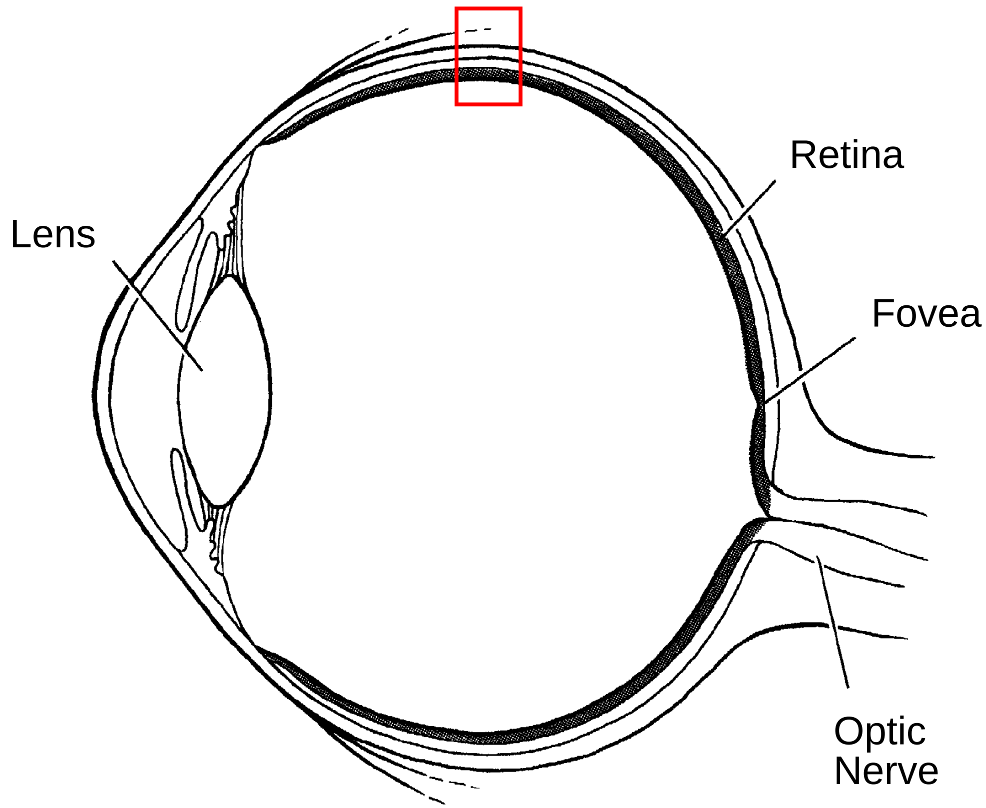
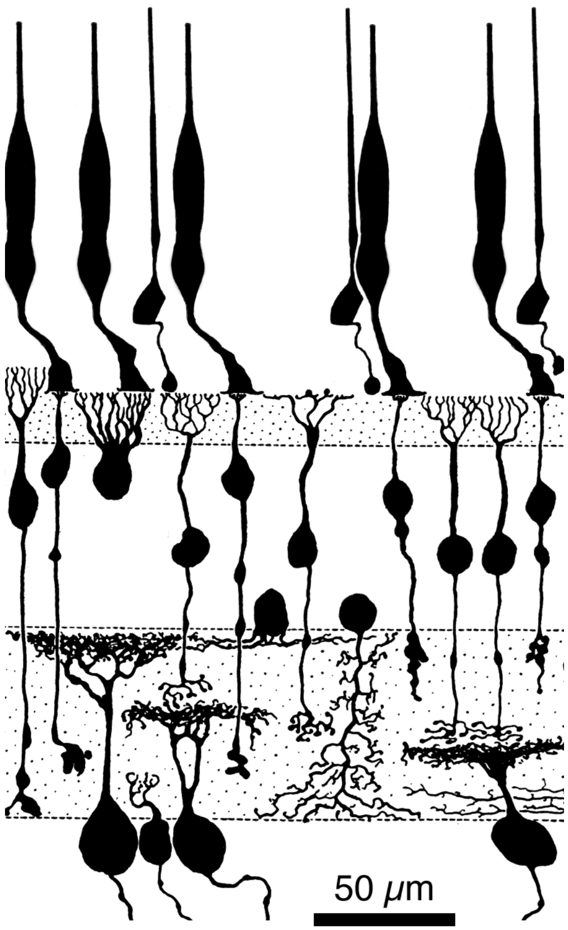
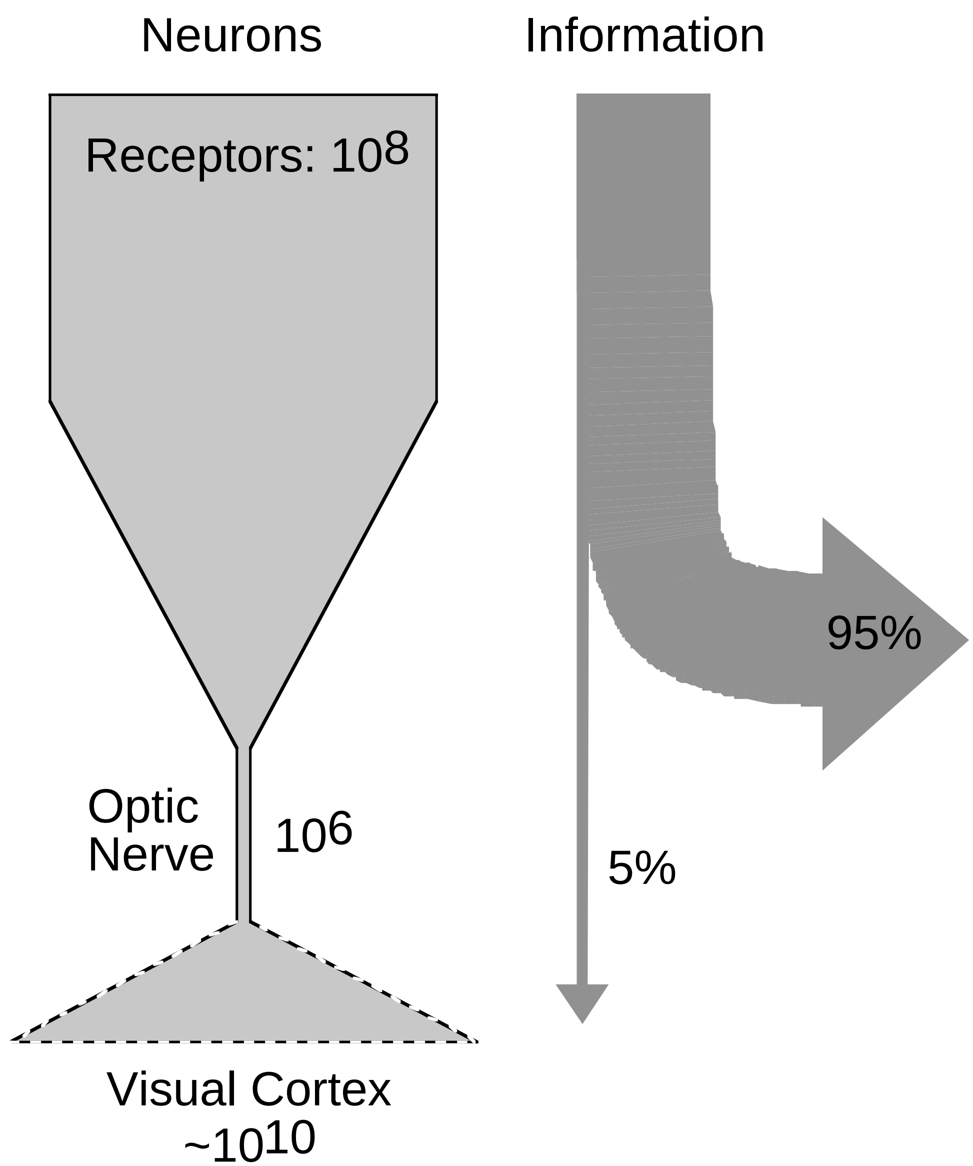
Adaptation in the Neural Code of the Retina



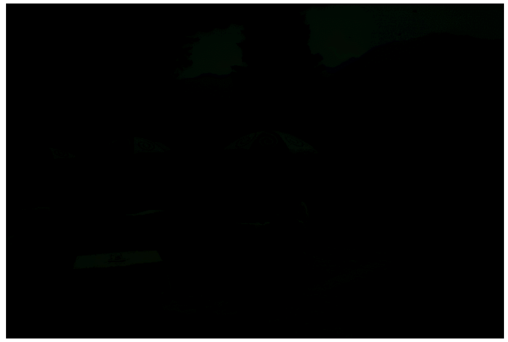
Optic Nerve Bottleneck

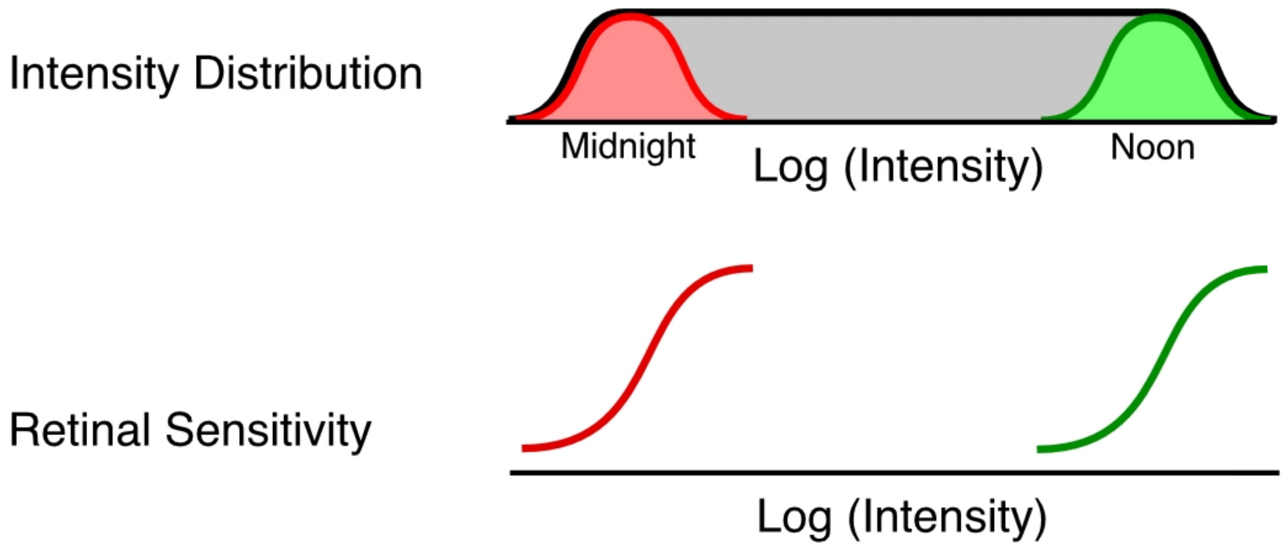


After Polyak 1941



Mean Intensity Varies a Lot, But Slowly

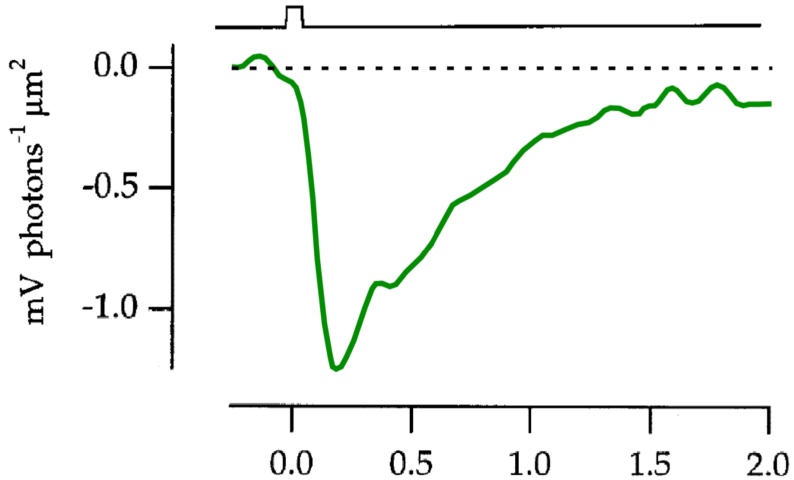




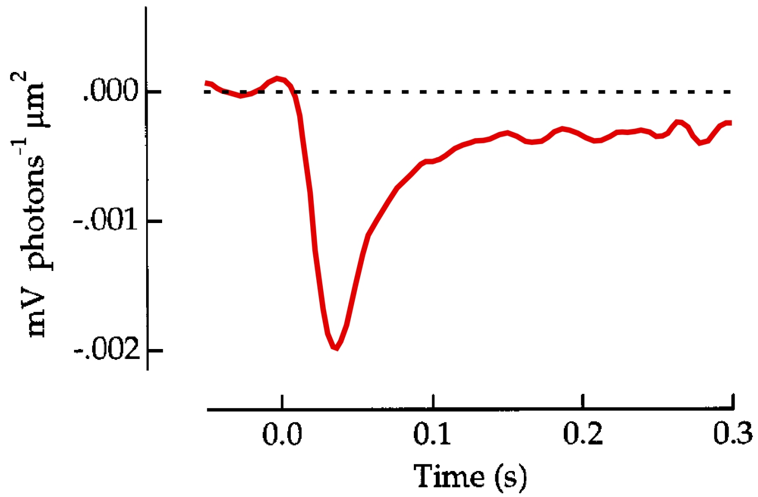
Light Adaptation: Evolutionary

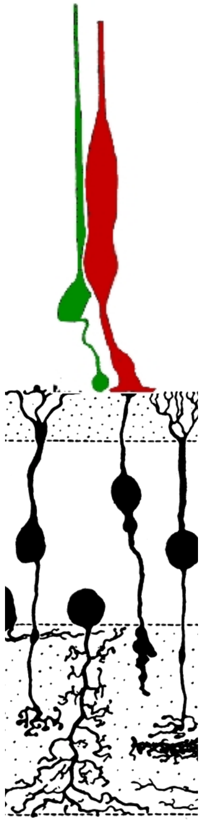
Rods and cones have 1000x different sensitivity to light

