Neural Computation on Natural Signals: Lessons from the Fly Visual System

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

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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)
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**Blowfly, Calliphora vicina**

![Blowfly Image]

Land and Collett, 1974

**The rocky road to perception**

![Image of Perception]

Adapted from Gary Larson

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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

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**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:

\[ V_{est}(t) = \left[ -\frac{\nabla_x C(x, t)}{\nabla_x C(x, t)} \right]. \]

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**How do animals estimate motion?**

Beetles and flies

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

Correlator model of motion detection (Reichardt, 1961)

Contrast dependence of optomotor turning response.

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

![Diagram of a correlator model](image)

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

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**Wide-field motion by spatiotemporal correlation**

\[
I(x,t) = I_0(x,t) + I_0(x+\psi x, t-\psi t),
\]

where \( I_0 \) has autocorrelation \( \chi_0(x,t) \):

\[
\chi_0(x,t) = \Omega(x) \Omega(t).
\]

Therefore, \( I \) has autocorrelation \( \chi(x,t) \):

\[
\chi(x,t) = 2 \cdot \Omega(x) \Omega(t) + [\Omega(x-\psi x) \Omega(t-\psi t) + \Omega(x+\psi x) \Omega(t+\psi t)]
\]

The brain detects this spatiotemporal correlation and interprets it as wide-field motion.

**To see motion you don’t need a moving object!**
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Inputs to motion computation in the fly retina

Fly brain: horizontal cross section

Kirschfeld, 1979

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

Kirschfeld, 1979

Typical laboratory experimental setup

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Response to motion depends on contrast

Response to motion: dependence on contrast and velocity

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**What does the fly do?**

<table>
<thead>
<tr>
<th>Low contrast pattern: biased estimator</th>
<th>High contrast pattern: unbiased estimator</th>
</tr>
</thead>
<tbody>
<tr>
<td>rate depends on velocity, and also depends on Contrast</td>
<td>rate depends on velocity, but is independent of Contrast</td>
</tr>
</tbody>
</table>

**Smooth transition**

**computation:** correlation

\[ V_{est}(t) = f_1[C(x,t)] \times f_2[C(x,t)] \]

**computation:** gradient ratio

\[ V_{est}(t) = \left[ \frac{\nabla_x C(x,t)}{\nabla_x C(x,t)} \right] \]

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**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...**

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The brain as a velocity estimator

The brain needs to know the conditional probability:

\[ P(\text{feature} | \text{input}) \]

Here:

- \text{feature} = V(t)
- \text{input} = (\&_x \text{C}, \&_x \text{C}).

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

We need to "know" \( P \):

\[ \text{measure } P[V(t) | \&_x \text{C}, \&_x \text{C}] \]

Measure visual input and full field motion

14-pixel line camera  rotation sensor  photodetector array

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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: \( P(\nabla,C,\nabla_x C,V) \), and the conditional distribution: \( P(V | \nabla,C,\nabla_x C) \).

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

\[
V_{\text{est}}(\nabla,C,\nabla_x C) = \int P(V | \nabla,C,\nabla_x C) \cdot V \, dV
\]

Local velocity estimates from photodetector signals

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Simple computations represented as contours

\[ Z = X \cdot Y \]
\[ Z = \frac{Y}{X} \]
\[ Z = \frac{X \cdot Y}{1 + 10X^2} \]

Conditional velocity distributions

contour plot of:

\[ V_{\text{est}}(\nabla C, \nabla_x C) = \int \rho(V | \nabla C, \nabla_x C) \cdot V \, dV \]

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Wide-field estimate = slope of best fitting line

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

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

Conditional velocity distributions

Contour plot of:

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

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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

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Velocity estimated from moving sinewave pattern and comparison to HI’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?
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**Setup for outdoor experiment**

- electrode holder and amplifier
- electrode
- fly
- rotation axis
- mounted on stepper motor

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

180° ≅ horizontal field of view of H1

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*Spike responses to repeated motion stimulus outdoors*

![Graph showing velocity over time for repeated motion stimulus]

*Detecting motion when the sun goes down*

![Graph showing velocity over time for detecting motion during sunset]

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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.

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**Spike timing and information transmission**

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

\[ S_{\text{total}} = -\sum_{W} P(W) \log_2[P(W)] \]

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:

\[ S_{\text{noise}} = \left\langle -\sum_{W} P(W|t) \log_2[P(W|t)] \right\rangle_t \]

The information transmitted is the difference of these two entropies:

\[ I = S_{\text{total}} - S_{\text{noise}} \]

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

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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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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.
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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 ...

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