Optical and Visual Characteristics of Animal Eyes

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**OPTICAL & VISUAL CHARACTERISTICS OF ANIMAL EYES**

15 November 2018 • 12:00 EST

Prof. Martin S. Banks, University of California Berkeley

Dr. Jenny Read, University of Newcastle

Dr. Benjamin Palmer, Weizmann Science Institute
Why do Animals have Pupils of Different Shapes?

Martin S. Banks & William W. Sprague
Optometry & Vision Science, UC Berkeley, USA

Jürgen Schmoll, Jared A.Q. Parnell, & Gordon D. Love
Physics, Durham University, UK
Vertical Slit Pupils

Domestic cat
Vertical Slit Pupils

Red fox
Vertical Slit Pupils

Gecko
Vertical Slit Pupils

Domestic cat
Lynx
Asian leopard
Ocelot
Red fox
Swift fox
Gecko
Galago
Crocodile
Alligator
Slow loris
English viper
Copperhead snake
Indian python and many other snakes
Black skimmer
Circular Pupils

Tiger
Circular Pupils

Human
Circular Pupils

- Tiger
- Human
- Lion
- Cougar
- Cheetah
- Leopard
- Jaguar
- Wolf
- Coyote
- Dog
- Rabbit
Horizontal Slit Pupils

Horse
Horizontal Slit Pupils

Elk
Horizontal Slit Pupils
Horizontal Slit Pupils

Horse
Sheep
Goat
Cow
Elk
Reindeer
Whitetail deer
Red deer
Llama
Moose
Some snakes
Categorizations

Pupil shape

vertical

sub-circular

circular

horizontal
<table>
<thead>
<tr>
<th>Pupil shape</th>
<th>Foraging mode</th>
</tr>
</thead>
<tbody>
<tr>
<td>vertical</td>
<td>prey</td>
</tr>
<tr>
<td>sub-circular</td>
<td>active predator</td>
</tr>
<tr>
<td>circular</td>
<td>ambush predator</td>
</tr>
<tr>
<td>horizontal</td>
<td></td>
</tr>
</tbody>
</table>
Categorizations

Pupil shape
- vertical
- sub-circular
- circular
- horizontal

Foraging mode
- prey
- active predator
- ambush predator

Diel activity
- diurnal
- polyphasic
- nocturnal

Brischoux, Pizzato, & Shine (2010), *Journal of Evolutionary Biology*
Foraging Mode, Diel Activity, & Pupil Shape

Banks, Sprague, Schmoll, Parnell, & Love (2015), Science Advances
Foraging Mode, Diel Activity, & Pupil Shape

<table>
<thead>
<tr>
<th>Pupil shape</th>
<th>Relative-risk ratio</th>
<th>Confidence interval</th>
<th>P</th>
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<tbody>
<tr>
<td>Circular</td>
<td></td>
<td></td>
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<tr>
<td>activity</td>
<td>1.18</td>
<td>(0.61, 2.17)</td>
<td>0.602</td>
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<tr>
<td>foraging</td>
<td>17.65</td>
<td>(6.71, 46.38)</td>
<td>&lt; 0.000001</td>
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<tr>
<td>Sub-circular</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>activity</td>
<td>4.28</td>
<td>(1.68, 10.90)</td>
<td>0.002</td>
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<tr>
<td>foraging</td>
<td>31.06</td>
<td>(9.01, 107.12)</td>
<td>&lt; 0.000001</td>
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<tr>
<td>Vertical slit</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>activity</td>
<td>6.21</td>
<td>(2.40, 16.05)</td>
<td>&lt; 0.000001</td>
</tr>
<tr>
<td>foraging</td>
<td>393.47</td>
<td>(96.93, 1597.19)</td>
<td>&lt; 0.000001</td>
</tr>
</tbody>
</table>

\[
RR(PupilShape, a_i, f_j) = \frac{p(PupilShape | a_i, f_j)}{p(HorzPupil | a_i, f_j)}
\]

\[
RRR(PupilShape, a_i, f_{j+1}) = \frac{RR(PupilShape, a_i, f_{j+1})}{RR(PupilShape, a_i, f_j)}
\]

\[a_i = \text{activity (}i = 1 \text{ for diurnal, 2 for polyphasic, 3 for nocturnal)}\]

\[f_j = \text{activity (}j = 1 \text{ for prey, 2 for active predator, 3 for ambush predator)}\]

\[\chi^2 = 219.9; \; p < 1 \times 10^{-15}\]

Banks, Sprague, Schmoll, Parnell, & Love (2015), *Science Advances*
1) Larger adjustments in pupil area with simple musculature (Walls, 1942; Detweiler, 1955).

