What makes insect vision special?

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Who am I?

• Vision scientist specialising in stereoscopic ("3D") vision
• Physics background
• Computational neuroscience in primates (human & non)
• Applications of stereo vision in eye clinic, entertainment, new displays...
• Recently moved into insect vision to study mantis stereopsis
Outline

• Background on insect vision
• Man vs mantis: motion perception
• Man vs mantis: stereopsis

People who did the work

• Vivek Nityananda – mantis behavioural experiments
• Ghaith Tarawneh – stimulus coding and modelling
• Ignacio Serrano-Pedraza – stimulus coding and modelling
Compound eyes

- Insect eyes are *compound* – made up of 100s to 1000s of little facets called ommatidia.
  - (Insects also have simple eyes called ocelli but these don’t usually form images – probably monitor brightness/flow.)
This has led to a widespread misconception...

Bryceson 1981
Images seen through a cleaned piece of cornea of an object (the number ‘7’) effectively at infinity
This is not how bugs actually see!
Compound eyes

Each facet collects light from a different direction. The end result is just a retinal image.
Compound eyes are inefficient

Out of all the rays of light coming from this direction, only the small bundle in the shaded region gets detected.
Compound eyes are inefficient

Out of all the rays of light coming from this direction, only the small bundle in the shaded region gets detected. Rays from a different direction are detected by a different ommatidium.
Simple eyes are more efficient

Rays from a given direction are collected all across the pupil and focused by the lens onto a single photoreceptor.

Mammals, birds, reptiles, fish, squid, octopods, spiders, insect ocelli...
Compound eyes are also low acuity

Kirschfeld 1976: If humans had compound eyes with no change in average acuity
Compound eyes

Cons:
• Low resolution – don’t show much detail.
• Low sensitivity – don’t capture much of the available light.

Pros:
• Nearly 360° (4π) field of view.
• Nearly infinite depth of field.
Variants of the compound eye

• Apposition
• Optical Superposition
• Neural Superposition

Image credits:

Blogger “Watcher” from Salt Lake City.
https://www.blogger.com/profile/02248341788957416471

The late Prof Matti Weckström
http://www.scholarpedia.org/article/Function_of_compound_eye
Rhabdomeres form waveguides, channeling light by internal reflection.
Ancestral eye of arthropods
Horseshoe crab, praying mantis, locust, beetles
Refraction Superposition Eye

Butterflies, moths
Crayfish
Diurnal flies
Superficially similar to a lightfield camera - a microlens array with a group of pixels under each lens - but not the same!
The pseudopupil
Ommatidia that you are looking directly at appear dark, because they absorb the light that would otherwise reflect off them in your direction. This is the pseudopupil.
Aside: Mantis shrimp pseudopupil

• Mantis shrimp have 3 pseudopupils in one eye.
• I.e. 3 regions of the eye look in the same direction.
• Monocular stereopsis?
Some insects have special forms of vision

Many insects have sensitivity to ultraviolet

– either because a single photoreceptor’s sensitivity extends into UV (e.g. mantis)

– or because they have dedicated photoreceptors for UV (e.g. bee)
Some insects have special forms of vision

Many insects have sensitivity to polarisation
  e.g. using for navigation (ants, bees, locusts...)

The compound eye is made up of many ommatidia. Each ommatidium contains a barrel shaped array of photoreceptors, through which light travels. Subsets of these photoreceptors project their polarization sensitive microvilli at perpendicular angles to one another. The orange and blue arrows in the right panel correspond to the polarization sensitivity of the colored photoreceptors.
**Man vs Mantis**

Visually guided pursuit predator.  
Diurnal.  
Two simple eyes.  
High-acuity fovea.  
Excellent resolution (0.007°)  
Variable focus, small depth of field.  
Eyes that move within head.  
High power consumption (~20W)  
Huge brain  
(~100,000,000,000 neurons)

Visually guided ambush predator.  
Diurnal.  
Two compound eyes.  
High-acuity fovea.  
Poor resolution (0.5°)  
Large depth of field.  
Eyes fixed on head.  
Low power consumption (~20mW)  
Tiny brain  
(~1,000,000 neurons)
Motion detection

