**Limulus eye: a filter cascade.**

1. **Light increment**
2. **Light decrement**

- **transduction and adaptation**
- **voltage to spike rate**

**Dynamic Response to Step Increase in Light Intensity**

1. **Light increment**
2. **Light decrement**

- **adaptation**
- **symmetrical (codes both)**
The Real World: An arbitrary stimulus

For linear systems……. IN OUT

an impulse an impulse response \( h(t) \)

\[ y(n) = \sum_{k=-\infty}^{\infty} h(k) \cdot x(n - k) \]

Dynamic Response to Step Increase in Light Intensity

1) Start in constant, low level light. Step increase in intensity for 2 sec. Decrease back to previous level.

2) Decrement in light intensity generates the reverse (mirror image)

Time invariant, linear system. Good fit to curve predicted from convolution

\[ y(t) = \int_{-\infty}^{\infty} h(\tau) \cdot x(t - \tau) \, d\tau \]

\[ x(t) \]

\[ h(t) \]
Convolution Result Predicts Dynamic Responses to Steps

Three alternative methods for estimating $h(t)$
- Response to impulse
- Response to noise
- Response to component sine waves

Cog. Sci. 28:147

The reverse correlation ("revcor") method (de Boer)

Spike Triggered Reverse Average
- Determine the average (most likely) stimulus waveform preceding a spike.
- Measured by "spike-triggered averaging" with a white noise stimulus.
- Revcor functions of low-CF auditory nerve fibers resemble the impulse response of a bandpass filter centered at the CF.
- Fourier transforms of revcor functions match the tip of pure-tone tuning curves over a wide range of noise levels.
- The revcor is an estimate of the crosscorrelation between stimulus and response.


Reverse correlation and Wiener filters
- Given a linear system, the crosscorrelation of the response $r(t)$ with a stationary, white noise input $w(t)$ is proportional to the system’s impulse response $h(t)$:

$$ \frac{1}{T} \int_{-\infty}^{\infty} w(t) r(t+\tau) d\tau \propto h(\tau), \text{ with } r(t) = \frac{1}{T} \int_{-\infty}^{\infty} h(\tau) w(t-\tau) d\tau $$

- The revcor is an estimate of the Wiener filter in the special case when $r(t)$ consists of impulses (spikes).

Linear systems analysis of audition
- Calculate the Fourier Transform of the impulse response to obtain the tuning curve of the auditory neuron.
Using Sine Wave Stimuli

- Amplitude is multiplied by the gain
- Phase is delayed or advanced (add phase shift to sine wave)
  Amplitude and phase are different for different frequencies.

Do this for all relevant frequencies

Stimulate at all relevant frequencies with sinewave stimuli.

Measure gain and phase

\[ k = \text{spring constant (N/m)} \]
\[ m = \text{mass (kg)} \]
\[ \omega = \text{frequency (radians/s)} \]

http://www.lcn.capra.org/~mmp/applist/damped/d.htm
**Separate Transfer Functions**
Data from Limulus (Knight et al., 1970)

- Generator potential in response to sinusoidally modulated light.
- Spike frequency in response to light (or to sinusoidally modulated current injection).
- Spike frequency in response to modulated light.

**Cascade Filter**

- Gain and Phase for Limulus Eye
- Spike rate in response to injected current
- Spike rate in response to light (observed and predicted)
Two Methods are Equivalent

Arbitrary Stimulus

Convert arbitrary stimulus waveform to sum of sines.

Calculate gain and phase shift for each frequency.

Sum up responses.

Compute predicted response.

Filtering an Impulse Stimulus

Arbitrary Stimulus

Compute predicted response.
Open circles: spike frequency recorded from eccentric cell A, while A is given a step increase in light.

Closed circles: constant illumination of ommatidium A while providing the step increase in light in B.

Lateral Inhibition also occurs in vertebrate retina

Receptive Field of Mammalian Ganglion Cell (S. Kuffler, 1953)

Lateral inhibition can be included in model

Linear cascade from one cell converts light to spike frequency.

Spikes from one cell inhibit neighbors (lateral inhibition).

Inhibition is mutual (varies with distance)

Steady State Response

What is the response to a point of light.

Center (immediately over the eccentric cell): excitation.

Surround (adjacent areas): inhibition.

In two dimensions

A Mexican Hat.

Spatial impulse response.
Lateral Inhibition Enhances Edges

Prediction by Convolution

Parallel Processing in Retina

Tiger salamander on electrode array.

Record simultaneously responses from 63 electrode array.
Characterize receptive field (spatial and temporal) of each ganglion cell using flickering checkerboard.

For one ganglion cell, center circular spot on receptive field; add surround grating.
Contribution from On Bipolar cells: APB added to ringers prior to recording (blocks the metabotropic glutamate receptor, knocking out "on" pathway.

Sharp electrodes for recording from amacrine cells.

Stimulus: circular spot, 800 microns diameter (slightly larger than RF. Surround flickering grating,
Intensity changes every 30 ms, pseudorandom level variation.
Grating flickers every .9 s.

A larger array for salamander studies: 512 electrodes

http://www.symmetrymagazine.org/cms/?pid=1000591

Lateral Inhibition
Lessons from Visual Coding

1. The goal: understand sensory coding. Vision: example of “frequency code”.
2. Visual processing includes:
   1. transduction,  2. encoding
3. Adaptation can be thought of as self inhibition.
4. Most sensory neurons behave as temporal filters: adaptation (tonic vs. phasic)
5. Linear systems analysis can also be used to describe spatial effects such as lateral inhibition.
6. Convolution can be used to predict responses to arbitrary stimuli.