# *Neural computation on natural signals: Lessons from the fly visual system*

with: Bill Bialek & Geoff Lewen

KITP, August 2004

*Good reason to study insect brains…*

"It is indubitable that zoologists, anatomists and psychologists have slighted the insects. Compared with the retina of these apparently humble representatives of life, ***the retina of the bird or the higher mammal appears as something coarse, rude, and deplorably elementary."***

(Ramon y Cajal, 1937)

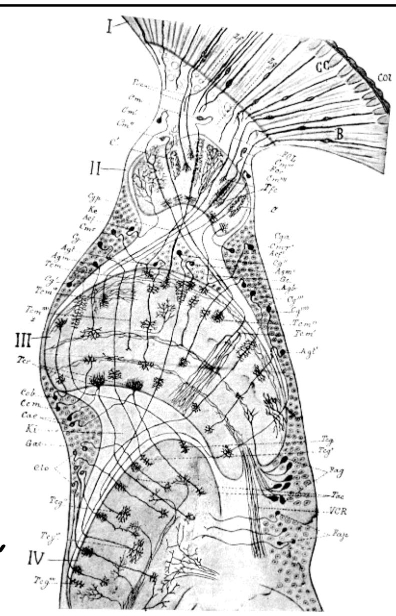
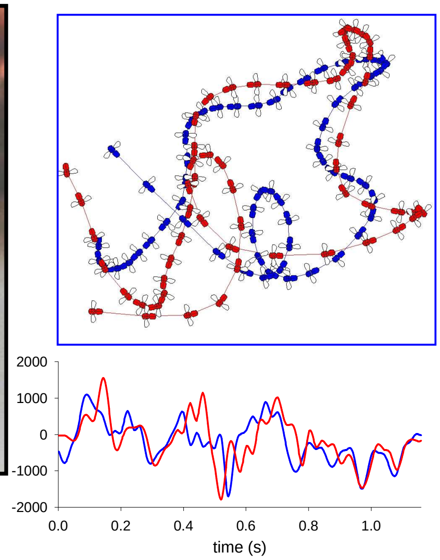


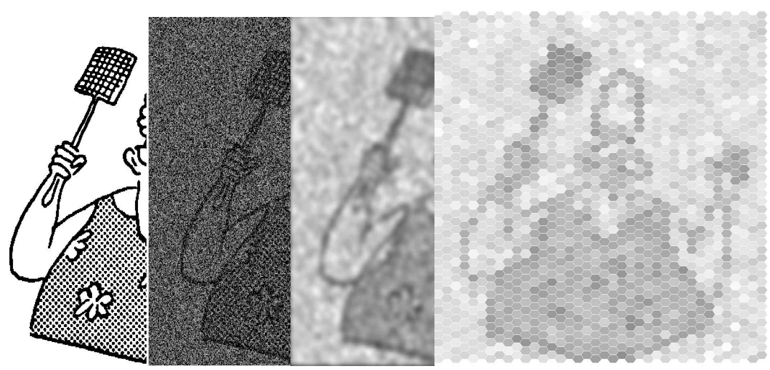

FIG. 77. DIAGRAM OF THE RETINA OF THE BEE. *I*, retina externa; *II*, retina intermediaria; *III*, retina profunda seu interna; *IV*, optic lobe; *Cor.*, corneolas; *CC*, crystalline cones; *B*, rods ending in the intermediate retina; *Cm*, neuron which receives the stimulus brought by the rods; *Tcm*, its termination in the deep retina; *Cg*, third neuron receiving the excitation, etc.

## *Blowfly,* Calliphora vicina

Land and Collett, 1974



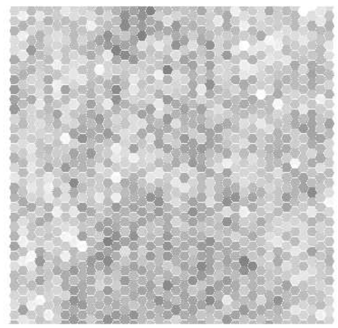

## *The rocky road to perception*



Adapted from Gary Larson

*Decision making in the ideal world…*

*and in the real world*



*From raw data to feature extraction*

Raw sensory input implicitly contains relevant features.
These are extracted by the brain through computation.

Making sense of neural signals:
- Input signals are complex, ambiguous, noisy
- Seldomly clear what feature is computed
- Input space is high-dimensional

Simplify: computation of motion in fly visual system
- Input signal and noise (photoreceptors) can be quantified
- Good guess for function in behavior: velocity estimation
- Reduced dimensionality: nearest neighbor interactions
- The problem is mathematically tractable
- Very important in the fly's life

*Computing velocity: the gradient model*

Rigid motion of contrast pattern : $C(x,t) = C\left[x - \int_0^t V(\tau)d\tau\right]$

($C$ contrast, $x$ position, $t$ time, $V$ velocity)

partial derivatives :

$$\nabla_t C(x,t) = -V(t) \cdot C',$$
$$\nabla_x C(x,t) = C'.$$

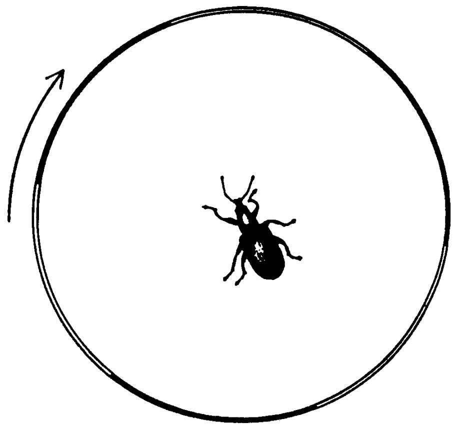
So, from the observed $C(x,t)$ we can

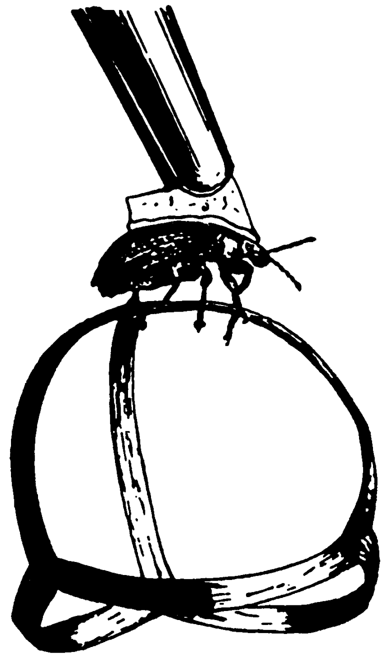
estimate velocity as follows : $V_{est}(t) = \left[-\frac{\nabla_t C(x,t)}{\nabla_x C(x,t)}\right].$

