BY **MIKE WOOD**

Why do animal eyes have pupils of different shapes?

I REMEMBER, WHEN I FIRST STARTED WRITING this column 11 years ago, discussing with the *Protocol* Editor, Beverly Inglesby, just what my allowed scope should be. We agreed that I could write about anything that interested me, whether or not it was directly related to entertainment technology. In practice, I've tried to keep topics at least loosely related to the field, but this issue I'm stretching that connection to the point of breaking. I don't care; I found a recent research paper fascinating, and I hope you'll indulge me. The topic at hand is the differing shape of the pupils in animals' eyes.

I'm sure we've all noticed that while the pupils in our eyes remain round as their size changes with brightness, cats have eyes with pupils that contract to a vertical slit, while sheep and goats also have slits, but this time the slit is horizontal. Why is this?

> **"... our pupils have an aperture range of about 4-stops while a cat has 8-stops or more ..."**

Up until very recently, the accepted wisdom was that slitted pupils allowed a much larger range of opening size and thus provided better vision in low light or at night. This is indeed true; a cat's eyes have a much greater range of opening of their iris than we do. They can vary the pupil area by as much as 300:1 whereas our own, round, pupils are limited to a measly 15:1 in comparison. That gives the cat a huge advantage as a predator. They can shrink their eyes to a narrow slit during bright daylight (the domestic cat is really a desert creature, and is evolved for full sun) or open them up wide to gather every last photon at night. We have to use sunglasses and night vision goggles to achieve the same range. To put this in familiar photographic terms, our pupils have an aperture range of about 4-stops while a cat has 8-stops or more. *Note: this doesn't mean that the human eye is limited to a range of brightness of only 4-stops, this is just the range of the physical change in the pupil aperture; the different sensitivity of rods and cones, chemical changes, and other adaptations by the eye effectively give us variable film speed as well, and, given the time to adapt, we can see a very large range of brightness. Still, whatever range we have, cats can do better and the size change in pupils is almost instantaneous!*

However, this isn't the whole story. An international research team led by Martin Banks from the University of California, Berkeley has recently shown that increased light level range isn't the only reason for slitted pupils. It's long been noticed that, amongst the animals with slitted pupils, those with the slit vertical, such as cats and snakes, tend to be nocturnal or ambush predators, while those with the slit horizontal, such as many herbivores, tend to be prey. The light level argument works equally for both slit orientations, so why should one orientation be preferred over another? In addition, there are almost no animals with diagonal slitted pupils. There must be something else going on here. *Note: Although there is not such strong evidence, it seems that active predators or foragers that are awake both day and night tend to have round pupils. That's where humans fit into this picture. Round is a good compromise.*

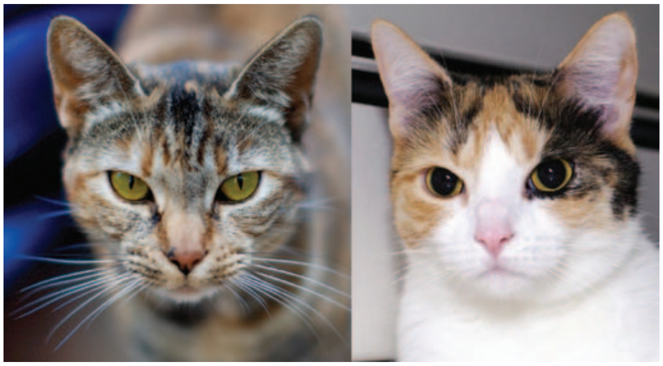

Figure 1 – Cats Eyes

The team found such strong correlation between slit pupil orientation and whether an animal was predator or prey that they set themselves the goal of determining what the advantages might be. "That is, why would a horizontally elongated pupil be advantageous for prey and a vertically elongated pupil be advantageous for ambush predators who are active at night and day?"

Looking first at the vertical slits of predator animals, what do predator animals need from their vision? Before they leap into action to catch their intended prey, they must be able to accurately estimate the distance to that prey. In general, binocular vision systems can provide three methods for estimating distance:

a. Stereopsis: This is the 3D effect provided by having two separated eyes, each with their own slightly different view point. *This provides our major depth cue for 3D vision and is the primary means used in 3D movies or television.*

b. Motion parallax: Image differences gathered as our head or body moves.

c. Defocus blur (a.k.a. "accommodation"): Objects at different distances have different lens focus.

