

# Outline

1. Introduction to neural circuits
2. Computational roles of feedback signals
3. Open questions, challenges, opportunities

# Biologically-inspired computation

*Claim (without proof):*

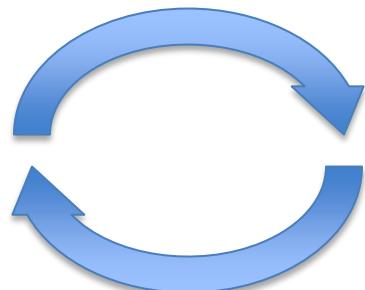
*over millions of years of evolution, “interesting” solutions to difficult problems have emerged through changes in neuronal circuits*

Theories

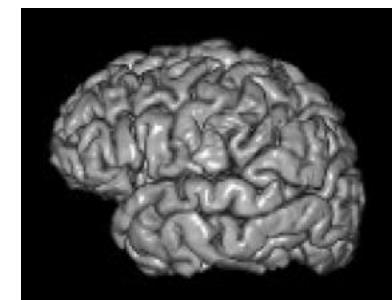
Technology developments

Computational models

Tools, models,  
hardware



Algorithms,  
solutions



Listening to neuronal  
circuits

Decoding activity

Writing-in information

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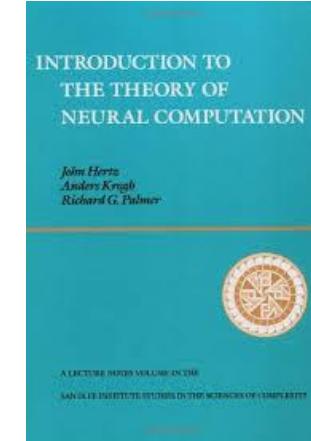
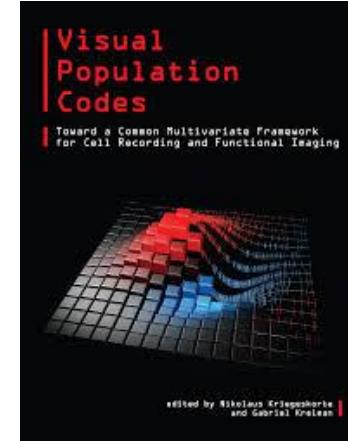
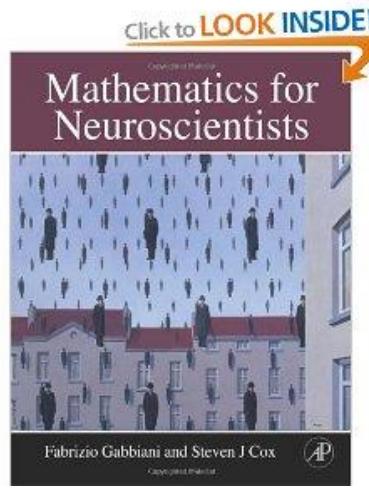
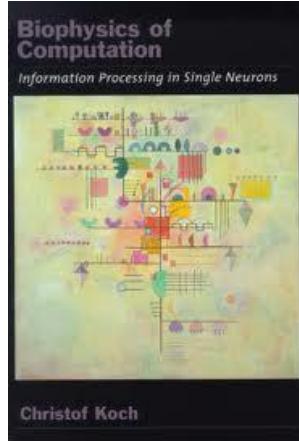
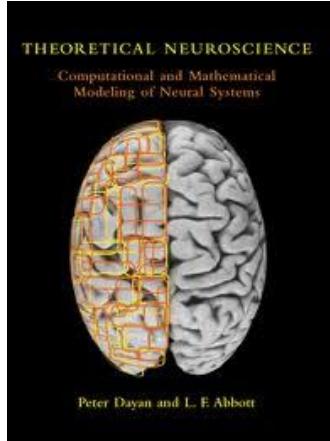
# Some features of brain-based computations

- Hardware and software that work for many decades
- Parallel computation (with serial bottlenecks)
- Reprogrammable architecture
- Single-shot learning
- “Discover” structure in data
- Fault tolerance
- Robustness to sensory transformations
- Component interaction and integration of sensory modalities

# Why study neural circuits?

- We can begin to explore high-level at the neural circuit level
- Golden age for neural circuits: opportunity to manipulate, disrupt and interact with neural circuits at unprecedented resolution
- Theories can be rigorously tested at the neural level
- Empirical findings can be readily translated into algorithms

# Recommended books



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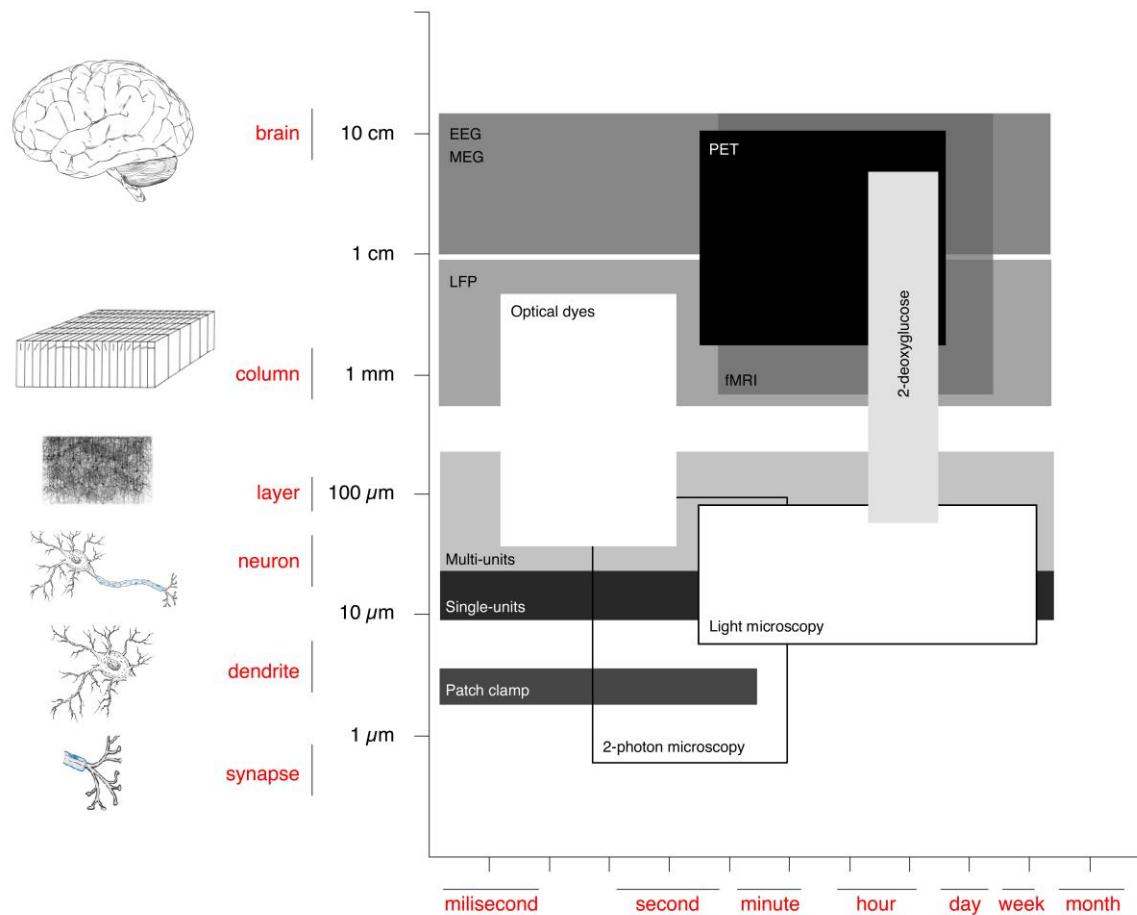
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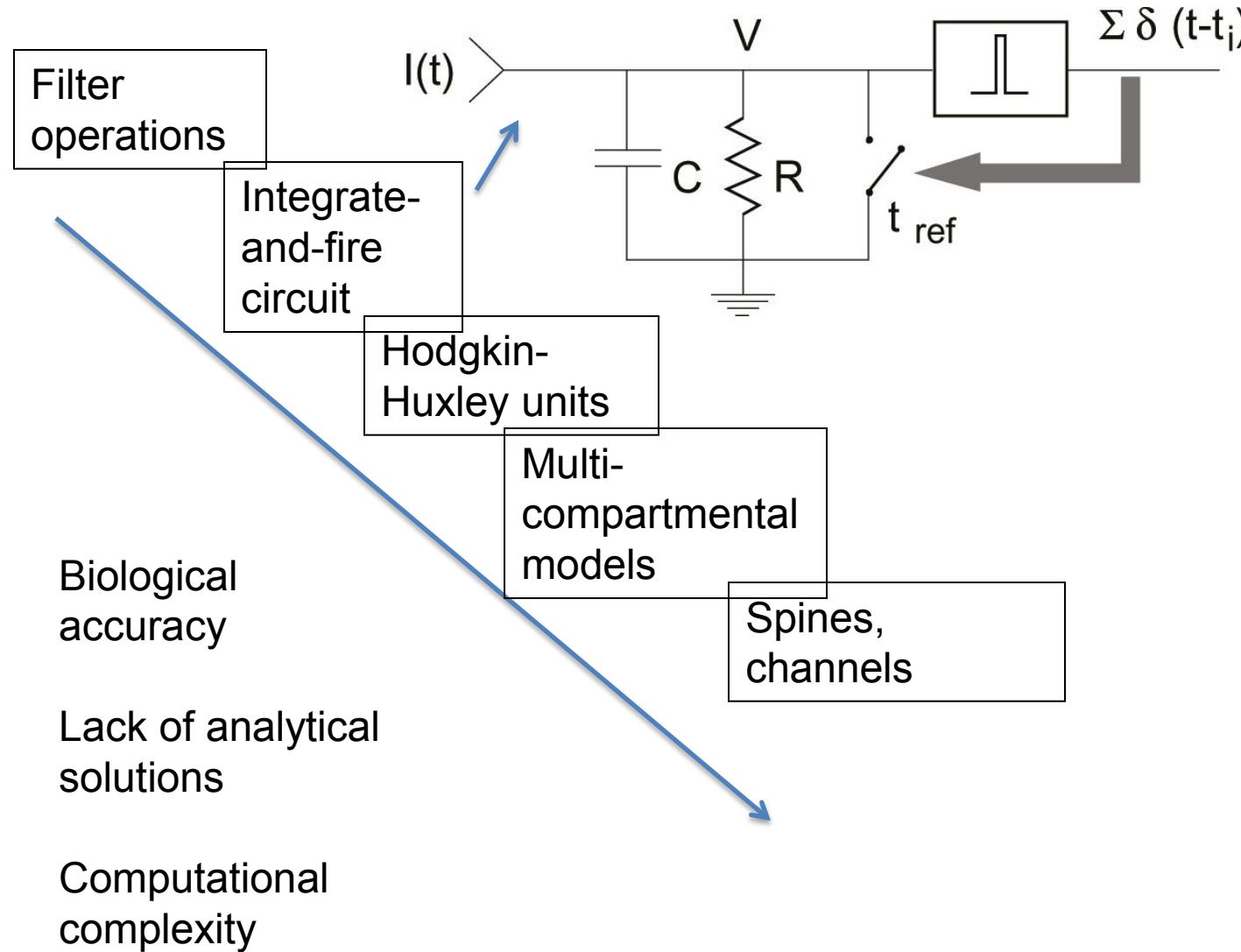
- Abbott and Dayan. Theoretical Neuroscience - Computational and Mathematical Modeling of Neural Systems [2001] (ISBN 0-262-04199-5). MIT Press.
- Koch. Biophysics of Computation [1999] (ISBN 0-19-510491-9). Oxford University Press.
- Gabbiani and Cox. Mathematics for Neuroscientists. [2010] (ISBN 978-0-12-374882-9). Academic Press.
- Kriegeskorte and Kreiman. Visual Population Codes. [2010] (ISBN 9780262016247). MIT Press.
- Hertz, Krogh, and Palmer. Introduction to the Theory of Neural Computation. [1991] (ISBN 0-20151560-1). Santa Fe Institute Studies in the Sciences of Complexity.