***How do animals estimate motion?***

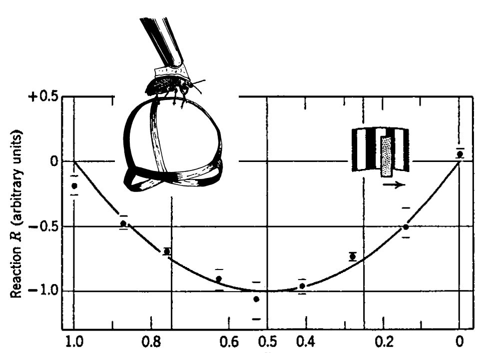
Beetles and flies

*Behavioral experiments on the Beetle* Chlorophanus, *(Reichardt, 1961)*

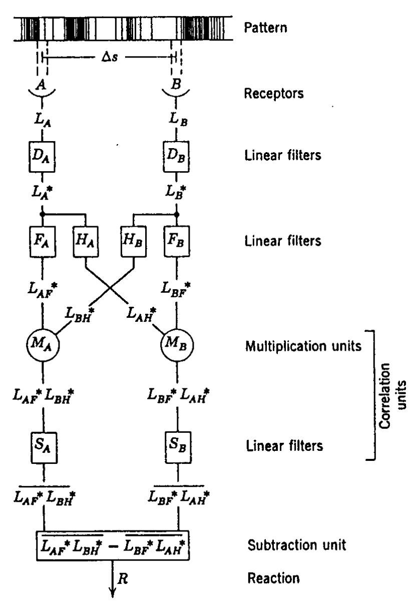




*Correlator model of motion detection (Reichardt, 1961)*

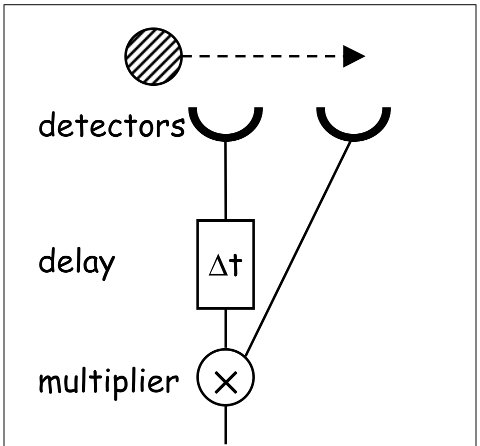



Contrast dependence of optomotor turning response.




Correlator model for the optomotor turning response.

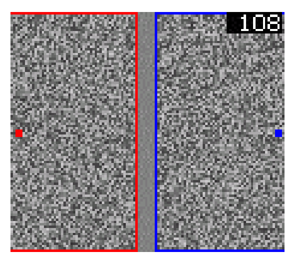
## *Simplified correlator model (Reichardt & Hassenstein, 1956)*




*Spatiotemporal correlation hallmark: response ∝ $C^2$*

*Problem: this is very different from pure velocity estimation.*
*Is this model generally valid?*
*Take a second look, in the fly visual system…*

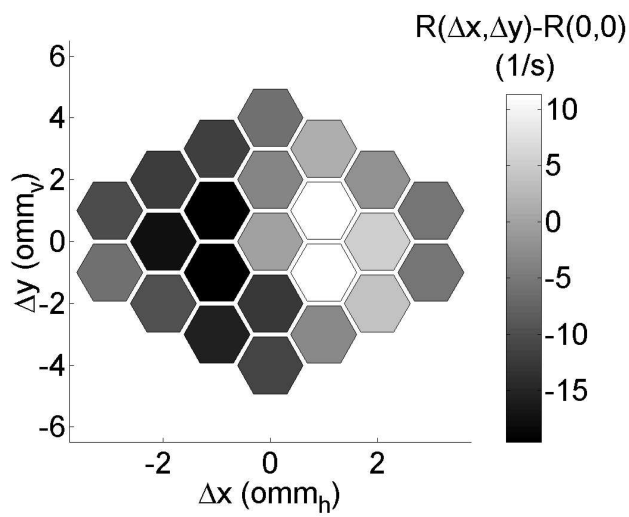
## *Wide-field motion by spatiotemporal correlation*



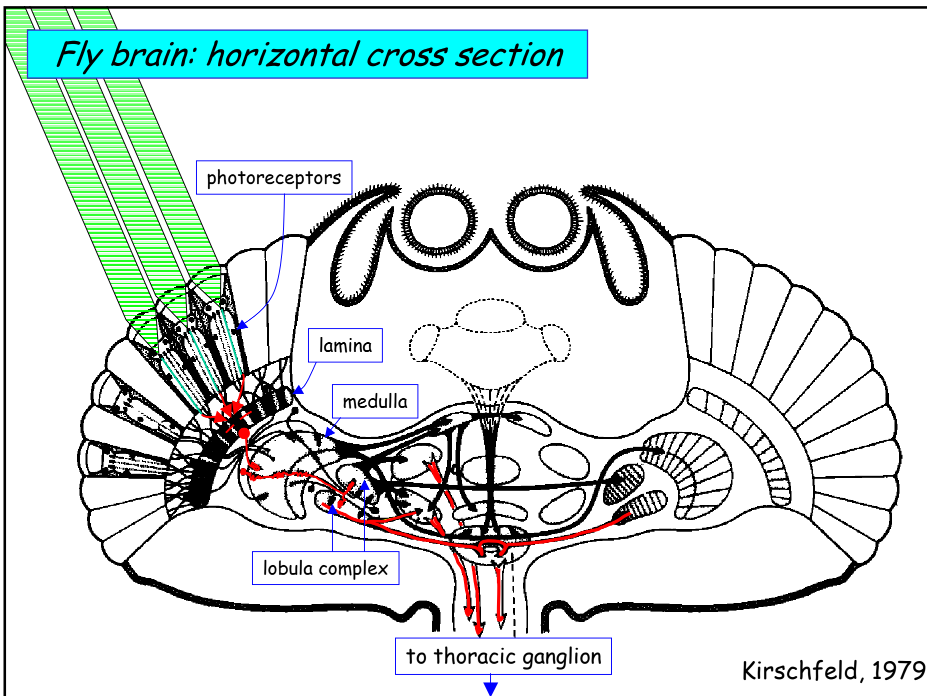

$I(x,t) = I_0(x,t) + I_0(x-\Delta x, t-\Delta t)$,
where $I_0$ has autocorrelation $\Phi_0(x,t)$:
$\Phi_0(x,t) = \delta(x)\cdot\delta(t)$.
Therefore, $I$ has autocorrelation $\Phi(x,t)$:
$\Phi(x,t) = 2\cdot\delta(x)\cdot\delta(t) + [\delta(x-\Delta x)\cdot\delta(t-\Delta t)+\delta(x+\Delta x)\cdot\delta(t+\Delta t)]$

