BY **MIKE WOOD**

Animal pupil shapes – Part 2

JUST OVER A YEAR AGO in this column, I wrote about some differences in animal eyes. In particular, the difference in pupil shape between predators and their prey. In that article I showed a figure which illustrated various pupil shape divergence, specifically contrasting those which are lines or slits in one orientation or another, and those which are circular, like our own.

> This is clearly a less than ideal layout for the human eye.

What I didn't include, although they were in my original source images, was the eye of a squid, octopus, or other cephalopod. I left them out on purpose, they are so different from the eyes of vertebrates that they deserve an article all their own.

Convergent evolution

The eyes of vertebrates, including ourselves, and the eyes of cephalopods including octopus and squid, appear to have evolved completely independently. (There is some discussion that they both may share a common very primitive gene, but this doesn't explain the wide differences that evolution then caused).

At first glance they are very similar. Each has an iris, a lens, a cornea, and a retina. However the apparent similarity of the structures masks significant differences in the detail and the way those eyes function.

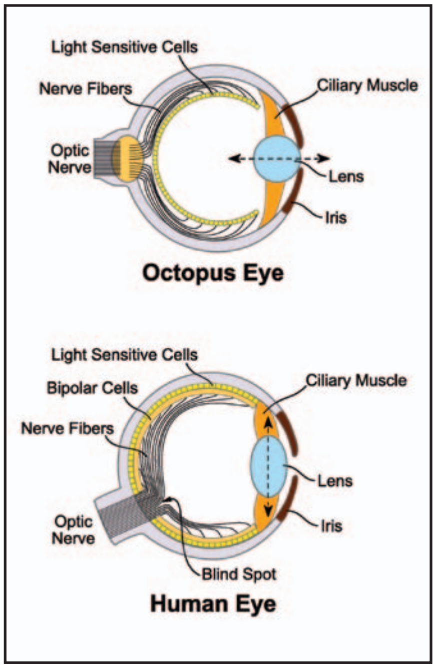

Figure 1

For example, as shown in **Figure 1**, although both eyes have lenses, the way that focusing occurs is completely different. Lenses in vertebrate eyes are flexible and we change the focus by contracting muscles around the outer edge which squeeze the lens in and change its shape thus altering its focal length. Cephalopod lenses, on the other hand, are stiff and have a fixed focal length. Focusing is achieved by moving the entire lens backwards and forwards, just as we might do in a camera.

The most significant difference however is in the orientation of the light sensitive cells in the retina. The sensitive cells in the eye of the octopus point toward the incoming light whereas our own rod cells and cone cells point backward and absorb light reflecting from the back of the eye. This is clearly a less than ideal layout for the human eye. Our apparently excellent vision involves seeing through a network of blood vessels, cells, and several layers of nerves proving connections between the cells. These cells are almost transparent but, even so, inevitably introduce scattering of the light and degrading our visual acuity. The blood vessels may be almost transparent, but the blood within them certainly isn't. We also have a blind spot where that network of nerves must pass through a hole in the retina. In contrast, the octopus eye seems much more logical. The retinal cells are positioned such that the end which is light sensitive is inwards, towards the lens. Thus light can pass unimpeded from the lens to those cells.

> Their vision is blurry, but the blurriness depends on the color.

Note: The reason why two completely opposite variants of eye design showed up is a great example of convergent evolution. That is, when two completely different evolutionary tracks converge on very similar optimal solutions. The differences described above can be seen by watching embryonic development. The vertebrate retina is a modification of the outer layer of the brain, our eyes develop from bulges in the brain's neural tube *that pinch in to form cavities. Over time, evolution progressively modified part of the brain for light sensitivity. Although the layer of light-sensitive cells gradually assumed a retina-like shape, the cells retained their original orientation, which included the nerve connections on the outer surface. Conversely, cephalopod eyes develop from skin cells which drop inwards to form a pit. These cells also retain their original orientation, but now the nerve connections are behind the cells, below the surface. A fundamental difference between modified brain cells and modified skin cells leads to these completely reversed structures. Once evolution had started down one of these tracks no simple or single mutation could change it, it quickly became hard-baked in. Vertebrate eyes may not be a great design, but they reached a point that was good enough such that there was no overriding evolutionary pressure to make them any better. The big plus point we have with eyes made from modified brain cells is that our eyes are smart and capable of a huge amount of pre-processing whereas invertebrate eyes are dumb and have to pass on the data raw.*