Rod



Cone





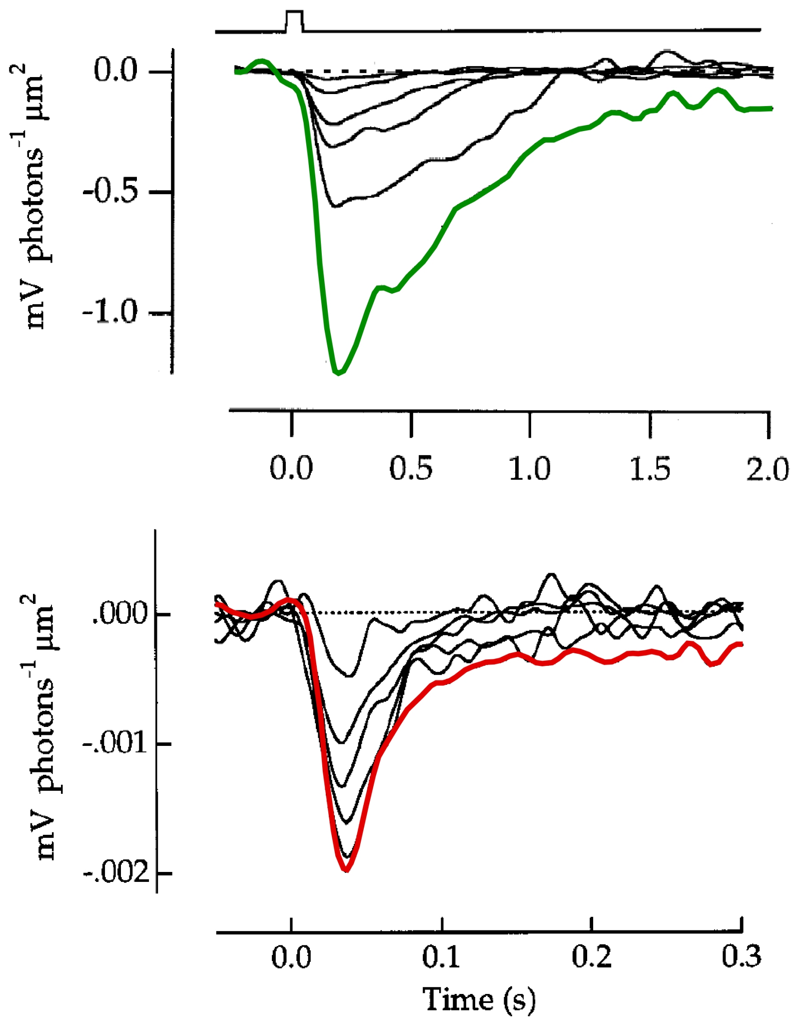
Schneeweis & Schnapf 1999, 2000

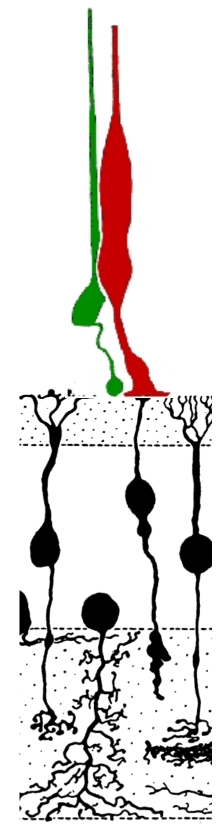
Light Adaptation: Dynamic

Sensitivity decreases with increasing background light

Rod

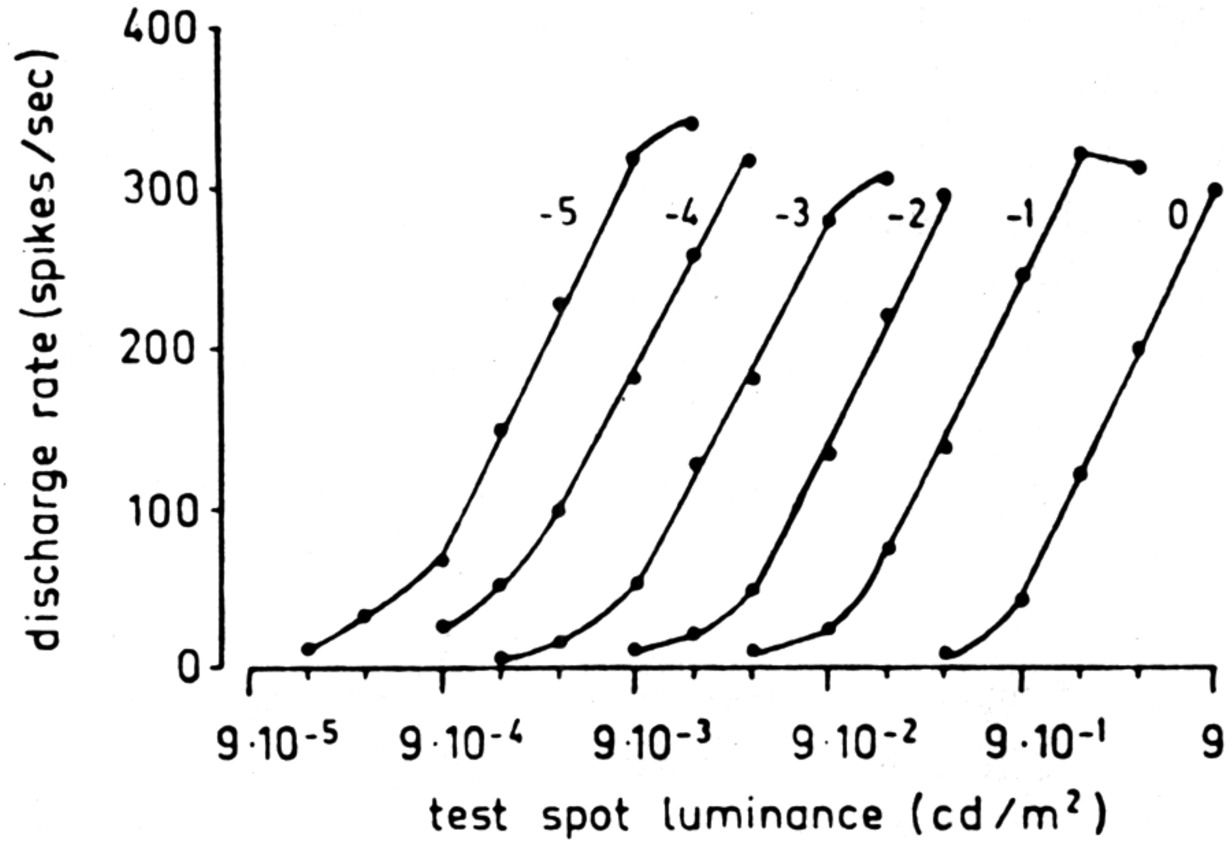
Cone





Schneeweis & Schnapf 1999, 2000

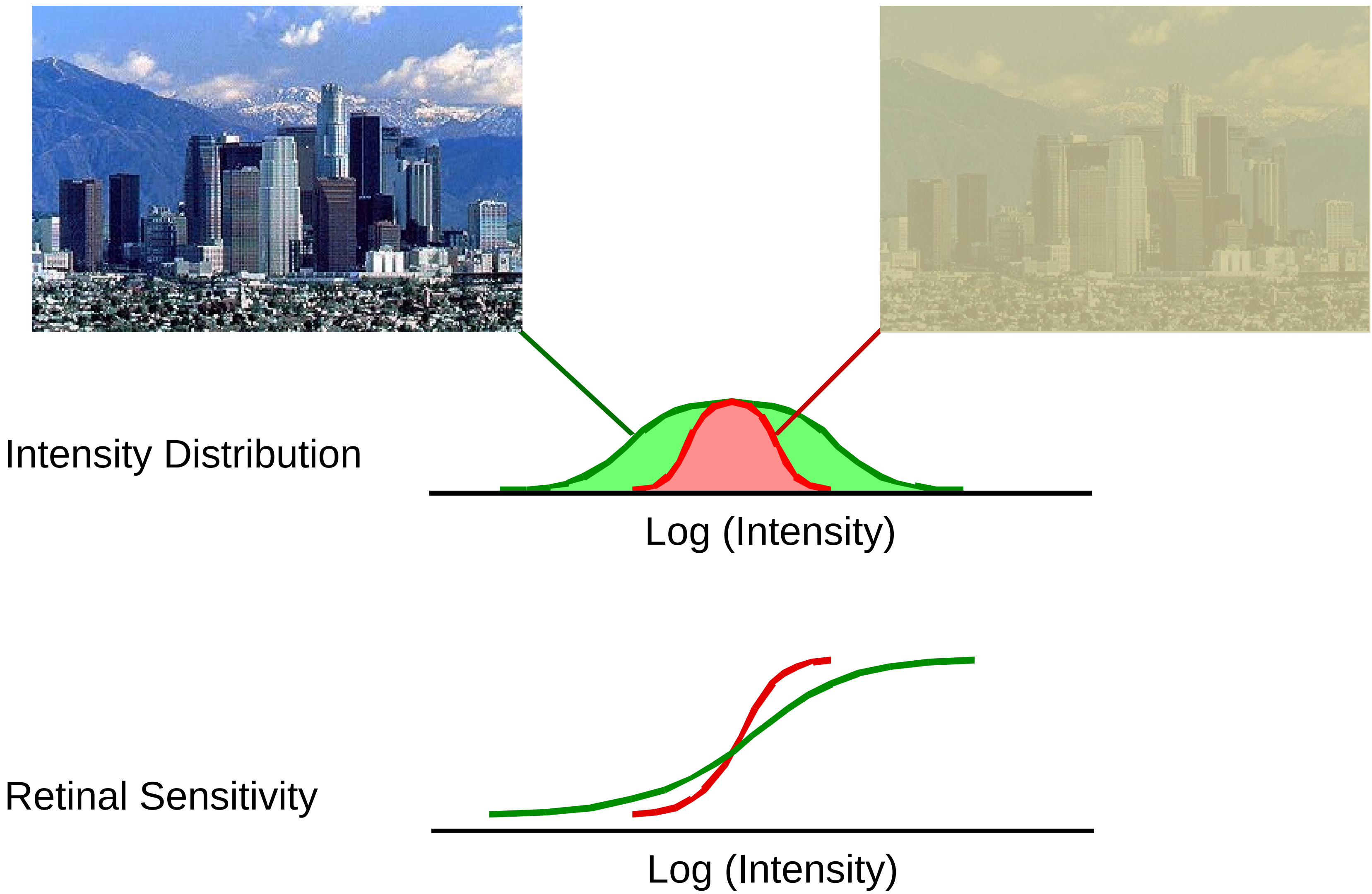
Ganglion Cells Report Intensity Ratios



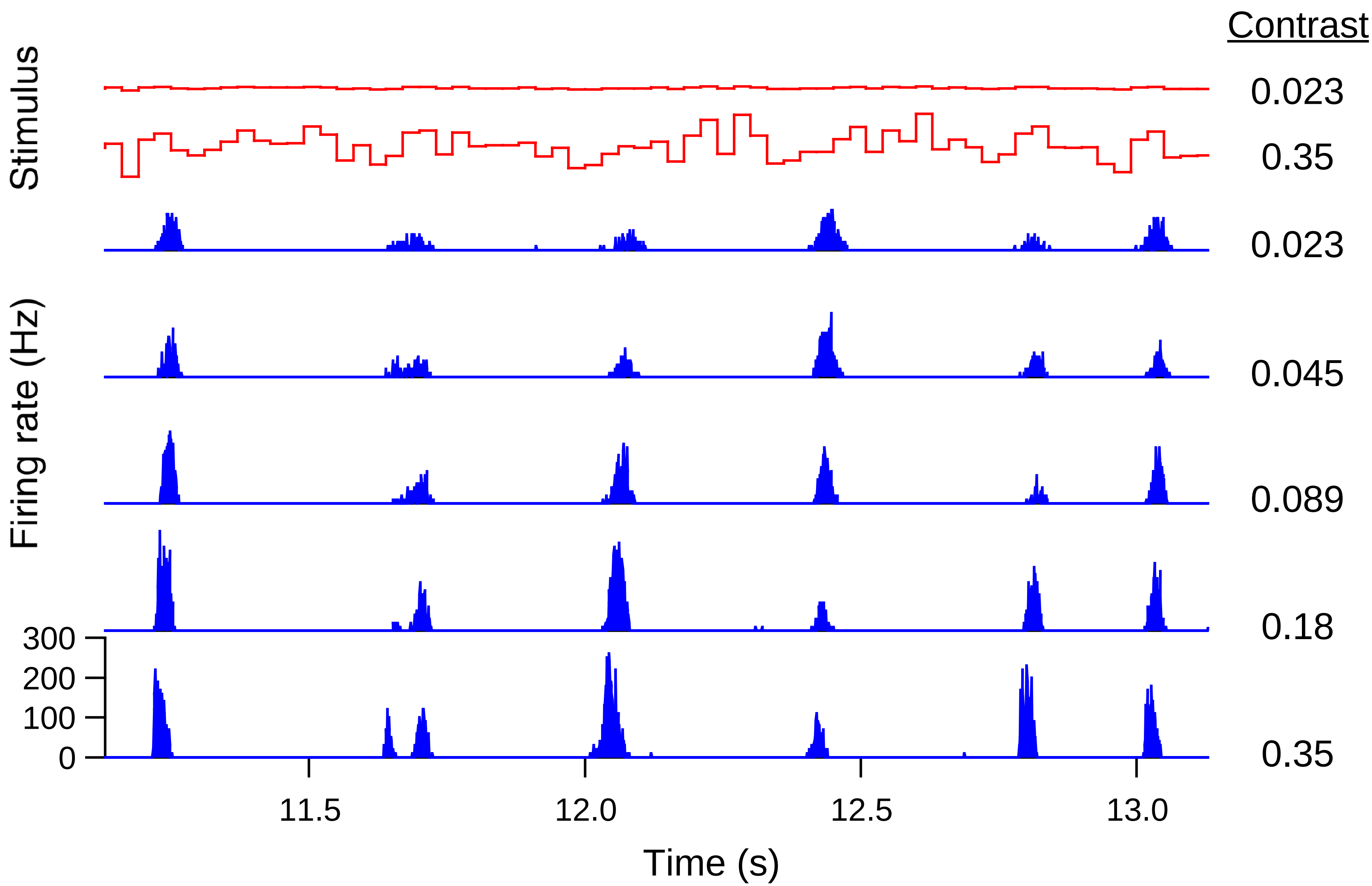
Response vs intensity for cat retinal ganglion cells adapted to increasing backgrounds.