# Methods to study the brain at different scales

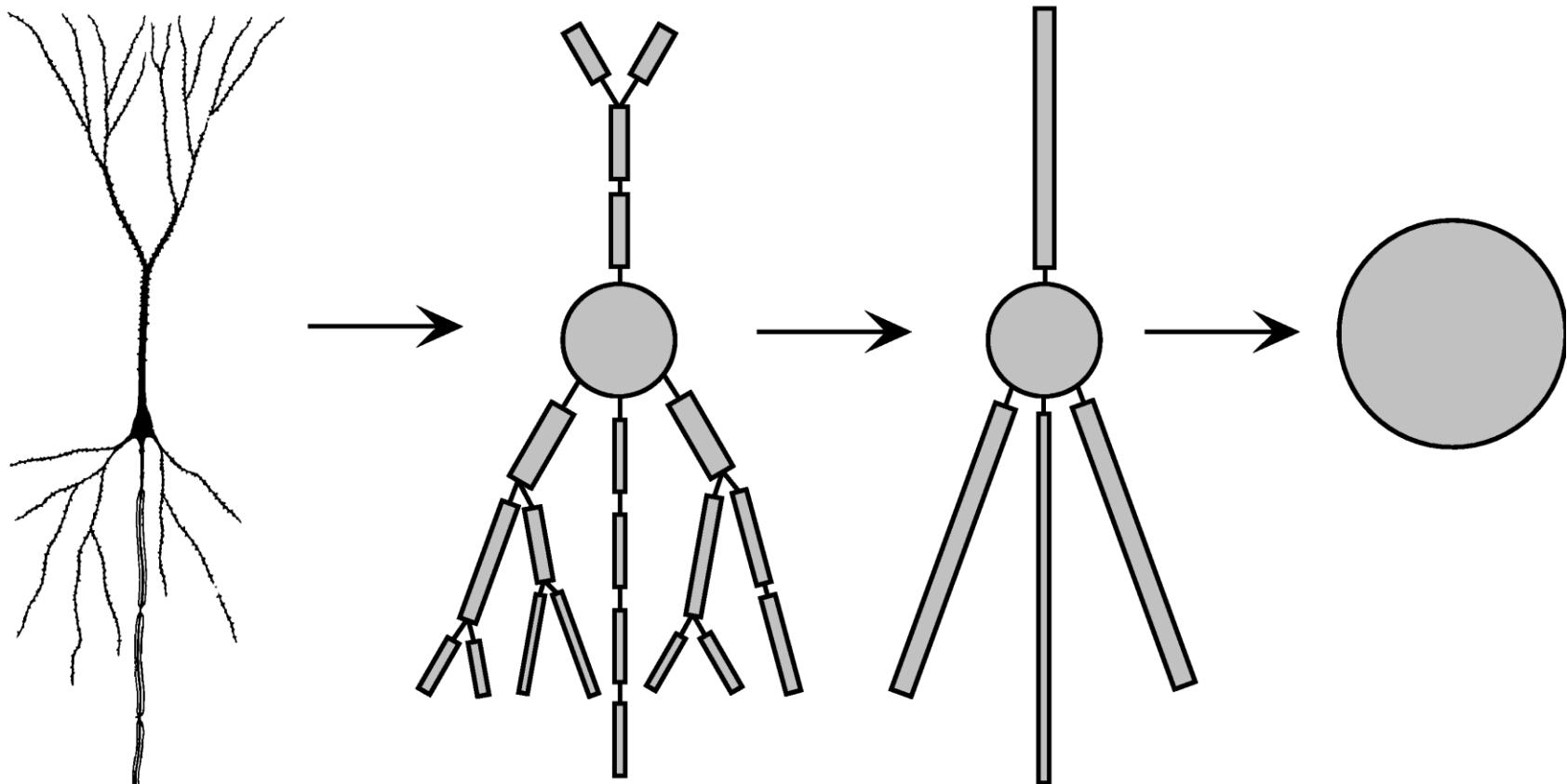


Courtesy of Elsevier, Inc., <http://www.sciencedirect.com>. Used with permission.  
Source: Kreiman, Gabriel. "Neural coding: computational and biophysical perspectives." Physics of Life Reviews 1, no. 2 (2004): 71-102.

# Simulating single neurons: A nested family of models



# Geometrically accurate models vs. spherical cows with point masses



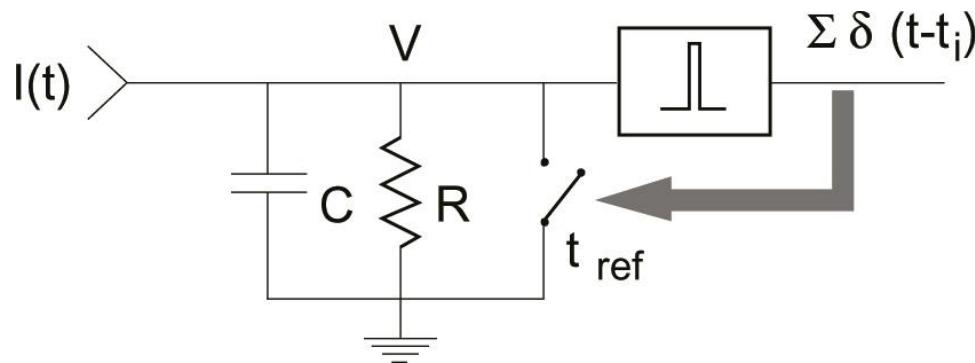
A central question in Theoretical Neuroscience:  
What is the “right” level of abstraction?