2) Preserves chromatic-aberration correction in some lenses when pupil is constricted (Malmström & Kröger, 2006; Land, 2006).

3) Vertical-slit pupil for terrestrial predators maximizes sharpness of horizontal contours such as horizon (Heath et al., 1969; Brischoux et al., 2010).
Large Adjustment in Area

Slit pupil allows large change in aperture size with simple musculature.

From Walls (1942)
Large Adjustment in Area

Hammond & Mouat (1985), *Experimental Brain Research*

Wilcox & Barlow (1975), *Vision Research*

de Groot & Gebhard (1952), *Journal of Optical Society of America*
1) Larger adjustments in pupil area with simple musculature (Walls, 1942; Detweiler, 1955).

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Why Vertical Slit Pupils?
Depth Cues

• Triangulation cues
  Binocular disparity (vergence)
  Motion parallax (head translation)
  Blur (accommodation)

• Perspective cues
  Linear perspective
  Texture gradient
  Relative size

• Light-transport cues
  Shading
  Aerial perspective
  Occlusion
Geometry of Binocular Disparity

\[ d = X_L - X_R \]

\[ d = \frac{Is}{z_0} \left( 1 - \frac{z_0}{z_1} \right) \]

\[ \delta \approx I \left( \frac{1}{z_0} - \frac{1}{z_1} \right) \]

\[ \delta \approx I(\Delta D) \]

Held, Cooper, O’Brien, & Banks (2010), ACM Transactions on Graphics
Geometry of Blur

\[
b = A \left| \frac{s}{z_0} \left( 1 - \frac{z_0}{z_1} \right) \right|
\]

\[
\beta \approx A \left| \frac{1}{z_0} - \frac{1}{z_1} \right|
\]

\[
\beta \approx A |\Delta D|
\]

Held, Cooper, O’Brien, & Banks (2010), ACM Transactions on Graphics
\[ \delta \approx I(\Delta D) \]

\[ \beta \approx A |\Delta D| \]

\[ \frac{\beta}{|\delta|} \approx \frac{A}{I} \]

Held, Cooper, O’Brien, & Banks (2010), *ACM Transactions on Graphics*
Astigmatic Depth of Field

\[ \beta_h \approx A_h \left| \frac{1}{z_0} - \frac{1}{z_1} \right| \]

\[ \beta_v \approx A_v \left| \frac{1}{z_0} - \frac{1}{z_1} \right| \]

\[ \frac{\beta_v}{\beta_h} \approx \frac{A_v}{A_h} \]
Solving the correspondence problem in stereopsis:

- Most disparities are horizontal, so must search for horizontal offset in two eyes that provides correct match.
- Can’t be done with horizontal contours.
- Thus, vertical contours provide better information for matching and therefore better information for depth from disparity (Walker, 1940; Ebenholtz & Walchli, 1965).
- Blur reduces precision of stereopsis (Goodwin & Romano, 1985).
- If animal is going to have a slit pupil, orientation should be vertical to minimize the relevant blur for stereopsis.
Depth from blur maximized by opening aperture

• For estimating distance of horizontal contours, vertical extent of pupil determines depth-of-field blur. Maximize pupil height.

• Vertical slit pupil aids distance estimation for vertical contours by facilitating stereopsis.

• Vertical slit pupil aids distance estimation for horizontal contours by maximizing depth-of-field blur.

• Thus, vertical slit pupil makes triangulation baseline simultaneously as wide and tall as possible.
Why Horizontal Pupils?
26 of 27 terrestrial prey animals in our database have laterality angles (the angle between the optic axes) greater than 87 deg.
With horizontal incidence, horizontal contours imaged in front of retina, & vertical contours behind retina creating very large astigmatism of oblique incidence.
Schematic Eye for Sheep

Coile & O’Keefe (1988), *Ophthalmic & Physiological Optics*
Image Quality for Circular & Vertical Pupils
Image Quality for Circular & Vertical Pupils

vertical sections
upper field

horizontal sections

lower field

upper field

lower field
Benefits of Horizontal Pupil

1) Increases effective field of view horizontally to enable detection of predators approaching along ground from various directions.

2) Reduces blur of horizontal contours near ground, even in eccentric view. Aids forward locomotion.
Prediction: Eye Rotation with Head Pitch
Conclusion

1) Slit pupils enable greater variation in retinal illumination in different light environments.

2) Vertical slits useful for terrestrial predators. Vertical contours imaged sharply, aiding depth from disparity. Short depth of field for horizontal contours, aiding depth from blur on foreshortened ground.

3) Horizontal slits useful for terrestrial prey. Expands effective field of view horizontally. Small vertical aperture minimizes blur of horizontal contours on foreshortened ground, which helps guide forward locomotion across uneven terrain.