Sakmann & Creutzfeld 1969

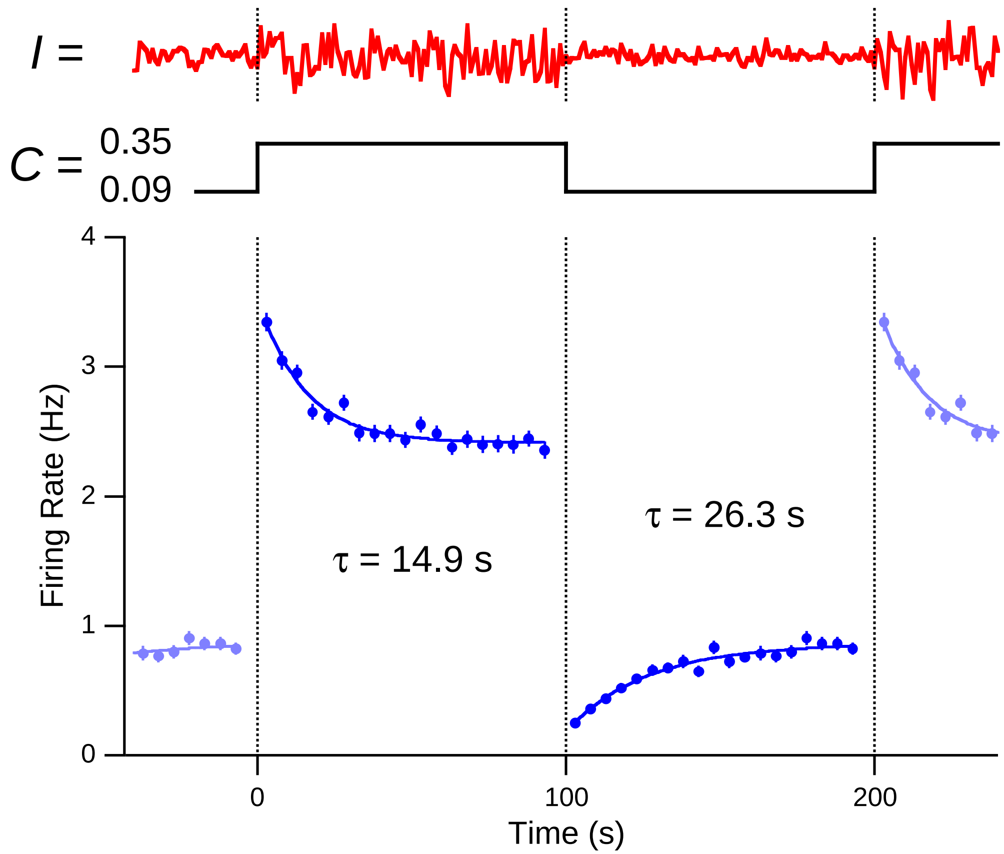
Contrast Varies, But Slowly



Response sensitivity adapts to stimulus contrast

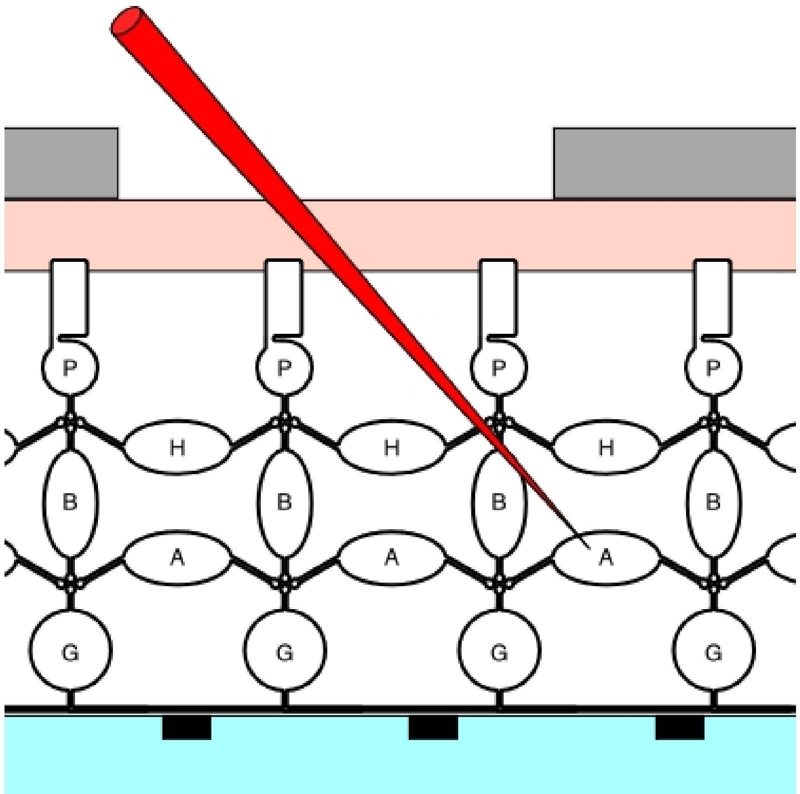


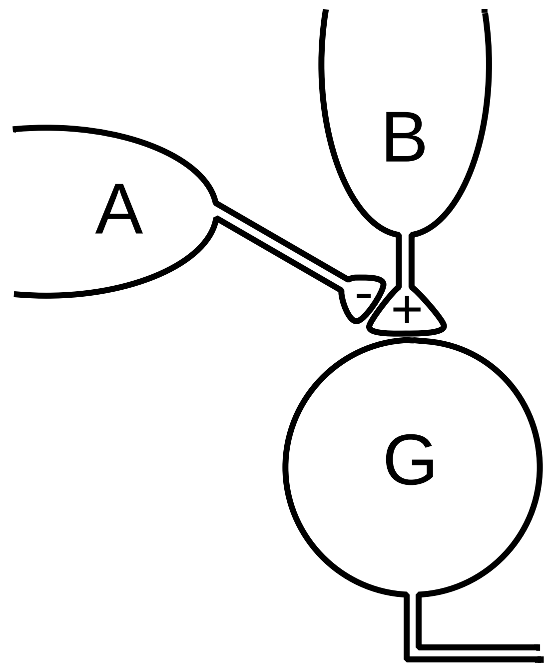
Contrast Adaptation Occurs over Seconds



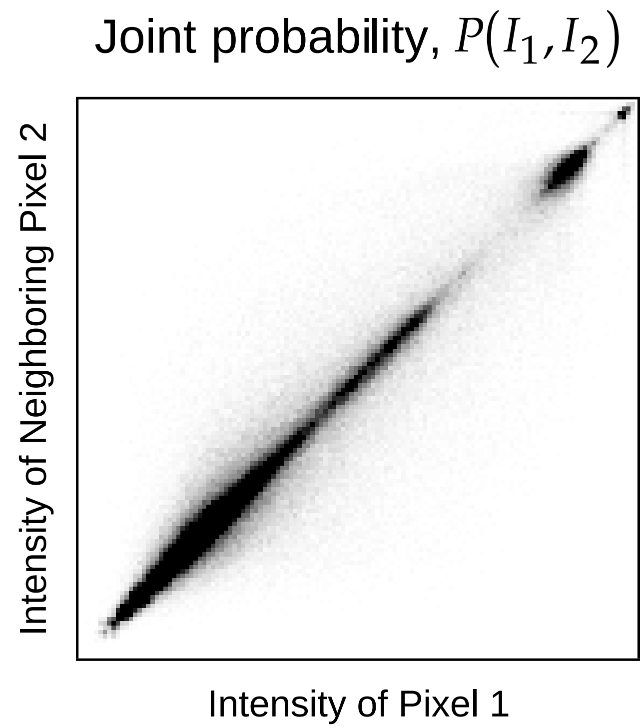
Smirnakis et al 1997

Probing the Origins of Contrast Adaptation



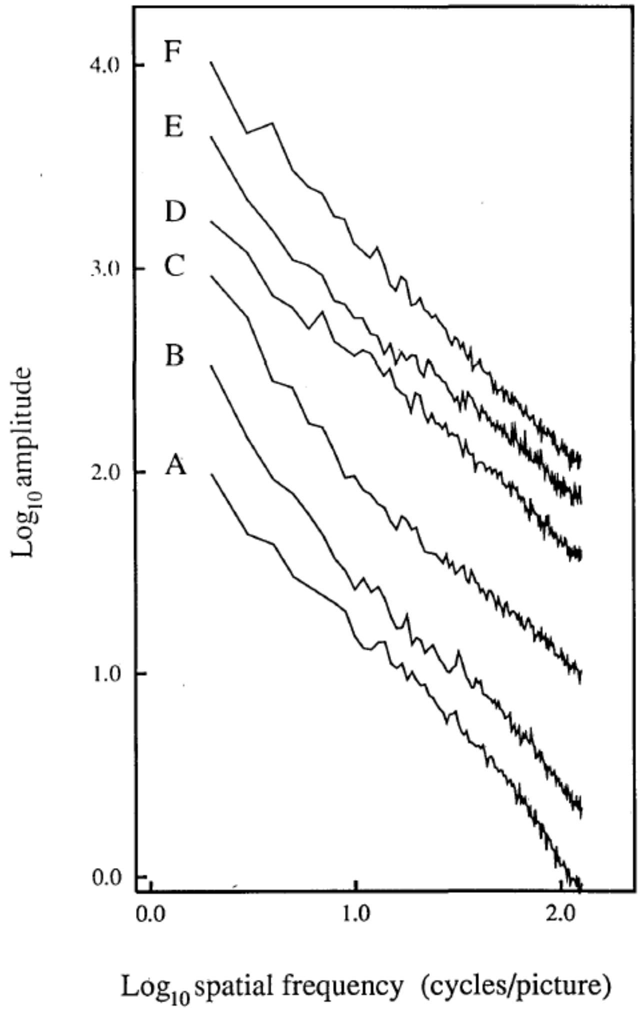


Natural Scenes Are Highly Correlated in Space



Natural Scenes Have 1/k^2 Spatial Power Spectra

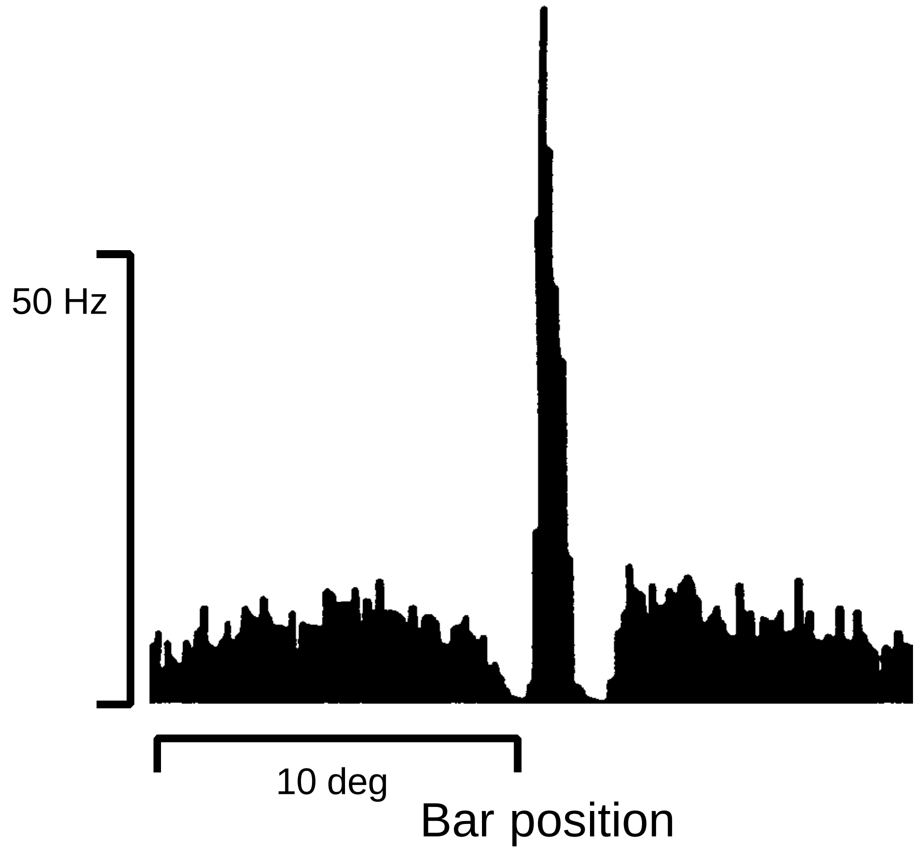
Amplitude Spectrum



Field 1987

Ganglion Cells Report Spatial Differences

Cat ganglion cell receptive field probed with a thin white bar

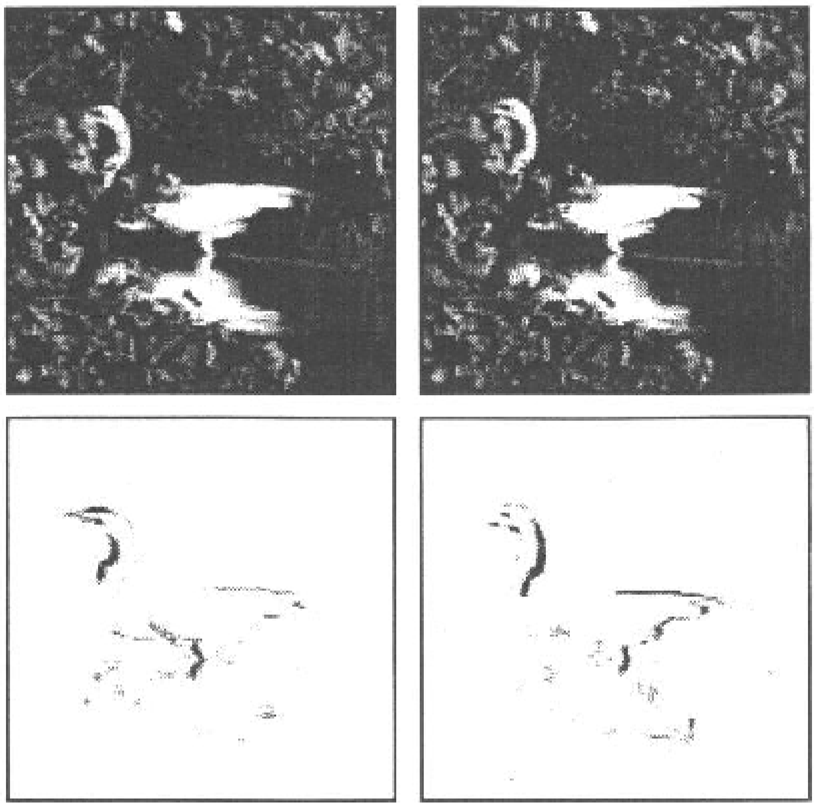


Rodieck & Stone 1965

Natural Scenes are Correlated in Time

t

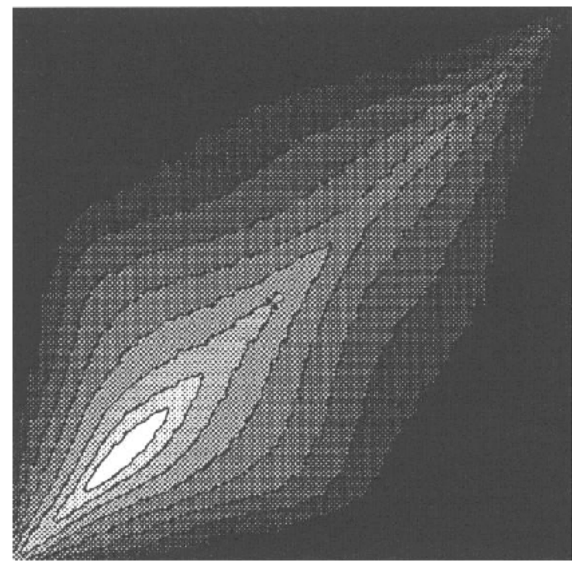
t + 33 ms



increases

decreases

Joint Probability

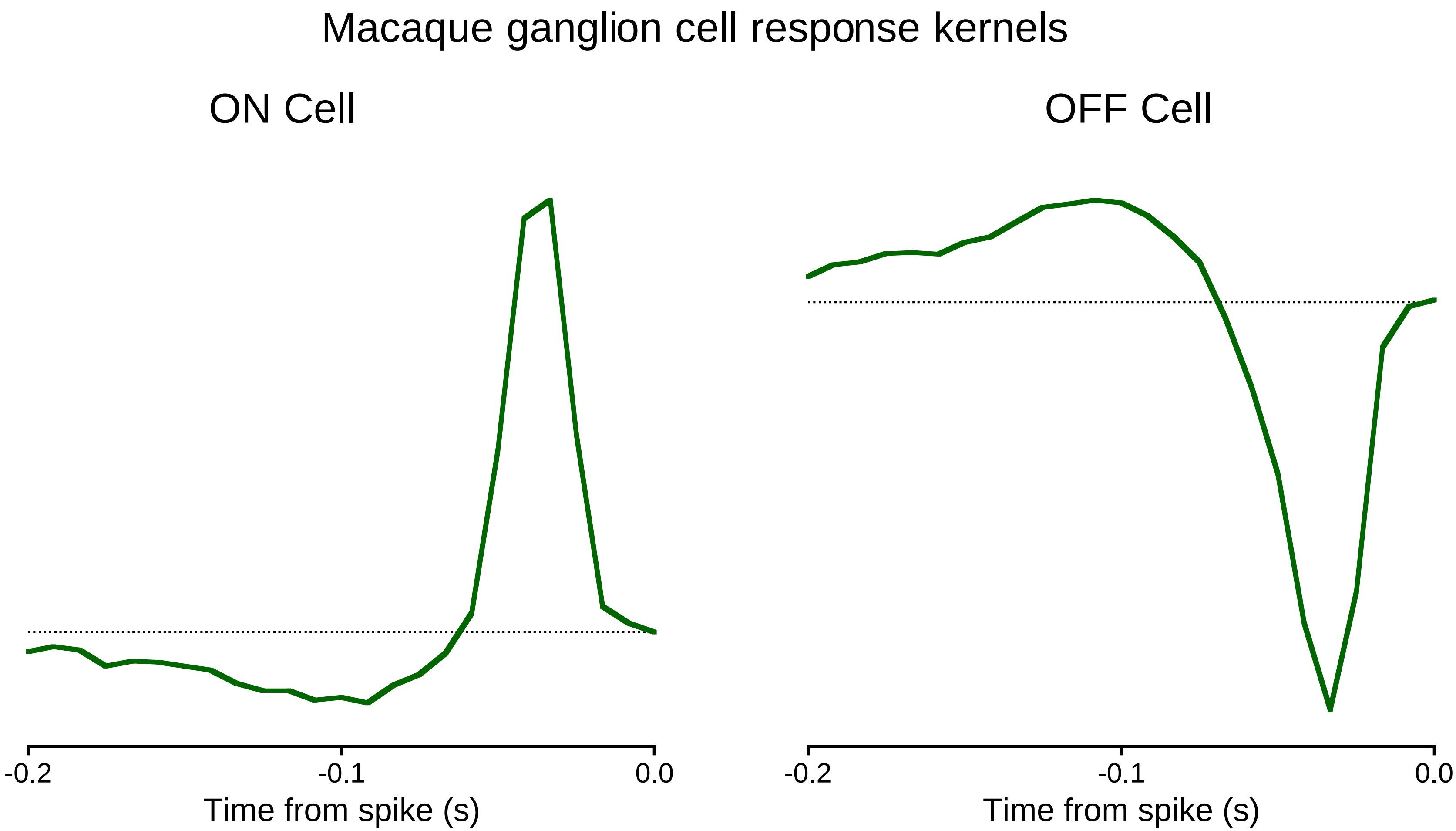