# The leaky integrate-and-fire model

- Lapicque 1907
- Below threshold, the voltage is governed by:

$$C \frac{dV(t)}{dt} = -\frac{V(t)}{R} + I(t)$$

- A spike is fired when  $V(t) > V_{thr}$  (and  $V(t)$  is reset)
- A refractory period  $t_{ref}$  is imposed after a spike
- Simple and fast
- Does not consider:
  - spike-rate adaptation
  - multiple compartments
  - sub-ms biophysics
  - neuronal geometry



# Leaky I&F neurons: a simple implementation

```
function [V,spk]=simpleiandf(E_L,V_res,V_th,tau_m,R_m,I_e,dt,n)

% ultra-simple implementation of integrate-and-fire model
% inputs:
% E_L = leak potential [e.g. -65 mV]
% V_res = reset potential [e.g. E_L]
% V_th = threshold potential [e.g. -50 mV]
% tau_m = membrane time constant [e.g. 10 ms]
% R_m = membrane resistance [e.g. 10 MΩ]
% I_e = external input [e.g. white noise]
% dt = time step [e.g. 0.1 ms]
% n = number of time points [e.g. 1000]
%
% outputs:
% V = intracellular voltage [n x 1]
% spk = 0 or 1 indicating spikes [n x 1]
```

```
V(1)=V_res; % initial voltage
spk=zeros(n,1);
for t=2:n
    V(t)=V(t-1)+(dt/tau_m) * (E_L - V(t-1) + R_m * I_e(t)); % Change in voltage at time t
    if (V(t)>V_th)
        V(t)=V_res;
        spk(t)=1;
    end
end
```

$$C \frac{dV(t)}{dt} = -\frac{V(t)}{R} + I(t)$$



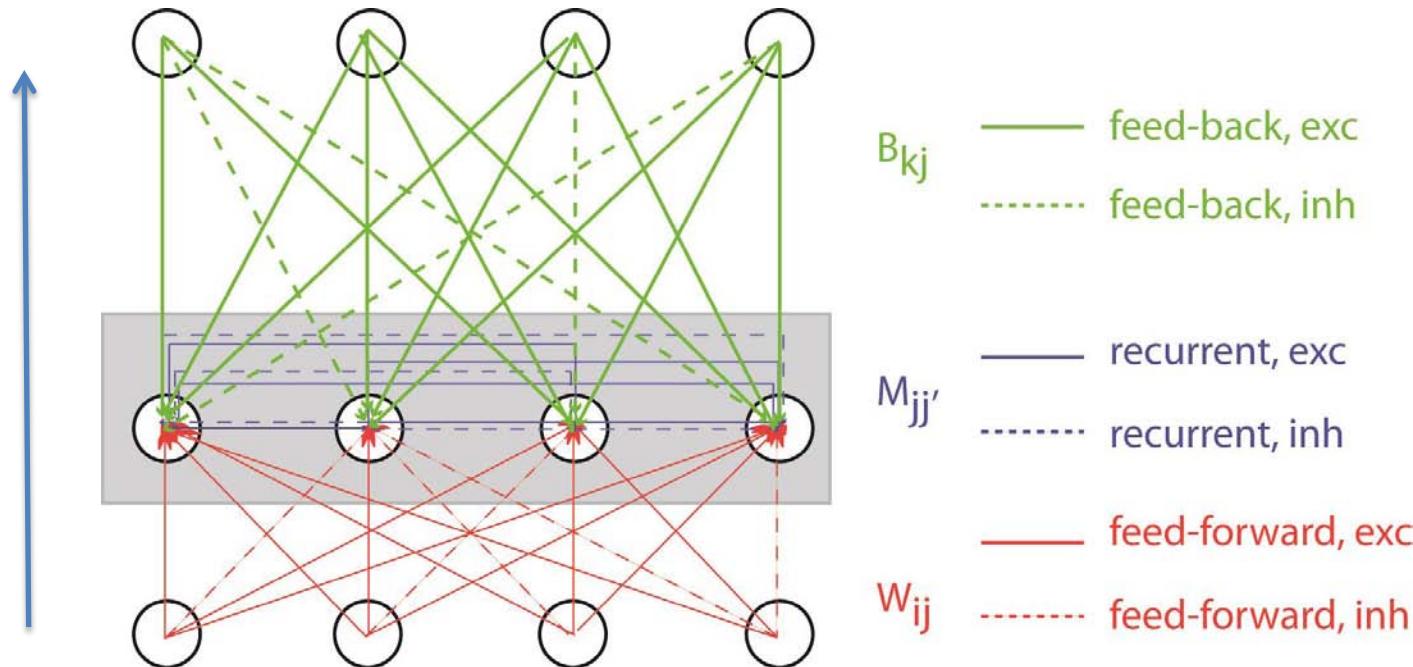
All of these lines are comments



This is the key line integrating the differential equation

```
% Emit a spike if V is above threshold
% And reset the voltage
```

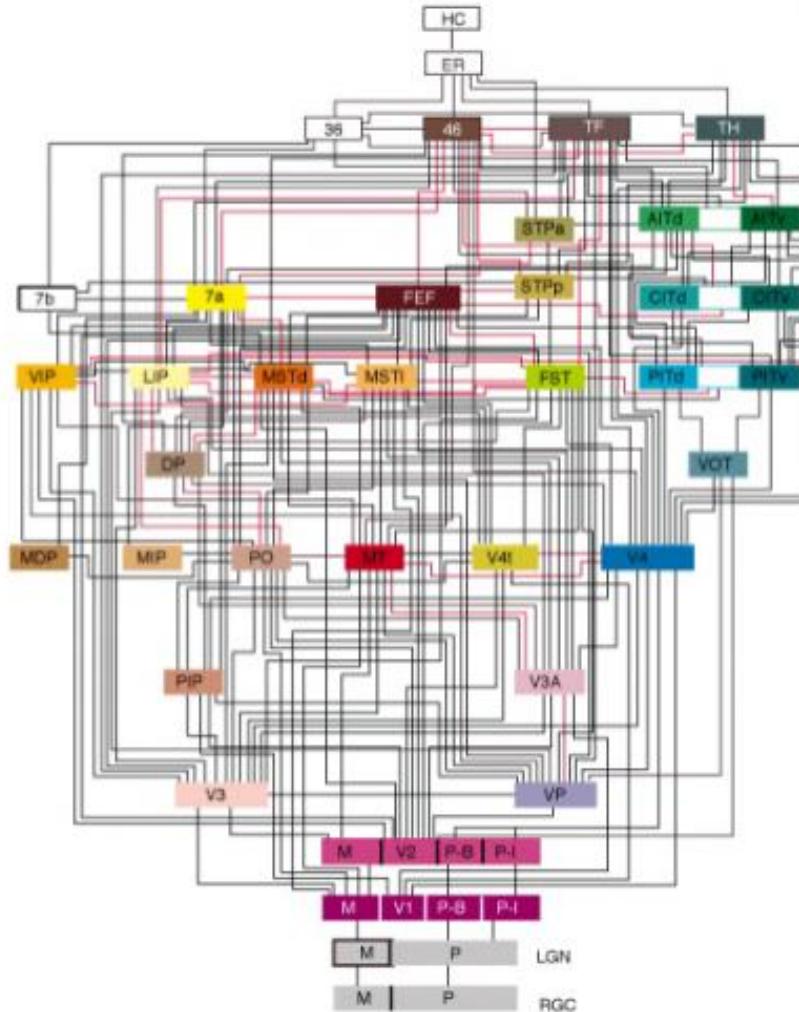
# Circuits – some basic definitions



Notes:

1. Connectivity does not need to be all-to-all
2. There are excitatory neurons and inhibitory neurons (and many types of inhibitory neurons)
3. Most models assume balance between excitation and inhibition
4. Most models do not include layers and the anatomical separation of forward and back pathways
5. There are many more recurrent+feedback connections than feed-forward connections (the opposite is true about models...)