Of these three depth cues, an ambush predator cannot use motion parallax as the required movement of their head or body would give away their position to the prey. That leaves stereopsis and defocus blur as possible mechanisms.

To use stereopsis to estimate distance, the brain must know that it is looking at the same object with both eyes. That is, we have to match a feature in one eye with the same feature in the other eye before we can estimate how far away it is. Now think about how our eyes, and those of predators, are positioned relative to each other—they are in a horizontal line, side by side. Thus, for stereopsis to work well, we need accurate recognition of contrast along that same horizontal axis and are therefore looking for sharp resolution of vertical lines in our subject. (If our eyes had evolved to be one above the other then horizontal lines would be better but, in general, most animals are bilaterally symmetrical about a vertical axis.)

What do we need to maximize defocus blur? We know, from our experience with cameras, that the best focus discrimination (or smallest depth of field) is when the camera aperture is as wide as possible. Similarly, we want the pupil as wide as possible to get the best discrimination with focus.

This gives us two goals we would like to meet with our perfect predator vision system:

a. Maximum sharpness for vertical lines for accurate stereopsis.

b. Maximum aperture for accurate defocus blur.

On the face of it, these two conditions are mutually exclusive; sharp focus needs a small aperture but defocus blur needs a large aperture. However, allow the aperture to be a shape other than round and we can find a solution. These conditions are both met simultaneously with a pupil which is narrow horizontally (for stereopsis on vertical lines), and wide vertically (for defocus blur on everything else). Precisely the arrangement of a cat's eye! **Figure 2** shows an illustration of the effect.

The white cross on the left is shown as it might appear at different distances to a vertical pupil. The vertical bar remains sharp while the horizontal gets increasingly blurred. The small picture on the right (From the UC Berkeley paper) was taken with a camera with a vertical slit iris and shows how a cat might see a bird. The

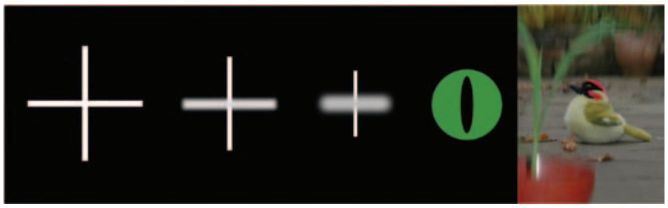

Figure 2 – Vertical Slit Pupil

horizontals of the nearby plant pot and the distant wall are both blurred. However, the vertical plant stem and sides of the plant pot remain relatively sharp while, at the critical focal distance, the prey is in sharp focus. The horizontal blur effect is most important when the eyes are close to the ground so these traits tend to be more important in smaller animals. For example, a domestic cat and other small cats have this adaptation, but large cats, such as lions, don't. Their increased height makes the adaptation less useful.

What about the prey animals? Their needs are different. They need to have as wide a field of view as possible at all times to be on the look out for predators. Ideally, they would have 360° of vision with maximum acuity at ground level where most attacks would come from. They also want to avoid being blinded by the sun. The team's results showed that a horizontal pupil does precisely this. It provides a broad horizontal field of view while minimizing glare from above. Couple that with the eye placement on the side of the head, instead of the front where it's needed for stereopsis, and you have an almost ideal panoramic view. No 3D vision, but all round warning of predators.

"Prey animals have one more trick with their eyes that is quite amazing and something I'd never realized before."

In addition, the team discovered that this shape of pupil also maximizes the acuity of horizontal contours (the opposite of our predator) which allows a sharper view of the ground and surrounding terrain. If you have eyes on the side of your head then, when you run forward, as far as your eyes are concerned, you are effectively running sideways and looking out of the corner of your eye! You need all the help you can get to avoid both obstacles and pursuing predators.

Prey animals have one more trick with their eyes that is quite amazing and something I'd never realized before. The wide field of view trick only works if the pupil is *always* horizontal and parallel with the horizon. So, how does a prey animal deal with changing head angles when bending down to graze, which is something a herbivore has to do for many hours a day? Perhaps surprisingly, (surprising to me as I'd never noticed it) the eyes of these animals rotate when they lower their heads such that the pupil remains horizontal. This might seem strange to us as we aren't able to rotate our eyes very much, if at all. Even stranger, when you think about it, is that, because the eyes are on opposite sides of the head then the eyes have to rotate in opposite directions (the scientific name for this eye motion is cyclovergence). It took the research team many hours of watching sheep and goats (and presumably trying to stay awake) at both Oakland Zoo in California and a farm in England to confirm that this is really the case! Martin Banks doubts that his team discovered this phenomenon, but could find no reference to it in the scientific literature, "I can't imagine that this missed everyone's attention for the last couple of hundred years." **Figure 3** shows the effect very clearly; the eye rotates so that the pupil remains horizontal even as the sheep tilts its head to graze.