Intensity at t+33ms

Intensity at t

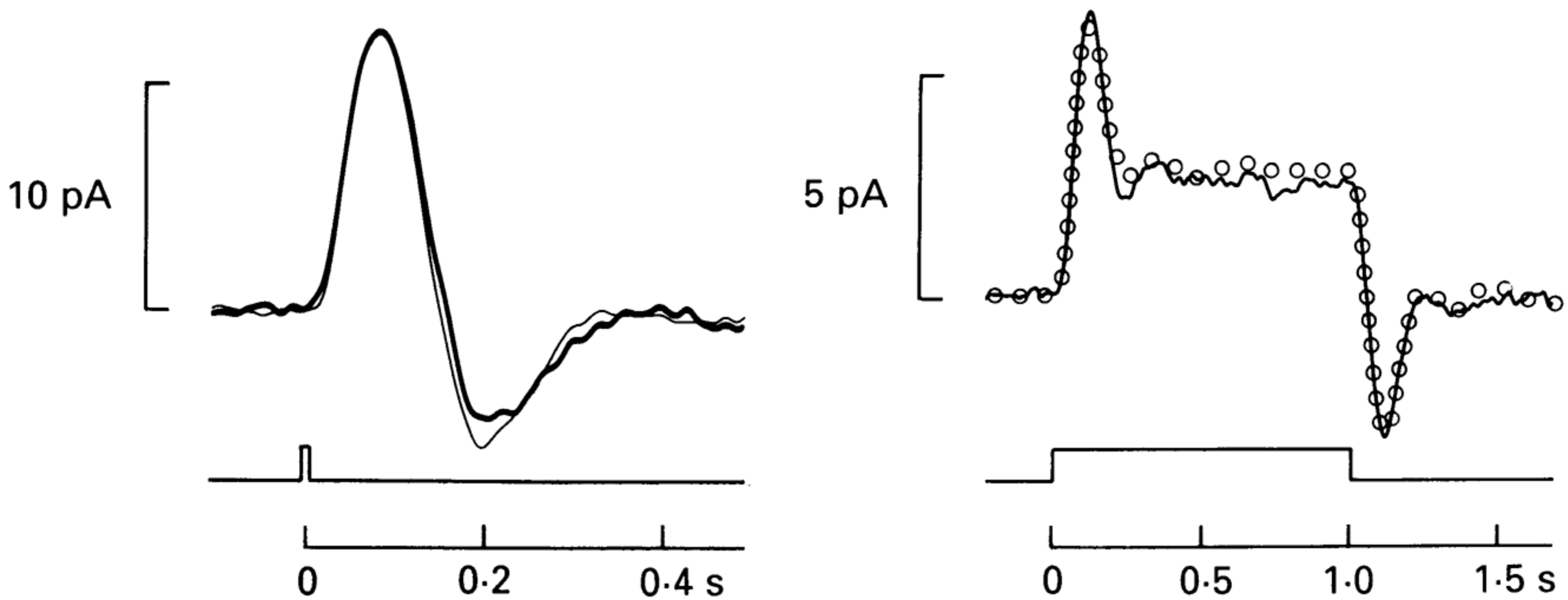
Dong & Atick 1995

Ganglion Cells Report Temporal Differences



Chichilnisky & Kalmar 2002

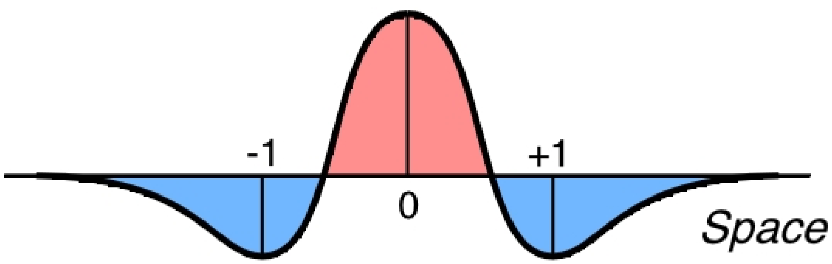
Cone Photoreceptors Compute Temporal Differences



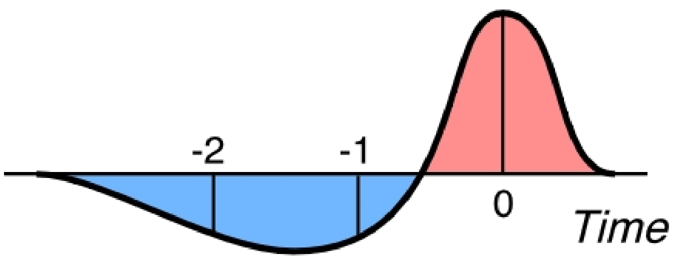
Macaque cone

Schnapf et al 1990

Predictive Coding



$$\text{Response} \approx \underbrace{I_0 - \underbrace{\frac{1}{2}\left(I_{-1} + I_1\right)}_{\substack{\text{Prediction for } I_0 \\ \text{from adjacent points}}}}_{\substack{\text{Deviation of } I_0 \\ \text{from prediction}}}$$

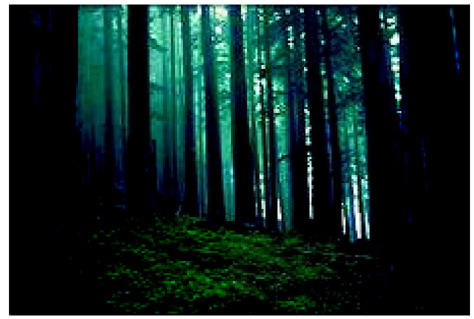


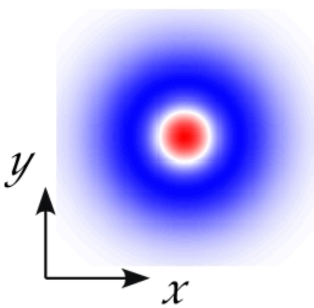
$$\text{Response} \approx I_0 - \frac{1}{2}\left(I_{-1} + I_{-2}\right)$$

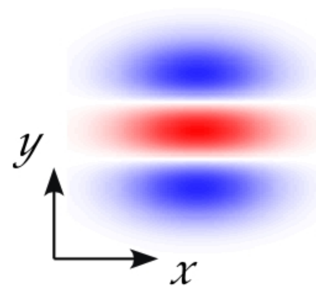
- Suppresses the predominant, predictable patterns.
- Enhances unexpected, novel features: e.g. edges, motion.
- Thought to be an evolutionary adaptation.