Supported by research grants from NIH & EPSRC.
Stereopsis in insects
The praying mantis versus a human observer
The geometry of stereo vision

left eye’s view  right eye’s view

right eye’s view  left eye’s view

disparity

mountain
tree
Stereo vision is hard

• To achieve stereoscopic or 3D vision, you have to:
  – detect an object in each eye independently
  – match up corresponding images of the same object
  – work out the disparity between them
  – convert that into an estimate of distance.

• Machine stereo algorithms are complex and computationally demanding, and actively under research.
Who has 3D vision?

Humans – we discovered that only in 1838

XVIII. Contributions to the Physiology of Vision.—Part the First. On some remarkable, and hitherto unobserved, Phenomena of Binocular Vision. By Charles Wheatstone, F.R.S., Professor of Experimental Philosophy in King’s College, London.

Received and Read June 21, 1838.
Who has 3D vision?

Other predatory mammals with front-facing eyes.
Who has 3D vision?

Prey mammals with side-facing eyes.
Who has 3D vision?

Predatory birds.
Who has 3D vision?

Predatory amphibians.
Who has 3D vision?

Predatory insects
– the praying mantis is the only invertebrate known to have stereo vision
How do we know mantids have stereo vision?

• First proved by Prof Samuel Rossel in 1983 using prisms
• Recently confirmed by my own group using a different approach.

Using colour to display 3D

Image as it appears on the experimental display.

Object for right eye drawn in blue.

Background drawn in blue + green (cyan)

Object for left eye drawn in green.

coloured filters placed over insect’s eyes

Image seen through blue filter, which blocks green light.

Image seen through green filter, which blocks blue light.
Using colour to display 3D

Image as it appears on the experimental display.

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Mantids don’t perceive colour

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Background drawn in blue + green (cyan)

Coloured filters placed over insect’s eyes

Mantids don’t perceive colour

So both eyes see a dark object on a bright background, but the position is different in each eye. This disparity can simulate depth.
Who has 3D vision?

Possibly many others –
it’s hard to prove a species has stereo vision, and most have not been investigated.
Who has 3D vision?

3D vision has evolved independently at least 4 times.

500 million years ago
Who has 3D vision?

• 3D vision seems to work very similarly in humans, monkeys, cats and owls
  – (the four species where it’s been most studied)
How to build a stereo system

• 3D vision seems to work very similarly in humans, monkeys, cats and owls
  – (the four species where it’s been most studied)
• Does this mean there is only one good way to do 3D vision?
• But human-style 3D vision is computationally demanding – can an insect brain implement it?
Man vs Mantis: Half a billion years of separate evolution.

Huge brain
(~100,000,000,000 neurons)
High power (~20W)

Tiny brain
(~1,000,000 neurons)
Low power (~20mW)
Human stereo vision

- We wanted to ask if mantis stereo vision is different from human stereo vision.
- So I first have to explain how human stereo vision works.
  – (oversimplifying massively in the interests of time!)
How do humans do 3D vision?

The visual cortex of our brain contains cells – neurons – which receive input from small patches of the left and right retinas.
Different neurons see different patches of the left and right images.
Different neurons see different patches of the left and right images.
Different neurons see different patches of the left and right images.
Different neurons see different patches of the left and right images.
Different neurons see different patches of the left and right images.
Different neurons see different patches of the left and right images.
Different neurons see different patches of the left and right images.

This neuron is seeing a match.
How do the neurons know which one is seeing the true match?

Neurons compute (roughly) the correlation coefficient between the image-patches in the two windows.
Compute correlation coefficient
Correlation is 1 when image-patches match

$r=1.0$
Correlation is 1 when image-patches match

The response of each neuron reflects the correlation between their left and right image-patches. The neuron with the largest response is the one that is seeing the correct match.
Similarities between machine and human stereo

Correlation between left and right images is a common “goodness of match” metric in “dense stereo” machine vision algorithms.
Correlation works for arbitrary images

E.g. “random dot patterns” where stereoscopic disparity is the *only* indication of depth
Evidence for correlation

• How do we know human stereo uses the correlation between left and right eyes?
  – Messing with interocular correlation messes up human stereopsis.
Normal, correlated random-dot pattern

Correlation equals +1 when image-patches match.

correlated dot-pair =

Left image                              Right image

Pixels right eye

Pixels in left eye

L         R                 L         R

or

[Images of correlated dot-pairs]
Anti-correlated random-dot patterns

So what happens if we totally mess with correlation?
Anti-correlated random-dot patterns

So what happens if we totally mess with correlation?

Now a black pixel in the left eye corresponds to a white pixel in the right eye and vice versa.

