

Detecting the Detector: A Widespread Animal Sense?

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ABSTRACT

A focusing eye acts as a high-performance retroreflector, potentially appearing millions of times brighter when illuminated from a distance than would a matte white surface of the same area. In particular an eye which either has a reflective tapetum near its focal plane, or is operating at f-number less than unity, returns around half of the light entering its pupil in a direction parallel to that in which it arrived.

To detect other animals by eyeshine in this way, however, the detector requires a light source, potentially giving its own position away. The ideal method is therefore to use a form of light which the other animal cannot see, or cannot discriminate from other light. Alternatively, emitting brief flashes of light whose duration is shorter than the time required for the other animal's pupil to contract, or its eyelid to operate, optimises detection while giving minimal useful information about the detector's position. Modulation of the source by the detecting animal will cause retroreflected light to vary in sync, potentially allowing the detector to distinguish retroreflected light from background illumination even when the latter is stronger.

In 2009 I pointed out^[1] that fluorescent rings around the eye of the triplefin blenny discovered by Michiels et al^[2] could allow it to detect other animals, such as potential prey or predators, in this way. The blenny's rings fluoresce red when illuminated with blue light: only blue light normally penetrates to the depth where it lives. Use of red thus maximizes sensitivity, and red may be invisible to other animals living at depth which have not evolved to see this colour.

Michiels et al continue to accumulate evidence supporting the theory^[3]. It had previously been suggested that fish living at great depth might emit light for similar reasons^[4]. However, little attention appears to have been paid to potential use of the mechanism by animals other than fish. In this paper I introduce circumstantial evidence that many other types of animal likely use it.

Animals which may plausibly detect others' eyes by retroreflection include:

ANIMAL	PROBABILITY
mantis shrimp	overwhelming
many squid, certain other cephalopods	very high
certain insects	high
some birds	possible

Mantis Shrimp

Circularly polarized light is rare in nature, but light reflected off a mantis shrimp's body parts becomes circularly polarized. Mantis shrimp also have the ability, perhaps uniquely among animals, to perceive circularly polarized light. More subtly, they can detect the full Stokes vector of incoming light: its combination of linear and circular polarization.^[5,6,7] This is perfect for eye-detection by retroreflection. Incoming circularly polarized light can come only from another mantis shrimp, or retroreflected from the eye of a different animal. A non-mantis-shrimp target is not able to discriminate the circularly polarized component from other light, so is not alerted to the fact it is being 'scanned'.

For the mechanism to be effective, there should be minimal angular distance between the light source and the associated detecting eye as seen from the position of the target. But it is also desirable for the light source to have absolute brightness, hence area, as large as possible. The whole body of the mantis shrimp creates circularly polarized light, which is optimal for detecting large-eyed predators at long distance. Mantis shrimp are preyed on by cephalopods, so this sense is potentially very useful for detection of large-eyed predators lurking in burrows: however cryptic the predator and dark its surroundings, if it can see the mantis shrimp, the mantis shrimp can see it. The mantis shrimp may even be able to deduce further information about the predator. Research on a computer input device which uses retroreflection of circularly polarized light to determine the direction a human eye is looking^[8] has shown that the retroreflected light acquires some linear polarisation, due to the alignment of fine nerve fibres at a given point on the eye's retina. In the case of a vertebrate eye, these fibres emanate radially from the 'blind spot': the direction and degree of linear polarisation acquired allows the direction the human eye is looking to be deduced by interrogation of a single point on the retina. While the wiring of nonvertebrate eyes

differs, the mantis shrimp may well be able to derive useful information from the light reflected from various target eye types.

If the predator-detection hypothesis is correct, it should be easy to obtain an obvious startle response from a mantis shrimp by unmasking an otherwise invisible artificial retroreflector, and/or by varying its reflection intensity and polarising properties in real time.

The mantis shrimp's puzzling ability to sense many different colours, yet with relatively poor overall colour discrimination^[9], is suggestive of optimisation to detect illumination at specific wavelengths, including retroreflection of such light. While daylight and moonlight are broad spectrum, light produced by organisms, whether by fluorescence or bioluminescence, tends to be closely centred about specific wavelengths.

Cephalopods

Many cephalopods are equipped with photophores mounted in locations including around the eye, upon the tentacles, and upon the mantle.^[10,11]

Particularly promising candidates for a retroreflective sense include:

1. The Dana octopus squid, which has lidded photophores at the ends of its arms.^[12]
2. The bioluminescent octopus *Stauroteuthis*.^[13]
3. The vampire squid, which is almost entirely covered in photophores.^[14,15]
4. The mesopelagic squid *Abralia veranyi*, whose subocular photophores emit short bright flashes.^[16]
5. *Chiroteuthis calyx* and *Galiteuthis phyllura*, which have photophores actually fused with the eyeball.^[17]
6. Humboldt squid, which flash red and white when hunting, and are capable of cycling through other colours too quickly for the human eye to detect.^[18]
7. The colossal squid. This image of a photophore embedded on the eyeball of a colossal squid^[19] is strongly reminiscent of the first crude rig of a retroreflection-based computer input device I developed many years ago, which used LEDs glued to the front of a large lens.

