# Optical and Visual Characteristics of Animal Eyes

Presented by:

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Applications of **Technical Group** 

### Welcome to Today's webinar!



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





#### Domestic cat





Red fox







Gecko







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





#### Horse





Elk













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

### Categorizations

#### Pupil shape

vertical



subcircular



circular



horizontal



### Categorizations

### Pupil shape

vertical



subcircular



circular





#### Foraging mode



active predator

ambush predator



### Categorizations

### Pupil shape

vertical



subcircular



circular





### Foraging mode



### Diel activity





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

vertical



subcircular



circular



horizontal



Pupil shape	Relative-risk ratio	Confidence interval	Р
Circular			
activity	1.18	(0.61, 2.17)	0.602
foraging	17.65	(6.71, 46.38)	< 0.00001
Sub-circular			
activity	4.28	(1.68, 10.90)	0.002
foraging	31.06	(9.01, 107.12)	< 0.00001
Vertical slit			
activity	6.21	(2.40, 16.05)	< 0.00001
foraging	393.47	(96.93, 1597.19)	< 0.00001

$$RR(PupilShape, a_{i}, f_{j}) = \frac{p(PupilShape | a_{i}, f_{j})}{p(HorizPupil | a_{i}, f_{j})}$$
$$RRR(PupilShape, a_{i}, f_{j+1}) = \frac{RR(PupilShape, a_{i}, f_{j+1})}{RR(PupilShape, a_{i}, f_{j})}$$

 $a_i$  = activity (*i* = 1 for diurnal, 2 for polyphasic, 3 for nocturnal)

 $f_j$  = activity (j = 1 for prey, 2 for active predator, 3 for ambush predator)

χ<sup>2</sup> = 219.9; p < 1 x 10<sup>-15</sup>

Banks, Sprague, Schmoll, Parnell, & Love (2015), Science Advances

### **Previous Hypotheses**

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



From Walls (1942)

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

### 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* 

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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



Held, Cooper, O'Brien, & Banks (2010), ACM Transactions on Graphics

### Geometry of Blur



$$b = A \left| \frac{s}{z_0} \left( 1 - \frac{z_0}{z_1} \right) \right|$$
$$\beta \approx A \left| \frac{1}{z_0} - \frac{1}{z_1} \right|$$
$$\beta \approx A \left| \Delta D \right|$$

Held, Cooper, O'Brien, & Banks (2010), ACM Transactions on Graphics

### Geometry of Disparity & Blur





Held, Cooper, O'Brien, & Banks (2010), ACM Transactions on Graphics

### Astigmatic Depth of Field





$$\beta_h \approx A_h \left| \frac{1}{z_0} - \frac{1}{z_1} \right|$$
$$\beta_v \approx A_v \left| \frac{1}{z_0} - \frac{1}{z_1} \right|$$

$$\frac{\beta_{\nu}}{\beta_{h}} \approx \frac{A_{\nu}}{A_{h}}$$

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?



### Lateral Eyes & Visual Field

26 of 27 terrestrial prey animals in our database have laterality angles (the angle between the optic axes) greater than 87 deg.



### Image Formation with Oblique Incidence

top view



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



## **Benefits of Horizontal Pupil**



- 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.

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**Questions?** 

## Stereopsis in insects The praying mantis versus a human observer





The Leverhulme Trust



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#### The geometry of stereo vision









#### 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.





#### 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.









#### Other predatory mammals with front-facing eyes.









#### Prey mammals with side-facing eyes.







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Predatory birds.











#### Predatory amphibians.











#### 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.

Rossel (1983) Binocular stereopsis in an insect. *Nature* 302: 821 Nityananda et al (2018) A novel form of biological 3D vision. *Current Biology* 28(4)





#### Using colour to display 3D





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#### Using colour to display 3D







#### Using colour to display 3D



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

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#### Possibly many others –

it's hard to prove a species has stereo vision, and most have not been investigated.











**Neuroscience** 

• 3D vision seems to work very similarly in humans, monkeys, cats and owls

- (the four species where it's been most studied)











Machines





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#### 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.







#### 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.

image in left retina

image in right retina





brain cell or neuron







1

.











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# 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





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# 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



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#### 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.





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correlated dot-pair =



#### Anti-correlated random-dot patterns

So what happens if we totally mess with correlation?



Pixels in left eye

Pixels right eye



#### 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.











#### Human stereo vision **doesn't work** in anti-correlated stereograms



black white

• 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"





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#### Human results



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

Distance from screen



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#### Mantis results



Near-perfect depth discrimination: Strike if disparity indicates prey within catch range; do not strike if disparity indicates otherwise.



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First time it's been demonstrated mantis stereopsis works in complex images where target is perfectly camouflaged





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# Humans can't discriminate depth in anti/un-correlated stereo images



Near perfect depth discrimination

At chance.

At chance.







#### Mantids can. Anti-correlated Uncorrelated Correlated Large dots Small dots Large dots Large dots Small dots Small dots 1.0 1.01 1.01 Strike probability 0.8 0.8 0.8 0.6 0.6 0.6 0.4 0.4 0.4 0.2 0.2 0.2 7.5 0 7.5 0 7.5 7.5 0 7.5 Undefined Undefined 0 7.5 Undefined 0 Undefined Undefined 0 Undefined

Distance from screen

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



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# 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



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Newcastle

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#### 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:



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#### 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



A. Levy-Lior, E. Shimoni, O. Schwartz, E. Gavish-Regev, D. Oron, G. Oxford, S. Weiner, L. Addadi, *Adv. Funct. Mater.* 2010.



B.A. Palmer, G.J. Taylor, V. Brumfeld, D. Gur, M. Shemesh, N. Elad, A. Osherov, D. Oron, S. Weiner, L. Addadi. *Science* **2017**.





D. Gur, B. Leshem, D. Oron, S. Weiner, L. Addadi, *J. Am. Chem. Soc.* 2014.



D. Gur, B. Leshem, M. Pierantoni, V. Farstey, D. Oron, S. Weiner, L. Addadi, J. Am. Chem. Soc. 2015.



D. Gur, B. A. Palmer, B. Leshem, D. Oron, P. Fratzl, S. Weiner, L. Addadi, *Angew. Chem*. 2015.



J. Teyssier, S. V. Saenko, D. van der Marel, M. C. Milinkovitch, *Nat. Commun*. 2015.









## Why Guanine?



A. Hirsch, D. Gur, I. Polishchuk, D. Levy, B. Pokroy, A.J. Cruz-Cabeza, L. Addadi, L. Kronik, L. Leiserowitz. *Chem. Mater.*, **2015**D. Gur, B.A. Palmer, S. Weiner, L. Addadi, *Adv. Funct. Mater.*, **2017**

# **Controlling Crystal Morphology**



# **Reflectivity in Vision**

B.A. Palmer, D. Gur, S. Weiner, L. Addadi, D. Oron, Adv. Mater., 2018

# Reflectivity in Vision: Light Concentration



Ostrocod Gigantocypris



"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 (f number) = f (focal length)/D (diameter of pupil) = 0.3



M.F. Land, Sci. Am. 239, 126-134 (1978)

# Reflectivity in Vision: Light-Doubling Tapeta



# Reflectivity in Vision: Image-formation







E. Young, Inside the Eye: Nature's Most Exquisite Creation, *Nat. Geo*. Feb **2016**.













B.A. Palmer, G.J. Taylor, V. Brumfeld, D. Gur, M. Shemesh, N. Elad, A. Osherov, D. Oron, S. Weiner, L. Addadi. Science 2017.



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