• Surprising similarity between insects and primates.
• Reichardt detector, first proposed for beetles, mathematically identical to motion energy model used to model primate motion perception.
Reichardt detector

(basic version)
Reichardt detector

time 1

moving object

delay
Reichardt detector

time 2

delay

moving object
Reichardt detector

time 2

delay

moving object
Reichardt detector

moving object

delay
Reichardt detector

(high-pass temporal filter) × (low-pass temporal filter)

(more realistic version)
Add in opponency: construct a mirror-image leftward motion sensor and subtract it from the rightward sensor.
spatial filters

temporal filters

separable responses

nonlinearity

opponency

Reichardt detector

Energy model

I(x,t)

SF_1(x) → TF_1(t) → A → + → AB'

SF_2(x) → TF_2(t) → A' → + → A'B

SF_1(x) → TF_1(t) → B → + → BA'

SF_2(x) → TF_2(t) → B' → + → (A-B')^2

Opponent Energy

(AB' - BA')

4(AB' - BA')
Man vs mantis: Motion perception

- Using the optomotor response to do mantis psychophysics and study their motion perception
Coded “left”
Coded “right”
Coded “no response”
Mantis psychometric function


Threshold contrast 0.3
Mantis contrast sensitivity function

• If you measure contrast thresholds for *sinusoidal grating stimuli* of different spatial and temporal frequencies, you can plot the contrast sensitivity function.

• The contrast sensitivity function is a very basic property of any visual system, saying what the animal can and cannot see.
Mantis contrast sensitivity function

Sensitivity = $1/\text{contrast threshold}$, plotted here as a function of spatial frequency for temporal frequency 8Hz

NB some insects have much better sensitivity to high temporal frequencies than humans.
Masking experiments

**Signal:** Lower frequency grating drifting smoothly to the *right*

**Noise:** Higher frequency grating jumping in phase *randomly*

Higher contrast thresholds are now needed to detect signal motion.
In humans, noise has the strongest masking effect when presented at the signal frequency

Figure 3: Effect of noise on mammalian motion detectors

In humans, this motion masking function gives you the contrast sensitivity function of each motion channel.
Not in mantises!
Not in mantises!

*Noise* at these very low spatial frequencies produces strong masking even though *signal* here elicits no response!
Man vs mantis: motion perception

• So in humans, masking reflects sensitivity
  – frequencies to which we are more sensitive produce stronger masking
• In mantises, it does not
  – low frequencies to which the mantis is not sensitive produce strong masking
• A qualitative difference in motion perception?
Man vs mantis: motion perception

• So in humans, masking reflects sensitivity
  – frequencies to which we are more sensitive produce stronger masking
• In mantises, it does not
  – low frequencies to which the mantis is not sensitive produce strong masking
• A qualitative difference in motion perception?
• In fact, no: a quantitative difference in spatial filters.
spatial filters
- SF1
- SF2

temporal filters
- TF1(t)
- TF2(t)

separable responses
- A
- A'
- B
- B'

nonlinearity
- A-B'
- A+B
- A'+B
- A'-B

opponency
- AB'
- BA'

Opponent Energy
- (AB'-BA')
- 4(AB'-BA')
Man vs mantis: motion perception

• A quantitative difference in spatial filters:
  • Insect spatial filters are lowpass.
  • The opponent step in motion detection cancels out the response to low-frequency signal, creating a bandpass contrast sensitivity function despite the lowpass front end.
  • Low-frequency noise does not cancel, adds variance, masks signal.
  • Human spatial filters are bandpass.
  • The opponency step doesn’t change the tuning.

Man vs mantis: Motion perception

- The basic computation for motion perception is surprisingly similar in insects and humans:
- Spatiotemporal filtering + nonlinearity + opponency.
- Different neural implementation.
- Different parameters (e.g. spatial bandwidth) produce qualitatively different behaviour (e.g. whether invisible noise can mask the signal).
Stereopsis
Stereo vision has evolved several times.

Stereo vision has evolved several times.

Stereo vision has evolved several times.

Stereo vision has evolved several times. The only invertebrate known to have stereopsis!

How do we know mantids have stereopsis?