# The visual system shows an approximately hierarchical architecture

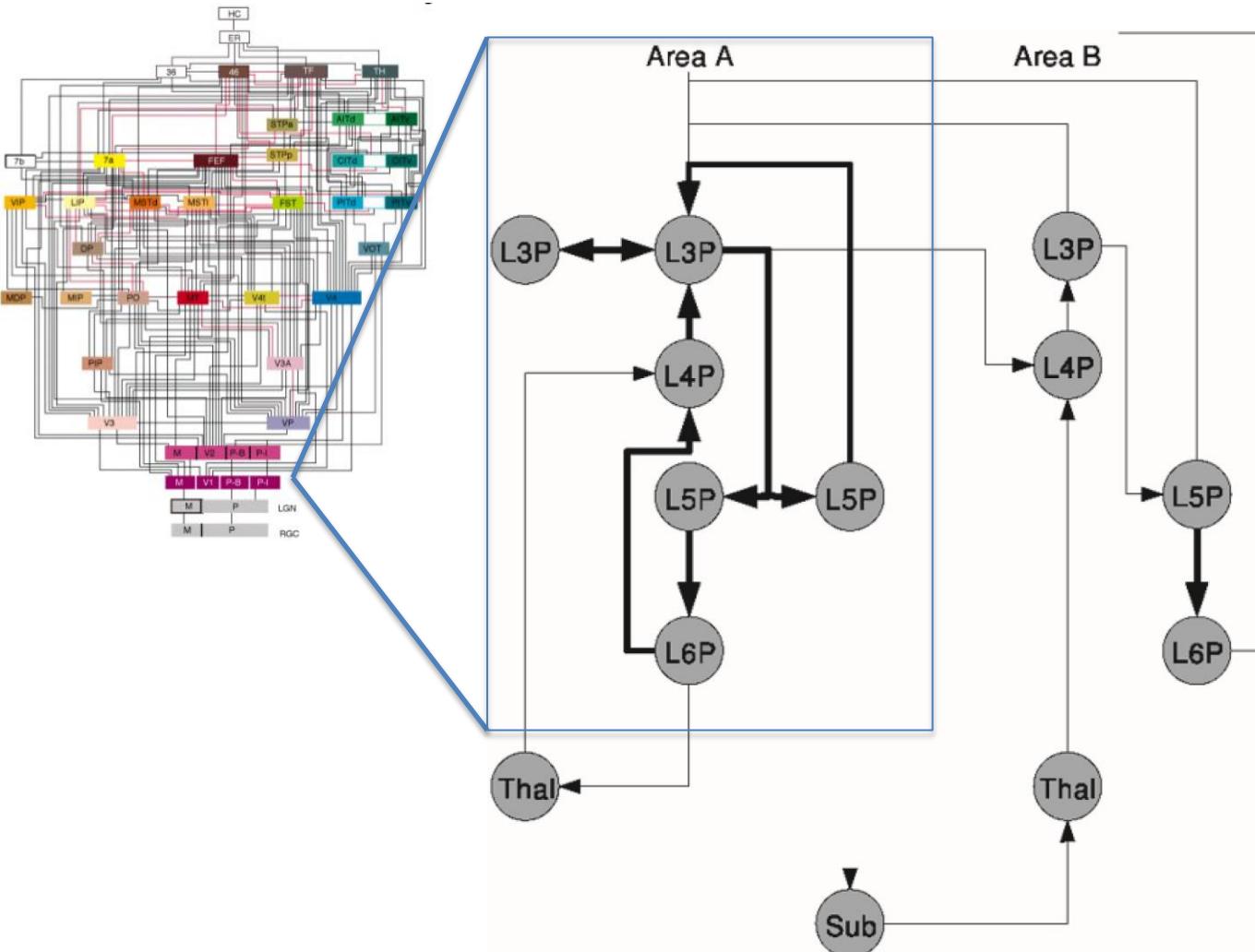


Felleman and Van Essen 1991

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Source: Felleman, Daniel J., and David C. Van Essen. "Distributed hierarchical processing in the primate cerebral cortex." *Cerebral cortex* 1, no. 1 (1991): 1-47.

# And a canonical microcircuit structure within each area



Douglas and Martin 2004

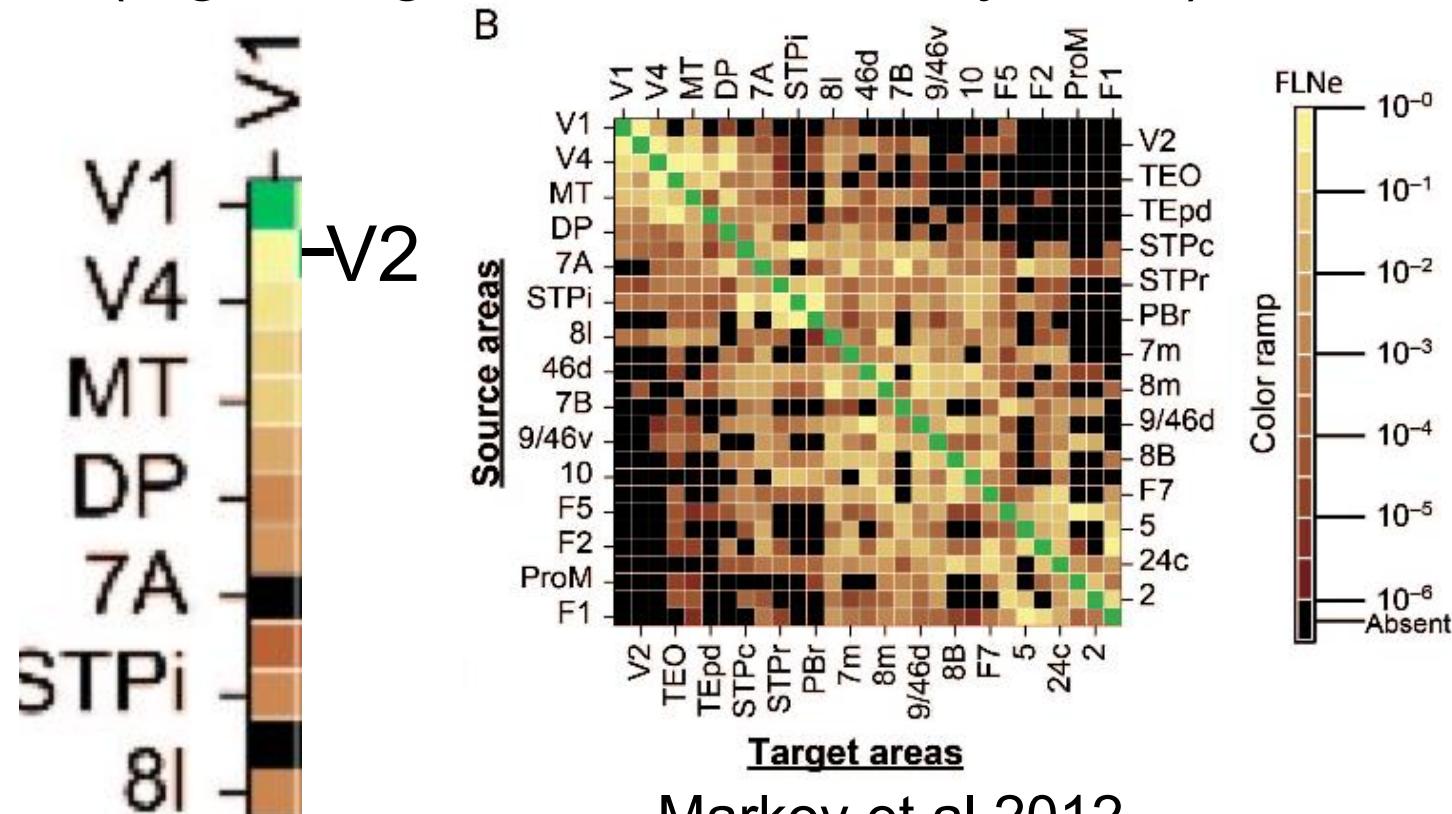
© Annual Reviews of Neuroscience. All rights reserved. This content is excluded from our Creative Commons license. For more information, see <https://ocw.mit.edu/help/faq-fair-use/>.  
Source: Douglas, Rodney J., and Kevan AC Martin. "Neuronal circuits of the neocortex." *Annu. Rev. Neurosci.* 27 (2004): 419-451.

# First order approximation: “Immediate” recognition as a hierarchical feed-forward process

1. Behavior: We can recognize objects within ~150ms (e.g. Potter et al 1969, Thorpe et al 1996)
2. Physiology: Visually selective responses to complex shapes arise within ~150 ms (e.g. Keysers et al 2001, Hung et al 2005, Liu et al 2009)
3. Computation: Bottom up computational models perform relatively well in basic object recognition (e.g. Fukushima 1980, Riesenhuber and Poggio 1999)

# Why are there so many feedback connections?

There are more horizontal + top-down projections than bottom-up ones (e.g. Douglas 2004, Callaway 2004)



What are feedback signals doing?

When?

Why?

How?

Markov et al 2012

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Source: Markov, Nikola T., M. M. Ercsey-Ravasz, AR Ribeiro Gomes, Camille Lamy, Loic Magrou, Julien Vezoli, P. Misery et al. "A weighted and directed interareal connectivity matrix for macaque cerebral cortex." Cerebral cortex (2012): bhs270.

