroll DC: Built-in polarizers form part of a compass organ in spiders. *Nature* 1999, **401**:470-472.
2. Land MF: **The morphology and optics of spider eyes**. In *Neurobiology of Arachnids.* Edited by Barth FG., Berlin: Springer Verlag; 1985:53-78.
3. Wehner R: **The perception of polarized light**. In *The Biology of Photoreception: Symposia of the Society for Experimental Biology XXXVI* 1983, **36**:331-369.
4. Freake MJ: **Evidence for orientation using the e-vector direction of polarized light in the sleepy lizard *Tiliqua rugosa***. *J Exp Biol* 1999, **202**:1159-1166.
5. Hawryshyn CW: **Polarization vision in fish**. *Am Sci* 1992 **80**:164-175.
6. Schwind R, Horvath G: **Reflection-polarization pattern at water surfaces and correction of a common representation of the polarization pattern of the sky**. *Naturwissenschaften* 1993, **80**:82-83.
7. Shashar N, Hanlon RT, Petz A de M: **Polarization vision helps detect transparent prey**. *Nature* 1998, **393**:222-223.
8. Marshall NJ, Cronin TW, Shashar N, Land MF: **Behavioural evidence for polarization vision in stomatopods reveals a potential channel for communication**. *Curr Biol* 1999, **9**:755-758.
9. Shashar N, Rutledge PS, Cronin TW: **Polarization vision in cuttlefish — a concealed communication channel?** *J Exp Biol* 1996, **199**:2077-2084.
10. Marshall NJ, Kent J, Cronin TWL: **Visual adaptations in crustaceans**. In *Adaptive Mechanisms in the Ecology of Vision.* Edited by Archer S, Djamgoz M, Lowe E, Partridge J, Vallerga S. London: Kluwer; 1999:285-387.
11. Bernard GD, Wehner R: **Functional similarities between polarization vision and color vision**. *Vision Res* 1977, **17**:1019-1028.
12. Labhart T: **Polarization-opponent interneurons in the insect visual system**. *Nature* 1988, **331**:435-437.
13. Foelix RF: *Biology of Spiders*, 2nd edn. Oxford: Oxford University Press; 1996.