Many cephalopods also have a higher density of retinal cells than we do, so should theoretically have higher visual acuity. As I'm sure you know, we have two main types of photo-receptors in our eyes, rods and cones. Rods are sensitive to brightness only while our cones are sensitive to ranges of wavelength in three types and are thus responsible for our color vision. Cephalopods have only a single type of photo-receptor, different from either our rods or cones. They are similar to our rods in that they are sensitive primarily to brightness. However, in some species, they are also sensitive to polarization.

With only a single brightness receptor octopuses and squids should be color blind. Hang on a minute, that doesn't seem right. How does that jibe with their well-known ability to change their skin color to match their surroundings? What's the point of being able to change color if you can't see it, and how on earth do they know what color to make if they are color blind?

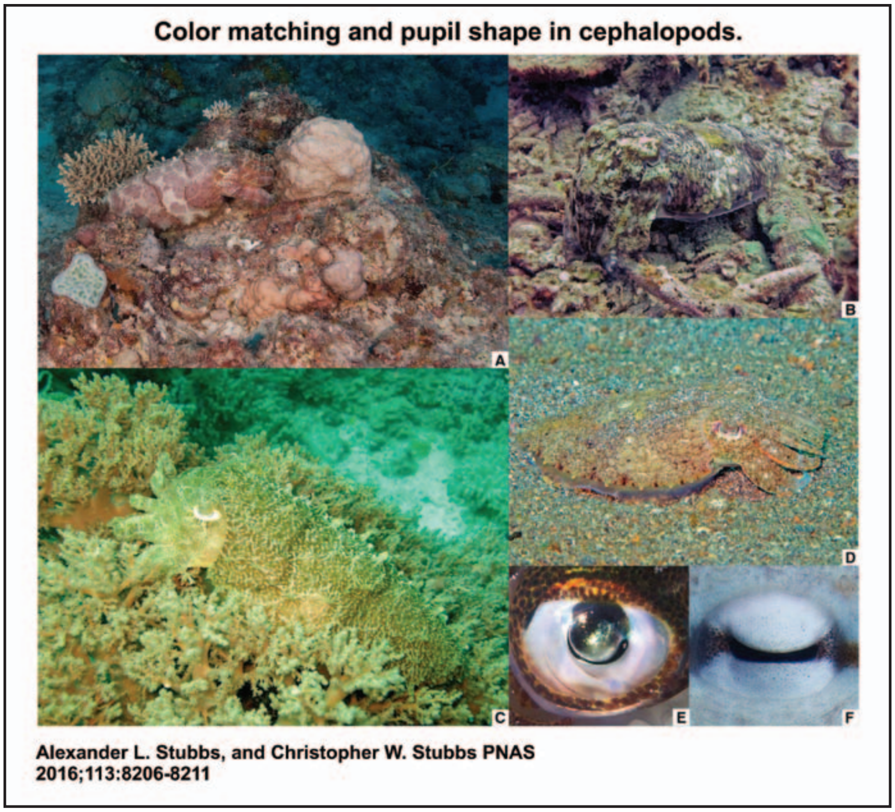

Figure 2

That leads us into the connection between this article and the one from last year concerning pupil shape. Octopus and squid pupils are very unusual, particularly in that they are asymmetrical. What could be the reason for this and what's it got to do with color?

How do color blind cephalopods see colors?

This apparent paradox has been studied for some time. One explanation could be that the chromatophores in the squid skin that are responsible for producing the color changes are also somewhat light sensitive. Thus it's possible that the skin itself detects color as it contacts the surface it wants to copy. This is generally accepted as likely, but it doesn't explain the color changes that squids undergo when courting when the skin is not touching anything. Why would a male cuttlefish risk flashing bright colors during a mating dance if the female couldn't even see them but a nearby fish could–and quickly eat him? It seems there must be something else going on as well.