The brain detects this spatiotemporal correlation and interprets it as wide-field motion.
⇒ ***To see motion you don't need a moving object!***

*Inputs to motion computation in the fly retina*

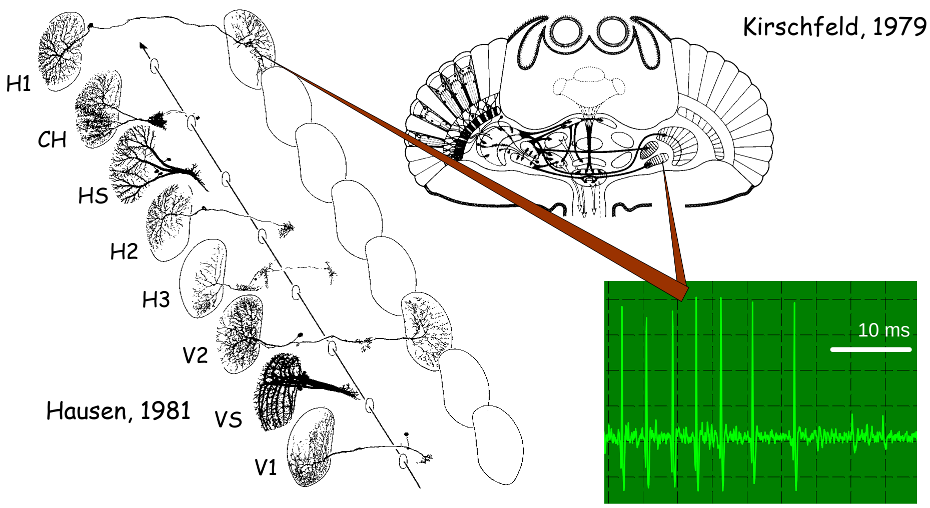



*Fly brain: horizontal cross section*

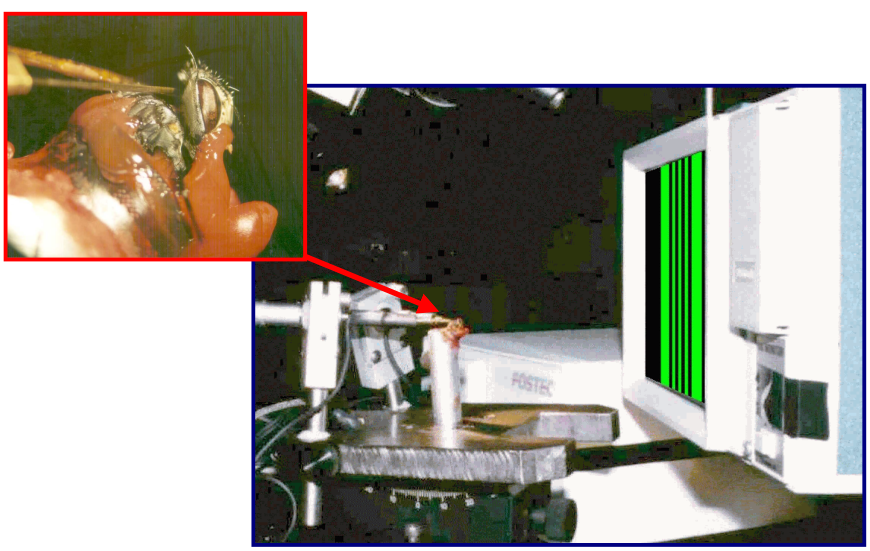


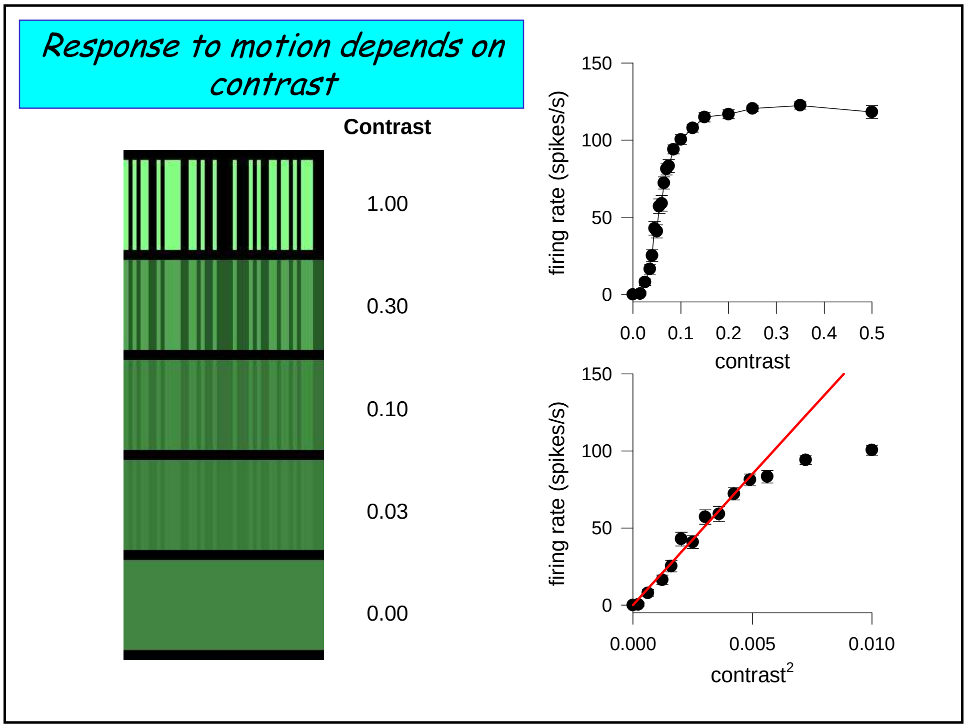

Kirschfeld, 1979

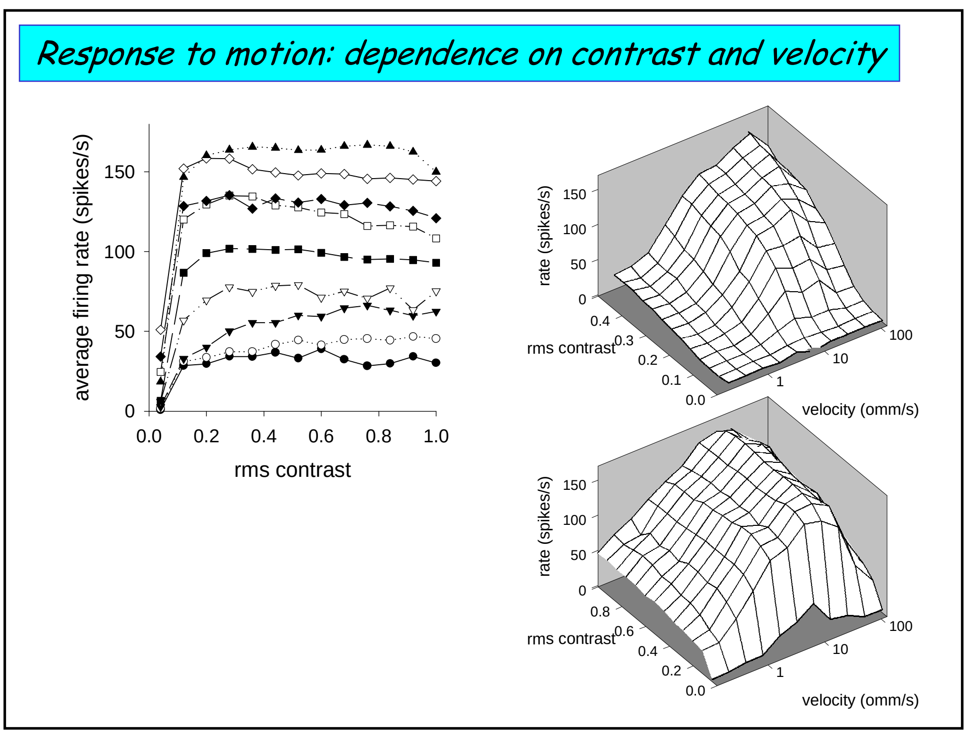
*Large-field tangential cells in the lobula plate: structure and signals*




*Typical laboratory experimental setup*




Response to motion depends on contrast
Contrast
1.00
0.30
0.10
0.03
0.00
firing rate (spikes/s)
150
100
50
0
0.0
0.1
0.2
0.3
0.4
0.5
contrast
firing rate (spikes/s)
150
100
50
0
0.000
0.005
0.010
contrast$^2$


Response to motion: dependence on contrast and velocity
average firing rate (spikes/s)
150
100
50
0
0.0
0.2
0.4
0.6
0.8
1.0
rms contrast
rate (spikes/s)
150
100
50
0
0.4
0.3
0.2
0.1
0.0
rms contrast
1
10
100
velocity (omm/s)
rate (spikes/s)
150
100
50
0
0.8
0.6
0.4
0.2
0.0
rms contrast
1
10
100
velocity (omm/s)

*What does the fly do?*

| ***Low contrast pattern:*** | ***High contrast pattern:*** |
| --- | --- |
| ***biased estimator*** | ***unbiased estimator*** |
| rate depends on velocity, and also | rate depends on velocity, but is |
| ***depends on Contrast*** | ***independent of Contrast*** |
| *computation: correlation* | *computation: gradient ratio* |