# Computational roles of feedback signals

1. Fundamental computations in V1
2. Visual search
3. Pattern completion

# Neurons in primary visual cortex show orientation tuning

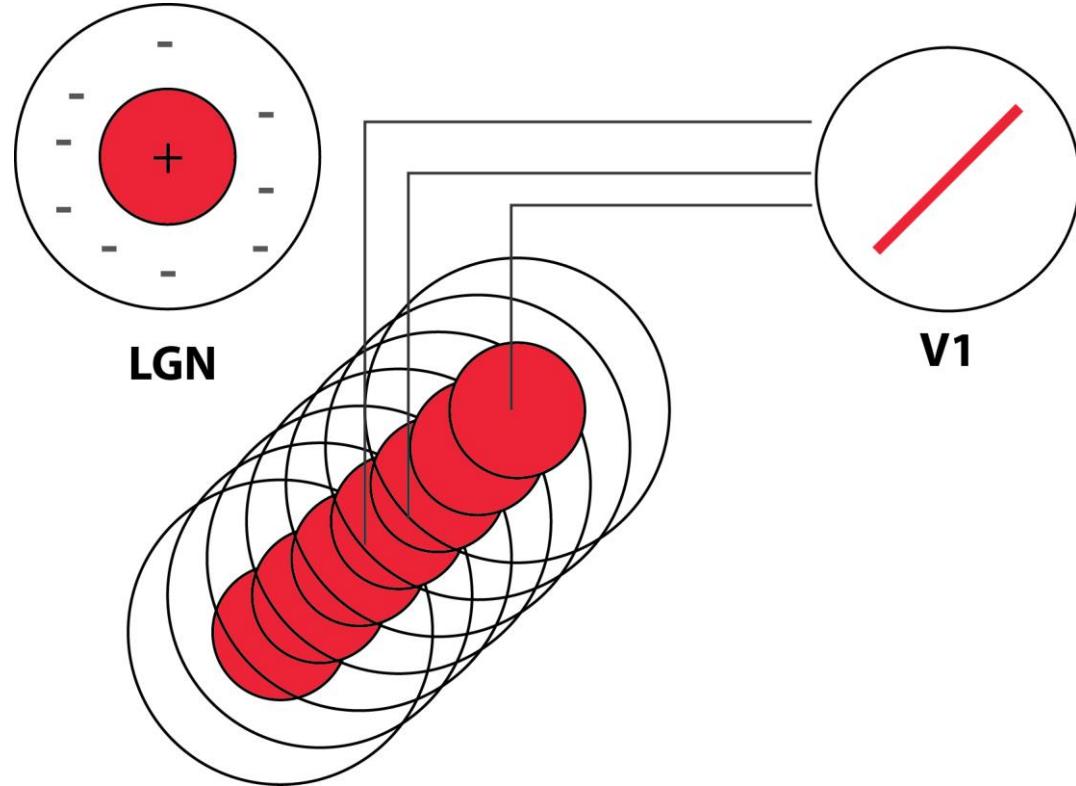
Gabor function

$$D(x,y) = \frac{1}{2\pi\sigma_x\sigma_y} \exp\left[-\frac{x^2}{2\sigma_x^2} - \frac{y^2}{2\sigma_y^2}\right] \cos(kx - \phi)$$

Image removed due to copyright restrictions. Please see the video.

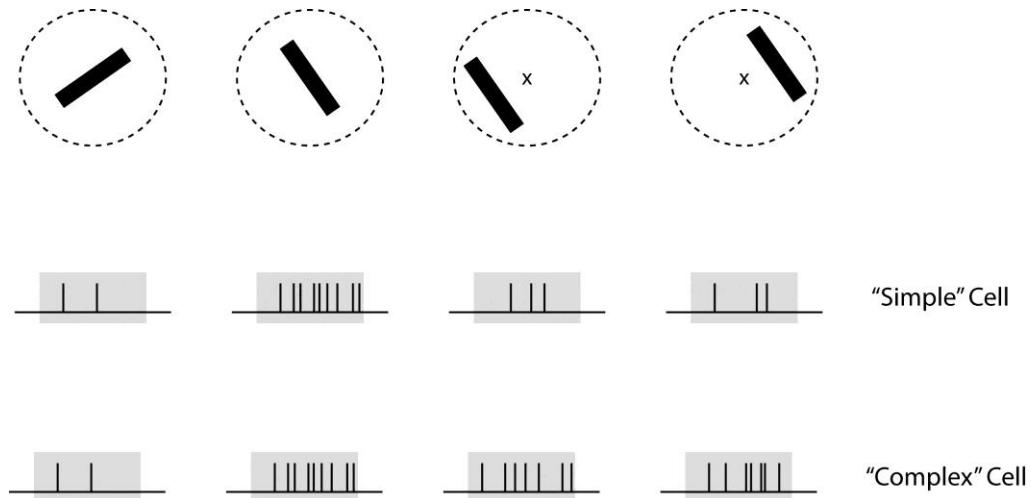
Source: Eye, Brain, and Vision. David H. Hubel. New York : Scientific American Library : Distributed by W.H. Freeman, c1988. ISBN: 0716750201.

# A simple model for simple cells



A feed-forward model for orientation selectivity in V1  
(by no means the only model)

# Complex cells show position tolerance



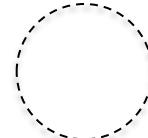
Stimulus: black bar

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Source: Hubel, David H., and Torsten N. Wiesel. "Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. "The Journal of physiology 160, no. 1 (1962): 106-154.