About a year ago, in 2016, a team from UC Berkeley and Harvard led by Alexander Stubbs proposed a different solution. They proposed a mechanism whereby a cephalopod can see color using their eyes with a single photoreceptor type, but using a mechanism that completely differs from our normal understanding of color vision.

Stubbs describes the key as that unusual asymmetric pupil shape. It allows light to enter from a great range of directions at the same time, not just straight on, and, critically, produces an asymmetric image on the retina.

The large aperture causes an optical problem familiar to all of us involved with lighting and imaging, chromatic aberration. The lens of a squid or octopus, like our own eye, acts like a simple single glass lens in that it doesn't bend light the same amount for every color.

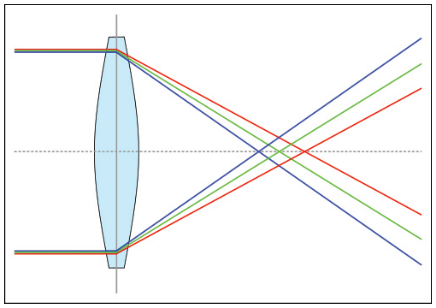

Figure 3 – Chromatic aberration

As shown in **Figure 3**, a simple lens bends shorter wavelengths, blue light, more than it does longer wavelengths, red light. This leads to a blurred, spread out, image on the retina. The smaller the pupil (or iris in a camera), the less this aberration so the sharper the image. Conversely, a large pupil, as you might get when you visit the optician and get your eyes dilated, leads to blurry images with colored fringing around the edges. In cameras and luminaires, we use combinations of lenses (known as achromatic) to reduce this problem, but it is still often noticeable. For example, the red or blue ring around the edge of a gobo is the result of chromatic aberration.

Cephalopod pupils are enormous, at least in one direction, so produce a large amount of chromatic aberration. This is the key to understanding how it might allow them to distinguish colors.

Figure 4 is taken from Stubbs' paper and explains the situation. A and B are eyes like our own with circular pupils. Chromatic aberration, when the eye is focused on green, produces a spread-out image with red focused behind the retina and blue focused in front. A large pupil, as shown in A, produces much more spreading than a smaller pupil, B.

Now take a look at C. This represents the wide U shaped pupil of a squid eye. In this case the chromatic aberration coupled with the pupil shape separates the incoming light into separate images. Green, which is where the eye is focused, remains in the center while blue and red each spread to their own sides of the retina. Blue in one direction, red in the other. Now by being able to recognize which portion of the retina is being stimulated, the squid has enough data to be able to distinguish the color components of the incoming light. It's acting just like a spectrometer where a prism spreads the light from a slit out into a rainbow spectrum of light. The position of the light on the receptor tells you the color.

There's also another possibility this opens. If the squid knows how far away an object is, such as by touching it with its arms, then it could use the differing focus it needs to use to keep various parts of the image in focus to determine what color each of those parts are. It's quite possible both these techniques are used. The touching focus distance method may be used when the squid needs good color discrimination to camouflage itself to the background, whereas the coarser image placement spectrometer mechanism might be used for longer distance color vision, such as the courtship dances of cuttlefish. "We propose that these creatures might exploit a ubiquitous source of image degradation in animal eyes, turning a bug into a feature," Stubbs said. "While most organisms evolve ways to minimize this effect, the U-shaped pupils of octopus and their squid and cuttlefish relatives actually maximize this imperfection in their visual system while minimizing other sources of image error, blurring their view of the world but in a color-dependent way and opening the possibility for them to obtain color information."