| $V_{est}(t) = F_1[C(x,t)] \times F_2[C(x,t)]$ | $V_{est}(t) = \left[-\frac{\nabla_t C(x,t)}{\nabla_x C(x,t)}\right].$ |

***Smooth transition***

***The fly computes motion, but does so in peculiar ways. Is there a "right" way? How should we even approach this question?***

Problems:

- Photon shot noise
- Diffraction and finite sampling
- Variations in illumination
- Variations in contrast
- Independently moving objects
- Components of translational motion, etc.

We'll take an experimental statistical approach…

## *The brain as a velocity estimator*

The brain needs to know the conditional probability:

$$P(feature|input)$$

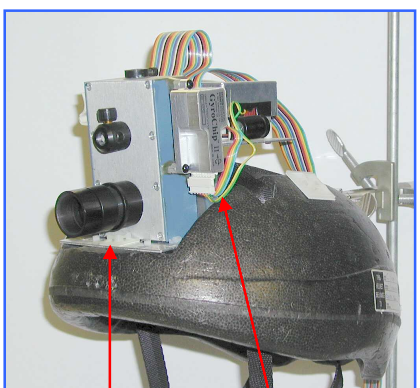
Here: $feature = V(t)$
$input = (\&_t C, \&_x C),$

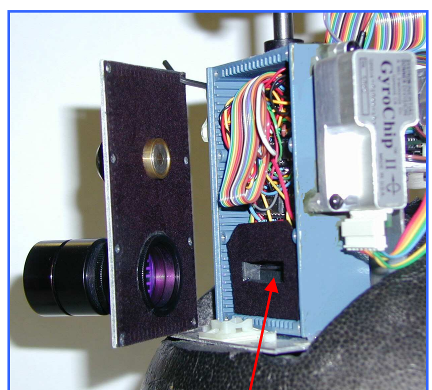
Here $\&_t C, \&_x C$ are "sufficient visual primitives"; they contain all raw data needed to compute velocity.

We need to "know" $P$:

$$measure\ \ P[V(t)\,|\,\&_t C, \&_x C]$$

## *Measure visual input and full field motion*





14-pixel line camera rotation sensor photodetector array

## *Sample joint distribution of natural velocity & contrast gradients*

Sample contrast as a function of space and time: $C(x,t)$,
and angular velocity of photodetector array: $V(t)$.

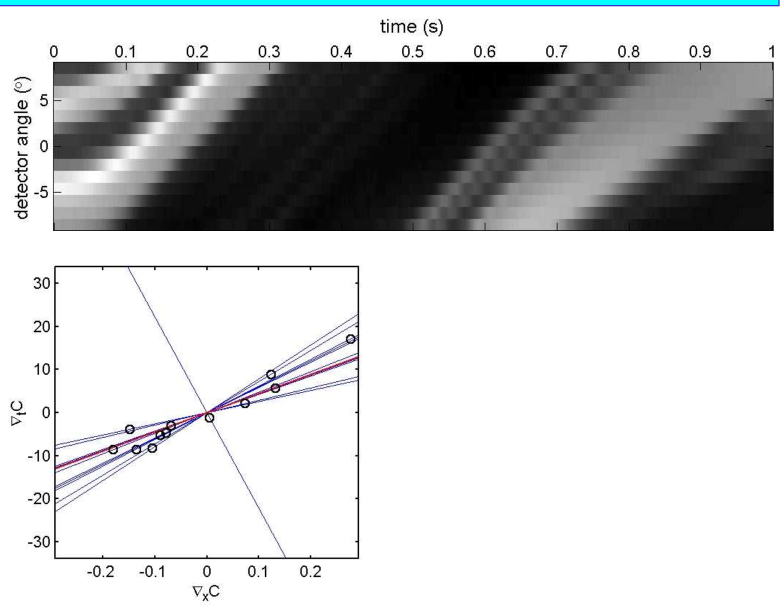
From this, get the joint distribution: $P(\nabla_t C, \nabla_x C, V)$,

and the conditional distribution: $P(V \mid \nabla_t C, \nabla_x C)$.