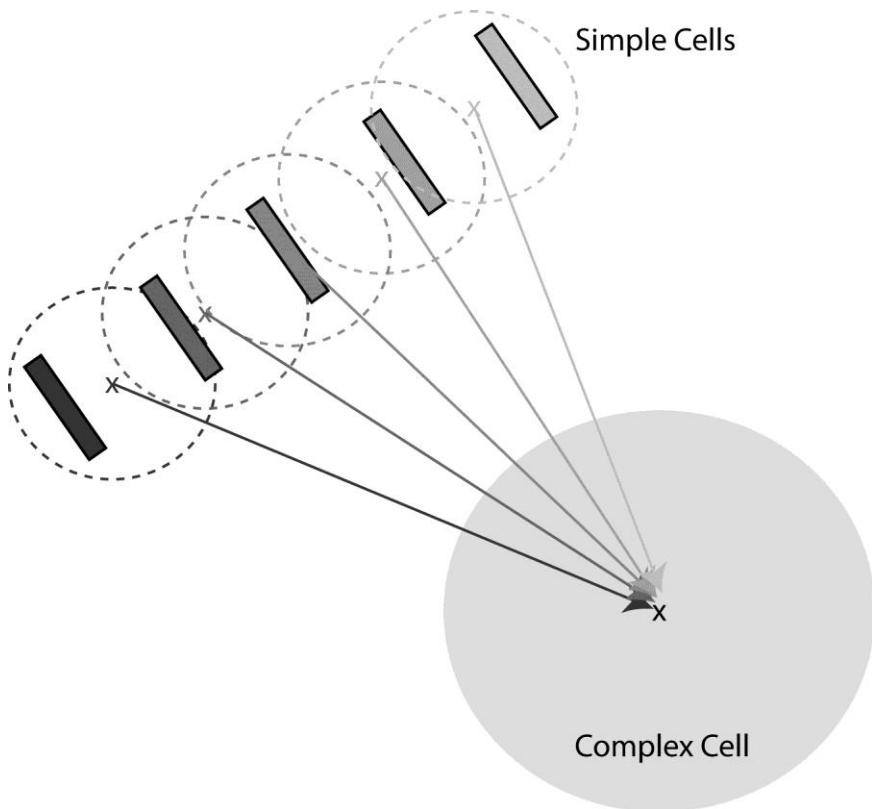


Stimulus presentation time



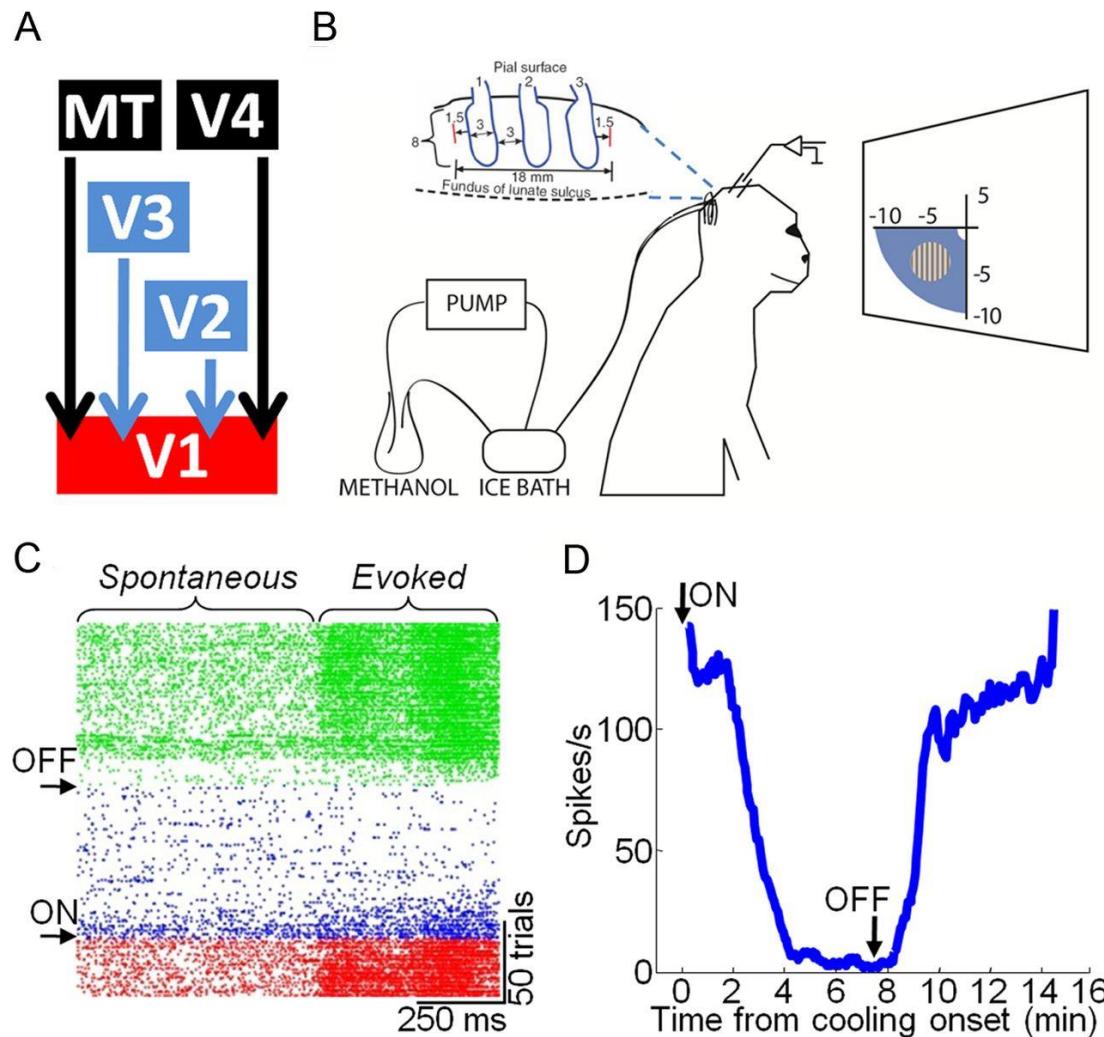
Receptive field

# A model to describe tolerance in complex cells



A feed-forward model  
describing the responses of  
complex cells arising from  
non-linear (e.g. OR, max)  
combination of inputs from  
multiple simple cells  
(by no means the only model)

# Reversible inactivation of V2/V3

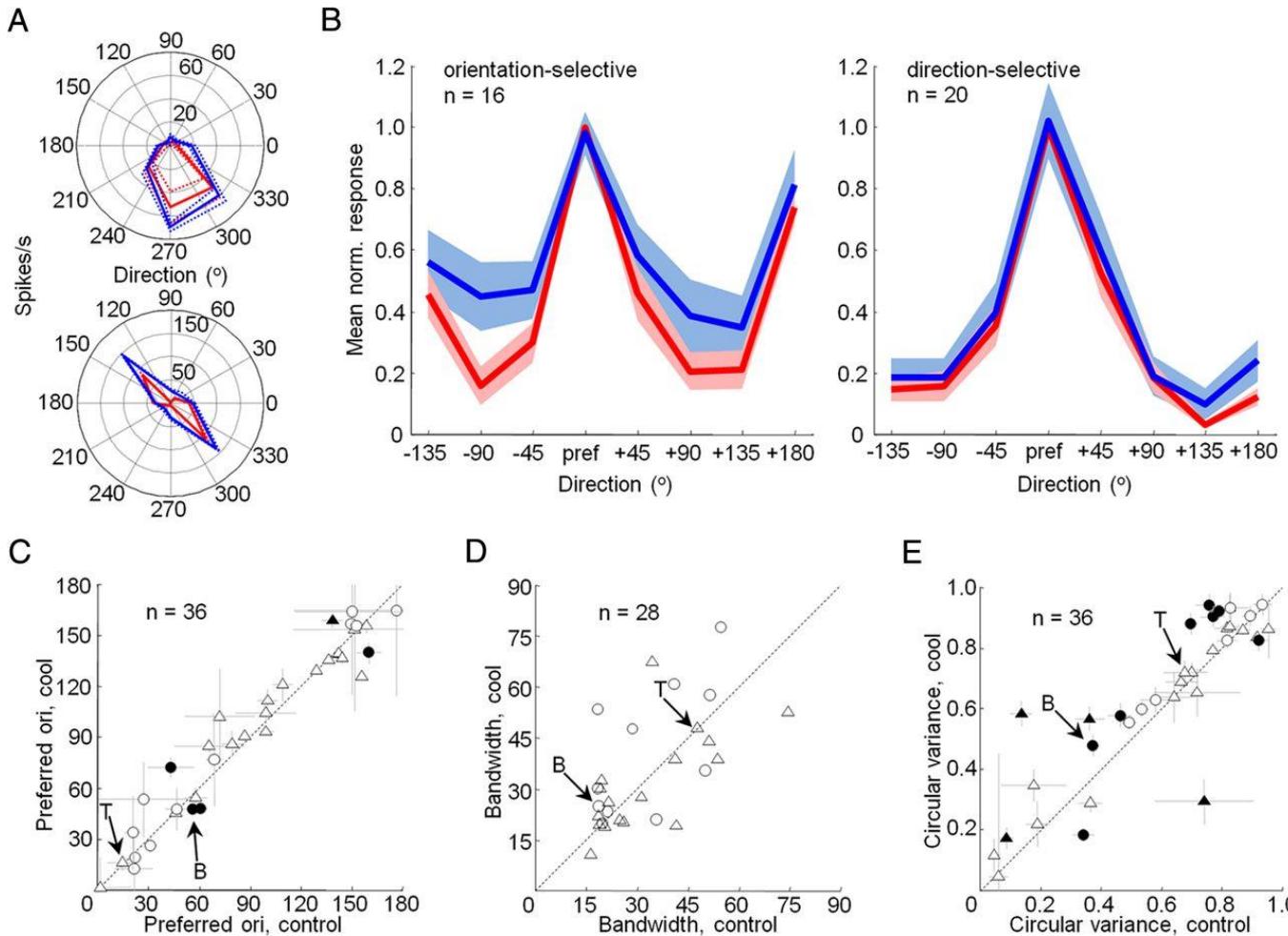


Courtesy of Society for Neuroscience. License CC BY NC SA.

Source: Nassi, Jonathan J., Stephen G. Lomber, and Richard T. Born.

"Corticocortical feedback contributes to surround suppression in V1 of the alert primate." *Journal of Neuroscience* 33, no. 19 (2013): 8504-8517.

# Feedback inactivation does not change orientation or direction selectivity



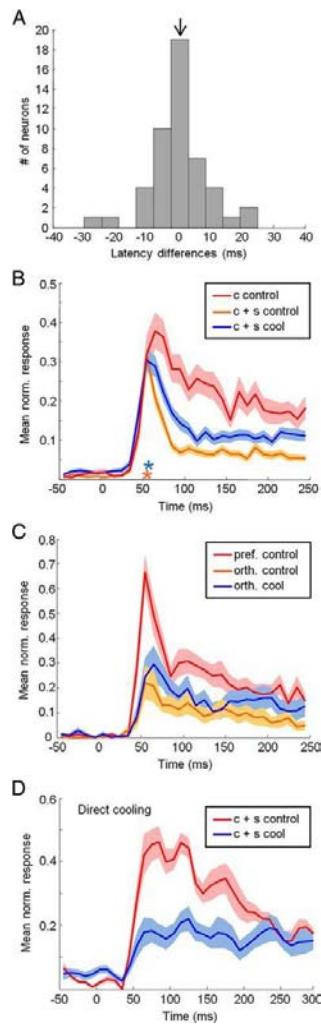
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Source: Nassi, Jonathan J., Stephen G. Lomber, and Richard T. Born.

"Corticocortical feedback contributes to surround suppression in V1 of the alert primate. "Journal of Neuroscience 33, no. 19 (2013): 85048517.