How do we know mantids have stereopsis?

Angle $\Delta = \text{binocular disparity}$.

How do we know mantids have stereopsis?

How do we know mantids have stereopsis?

How do we know mantids have stereopsis?

How do we know mantids have stereopsis?

- The pattern of strike errors indicates the mantis is using the binocular disparity $\Delta$ to judge distance.

Man vs mantis: stereopsis

• We’ve seen that in motion, insects and humans make similar computations. Is the same true for stereopsis?

• Two possible outcomes:
  1. Insect stereo is broadly similar to human stereo
     (at least in initial stages, e.g. how stereo correspondence is achieved)
     ⇒ New insights for understanding our own.
  2. Insect stereo is completely different
     ⇒ New ideas for machine stereo (esp simple, cheap)
What can stereopsis do?

**Range-finding:**
Find the distance to an object by triangulation without moving.
What can stereopsis do?

*Range-finding:*
Find the distance to an object by triangulation without moving. 
Human stereopsis is terrible at this! But our stereopsis can *break camouflage:* detect objects that are invisible monocularly.
Human stereopsis

• Can break camouflage.
• Does not require monocularly-visible objects.
• Works by computing the **interocular cross-correlation**
  – the correlation between left and right-eye images
• Many machine “dense stereo” algorithms work in a very similar way.
• What about insects?
How to display *arbitrary* 3D images like random dot patterns?

Prisms can shift the whole scene nearer or further, but that’s all.

To display more complex stimuli, we came up with an alternative approach:
National Geographic documentary: “Explorer: Eyes Wide Open”
Demonstrating mantis stereo vision

“Crossed disparity”
= in catch range.

“Uncrossed disparity”
= undefined distance.

3D glasses for insects

• So far this basically replicates Rossel with a different display technology.
• This proves that our 3D glasses do work and create a valid depth percept for insects.
• Now we can do experiments to probe how their 3D vision works and whether it is the same as our own.
• Q1: Can mantis stereopsis break camouflage?
Prey motion is required
Random dot stereogram: camouflaged target

no good for mantises as nothing moves
The *dynamic* random dot stereogram
An (even more) beautifully unnatural stimulus: the dynamic random dot stereogram.

• With a dynamic random-dot stereogram, we could hide the motion and have a moving object defined purely by disparity!
• So we tried that... the mantids didn’t respond.
• Hard to interpret a null result:
  – They can’t extract disparity in these images because their visual systems are not cross-correlating the two eyes’ images?
  OR
  – Mantids can see the moving object but are so freaked out by the unnatural stimulus that they don’t display their natural behaviour?

• Q1: Can mantis stereopsis break camouflage?
• A1: No evidence that it can.
A compromise: RDS with a motion cue

• Monocular motion reveals the target *location*  
  – it breaks the target’s camouflage, which is perfect in any frame  
• but it doesn’t specify the target *distance*  
  – only the disparity does that.
Humans can see depth in such stimuli

“disparity” (cm in front of / behind screen)

Near perfect depth discrimination
– always respond “near” if
disparity implies disk in front of
screen, almost always respond
“far” if behind.

5 human observers;
data collected by
Jonathon Marshall
Mantises see depth in these stimuli too

Disparity condition

Combined results for 17 insects.

Mean strikes/trial

strike at crossed disparity simulating prey within catch range

rarely strike at other configurations
Q2: Does mantis stereopsis still work with more complex scenes, when the target has the same pattern as the background?
A2: Yes.
Man vs mantis: stereopsis

Q2: Does mantis stereopsis still work with more complex scenes, when the target has the same pattern as the background?
A2: Yes.

Q3: How does it work? Are they detecting interocular cross-correlation?

To address this, we disrupted interocular cross-correlation in two ways.
Normal, correlated random-dot pattern

Left image                              Right image

correlated dot-pair = 

\[
\begin{array}{cc}
L & R \\
\text{or} & \\
\end{array}
\]

\[
\begin{array}{cc}
\text{L} & \text{R} \\
\end{array}
\]

Pixels right eye

Pixels in left eye
Anti-correlated random-dot patterns

Left image                              Right image

black     white

anti-correlated dot-pair =                         or

L         R                 L         R

Pixels in left eye

Pixels right eye
Anti-correlated stereograms give no depth percept

Correlated  Anti-correlated
Anti-correlated version
Human results

Correlated

Anti-correlated

“disparity” (cm in front of / behind screen)

Near perfect depth discrimination – always respond “near” if disparity implies disk in front of screen, almost always respond “far” if behind.