The "best estimate" of velocity, given the time and space gradients, is the conditional mean:

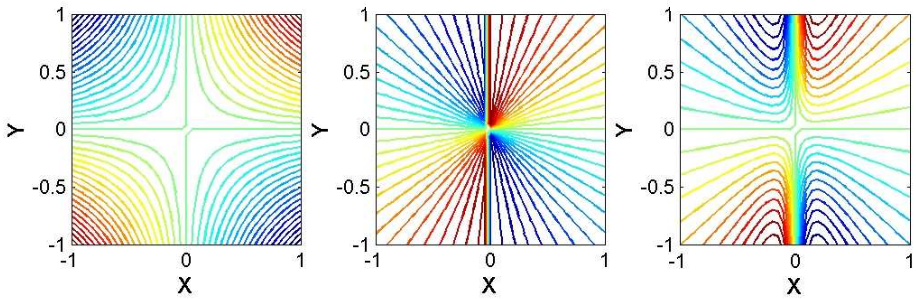
$$V_{est}(\nabla_t C, \nabla_x C) = \int P(V \mid \nabla_t C, \nabla_x C) \cdot V dV$$

## *Local velocity estimates from photodetector signals*

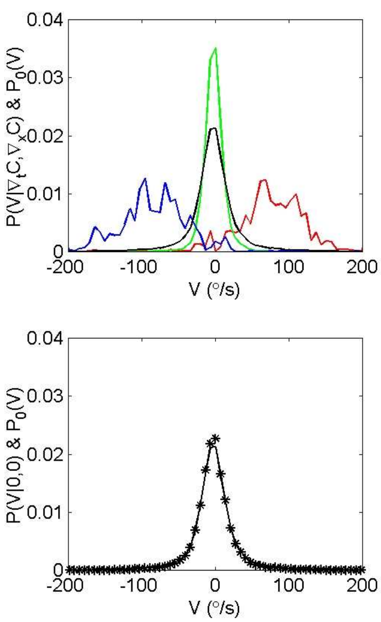


## *Simple computations represented as contours*

$$Z = X \cdot Y \qquad Z = \frac{Y}{X} \qquad Z = \frac{X \cdot Y}{1 + 10X^2}$$

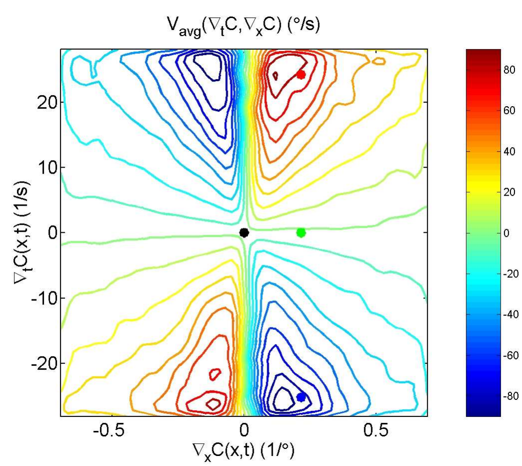



## *Conditional velocity distributions*




contour plot of:

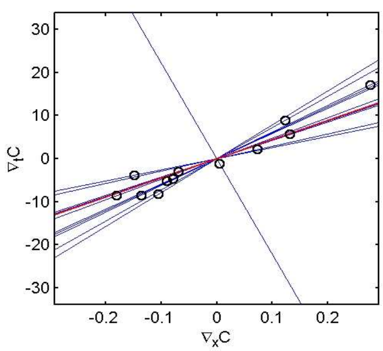
$$V_{est}(\nabla_t C, \nabla_x C) = \int P(V | \nabla_t C, \nabla_x C) \cdot V dV$$



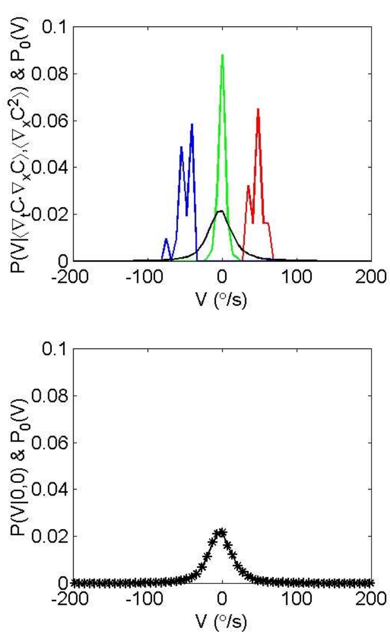
## *Wide-field estimate = slope of best fitting line*

Fit $Y = \alpha \cdot X$, based on measurements $\{X_i, Y_i\}$.

Least - squares estimate of $\alpha$ : $\alpha_{est} = \dfrac{\sum_i X_i \cdot Y_i}{\sum_i X_i^2} = \dfrac{\langle X \cdot Y \rangle}{\langle X^2 \rangle}$

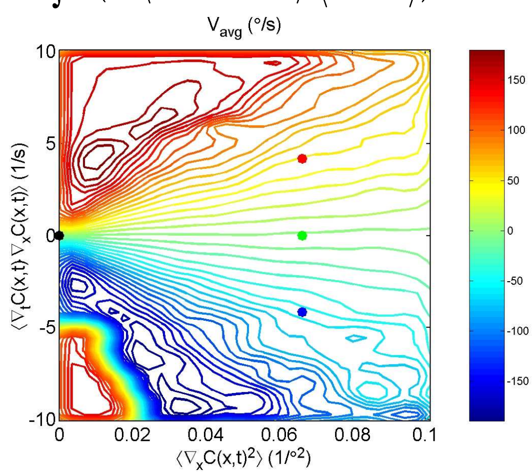



## *Conditional velocity distributions*

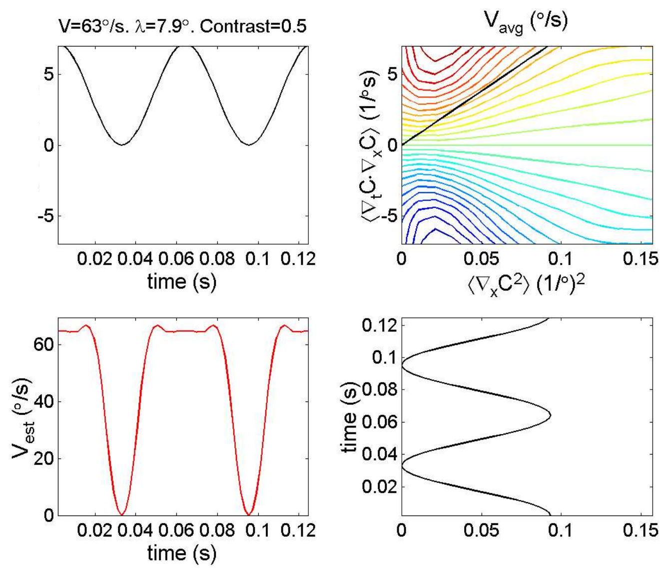



contour plot of:

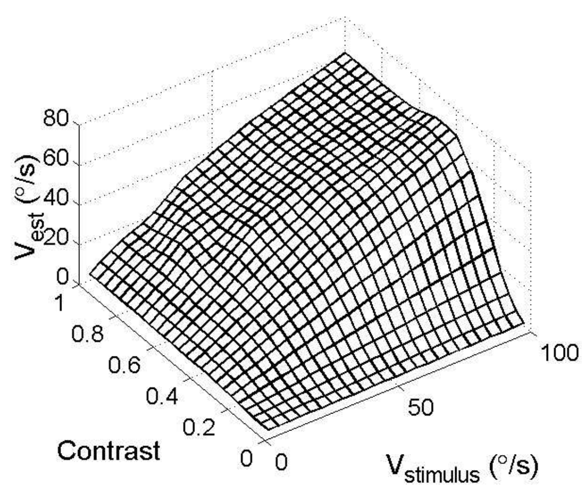
$$V_{est}\left(\langle \nabla_t C \cdot \nabla_x C \rangle, \langle \nabla_x C^2 \rangle\right) = \int P\left(V \mid \langle \nabla_t C \cdot \nabla_x C \rangle, \langle \nabla_x C^2 \rangle\right) \cdot V dV$$



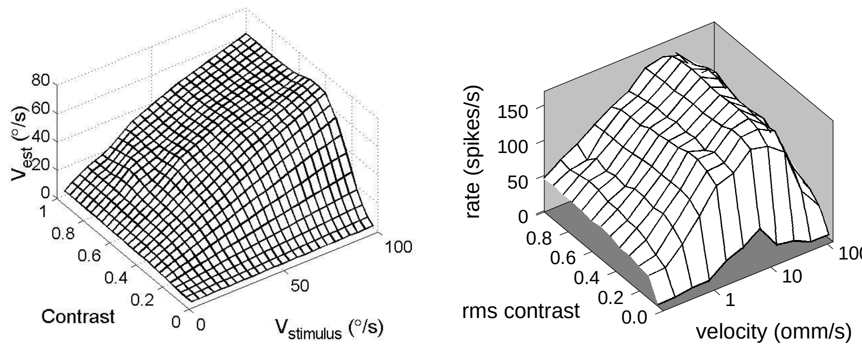
*Velocity estimated from moving sinewave pattern*



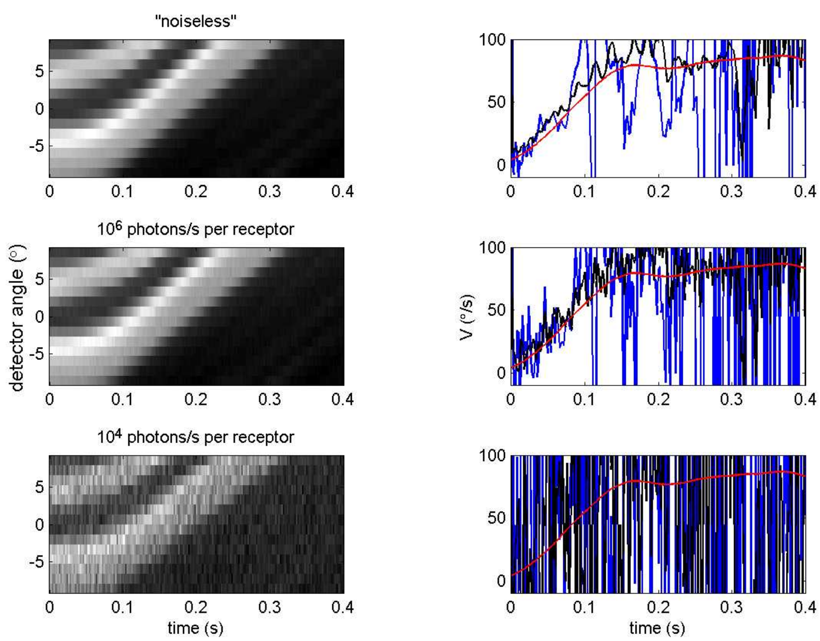

*Velocity estimated from moving sinewave pattern: the optimal estimator is biased at low contrast!*



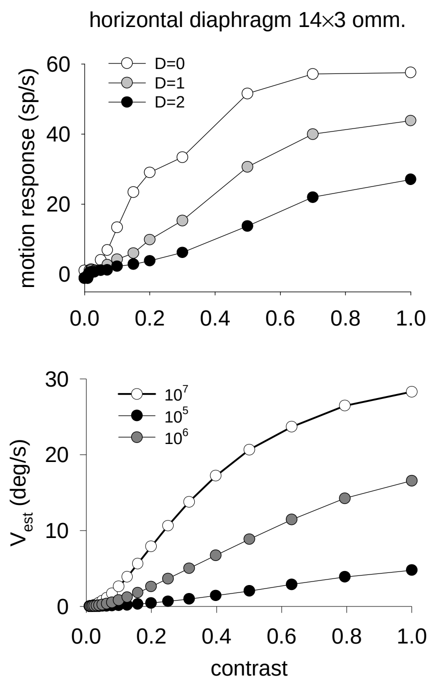
*Velocity estimated from moving sinewave pattern: comparing H1 and the optimal estimator*




*Detecting motion at different light intensities*



*Velocity estimated from moving sinewave pattern and comparison to H1's response: contrast dependence at different luminances*

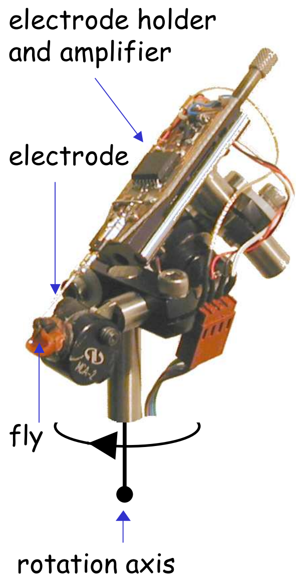



***Recapitulation***

- *Optimal velocity estimators must compute biased velocity estimates: the less reliable the input, the larger the bias. The fly has similar bias, suggesting that it approaches optimal computation.*
- *Fly and optimal estimator combine the behavior of two well-known models of motion detection.*

