Adaptation, Detection and Prediction in Retinal Circuits

Stephen A. Baccus
Stanford University School of Medicine, Department of Neurobiology
Understanding the brain

Function

Computation

Theory

Mechanism

Intensity

Pixel 1

Intensity

Pixel 2

0

100

200

0

200
What does the retina do?

Visual stimuli → Retina → Higher brain

Compress, Filter, Adapt

Detect, discriminate, predict, act

Visual stimuli → Retina → Higher brain

Detect, discriminate

Visual stimuli → Retina → Higher brain

Detect, Predict

Visual stimuli → Retina → Higher brain
What’s in the retina?

Photoreceptors
Intensity, wavelength, adapt

Horizontal cells
Spatial filtering, RF surround

Bipolar cells
On and Off, Different dynamics, ~ 12 types

Amacrine cells
Diverse and inhibitory, ~ 30 types, some linear, most nonlinear
most have unknown function

Ganglion cells
~20 types, responses vary in polarity, dynamics, nonlinearity,
adaptation, preferred features

IPL
~10 ‘layers’, different signals, many neurons in single layers

Mosaics
Cells of a given type tile the retina

Masland (2001)
What’s in the retina?

- Diversity of interneurons
- Synchrony
- Layered organization
- Different temporal channels
- Recurrent ‘excitation’ (disinhibition)

Masland (2001)
What’s in the retina? What limits the retina?

- Diversity of interneurons
- Synchrony
- Layered organization
- Different temporal channels
- Recurrent ‘excitation’ (disinhibition)

- Efficient use of wiring
- Noise
- Limited dynamic range

Masland (2001)

Photoreceptors
Horizontal cells
Bipolar cells
Amacrine cells
Inner plexiform layer
Ganglion cells
What does the retina do?

Adaptation

Luminance
  Barlow et al., (1957)

Contrast
  Shapley & Victor (1978)

Patterns
  Hosoya et al., (2005)
### Functional importance of adaptation

- **Input (Light intensity)**
- **Output**
- **Probability**

<table>
<thead>
<tr>
<th>Intensity</th>
<th>Time</th>
<th>Probability</th>
<th>Input (Light intensity)</th>
<th>Output</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Blakemore & Campbell, 1969**

**Shapley & Victor, 1979**

**Smirnakis et al., 1997**

- **Luminance adaptation**
- **Contrast adaptation**
Efficient use of dynamic range – under specific conditions

Additive noise

Tradeoff of information and energy efficiency

Energy efficiency

Maximization of information

Intensity

Output

Laughlin, 1981

Rate (Hz)

Berry & Meister, 1997

3 mV

1 s

0 200ms

100

0
Given a rate constraint, the retina maximizes information.

Poisson noise & rate constraint

Pitkow & Meister, 2012
Common properties of contrast adaptation

<table>
<thead>
<tr>
<th>Kinetics</th>
<th>Avian auditory forebrain</th>
<th>Vertebrate retina</th>
<th>Fly motion sensitive neuron H1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delay</td>
<td>Change quickly</td>
<td>Changes quickly</td>
<td></td>
</tr>
<tr>
<td>Gain</td>
<td></td>
<td></td>
<td>Changes slowly</td>
</tr>
</tbody>
</table>

Nagel & Doupe, 2006
Fairhall et al., 2001
Theory of maximizing information in a noisy neural system

Natural visual scenes are dominated by low spatial and temporal frequencies

The retina adapts in multiple ways

- Through evolution, luminance, contrast (also patterns)
- Increases information about the scene
- Scene statistics are important
- Energy usage also appears important
- In some cases optimal models predict retinal properties
Correlation structures vary during natural vision

Spatial Frequency  Orientation  Motion
Generalized Predictive Adaptation

Spatial frequency  Spatial correlations  Temporal correlations  Spatio-temporal correlations

Normalized sensitivity to novel stimulus: $S_B(B) / S_B(A)$ vs $S_B(B) / S_B(A)$

Normalized sensitivity to adapting stimulus: $S_B(B) / S_B(A)$ vs $S_B(B) / S_B(A)$

Hosoya et al., 2005
Properties of feature detection

- Selectivity
- Invariance
Models of selectivity and invariance in primary visual cortex

Hubel & Wiesel, 1963

Rust et al., 2005
What’s moving: the eye or the object?

