Neural circuits for direction selectivity in visual cortex

Wyeth Bair

Biological Structure
University of Washington
Seattle, WA
Macaque visual cortex

Felleman and van Essen (1991)

David C. van Essen, In: Visual Neurosciences, 2003 (L. Chalupa, J. Warner, eds.)
The visual motion pathway from retina to V1

Primary Visual Cortex

Layer 4C

LGN
Relay cells

Retina
Ganglion
Bipolar
Horizontal
Photoreceptors

Visual Stimuli
The visual motion pathway from retina to V1

- **Photoreceptors**
- **Horizontal**
- **Bipolar**
- **Ganglion**
- **LGN**
- **Layer 4C**
- **Primary Visual Cortex**

**Receptive fields**
The visual motion pathway from retina to V1

- **Photoreceptors**
  - Horizontal cells
  - Bipolar cells
  - Ganglion cells

- **Relay cells**
  - LGN
  - Layer 4C

- **Primary Visual Cortex**

- **Receptive fields**
The visual motion pathway from retina to V1

- Photoreceptors
- Horizontal Cells
- Bipolar Cells
- Ganglion Cells
- LGN Relay Cells
- Layer 4C
- Primary Visual Cortex
- Receptive fields
The visual motion pathway from retina to V1

Primary Visual Cortex
Layer 4C
LGN
Relay cells
Retina
Ganglion
Bipolar
Horizontal
Photoreceptors

Visual Stimuli

Receptive fields

center-surround

spot

M
P

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The visual motion pathway from retina to V1

Photoreceptors

Horizontal

Bipolar

Ganglion

Relay cells

LGN

Layer 4C

Visual Cortex

Primary

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PATHWAY

FROM

RETINA

TO

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ANGLION

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EAY

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CEPTIVE

FIELDS

SPOT

VISUAL

3TIMULI
The visual motion pathway from retina to V1

Primary Visual Cortex
Layer 4C
LGN
Relay cells
Retina
Ganglion
Bipolar
Horizontal
Photoreceptors

Receptive fields
orientation selective
unoriented
center-surround
center-surround
spot

Visual Stimuli
The visual motion pathway from retina to V1

- **Primary Visual Cortex**
  - Layer 4C
  - LGN
  - Relay cells

- **Retina**
  - Ganglion
  - Bipolar
  - Horizontal
  - Photoreceptors

- **Receptive fields**
  - Direction selective
  - Orientation selective
  - Unoriented
  - Center-surround

- **Visual Stimuli**
Direction Selective (DS) Neurons

**V1 complex DS neuron**

receptive field

- Anti-preferred direction
-Preferred direction

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ds_bar1.ai
Direction Selective (DS) Neurons

**V1 complex DS neuron**

receptive field

Anti-preferred direction

Preferred direction

.../talk/10/berlin/fig/ ds_bar2.ai
Direction Selective (DS) Neurons

V1 complex DS neuron

receptive field

Anti-preferred direction

Preferred direction

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Direction Selective (DS) Neurons

V1 complex DS neuron

receptive field

Anti-preferred direction

Preferred direction

../talk/10/berlin/fig/  ds_bar2_left.ai
Direction Selective (DS) Neurons

V1 complex DS neuron

receptive field

Anti-preferred direction  Preferred direction

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Direction Selective (DS) Neurons

V1 complex DS neuron

receptive field

Anti-preferred direction

Preferred direction

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ds_bar2_right.ai
Direction Selective (DS) Neurons

V1 complex DS neuron

receptive field

Anti-preferred direction

Preferred direction

Linear filter model

E.g., motion energy (ME) model.
Temporal integration in visual cortex

Adaptive temporal integration (ATI)

Temporal integration is longer for slower stimulus motion, and shorter for faster motion, as measured in the spike trains of complex DS neurons in V1 and V5/MT (Bair and Movshon, 2004).
As one changes the characteristics of $s(t)$, changes can occur both in the *feature* and in the *decision function*
Preferred

Anti-preferred

Binary, random motion sequence

Equivalent temporal frequency (TF)

Fastest TF = 25 Hz  (1/4 cycle at 100 frames/s)
**Binary, random motion sequence**

*Equivalent temporal frequency (TF)*

Fastest TF = 25 Hz  (1/4 cycle at 100 frames/s)
Binary, random motion sequence

Equivalent temporal frequency (TF)

Fastest TF = 25 Hz  (1/4 cycle at 100 frames/s)
Binary, random motion sequence

Equivalent temporal frequency (TF)

Fastest TF = 25 Hz  (1/4 cycle at 100 frames/s)
Binary, random motion sequence

Equivalent temporal frequency (TF)