***But is this all relevant to a real fly?***

## *Setup for outdoor experiment*

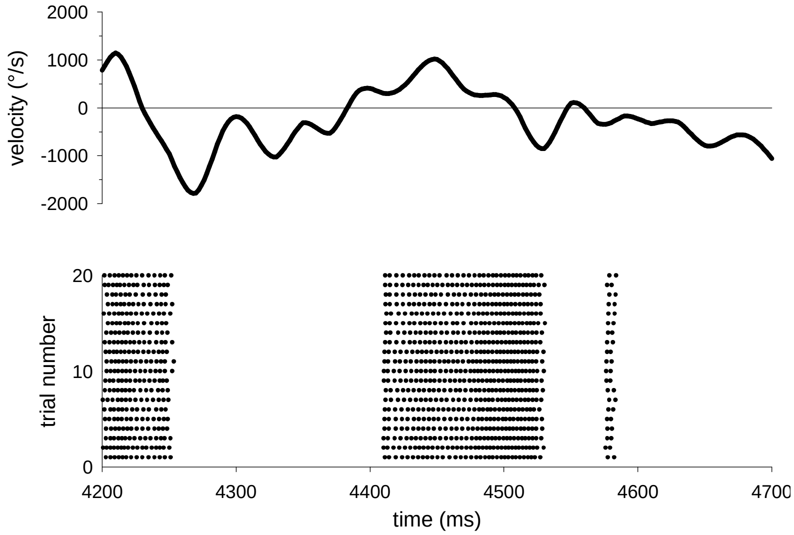



mounted on stepper motor

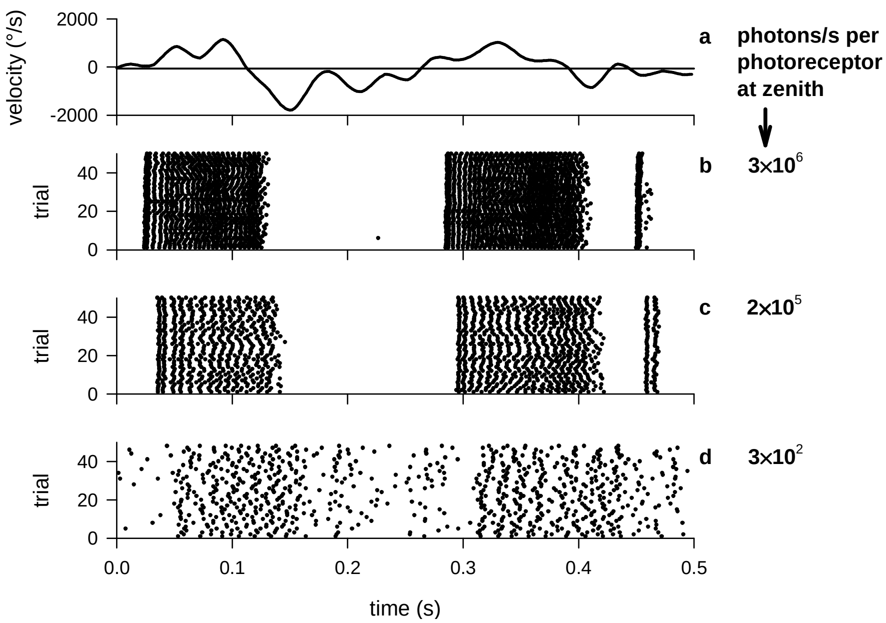
## *Visual stimulus and neural response in outdoor experiment*

180° ≅ horizontal field of view of H1

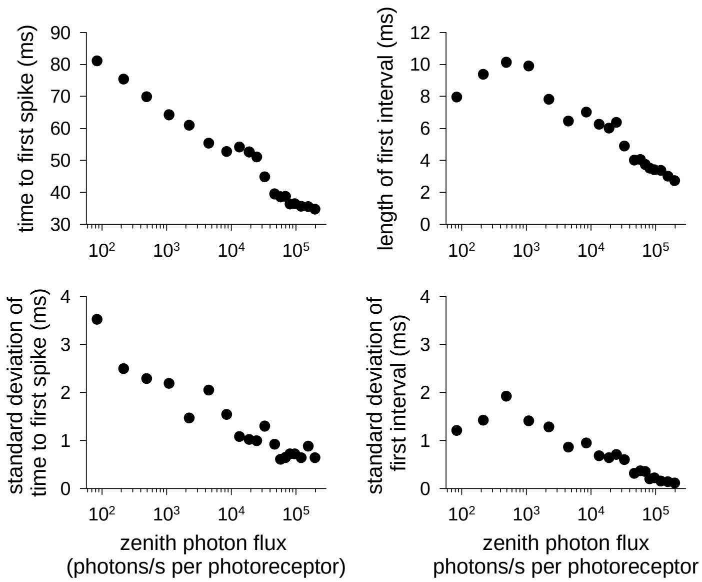
## *Spike responses to repeated motion stimulus outdoors*




## *Detecting motion when the sun goes down*



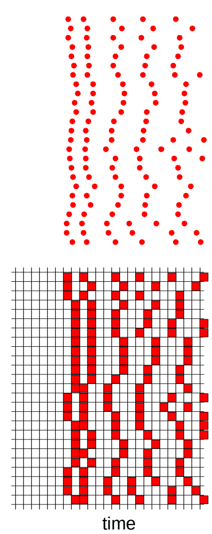
## *Spike timing precision as a function of light level*

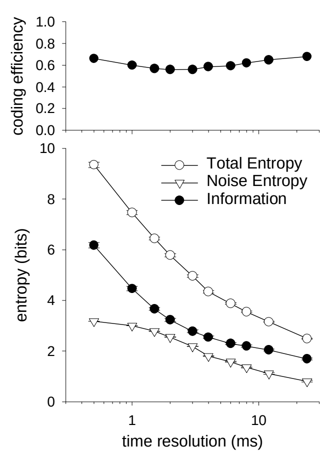



## *Time resolution and information transmission*

*25 samples of spike trains, each 24 ms long.*

*Spike trains at 1 ms resolution, forming binary words.*



## *Spike timing and information transmission*

Intuitively: information carrying capability goes up if time resolution improves. This is quantified by the total entropy:

$$S_{total} = -\sum_W P(W)\log_2[P(W)]$$

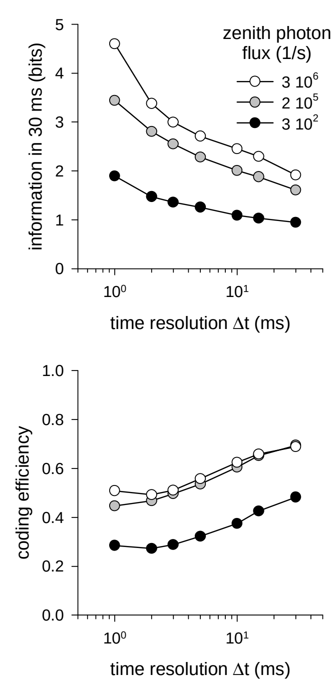
This specifies an upper bound on information transmission, which is only realized if all capacity is used to encode signals. This is not generally true; the discrepancy is measured by the noise entropy:

$$S_{noise} = \left\langle -\sum_W P(W \mid t)\log_2[P(W \mid t)] \right\rangle_t$$