Especially in the case of deep sea creatures presumed to have low population density, such as colossal squid, ocular retroreflection might be used for intraspecific detection of potential mates. This would allow one sex (probably the female) to remain

stationary and well concealed from detection by other means, e.g. in the mouth of a dark cave or burrow, while the other sex takes the risk of emitting light and travelling significant distances.

In this case, in contrast to a predator-prey arms race, it is in the interests of both animals to maximize retroreflection, with the reflective tapetum in the focal plane. Assuming blue light of wavelength ~500 nm is used, at which absorption by water is minimised, that 50% of light incident is retroreflected allowing for absorption by retinal and other tissue, and that a diffraction-limited return beam is produced from an 80 mm aperture, the beam will be ~15 microradians wide, and the aperture will appear ~10 billion times brighter than a matte white surface of corresponding area, ~100 million times brighter than the squid's entire body. In practice water transparency and clarity will be limiting factors, but a functional detection range of the order of tens of metres is likely.

It is possible that light retroreflected from a potential mate's eye might have uses in mate selection. For example, in humans macular degeneration is a sign of aging; it has also been claimed^[20] that Alzheimer's disease can be diagnosed and predicted noninvasively using an ophthalmoscope. In humans, and presumably other animals, there is genetic variation causing individuals to have slightly different eye pigments in their colour-detection cells, so they see a slightly different range of colours. In an animal which sees many colours, close inspection of another's eye might tell you how closely related you are, serving a similar function to selection by MHC (major histocompatibility complex) in mammals, enabling the animal to select mates which are neither too closely nor too distantly related.

The partners can also exchange information intentionally. Obviously the active signaller can choose the colour and timing of light flashes emitted. However the passive partner can also signal. Just by changing the focusing of her eye slightly, causing her tapetum to be slightly closer to or further from the focal plane, she can greatly vary the brightness of the light returned to the signaller, potentially with rapid temporal modulation: an effective and private communication channel. Humans may not have a monopoly on eye flirting.

Crustaceans

Many euphausiids, commonly known as krill, have bioluminescence, including on their eyestalks, which could well be used for retroreflective eye-detection.^[21]

Insects

Many insects are preyed on by spiders: it would be advantageous if they could detect spiders even when the latter are in shadow. Beetles are promising candidates for using detection by retroreflection: those with bioluminescence which can be rapidly switched on and off, such as fireflies and glow worms; or with a continuous glow whose intensity can be modulated, such as porphyri; also those with iridescent surfaces whose orientation with respect to incident sunlight or moonlight can be rapidly changed, e.g. wing cases.

Examples of spider types which could readily be detected include:^[22]

1. Wolf spiders, which tend to hunt in low light levels, at dusk and by moonlight, have large posterior eyes with well developed tapeta, easily detectable by retroreflection.
2. Net-casting *Deinopis* spiders have two enlarged eyes which lack a tapetum but operate at very low f-number ~ 0.58 , so will be readily detectable by retroreflection.
3. Jumping spiders, typically hunting by daylight, have large well-focused middle front eyes which should retroreflect significantly.

Birds

Birds with iridescent plumage in sunlight might be able to detect predators in shadow, such as cats, by retroreflection from the predator's eyes. Iridescent head plumage is particularly suggestive.

Others

The detectability of the focusing eye may be merely a specific example of a more general phenomenon. There is a military example in unclassified open literature: the memoirs of a World War 2 U-boat captain^[23]. The Allies had aircraft with radar which could detect a surfaced submarine. The Germans developed a receiver which could detect the radar signals at great distance, allowing the submarine to dive before it came within detection range. But the Allies found they could transmit a different signal at a frequency which was not absorbed by the detector circuitry, so did not alert the U-boat, but instead caused the detector to resonate, retransmitting a powerful signal on which the aircraft could home.

Thermodynamically, it is trivially true that detection requires absorption of energy, which is itself detectable. It has been pointed out in critiques of H G Wells's *The*

Invisible Man that unless the invisible man is blind, at least his retinas must absorb some light, and therefore be visible. Something like this is seen in transparent water-dwelling animals whose most visible parts are their eye parts.

It is tempting to extrapolate the visible-detector problem into an empirical rule that a detector of any kind of energy can be ‘tricked’ into betraying its presence: the more powerful and specific the detector’s ability, the more powerful and specific is the revealing signal it can be made to produce. If this speculation is true, a novel and fundamental evolutionary arms race has been discovered, and we should search for further biological examples of such detector-sensing capability, including ones whose specific mechanism is not immediately clear to us.

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