Fastest TF = 25 Hz  (1/4 cycle at 100 frames/s)
Preferred

Anti-preferred

**Binary, random motion sequence**

**Equivalent temporal frequency (TF)**

Fastest TF = 25 Hz  (1/4 cycle at 100 frames/s)
Reverse correlation: the spike-triggered average

![Diagram showing reverse correlation process]

Spike-conditional ensemble

spike-triggered average
Spike-triggered Average (STA)

Velocity (normalized)

Time relative to spike (ms)
V1 complex DS cell

![Graph showing V1 complex DS cell response to different TF (Hz) and Time relative to spike (ms).](image)
V1 complex DS cell

Rate (spikes/s)

TF (Hz)

Time relative to spike (ms)

Velocity (normalized)
V1 complex DS cell

TF (Hz)

Rate (spikes/s)

Velocity (normalized)

Time relative to spike (ms)
Summary of experimental findings

Time

Space
Summary of experimental findings

Adaptive temporal integration (ATI)

Temporal integration appears to change with the statistics of the motion (Bair & Movshon, 2004).
The Motion Energy Model

\[ G(r,t) = \frac{1}{(2\pi)^{3/2} \sigma_r \sigma_t} \ e^{\left(\frac{-|\mathbf{n}|^2 - t^2}{2\sigma_r^2}\right)} \ e^{-i \ 2\pi \ (f_r \ \mathbf{n} \cdot \mathbf{r} + f_t \ t)} \]

\[ n = (\cos \theta, \sin \theta) \]

\[ r = (x,y) \]

\[ ME(r,t) = |G(r,t) \ast s(r,t)|^2 \]

Adelson & Bergen (1985) J Opt Soc Am A
Temporal Integration in the Motion Energy Model

model filter

STAs

Time relative to spike (ms)

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Temporal Integration in the Motion Energy Model

model filter

STAs

slow

0.1 Hz

fast

25 Hz

DS neuron

Time relative to spike (ms)
Visual motion pathway, retina to V1

**Primary Visual Cortex**

**Layer 4C**

**LGN**

**Relay cells**

**Retina**

**Ganglion**

**Bipolar**

**Horizontal**

**Photorec.**

**Visual Stimuli**

**Receptive fields**
- direction selective
- orientation selective
- unoriented
- center-surround
- center-surround
- spot

**How could ATI arise?**

- Changes in the retina
- Cortical normalization
- Adaptation at the soma
- Non-linear interaction at spike generation
- Parallel pathways: convergence of fast and slow channels
Mask Stimulus
Results for one
V1 complex DS cell
Results for two V1 complex DS cells

![Graphs showing firing rate changes with different target and mask states.]

- **Target State**: The graphs compare different firing rates between fast and slow target states.
- **Mask State**: The bars on the right show the firing rates for different mask states.

**Graph Key**:
- Slow Target
- Fast Target
- Slow Target, Slow Mask
- Fast Target, Slow Mask
- Slow Target, Fast Mask
- Fast Target, Fast Mask

**Diagrams**:
- Top diagram: Plot of Slim Direction (prob) over Time (ms) for Cell_111_032.
- Bottom diagram: Plot of Target Direction (prob) over Time (ms) for Cell_118_019.
Database Summary

Fast Target vs Slow Target

Slow Target, Masked vs Slow Target

Fast Target, Masked vs Fast Target

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mask_scat.ai
Visual motion pathway, retina to V1

How could ATI arise?

- Changes in the retina
- Cortical normalization
  - Adaptation at the soma
  - Non-linear interaction at spike generation
- Parallel pathways: convergence of fast and slow channels

ATI is channel specific.
Noise-driven adaptation: in vitro and 
mathematical analysis

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Abstract

Variance adaptation processes have recently been examined in cells of the fly visual system and various vertebrate preparations. To better understand the contributions of somatic mechanisms to this kind of adaptation, we recorded intracellularly in vitro from neurons of rat sensorimotor cortex. The cells were stimulated with a noise current whose standard deviation was varied parametrically. We observed systematic variance-dependent adaptation (defined as a scaling of a nonlinear transfer function) similar in many respects to the effects observed in vivo. The fact that similar adaptive phenomena are seen in such different preparations led us to investigate a simple model of stochastic stimulus-driven neural activity. The simplest such model, the leaky integrate-and-fire (LIF) cell driven by noise current, permits us to analytically compute many quantities relevant to our observations on adaptation. We show that the LIF model displays “adaptive” behavior which is quite similar to the effects observed in vivo and in vitro.