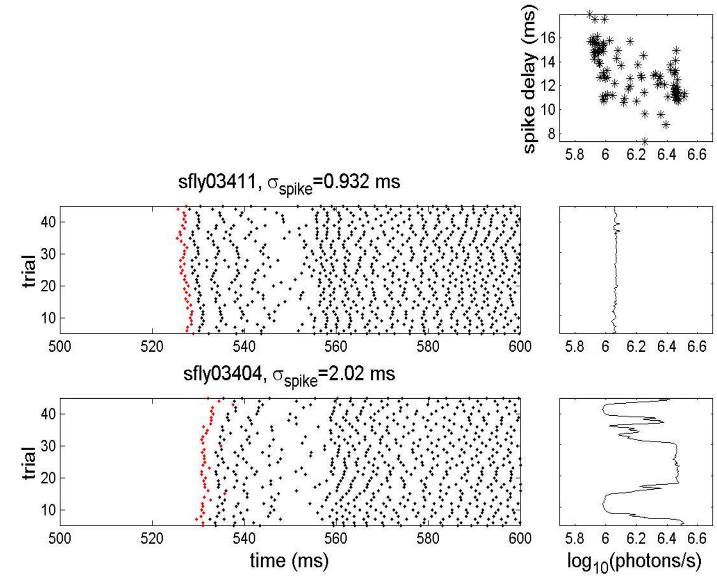
The information transmitted is the difference of these two entropies:

$$I = S_{total} - S_{noise}$$

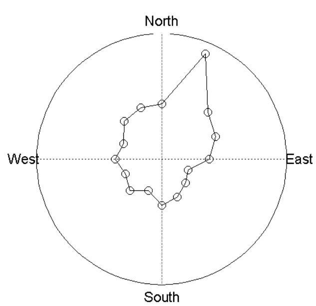
## *Information as a function of time resolution and light level*



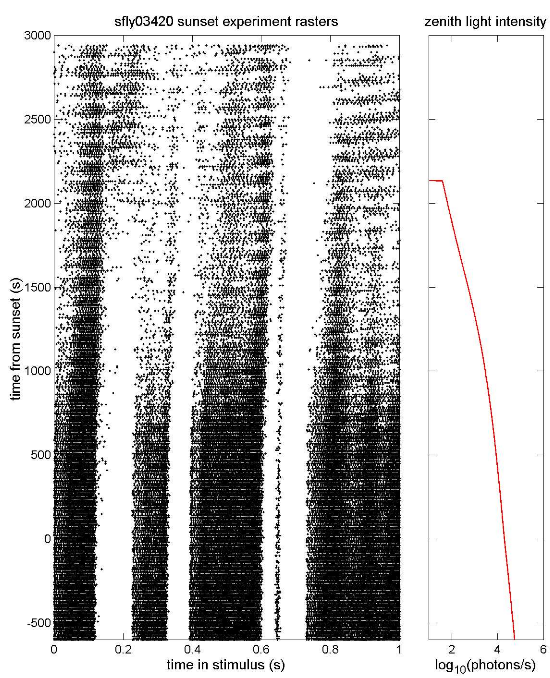
*Fluctuations in mean light level produce variations in spike timing*




*At lower input SNR, details matter more*




Light intensity as a function of azimuth angle



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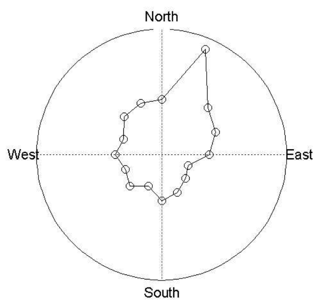
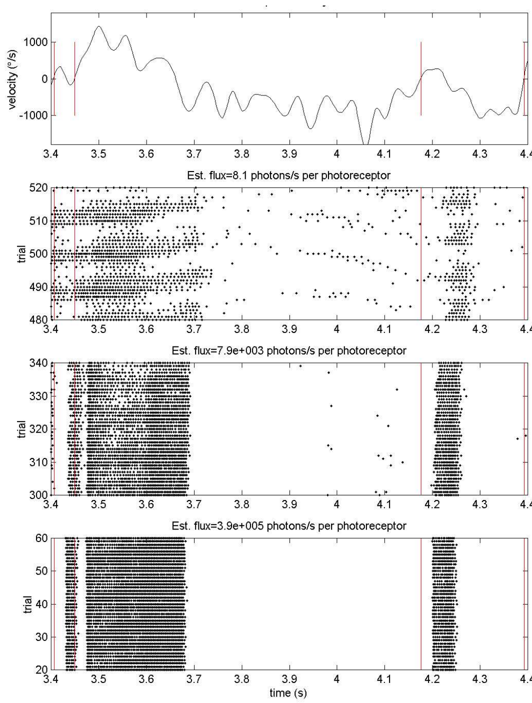



Light intensity as a function of azimuth angle



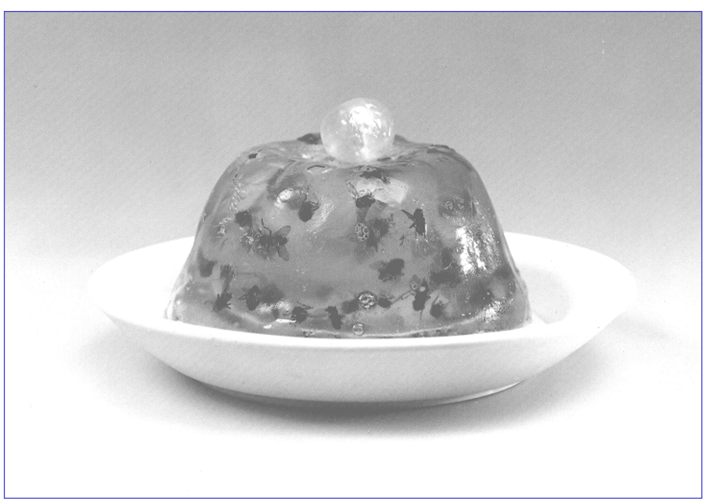

## *Recapitulation*

- *Optimal velocity estimators must compute biased velocity estimates: The less reliable the input, the larger the bias. The fly has similar bias, suggesting that it approaches optimal computation.*
- *Fly and optimal estimator combine the behavior of two well-known models of motion detection.*
- *In natural conditions, precision is limited by external noise. It makes sense to build computational strategies that take input reliability into account.*

*Some things to do…*

- Study dynamics of motion estimation and coding
- Two-dimensional optical input, 3 axes of rotation
- Move fly along 3-D trajectories

*Have a good lunch …*



Weidema