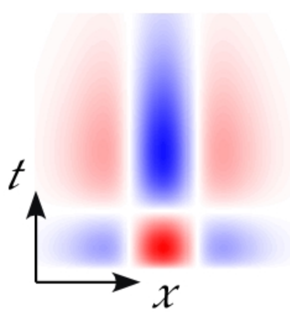
Attneave, Barlow, Srinivasan, Laughlin, Atick, et al

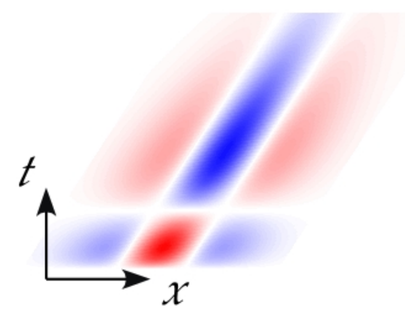
Dynamic Adaptation to a Change in Correlations?



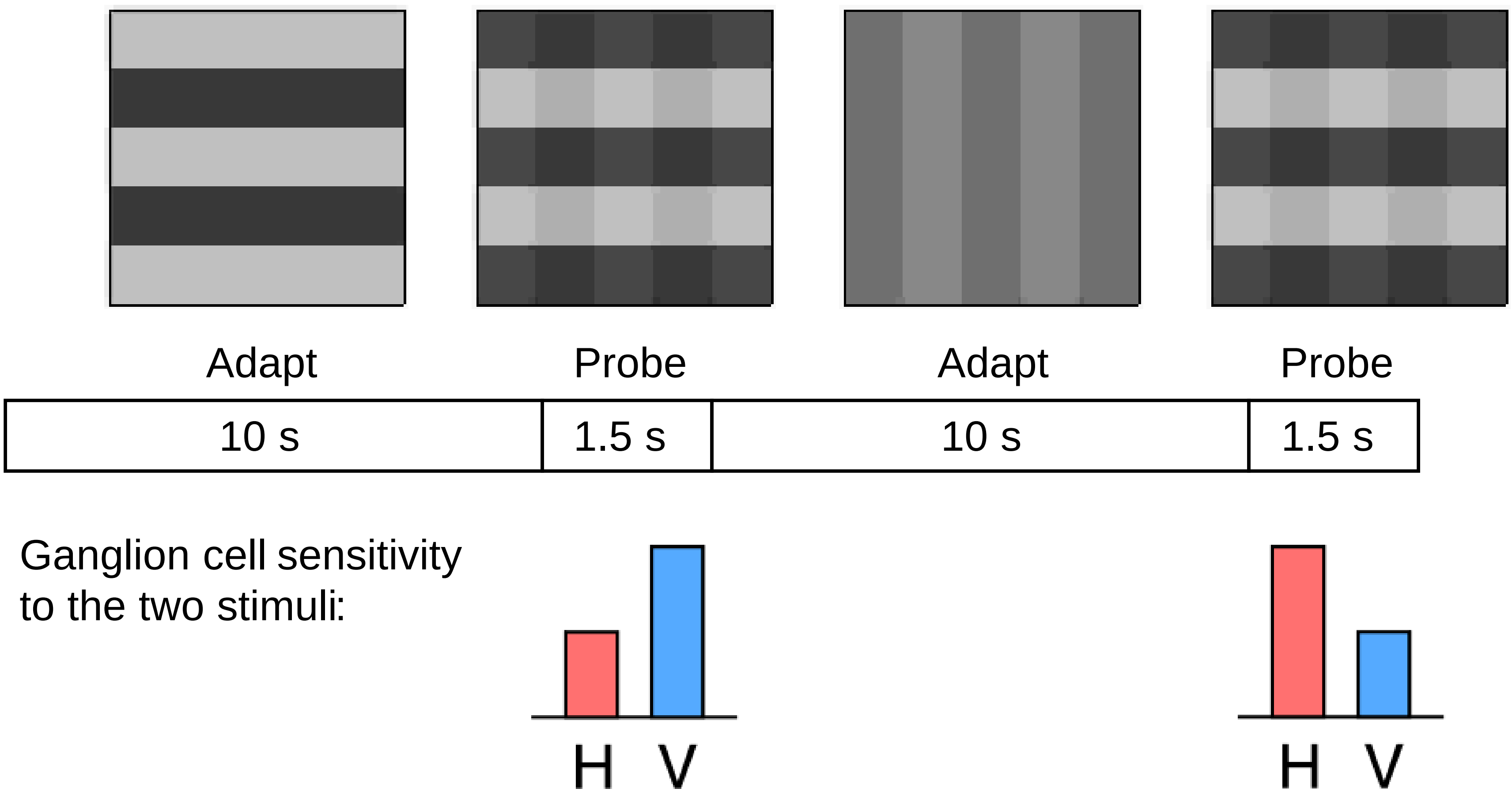






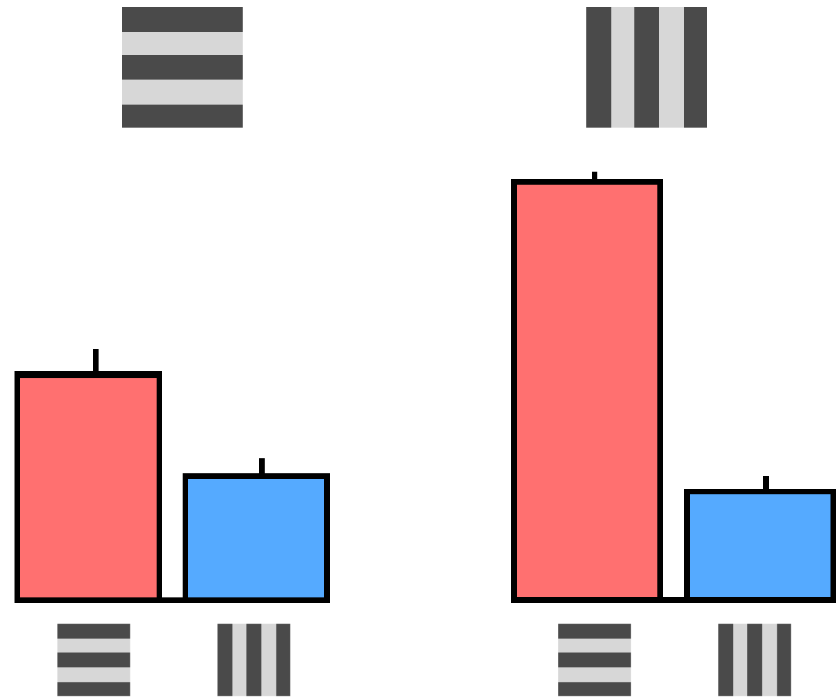


Probing Adaptation to Correlations

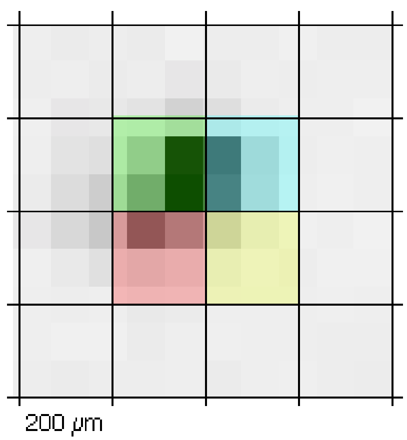


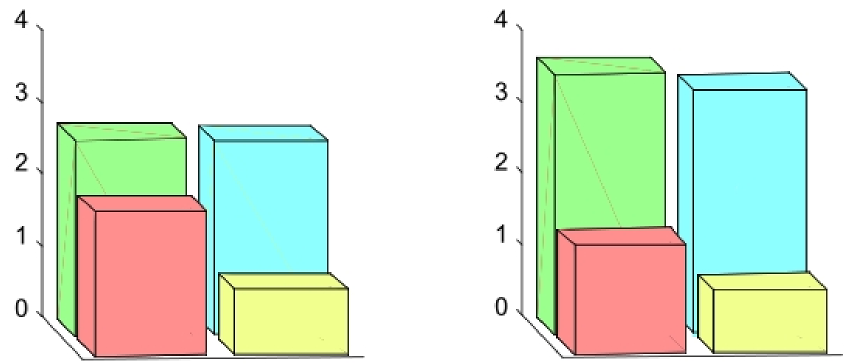
Oriented Patterns Modify Receptive Fields

After adaptation to:

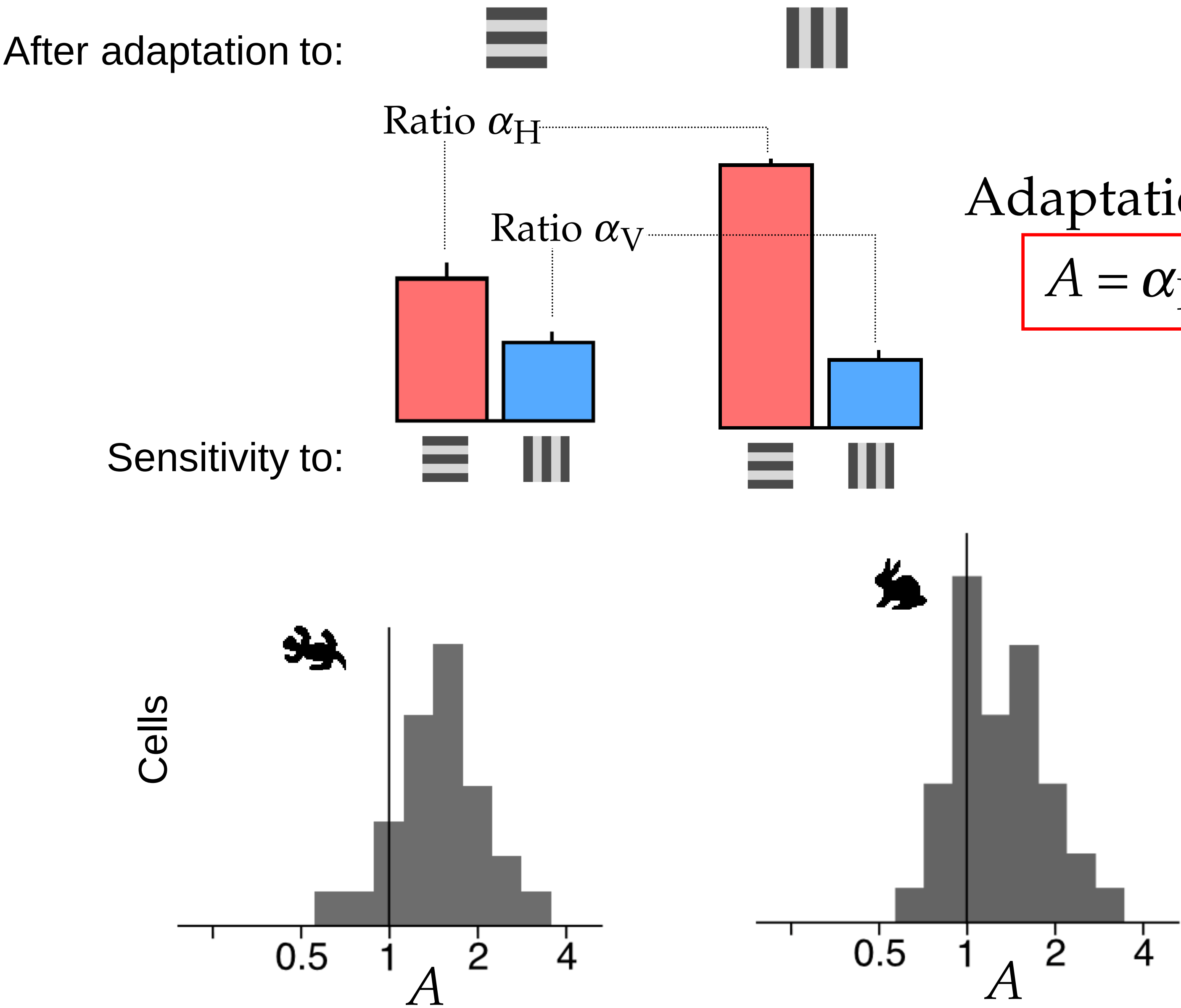


Sensitivity to:





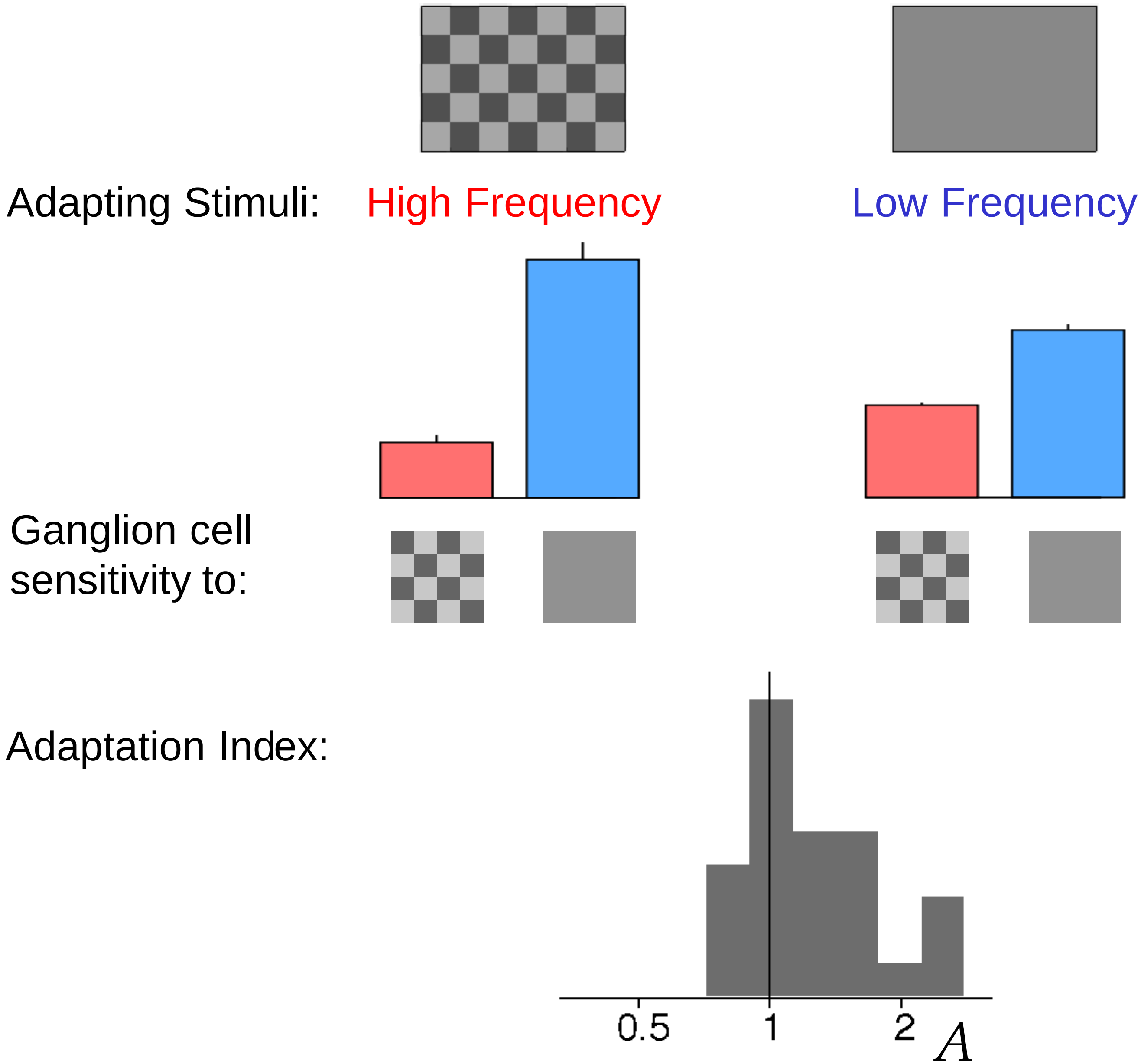
Many Ganglion Cells Adapt to Oriented Patterns