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Keywords: Adaptation; Noise; Integrate-and-fire; Fokker–Planck

It is widely understood that sensory neurons adapt to the prevailing statistics of their inputs [10]. Fairhall et al. [5] recently reported one such adaptation process in the fly visual system; they described a motion-sensitive neuron that appears to scale its input–output function to adapt its firing rate to the variance of the observed motion signal. However, the mechanisms underlying this type of contrast-dependent adaptation are unknown; specifically, it is unclear whether the observed phenomena arise from network

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Intrinsic Gain Modulation and Adaptive Neural Coding

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Abstract

In many cases, the computation of a neural system can be reduced to a receptive field, or a set of linear filters, and a thresholding function, or gain curve, which determines the firing probability; this is known as a linear/nonlinear model. In some forms of sensory adaptation, these linear filters and gain curve adjust very rapidly to changes in the variance of a randomly varying driving input. An apparently similar but previously unrelated issue is the observation of gain control by background noise in cortical neurons: the slope of the firing rate versus current (f-I) curve changes with the variance of background random input. Here, we show a direct correspondence between these two observations by relating variance-dependent changes in the gain of f-I curves to characteristics of the changing empirical linear/nonlinear model obtained by sampling. In the case that the underlying system is fixed, we derive relationships relating the change of the gain with respect to both mean and variance with the receptive fields derived from reverse correlation on a white noise stimulus. Using two conductance-based model neurons that display distinct gain modulation properties through a simple change in parameters, we show that coding properties of both these models quantitatively satisfy the predicted relationships. Our results describe how both variance-dependent gain modulation and adaptive neural computation result from intrinsic nonlinearity.


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Introduction

An f-I curve, defined as the mean firing rate in response to a stationary mean current input, is one of the simplest ways to characterize how a neuron transforms a stimulus into a spike train output as a function of the magnitude of a single stimulus parameter. Recently, the dependence of f-I curves on other input statistics such as the variance has been examined: the slope of the f-I curve, or gain, is modulated in diverse ways in response to different intensities of added noise [1–4]. This enables multiplicative control of the neuronal gain by the level of background synaptic activity [1]: changing the level of the background synaptic activity is equivalent to changing the variance of the noisy balanced excitatory and inhibitory input current to the soma, which modulates the gain of the f-I curve. It has been demonstrated that such somatic gain modulation, combined with saturation in the dendrites, can lead to multiplicative gain control in a single neuron by background inputs [5]. From a computational perspective, the sensitivity of the firing rate to mean or variance can be thought of as distinguishing the neuron’s function as either an integrator (greater sensitivity to the mean) or a differentiator/coincidence detector (greater sensitivity to fluctuations, as quantified by the variance) [3,6,7].

An alternative method of characterizing a neuron’s input-to-output transformation is through a linear/nonlinear (LN) cascade model [8,9]. These models comprise a set of linear filters or receptive field that selects particular features from the input; the filter output is transformed by a nonlinear threshold stage into a time-varying firing rate. Spike-triggered covariance analysis [10,11] reconstructs a model with multiple features from a neuron’s input/output data. It has been widely employed to characterize both neural systems [12–15] and single neurons or neuron models subject to current or conductance inputs [16–19].

Generally, results of reverse correlation analysis may depend on the statistics of the stimulus used to sample the model [15,19–25]. While some of the dependence on stimulus statistics in the response of a neuron or neural system may reflect underlying plasticity, in some cases, the rapid timescale of the changes suggests the action of intrinsic nonlinearities in systems with fixed parameters [16,19,25–29], which changes the effective computation of a neuron.

Our goal here is to unify the f-I curve description of variance-dependent adaptive computation with that given by the LN model: we present analytical results showing that the variance-dependent modulation of the firing rate is closely related to adaptive changes in the neuron’s LN model if a fixed underlying model is assumed. When the model relies only on a single feature, we find that such a system can show only a single type of gain modulation, which accompanies an interesting asymptotic scaling behavior. With multiple features, the model can show more diverse adaptive behaviors, exemplified by two conductance-based models that we will study.