As well as octopus, squid, and other cephalopods, Stubbs has suggested that this mechanism may even be the basis of color vision in dolphins, which have U-shaped pupils when contracted. "Their vision is blurry, but the blurriness depends

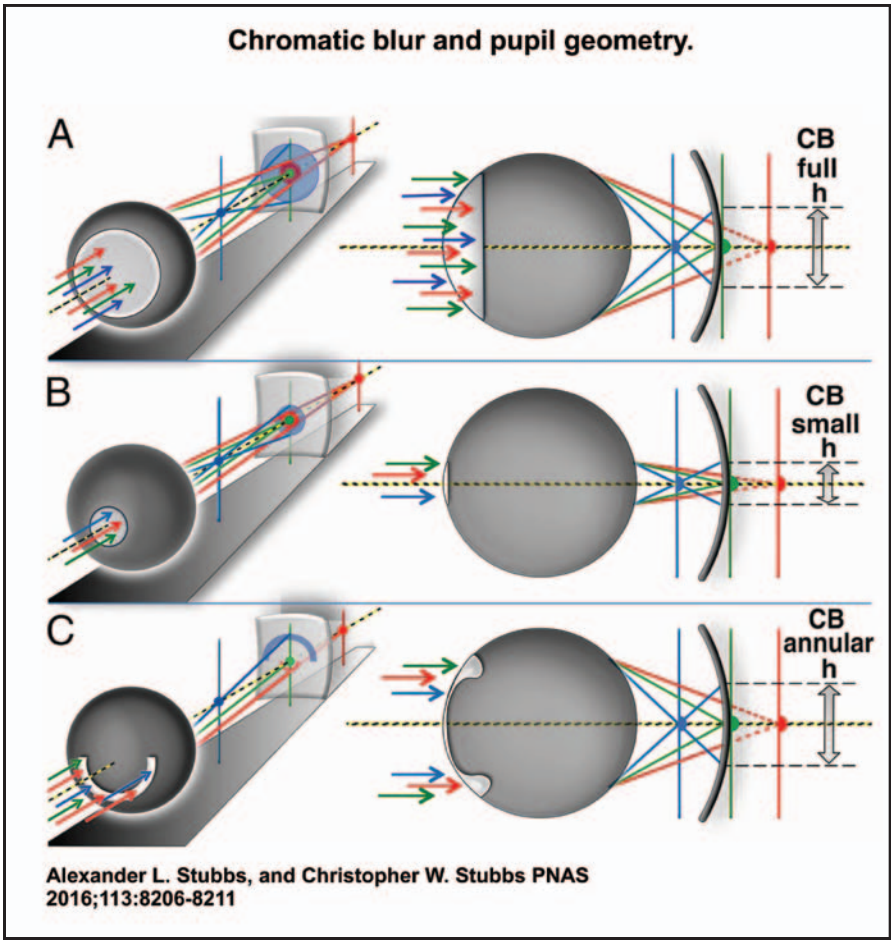

Figure 4 – Chromatic aberration in eye

on the color," Stubbs said, talking about squids. "They would be comparatively bad at resolving white objects, which reflect all wavelengths of light. But they could fairly precisely focus on objects that are purer colors, like yellow or blue, which are common on coral reefs and rocks and algae. It seems they pay a steep price for their pupil shape but may be willing to live with reduced visual acuity to maintain chromatically-dependent blurring, and this might allow color vision in these organisms."

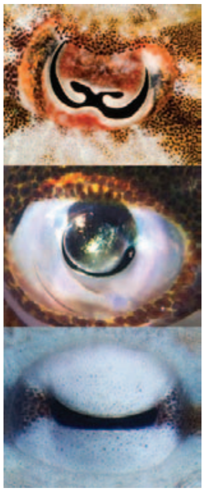

Figure 5 – Cephalopod eyes

Stubbs also reports that cephalopods may not be losing much color information by having only one type of photoreceptor. Underwater longer wavelengths, such as red, get blocked very quickly, so it's only a reduced range of green–blue light that penetrates to where these creatures live. The low light levels mean that a single photoreceptor, which is sensitive to low level light of any wavelength, could well be a better solution than an eye like our own. We need a lot of light to see in color, perhaps more than an octopus requires. ■

Mike Wood runs Mike Wood Consulting LLC, which provides consulting support to companies within the entertainment industry on product design, technology strategy, R&D, standards, and Intellectual Property. A 40-year veteran of the entertainment technology industry, Mike is a past President of ESTA and Co-Chair of the Technical Standards Council. Mike can be reached at mike@mikewoodconsulting.com.

Spectral discrimination in color blind animals via chromatic aberration and pupil shape
Authors: Alexander L. Stubbs and Christopher W. Stubbs
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