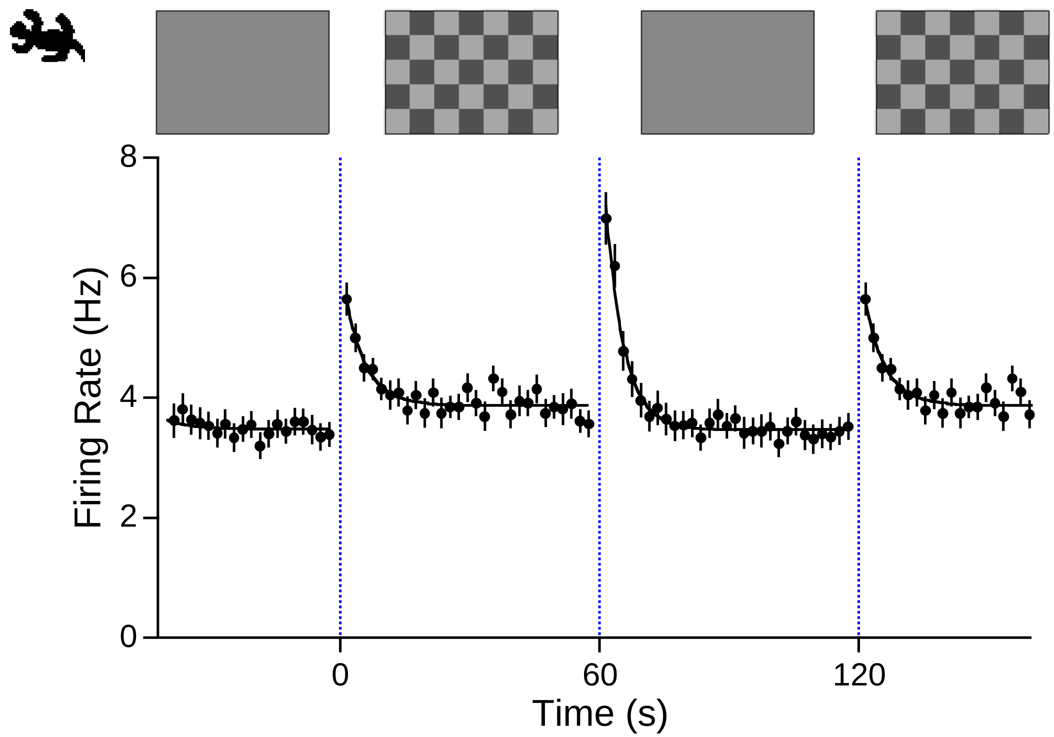
Adaptation Index:

$$A = \alpha_H / \alpha_V$$

Receptive Fields Adapt to Spatial Frequency



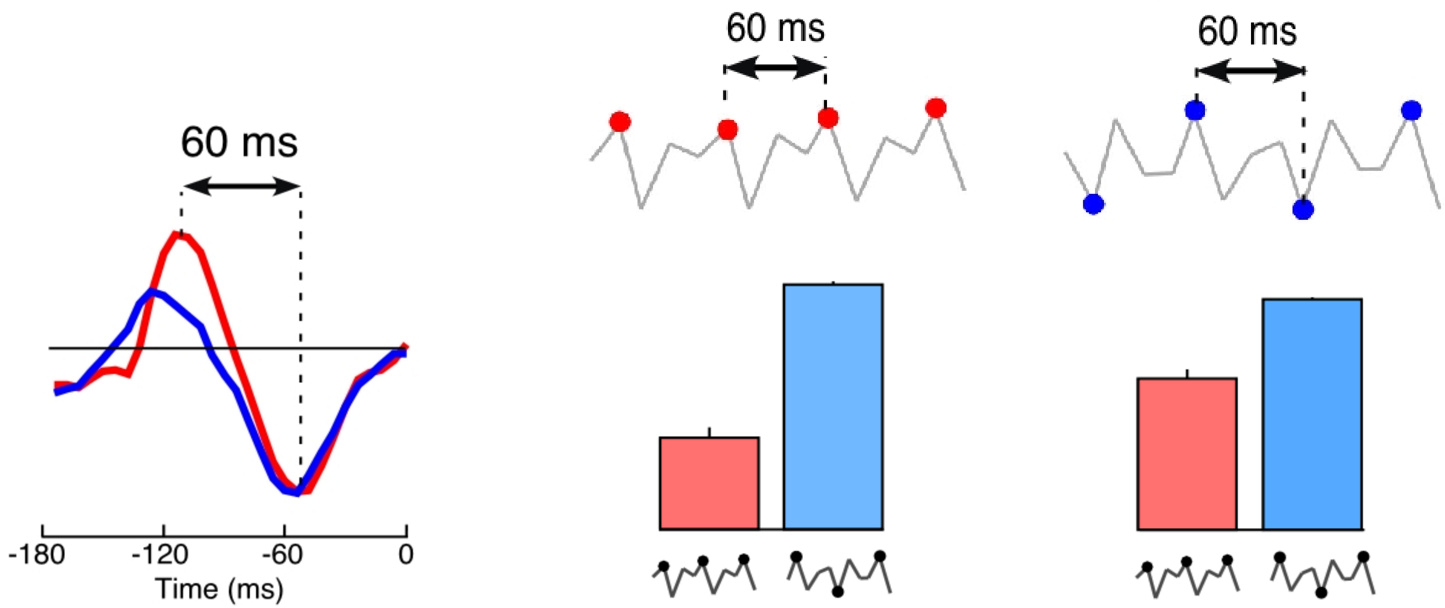
Pattern Adaptation Occurs Over Seconds



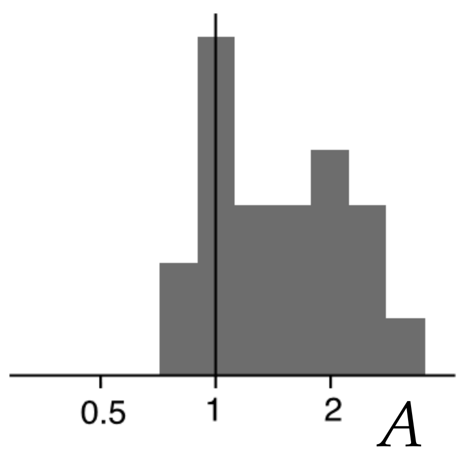
Smirnakis et al 1997

Filter Functions Adapt to Temporal Correlations

Adapting Flicker Stimuli: Positive Correlation Negative Correlation

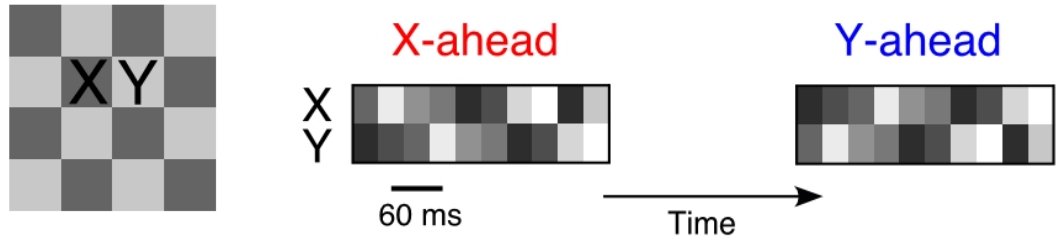


Adaptation Index:

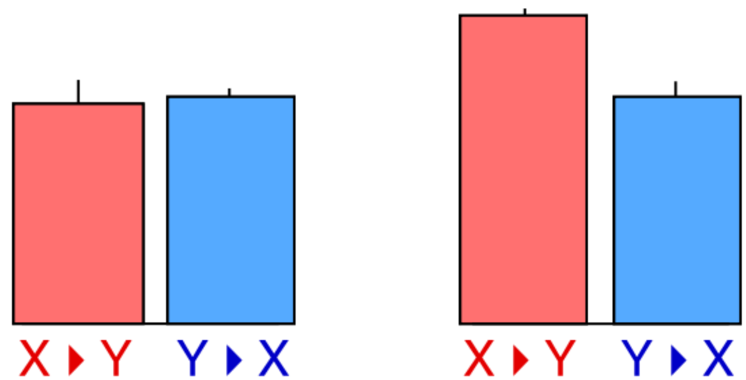


Responses Adapt to Space-Time Correlations

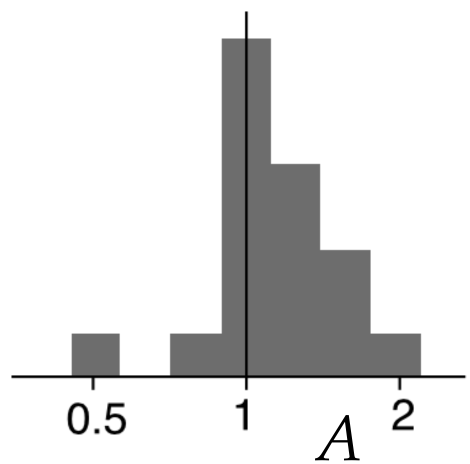
Adapting Stimuli:



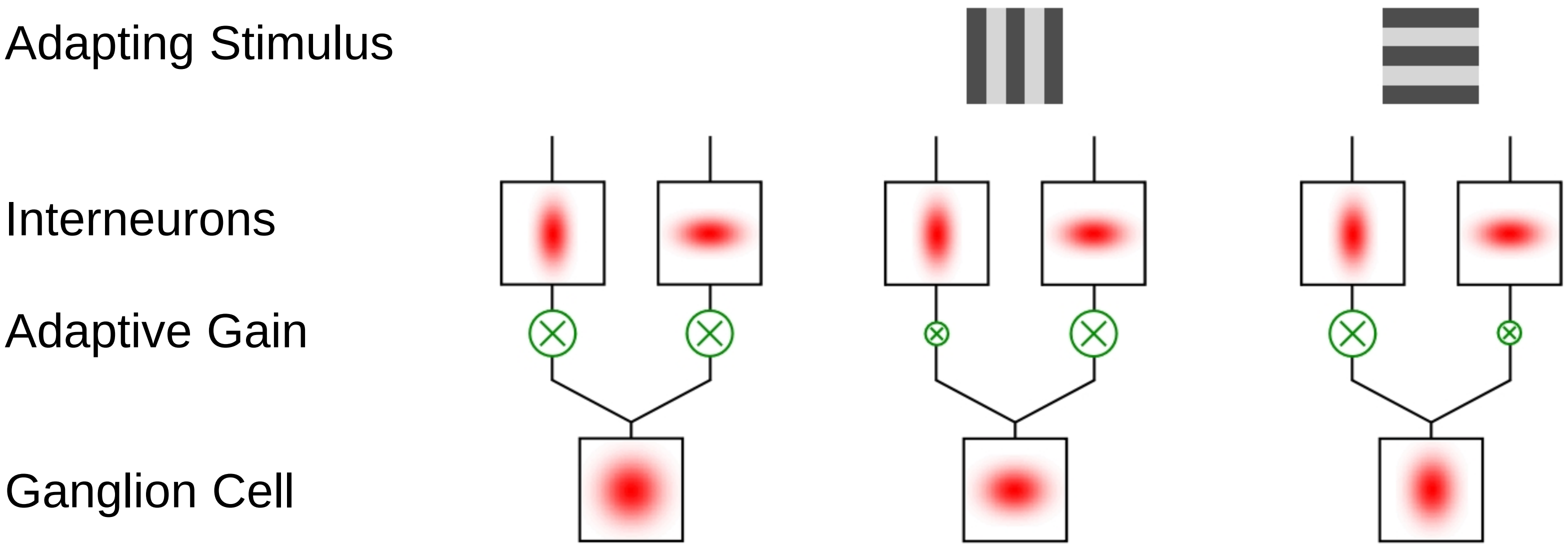
Ganglion cell sensitivity:



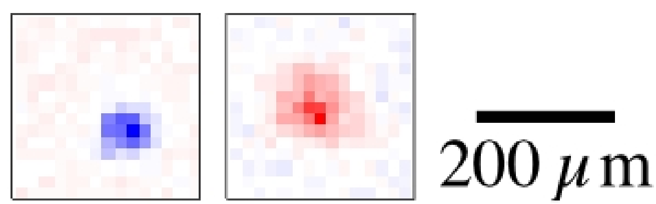
Adaptation Index:



Parallel Channels Hypothesis

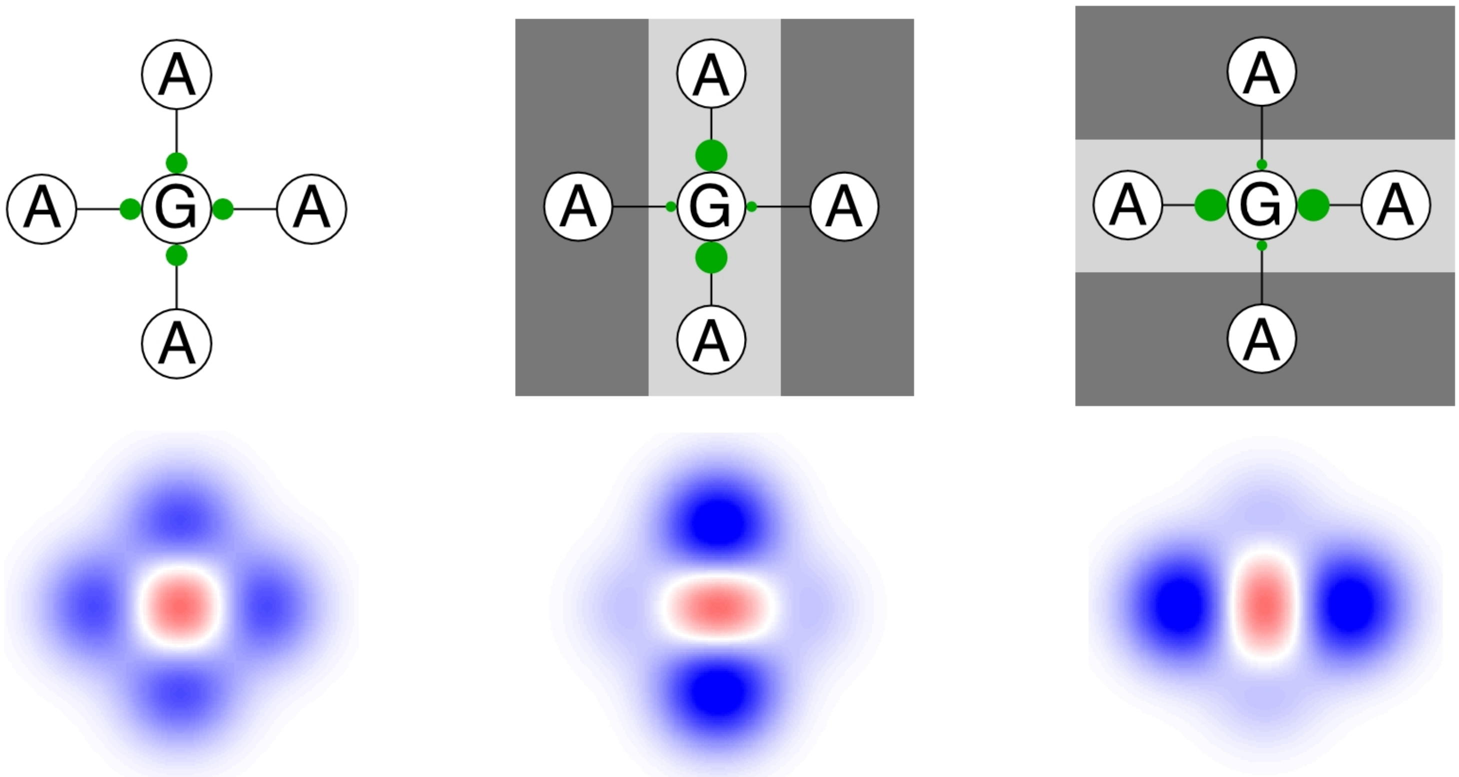


But... • Interneurons are not very selective, e.g. bipolar cells:



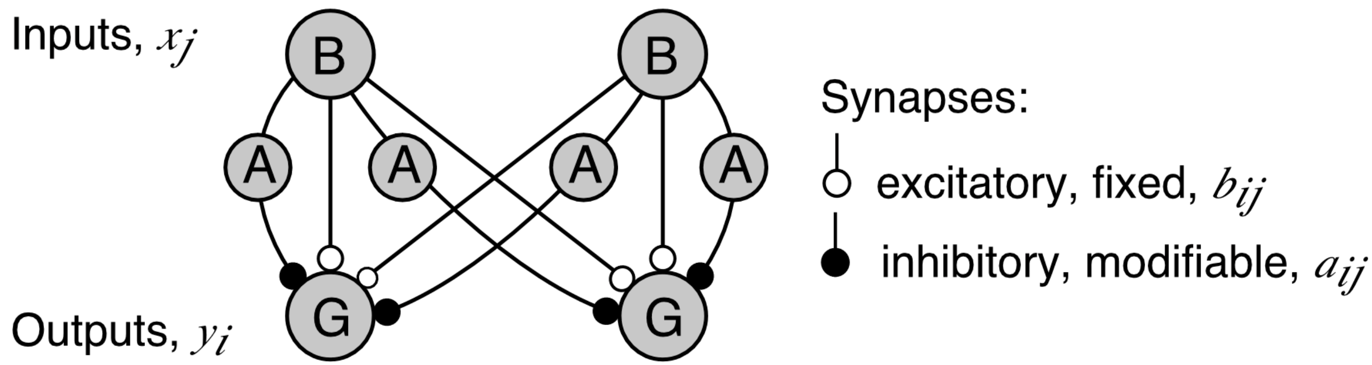
• Requires interneurons selective for many kinds of patterns, spatial, temporal, spatio-temporal...

Adaptive Network Hypothesis



- Connections are plastic using anti-Hebbian rule: If AC and GC strongly correlated, then inhibition strengthens.
- ACs “try to predict” GC signal based on signals at other points in space. Successful predictions get subtracted.
- Other forms of prediction across space and time, using amacrine cells of diverse types: small, large, transient, sustained,...

Anti-Hebbian Synaptic Plasticity



Linear processing:

$$y_i = \sum_j \left(b_{ij} + a_{ij}\right) \cdot x_j$$

Synaptic plasticity:

$$\frac{d}{dt} a_{ij} = -\frac{1}{\tau} a_{ij} - \beta \left\langle y_i x_j \right\rangle \qquad \tau, \beta > 0$$

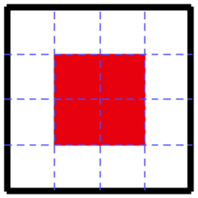
Decay term

Anti-Hebbian term:
More inhibition when pre and post-synaptic neurons are correlated.

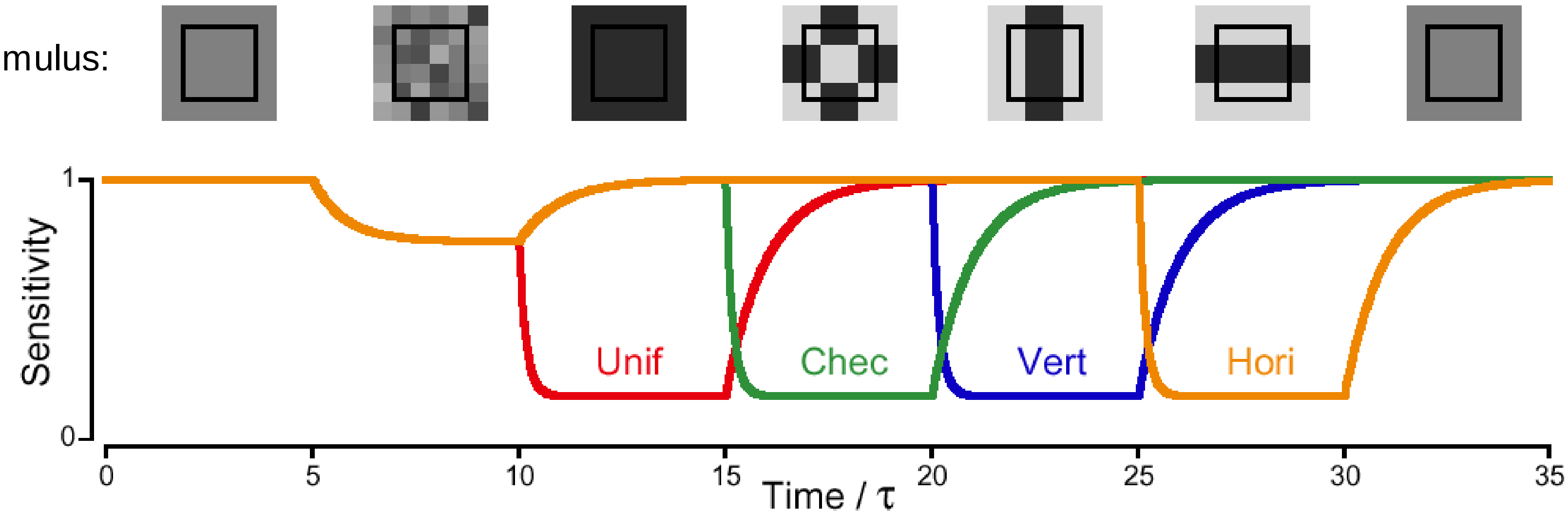
Foldiak, Barlow

Model Adaptation to Grating Stimuli

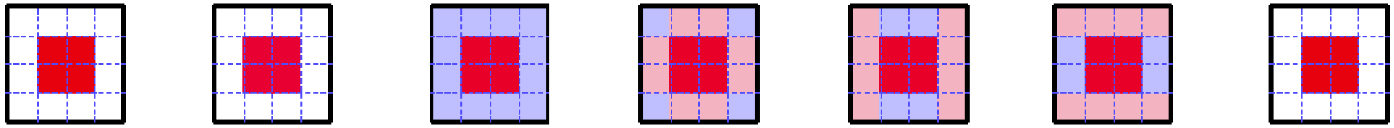
Ganglion cell starts with non-oriented receptive field:



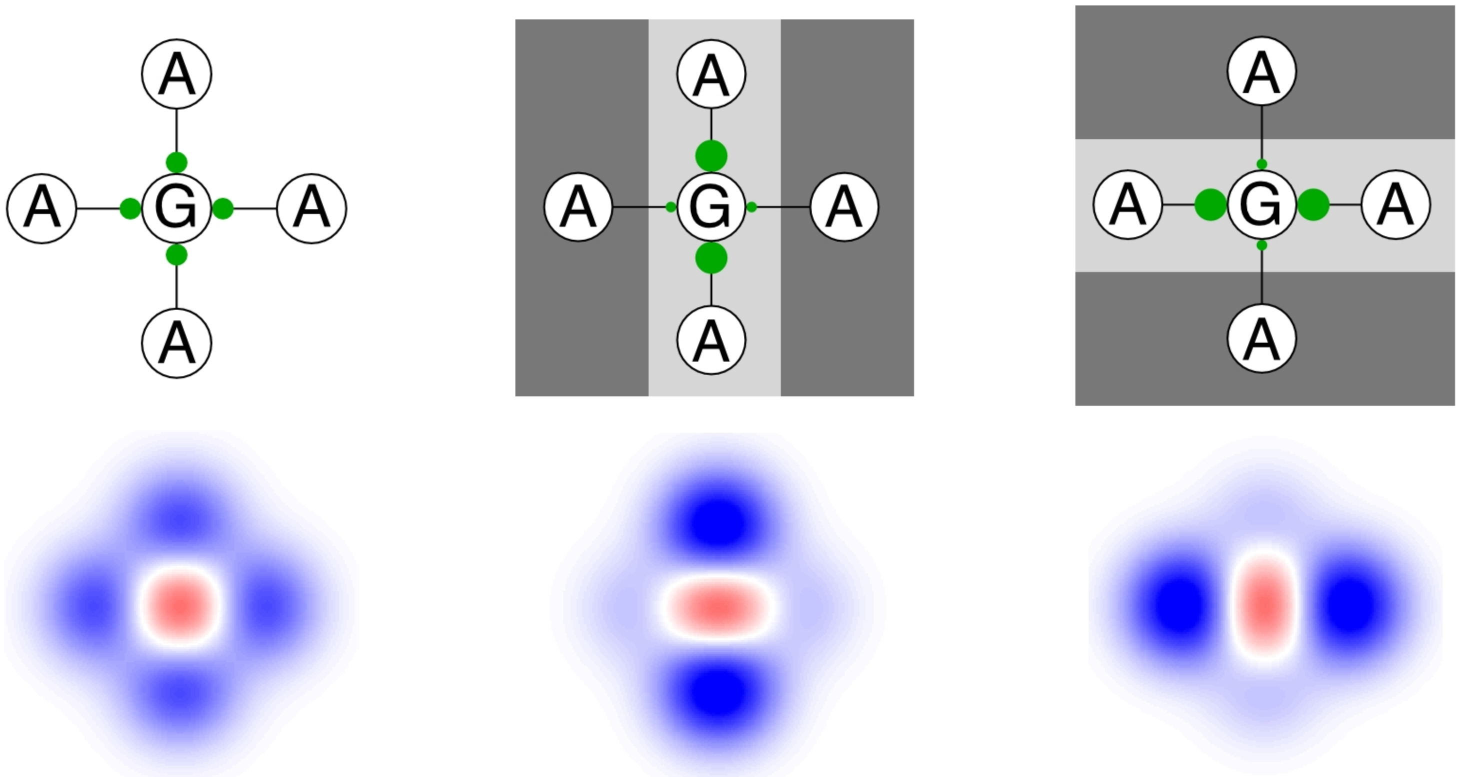
Adapting stimulus:

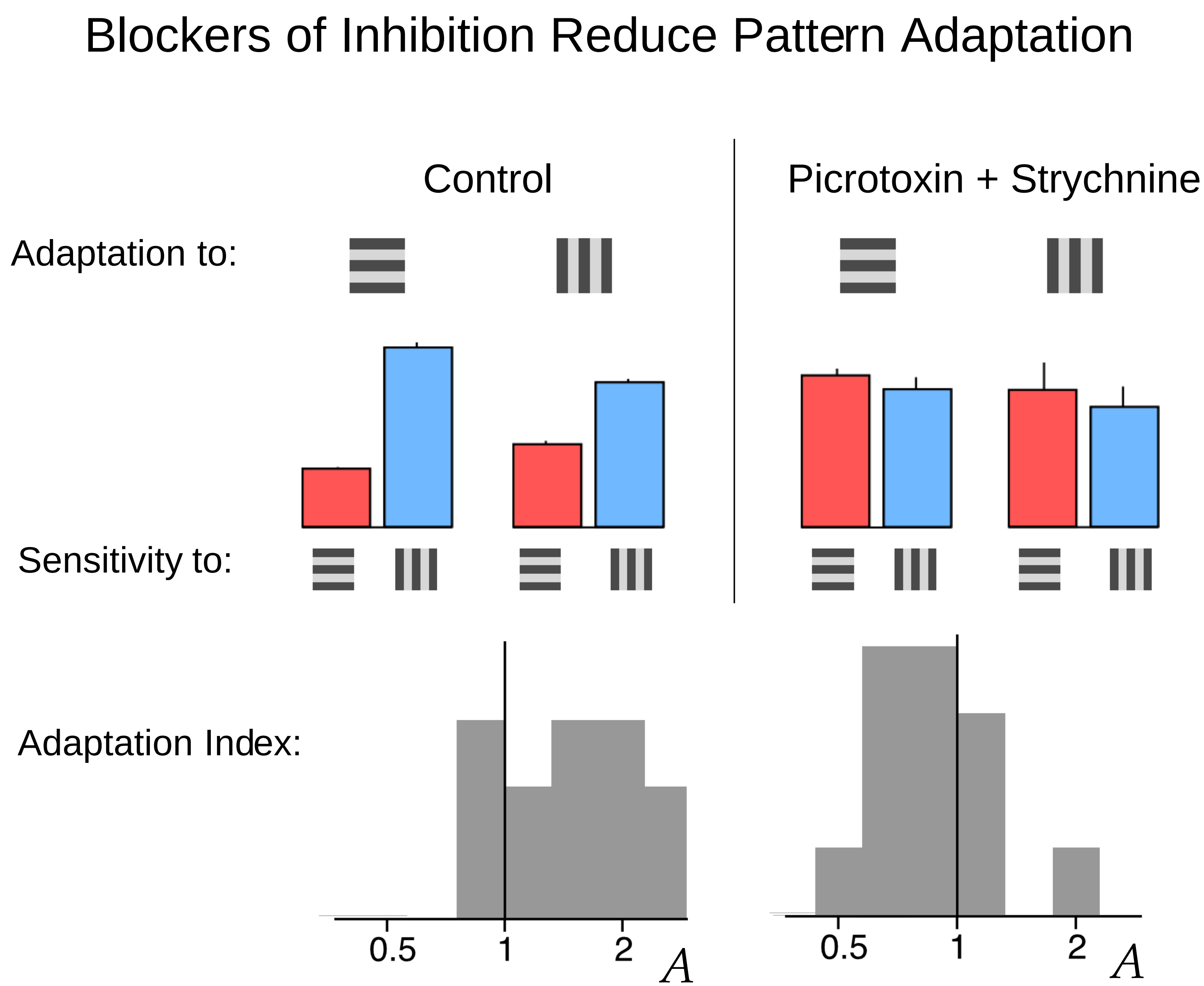


Receptive field:

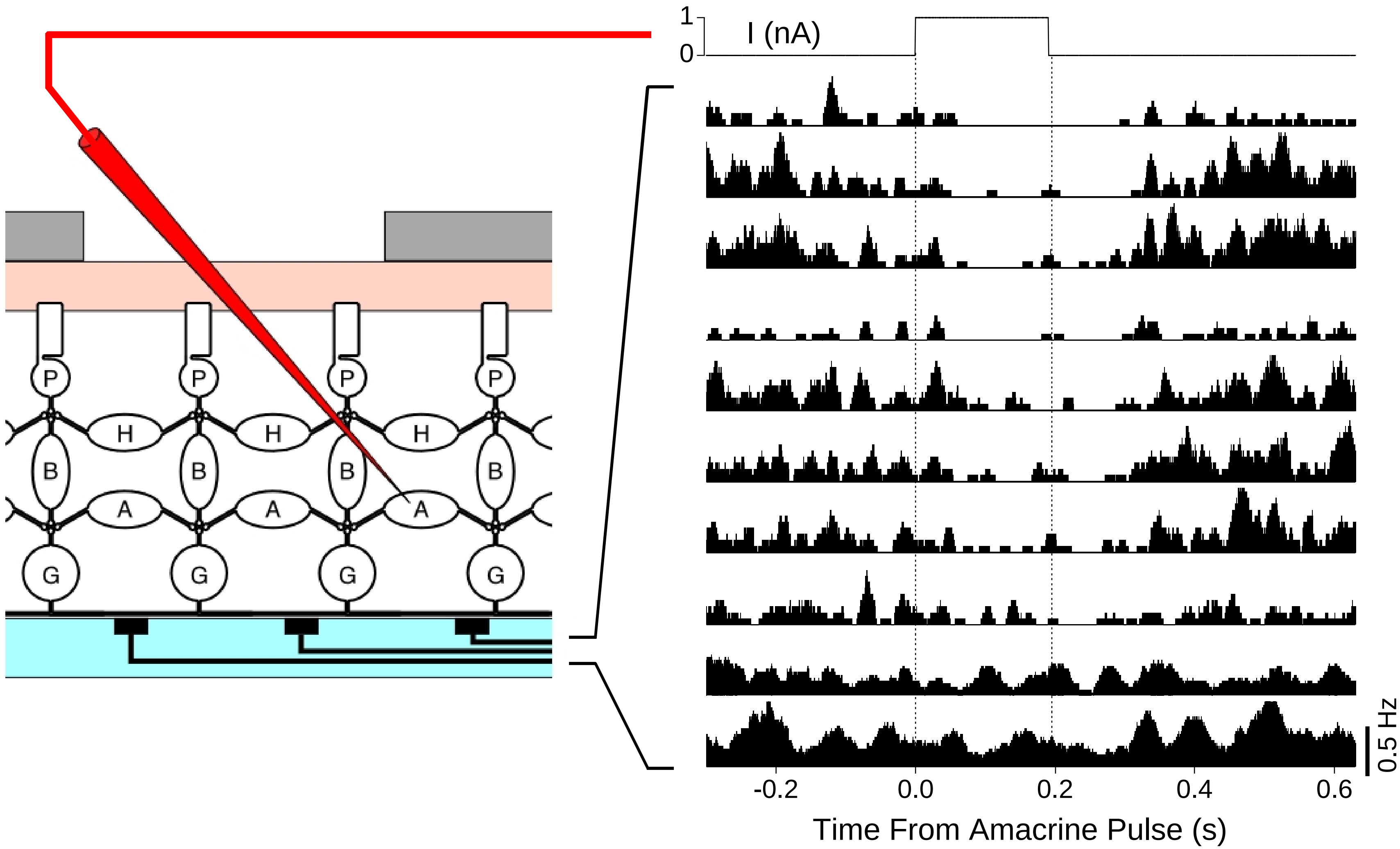


Adaptive Network Hypothesis

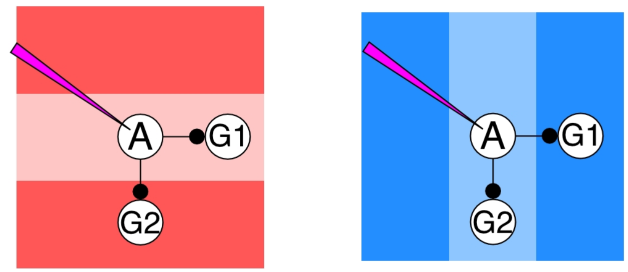


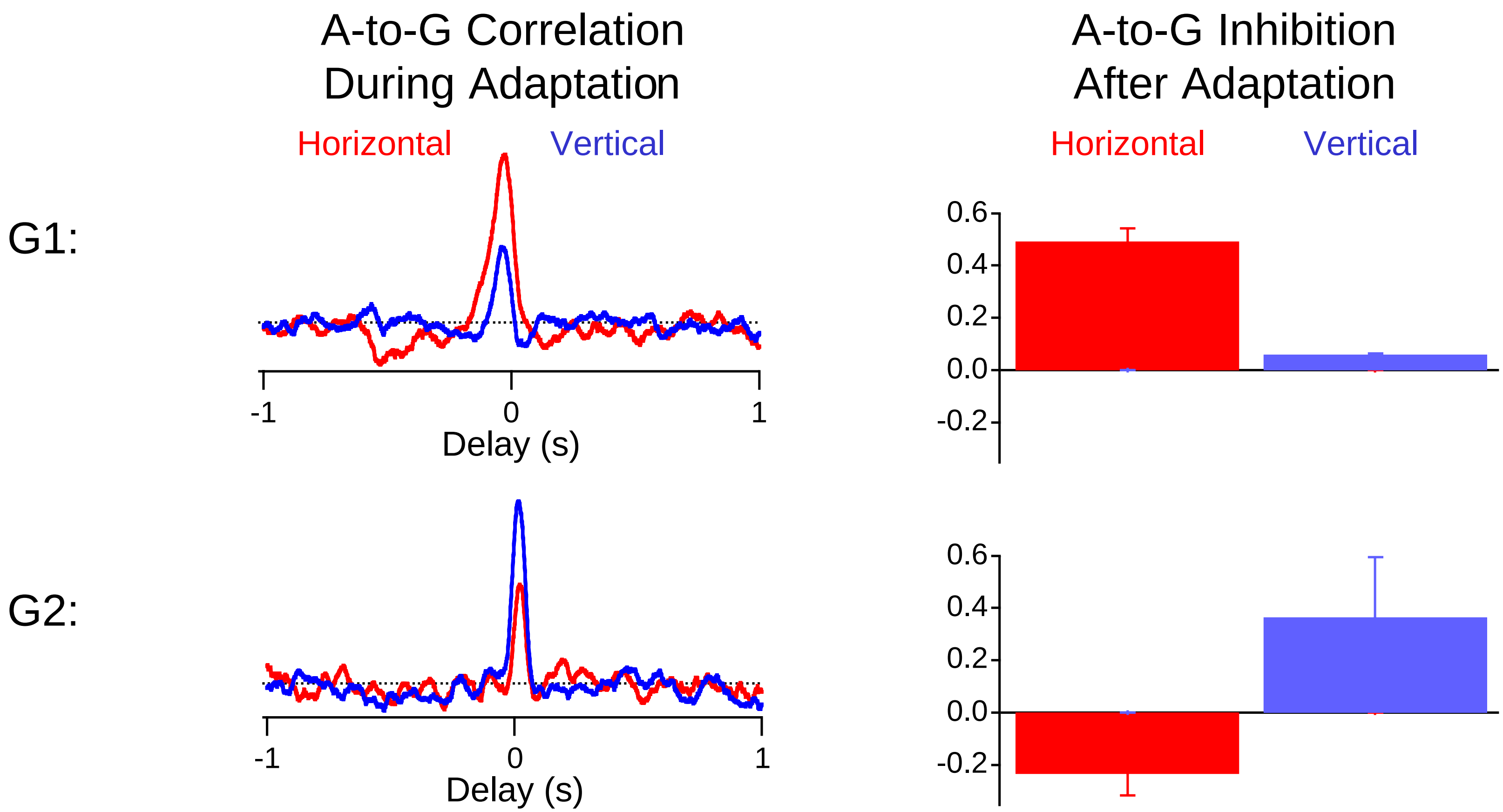

Blockers of Inhibition Reduce Pattern Adaptation
Control
Picrotoxin + Strychnine
Adaptation to:
Sensitivity to:
Adaptation Index:
0.5
1
2
A
0.5
1
2
A

Probing the Inhibitory Strength of Amacrine Cells



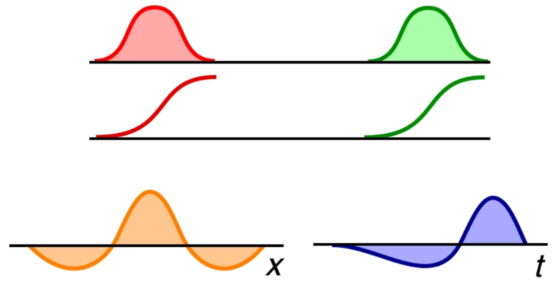
Amacrine-to-Ganglion Cell Inhibition is Modulated by Pattern Adaptation



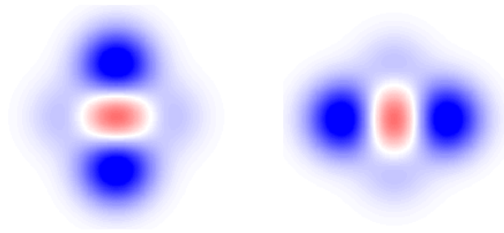


Conclusions

Much of retinal adaptation can be understood as **suppressing predictable signals**.



The rules used for prediction **adjust dynamically** to a change in the correlation structure of the visual input. This adaptation serves to **emphasize novel features**. It can make a substantial contribution to various pattern adaptations in human perception.



Dynamic predictive coding could be implemented through **anti-Hebbian synaptic plasticity** at inhibitory synapses.