Results

Diverse Variance-Dependent Gain Modulations without Spike Rate Adaptation

Recently, Higgs et al. [3] and Arsiero et al. [4] identified different forms of variance-dependent change in the f-I curves of
Results for two V1 complex DS cells

<table>
<thead>
<tr>
<th>Target State</th>
<th>Mask State</th>
<th>Firing Rate (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slow</td>
<td>None</td>
<td>0</td>
</tr>
<tr>
<td>Slow</td>
<td>Fast</td>
<td>50</td>
</tr>
<tr>
<td>Slow</td>
<td>Slow</td>
<td>30</td>
</tr>
<tr>
<td>Slow</td>
<td>Fast</td>
<td>80</td>
</tr>
<tr>
<td>Slow</td>
<td>None</td>
<td>100</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Target State</th>
<th>Mask State</th>
<th>Firing Rate (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fast</td>
<td>None</td>
<td>0</td>
</tr>
<tr>
<td>Fast</td>
<td>Fast</td>
<td>50</td>
</tr>
<tr>
<td>Fast</td>
<td>Slow</td>
<td>30</td>
</tr>
<tr>
<td>Fast</td>
<td>Fast</td>
<td>80</td>
</tr>
<tr>
<td>Fast</td>
<td>None</td>
<td>100</td>
</tr>
</tbody>
</table>

Graphs show the Slim Direction (prob) and Target Direction (prob) over time (ms) for different conditions of targets and masks.
Comparing Target and Mask STAs

Target + Mask

Target, Slow
Mask, Fast

Cell 118_019

Time (ms)
Comparing Target and Mask STAs

Target + Mask

Ori A

Ori B

Cell's Preferred Direction

Time (ms)

Stimulus Direction (prob)

Target, Slow
Mask, Fast

Cell_118_019

-200 -150 -100 -50 0

0.3

0.0

0.3

0.0

0.0

-200 -150 -100 -50 0

Cell_125_005

Ori A, Slow
Ori B, Fast

Ori A, Fast
Ori B, Slow

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mask_mte.ai
Comparison of STA width for Fast vs. Slow Components

n = 8 V1 DS neurons
Data collected in Kohn Lab.

Coloured pairs show two results from the same cell (ori1 fast vs ori2 slow; and ori2 fast vs ori1 slow)
Comparing Target and Mask STAs

Multitemporal encoding
Noisy input to leaky integrate-and-fire unit

random binary noise

+ GWN

LIF unit

spike train

Rate (spikes/s)
0 20 40
Mean, \( \mu \) (nS)
0 20 40
SD, \( \sigma \) (nS)
0 20 40

Input

0

Rate (spikes/s)
0 20 40
Mean, \( \mu \) (nS)
0 20 40
SD, \( \sigma \) (nS)
0 20 40

Time relative to spike (ms)

0

Low noise

High noise
Multitemporal Encoding in Models

Linear integrate and fire, with binary, white noise inputs

Low SD → + → LIF → High SD

- Low SD isolated
- Low SD combined
- High SD isolated
- High SD combined

STA Amplitude

Time (ms)
Multitemporal Encoding in Models

Linear integrate and fire, with binary, white noise inputs

Spiking network of conductance-driven leaky I & F neurons

Low SD
High SD

Low SD isolated
Low SD combined
High SD isolated
High SD combined
Visual motion pathway, retina to V1

**Primary Visual Cortex**
- Layer 4C
- LGN (Relay cells)

**Retina**
- Ganglion
- Bipolar
- Horizontal
- Photorec.

**Visual Stimuli**

**Receptive fields**
- Direction selective
- Orientation selective
- Unoriented
- Center-surround
- Spot

**How could ATI arise?**
- Changes in the retina
- Cortical normalization
- Adaptation at the soma
- Non-linear interaction at spike generation
- Parallel pathways: convergence of fast and slow channels

**ATI is channel specific.**
**Multitemporal encoding in DS neurons.**
Summary

Channel-specific control of temporal integration

No evidence for cortical normalization

Multitemporal encoding - the multiplexing of distinct temporal signals, reflected in the spike discharge of a single neuron

A parallel pathway model can account for the data.
A principled approach to modelling

**Modularity** - local representation of computation
**Emulation** - responses resemble those recorded in major cell classes
**Applicability** - accept arbitrary, time-varying stimuli
**Accessibility** - available on the web, fast computation is cheap

Online: [www.iModel.org](http://www.iModel.org)
Spiking Units

Conductance-driven leaky integrate-and-fire (LIF) units

\[
C \frac{dV}{dt} = g_{\text{ex}}(V_{\text{ex}} - V) + g_{\text{in}}(V_{\text{in}} - V) + g_{\text{leak}}(V_{\text{rest}} - V)
\]

Noise is added to \( g \)’s

Non-linear interactions between “dendritic” inputs
A circuit implementation for building V1 DS neurons
A circuit implementation for building V1 DS neurons

- Populations of conductance-driven spiking units
- Physiological RF attributes: ON/OFF, orientation, spatial frequency & phase
- Physiologically realistic synaptic time course
- Driven by a wide variety of visual stimuli
Creating Direction Selectivity