Basically at chance – always respond “near” regardless of disparity sign.

5 human observers; data collected by Jonothon Marshall
Human stimulus – uncorrelated
Humans can’t discriminate depth in anti/un-correlated stereo images

Correlated

Anti-correlated

Uncorrelated

“disparity” (cm in front of / behind screen)

Near perfect depth discrimination – always respond “near” if disparity implies disk in front of screen, almost always respond “far” if behind.

Basically at chance – always respond “near” regardless of disparity sign.
Humans can’t discriminate depth in anti/un-correlated stereo images

• This is what we expected.
• Human stereopsis works by cross-correlation, so messing with correlation destroys our stereopsis.

• What about mantises?
Remember they could do correlated..
Mantids *can* discriminate depth in anti/un-correlated stereo images!

Combined results for 17 insects, all 6 conditions randomly interleaved.

Combined results for 6 insects in separate experiment.
Man vs mantis

- Insects were able to discriminate depth in these images.
- Undergraduates were not.

$10^6 \text{ mm}^3, 10^{11} \text{ neurons}$

$10^1 \text{ mm}^3, 10^6 \text{ neurons}$

5 orders of magnitude
Could mantis stereopsis be built on Reichardt detectors?

• Filter the monocular stimuli so as to extract motion:

• You could then perceive depth based on the disparity of the moving region.

Does mantis stereopsis use motion direction?

• Seems like direction of motion would be a helpful cue in matching up the two eyes’ images.
• We tested if mantises use this.
“Vertical motion” stimulus with matching motion (down/down)
“Vertical motion” stimulus with different motion (up/down)
“Vertical motion” results

Mean number of strikes per trial

Up-Up

n=4 animals, 10 reps
“Vertical motion” results

Mean number of strikes per trial

<table>
<thead>
<tr>
<th>Up-Up</th>
<th>Down-Down</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="Up-Up.png" alt="Graph" /></td>
<td><img src="Down-Down.png" alt="Graph" /></td>
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</tbody>
</table>

Graphs show the mean number of strikes per trial for Up-Up and Down-Down motions.

n=4 animals, 10 reps
“Vertical motion” results

Mean number of strikes per trial

<table>
<thead>
<tr>
<th>Direction</th>
<th>n=4 animals, 10 reps</th>
</tr>
</thead>
<tbody>
<tr>
<td>Up-Up</td>
<td></td>
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<tr>
<td>Down-Up</td>
<td></td>
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<tr>
<td>Up-Down</td>
<td></td>
</tr>
<tr>
<td>Down-Down</td>
<td></td>
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</tbody>
</table>

n=4 animals, 10 reps
“Vertical motion” results

- Mantids don’t care at all if the motion direction matches!
- Mantis stereopsis clearly does not require matching motion direction in the two eyes.
- This suggests that the *local* cue is temporal change, not directional motion.
- (“Global” motion of prey item may be required.)
Man vs mantis: stereopsis

• Unlike motion, insect and human stereopsis seem to work quite differently.

• Mantis stereopsis
  – doesn’t need visual experience during development.
  – doesn’t work at all on single image-pairs.
  – can’t break camouflage.
  – doesn’t require correlation between images.
  – uses regions of change as matching primitives.
  – can discriminate depth when humans can’t.

• Computationally cheap way to get a yes/no answer to “is there a moving object in my strike zone?”
  – possibly of interest in mobile autonomous applications.
Summary: How is insect vision special?

- Multiple low-resolution visual sensors.
- Large depth of field, 360° view.
- Some have very high temporal sensitivity.
- Some are sensitive to UV, linear polarisation.
- Motion computation much like our own.
- Stereo computation very different (and based on motion).
- Incredibly successful low-power autonomous systems which we can certainly learn from!