Nassi et al 2013

# Temporal dynamics of feedback inactivation effects

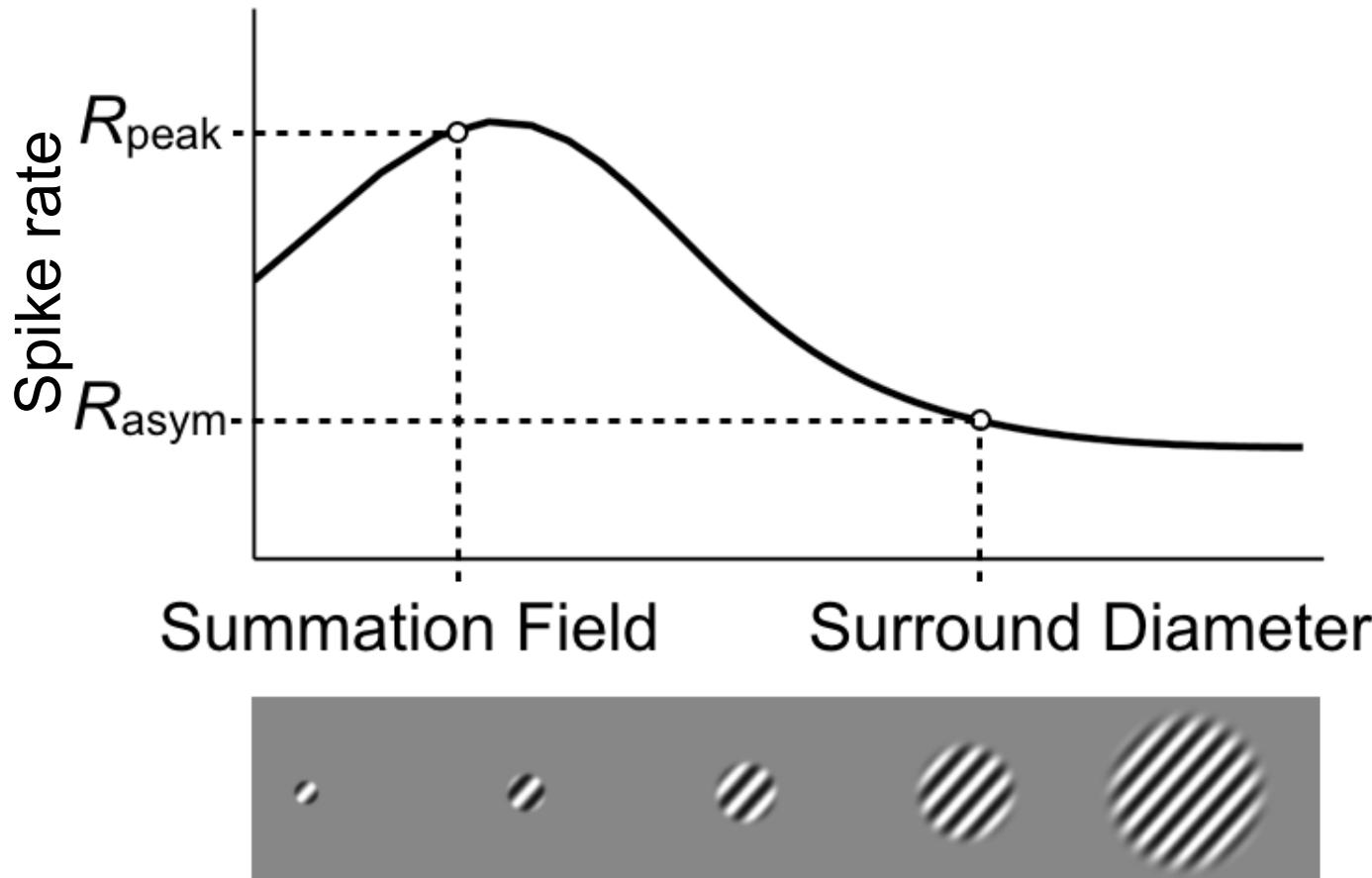


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Source: Nassi, Jonathan J., Stephen G. Lomber, and Richard T. Born.

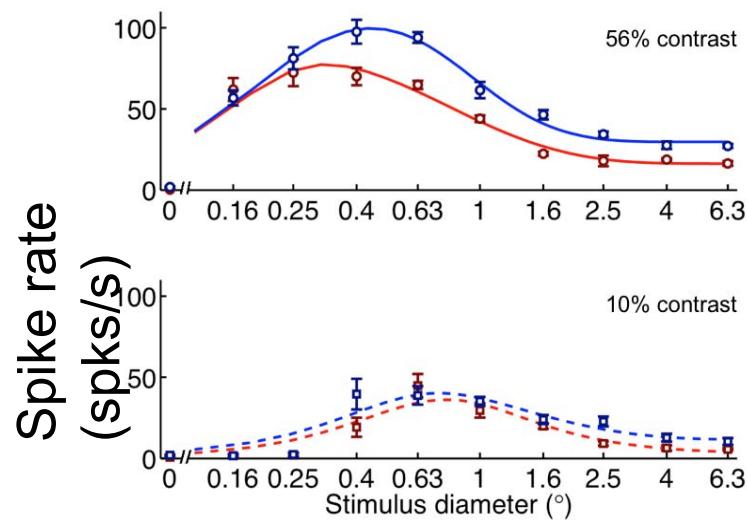
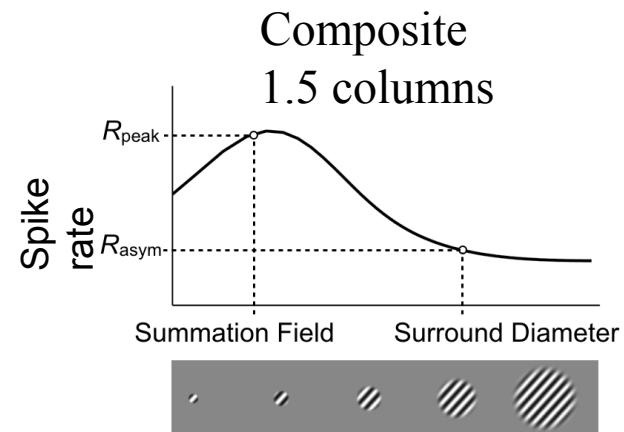
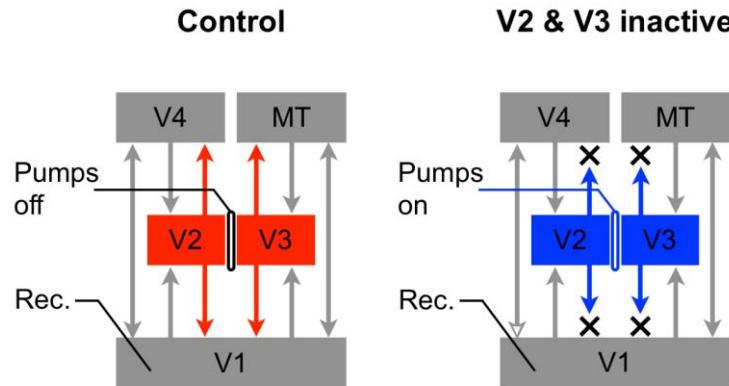
"Corticocortical feedback contributes to surround suppression in V1 of the alert primate. "Journal of Neuroscience 33, no. 19 (2013): 85048517.

# Area summation curve in V1



Courtesy of Frontiers in Systems Neuroscience. Used with permission.  
Source: Nassi, Jonathan J., Camille Gómez-Laberge, Gabriel Kreiman, and Richard T. Born. "Corticocortical feedback increases the spatial extent of normalization." *Frontiers in systems neuroscience* 8 (2014): 105.

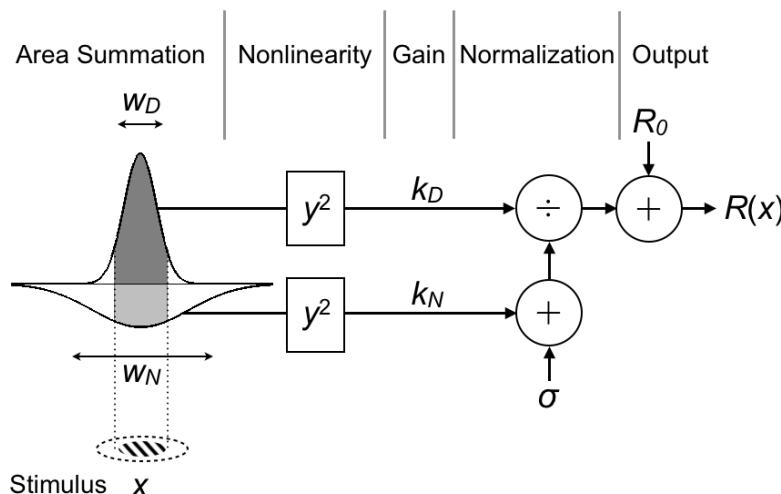
# Feedback inactivation leads to reduced surround suppression



Courtesy of Frontiers in Systems Neuroscience. Used with permission.