Direction tuning curve

Direction of motion (deg)
Creating Direction Selectivity

**Direction tuning curve**

Direction of motion (deg)

**Reichardt mechanism**

Reichardt (1957)
Creating Direction Selectivity

**Direction tuning curve**

**Reichardt mechanism**

Reichardt (1957)

- anti-pref.
- preferred

Direction of motion (deg)
Creating Direction Selectivity

Direction tuning curve

Reichardt mechanism
Reichardt (1957)

Tilted X-T filter
Adelson & Bergen (1985)
Creating Direction Selectivity

Direction tuning curve

Reichardt mechanism
Reichardt (1957)

Tilted X-T filter
Adelson & Bergen (1985)
Creating Direction Selectivity

**Direction tuning curve**

Direction of motion (deg)

**Reichardt mechanism**

Reichardt (1957)

- preferred
- anti-pref.
Creating Direction Selectivity

**Direction tuning curve**

Direction of motion (deg)

**Reichardt mechanism**
Reichardt (1957)

anti-pref.  preferred

**Network implementation**

Torre and Poggio, 1978
Koch, Poggio & Torre, 1983
Polsky et al., 2004
Presynaptic Delay: Delay in Inputs

Temporal diversity in V1 and LGN
Adelson and Bergen (1985)
De Valois and Cottaris (1998)

LGN temporal filters

20 ms

Single-filter DS model
Postsynaptic Delay: Delay in Dendrites

Non-linear subunit

Delay

IN → EX
LGN

Subunit interaction

20 ms

mask

DS

Dendritic subunits

Torre and Poggio, 1978
Branco et al., 2010

ds_post.ai
Comparing models with pre- and postsynaptic DS delays
Comparing models with pre- and postsynaptic DS delays

Drifting Gratings

Direction

Temporal Frequency

Postsynaptic Delay

Presynaptic Delay

DS

EX

LGN

DS

EX

LGN
Comparing models with pre- and postsynaptic DS delays

Drifting Gratings

1D White Noise

Direction

Temporal Frequency

Firing Rate

DS

LGN

EX

EX

Postsynaptic Delay

Presynaptic Delay
Model Demo
Multitemporal Encoding in Models

Linear integrate and fire, with binary, white noise inputs

Low SD → I → LIF → High SD

Spiking network of conductance-driven leaky I & F neurons

Low SD isolated
- Low SD combined
- High SD isolated
- High SD combined

DS Cell

Slow Target (6 Hz)
Fast Target (25 Hz)

High TF Channel Narrow Kernel
Low TF Channel Broad Kernel

STA Amplitude

Time (ms)

E

Ori A, Slow
Ori B, Fast

Ori A, Fast
Ori B, Slow

STA Amplitude

Time (ms)
**DS_Post_Fac**
Direction Selective, Post-Synaptic, Faculatory

**Summary**
Complex direction selective (DS) cells are created within a spiking network model from pair-wise interactions of spiking inputs from non-DS, orientation-tuned simple cells. The DS interaction involves (i) cell pairs with spatial RFs that are phase-offset by about 90 deg, (ii) a temporal delay that is implemented post-synaptically (relative to the synapse at the transformation from non-DS to DS), and (iii) a facilitatory interaction. This is a hierarchical model containing four distinct populations of spiking units: LGN (ON and OFF center), V1 simple inhibitory, simple excitatory, and complex DS. The spiking cells are conductance-driven integrate and fire units modeled on those of Troyer et al. (1998)

**Results**
To be added. Under development. Apr 2010.

**References**

(A) Organization of the four populations of spiking units: LGN-lateral geniculate nucleus, IN-inhibitory V1 simple cells, EX-excitative V1 simple cells, DS-direction selective V1 cells.

(B) A population of four V1 DS complex cells.

(C) Within a 12,12,4 (x,y,z) lattice of V1 inhibitory simple cells (IN), cells in the 3rd z-layer that are presynaptic to the white-circled cell in (D) are shown in color. Colors indicate preferred orientation (see orientation key between panels C and D).

(D) The 12,12,4 lattice of V1 excitatory simple cells (EX) is shown where color indicates orientation (see orientation key). The white-circled cell gets IN inputs as marked in (C) and
iModel Tools

Model Viewer

Response Viewer / Analyzer

Synaptic weight patterns

Stimulus Editor/Player

Neuronal responses: action potentials
Summary

We developed a set of spiking network models for DS circuits motivated by several popular theories.

The models offer insight for developing experimental solutions to some of the fundamental questions about DS neurons.

We are developing interactive tools to make it easy for others to explore and test the models.
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