The Real World + Fixational Eye - movements = Retinal Image

Eye motion

Object motion

0.5 degree
What’s moving: the eye or the object?

The Real World + Fixational Eye - movements = Retinal Image

Ganglion cell receptive field

Rabbit fixational eye movements

Random walk

Ölveczky, Baccus & Meister (2003)

0.5 s

50 µm

800 µm

Object

Background
Object motion sensitive ganglion cells

Differential motion (Object + Eye)

Global motion (Eye Only)

Rabbit “ON Brisk Transient”

Salamander “Fast OFF”
Properties of the Object Motion Sensitive (OMS) Circuit

Global motion

Image

Time

Selective for differential motion

Differential motion

Object

Background

Invariant to the spatial pattern
Simplified model of the OMS circuit

Victor, 1987
Simplified model of the OMS circuit

Victor, 1987
Improved model of the OMS excitatory input

Stimulus $s(x,y,t)$

Bipolar cell

spatio-temporal receptive field

Center

Surround

Time

$\mathcal{F}(x,y,t) = \int_0^T \int \int s(x,y,\tau) F(x,y,t-\tau) \, dx \, dy \, d\tau$

Bipolar cell response

Bipolar to ganglion cell rectifier

OMS ganglion cell

Data

Model

Polyaxonal amacrine cells have a small receptive field (input) and a large projective field (output).
Object motion sensitive circuit and model
Object motion sensitive circuit and model
Apparent motion percept reflecting eye movements

Stimulate center with horizontal eye movements, surround with vertical eye movements
Object motion sensitive circuit and model

Invariance
Arises through summation.
Rectification preserves sensitivity.

Selectivity
Arises by temporal comparison of sparse excitation and inhibition.
Sparseness arises due to a high threshold.
Invariance is an essential component of selectivity.
Basic signal detection

\[ P(v, n) \]

\[ P(v, s) = P(v, n) + P(v, s) \]

\[ P(v) = P(v, n) + P(v, s) \]

Bayes’ rule

\[ P(s \mid v) = \frac{P(v, s)}{P(v)} \]

Kording & Wolpert, 2006
Stocker & Simoncelli, 2007
Beck ... Pouget, 2008
Stimulus representing camouflaged object
Sensitization predicts the location of an object

The retina exhibits several predictive phenomena
Sensitization
Motion Anticipation
Periodic stimuli
Deep Learning to Understand the Retina

McIntosh, L., Maheswaranathan, N., Nayebi, A., Ganguli, S., Baccus, S.A.
Performance of Convolutional Neural Network models

Retinal reliability
Comparing internal structure of CNNs and retina
Figure 4

0.4 - 0.4 Correlation

Amacrine cells
Bipolar cells
Horizontal cells

1st layer subunits
2nd layer subunits
3rd layer subunits

Data CNN

Time (s)
RF width (microns)
300
0

Model
Data

B

1st Layer
2nd Layer

Correlation

Subunits

C

Bipolar cells
Amacrine cells

LN CNN
LN CNN
Rapid dynamics of context-dependent feature encoding
Polarity Reversal

t = 40.14 s  t = 41.14 s  t = 42.27 s

Omitted Stimulus Response

Rate (Hz)

S&m

Stim
WN
NS

Rate (Hz)

Time (ms)

Motion Anticipation

Model population response

Normalized Rate

Position (µm)

Motion Reversal

CNN model

Schwartz et al. (2007)

Rate (Hz)

Time from Reversal (s)
Deep learning models of the retina are much more accurate than previous models.

They match the internal structure of the retina.

These models generalize to unseen stimuli.

They provide a rich framework for generating new hypotheses about retinal computation.
Research Associate
Michael Menz

Postdoctoral Fellows
Pablo Jadzinsky
Juyoung Kim

Graduate Students
David Kastner
Yusuf Ozuysal
Bongsoo Suh
Ben Naecker
Niru Maheswaranathan
Lane McIntosh

Surya Ganguli