Correlation = -1.
**Anti-correlated random-dot pattern**

Correlation equals -1 when image-patches originally matched. Correlation never equals +1.

Anti-correlated dot-pair = \[ \begin{array}{c} L \quad R \\ \bullet \quad \circ \\ \circ \quad \bullet \end{array} \] or \[ \begin{array}{c} L \quad R \\ \circ \quad \bullet \\ \bullet \quad \circ \end{array} \]
Human stereo vision *doesn’t work* in anti-correlated stereograms

- Messing up the relationship between the pattern in left and right eyes stops stereo vision working (unsurprisingly!)
Do mantids use cross-correlation?

- Mantids only strike at things they think are prey.
- And they only eat live prey.
- So they only strike at things that move (like our “simulated bug”)
- To use random-dot patterns with mantids, we had to make a random-dot pattern with a moving “simulated bug”.
Random dot pattern with moving “prey”
Human results

Near perfect depth discrimination: Respond “near” if disparity implies disk in front of screen, usually respond “far” if behind.

Distance from screen

Further than screen  Nearer than screen
Mantis results

Near-perfect depth discrimination: Strike if disparity indicates prey within catch range; do not strike if disparity indicates otherwise.
First time it’s been demonstrated mantis stereopsis works in complex images where target is perfectly camouflaged
Humans can’t discriminate depth in anti/un-correlated stereo images

**Correlated**

- Near perfect depth discrimination

**Anti-correlated**

- At chance.

**Uncorrelated**

- At chance.

Disparity-defined depth (cm in front of / behind screen)
Mantids can.

Unlike humans, mantids *can* discriminate depth in anti/un-correlated stereo images!
Man vs Mantis

- Praying mantids could use their 3D vision to correctly discriminate depth in these highly unnatural stimuli.
- Undergraduates could not.
Moving or not moving?

• Mantis stereo vision requires movement, but does not require anything to move.
• It requires “second order” but not “first order” motion.
“Luminance flip” stimulus

- Dots change from black to white and vice versa as “target” passes over them.
- “Second-order” motion – we see motion but nothing actually moves across the screen.
- Location is offset between left and right eye videos (disparity)
Mantids can discriminate depth in this “luminance flip” video.
Our current understanding of mantis stereo vision

- Mantis stereo vision is based on temporal change.
- Their visual system passes the inputs to each eye through a high-pass temporal filter.
- This extracts regions where things are changing:

![Video of "luminance flip" stimulus as it enters the eye](image1)

![Video after processing by mantis visual system (high-pass filtered and rectified)](image2)

- They then extract the disparity of the moving region – possibly by cross-correlation.
Mantis vs human stereopsis

• Mantis stereopsis is fundamentally different to human:
  – Human stereopsis is based on the detailed pattern of light and dark in the two eyes.
  – Mantis stereopsis is based on image change over time, and doesn’t care about the detailed pattern of light and dark.

• Pros and cons:
  – Mantis stereopsis is presumably less costly to implement (number of neurons, spikes).
  – Mantis stereopsis is more robust to low interocular correlation.
  – Mantis stereopsis fails totally with static images.
Summary

• Praying mantids are the only invertebrate known to have stereopsis.

• Mantis stereopsis is fundamentally different from human
  – it works on change over time, not the pattern of light and dark.

• However subsequent processing may be similar to ours
  – may work by cross-correlating left and right video streams.

• Brain circuits underlying mantis stereopsis are surprisingly complex
  – multiple classes of disparity-selective neurons, and multiple feedback loops.

• This is still simpler than our own stereo vision and may be a valuable
  source of inspiration for new forms of machine stereo.
Optically Functional Organic Crystals in Animal Vision

OSA webinar, Nov 2018
Guanine


Crystal Morphology and Organization

Crystal Morphology and Organization

Crystal Morphology and Organization

Crystal Morphology and Organization

Why Guanine?


Controlling Crystal Morphology

Reflectivity in Vision

Reflectivity in Vision: Light Concentration

“The paired eyes have huge metallic-looking reflectors behind them, making them appear like the headlamps of a large car; they look out through glass-like windows in the otherwise orange carapace and no doubt these concave mirrors behind serve instead of a lens in front” (Hardy 1956).

\[
N (\text{f number}) = \frac{f (\text{focal length})}{D (\text{diameter of pupil})} = 0.3
\]

Ostrocod Gigantocypris

M.F. Land, Sci. Am. 239, 126-134 (1978)
Reflectivity in Vision: **Light-Doubling Tapeta**
Reflectivity in Vision: Image-formation


The Image Forming Mirror in the Eye of the Scallop

The Image Forming Mirror in the Eye of the Scallop

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