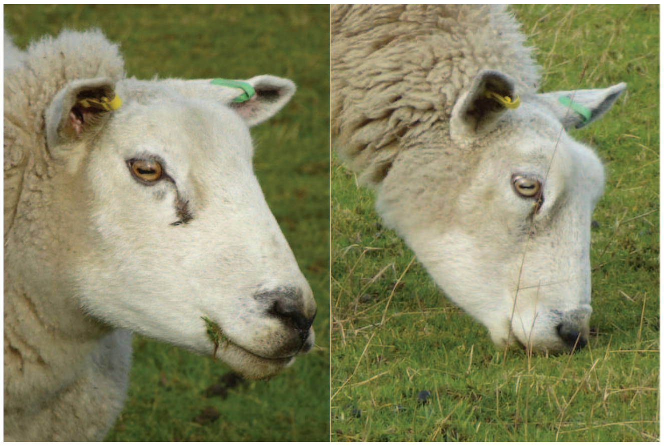

Figure 3 – Sheep's eye and cyclovergence

The researchers found this same evolution in retina shape to deal with the same problems has happened many times in different species in what looks like a textbook example of parallel evolution. For example, small canines such as foxes, small cats, snakes, crocodiles, and many lizards often exhibit the vertical slit pupil that is ideal for small predators. Wolves do as well, but as taller animals, the effect is less pronounced.

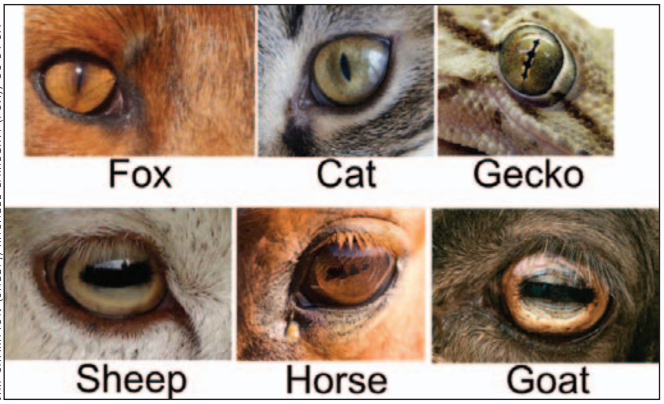

Figure 4 – Parallel Evolution

So, what is my tenuous link from all this to entertainment technology? Pretty weak, I'm afraid. It did occur to me that, as humans, we are predisposed to develop symmetrical optical systems because our eyes are also symmetrical. We use non-symmetrical optics in items such as the anamorphic lenses used to project wide-screen movies, but they are somewhat unusual. The inevitable anthropomorphism of everything we do tends to result in symmetrical optical systems.

Another link is perhaps the problems of depth perception on a stage. The audience is seated at a distance from the stage, which is often relatively shallow. This arrangement causes problems for the three depth perception cues we discussed earlier. Stereopsis and defocus blur are minimized because of the viewing distance and shallow depth, and motion parallax is all but removed because we are in a seat and can't move! It is thus left to the design team to offer other help in bringing out the performers from the background. Lighting, costume and scenic design, and blocking all help in assisting the audience's depth perception. One of the most familiar lighting assists is perhaps the use of edge or rim lighting to accentuate a dancer. The halo of light around the performer helps to separate them from the background and visually pull them towards us. We also know that warm colors tend to appear closer to us than cooler ones and use that in our designs. Strong vertical elements in a set design can also help us with stereopsis, in the same way it assists predators.

Whatever the connection, I found this whole topic fascinating. The original research paper is much more detailed than I've reported and I encourage you to read it, the details are below. Also, take a look at sheep or goats next time you see them and confirm for yourself that their eyes really do stay horizontal as they tilt their heads!

Thanks to Martin Banks, University of California, Berkeley for permission to use text and figures. ■

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 35-year veteran of the entertainment technology industry, Mike is the Immediate Past Chair of the PLASA Governing Body and Co-Chair of the Technical Standards Council. Mike can be reached at mike@mikewoodconsulting.com.

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