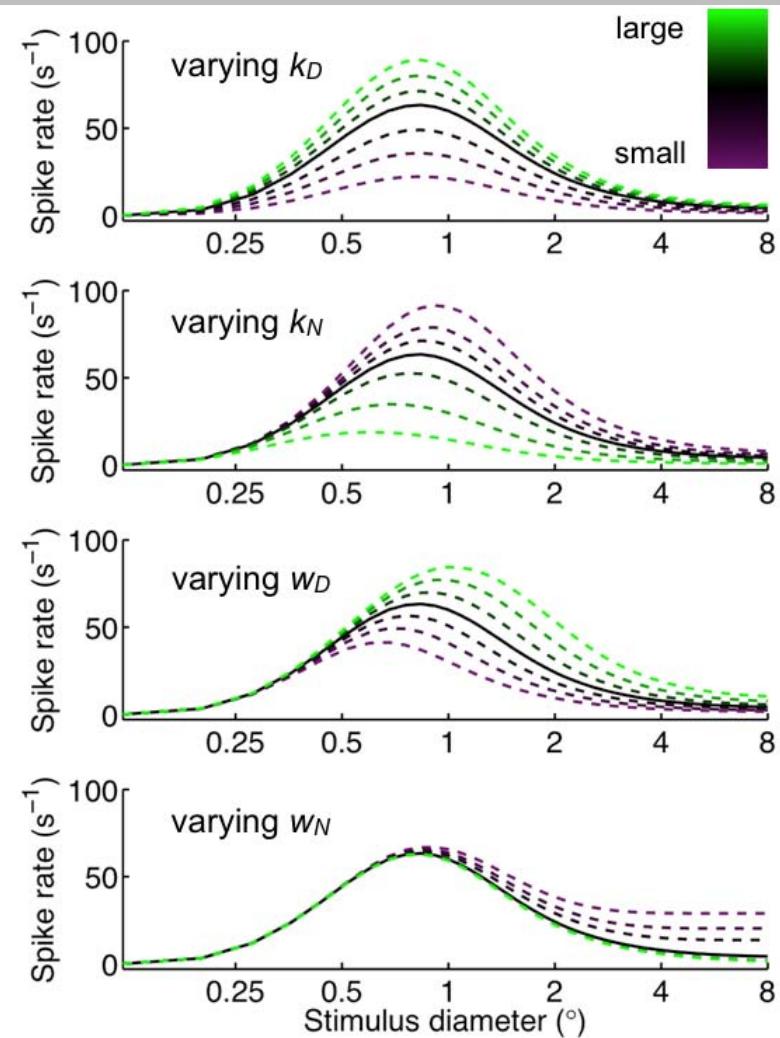
Source: Nassi, Jonathan J., Camille Gómez-Laberge, Gabriel Kreiman, and Richard T. Born. "Corticocortical feedback increases the spatial extent of normalization." *Frontiers in systems neuroscience* 8 (2014): 105.

# A simple normalization model to explain area summation curves



$$R_{ROG}(x) = R_0 + \frac{D(x)}{\sigma + N(x)}$$

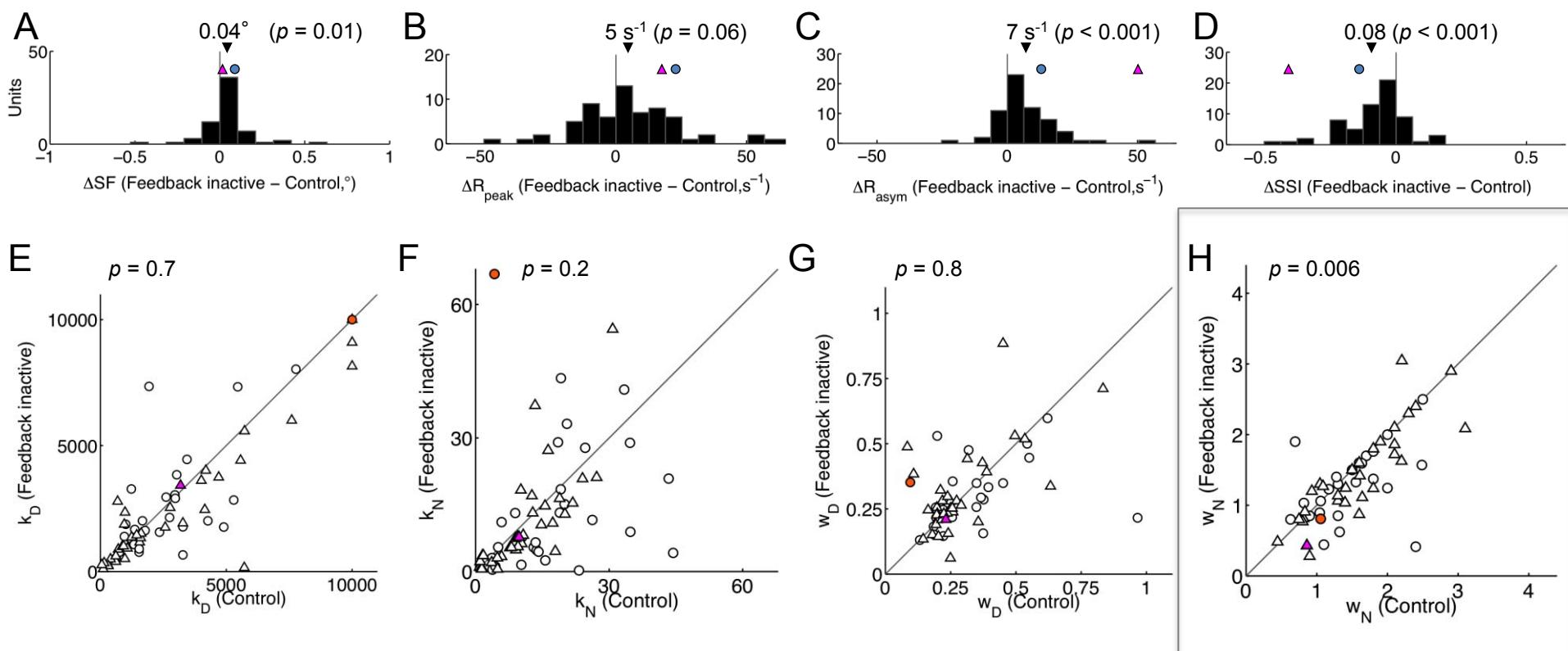
$$R_{ROG}(x) = R_0 + \frac{k_D [w_D \operatorname{erf}(x/2w_D)^2]}{\sigma + k_N [w_N \operatorname{erf}(x/2w_N)^2]}$$



Courtesy of Frontiers in Systems Neuroscience. Used with permission.

Source: Nassi, Jonathan J., Camille Gómez-Laberge, Gabriel Kreiman, and Richard T. Born. "Corticocortical feedback increases the spatial extent of normalization." *Frontiers in systems neuroscience* 8 (2014): 105.

# Feedback increases the normalization width: $w_N$



Courtesy of Frontiers in Systems Neuroscience. Used with permission.

Source: Nassi, Jonathan J., Camille Gómez-Laberge, Gabriel Kreiman, and Richard T. Born. "Corticocortical feedback increases the spatial extent of normalization." *Frontiers in systems neuroscience* 8 (2014): 105.

# Computational roles of feedback signals

1. Fundamental computations in V1
2. **Visual search**
3. Pattern completion

Picture of Waldo removed due to copyright restrictions

# Feedback signals in visual search

Figure removed due to copyright restrictions. Please see the video.

Source: Miconi, Thomas, Laura Groomes, and Gabriel Kreiman.

"There's Waldo! A normalization model of visual search predicts single-trial human fixations in an object search task."Cerebral Cortex (2015): bhv129.

# The model can search for objects in cluttered images

Figure removed due to copyright restrictions. Please see the video.  
Source: Miconi, Thomas, Laura Groomes, and Gabriel Kreiman.  
"There's Waldo! A normalization model of visual search predicts  
single-trial human fixations in an object search task."Cerebral  
Cortex (2015): bhv129.

# The model's performance is comparable to human performance in the same visual search task

Figure removed due to copyright restrictions. Please see the video.

Source: Miconi, Thomas, Laura Groomes, and Gabriel Kreiman.

"There's Waldo! A normalization model of visual search predicts single-trial human fixations in an object search task."Cerebral Cortex (2015): bhv129.

# Consistency metrics

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Source: Miconi, Thomas, Laura Groomes, and Gabriel Kreiman.

"There's Waldo! A normalization model of visual search predicts single-trial human fixations in an object search task."Cerebral Cortex (2015): bhw129.

# Computational roles of feedback signals

1. Fundamental computations in V1
2. Visual search
3. **Pattern completion**



Image by Hanlin Tang

Courtesy of Hanlin Tang. Used with permission.

# Inference and pattern completion as a hallmark of intelligence

A, C, E, G,



I

1, 2, 3, 5, 7, 11,



13

V-s-a- R-c-g-i-i-n



Visual Recognition

Even though it was raining heavily,  
Jonathan decided to go out without  
an



Umbrella

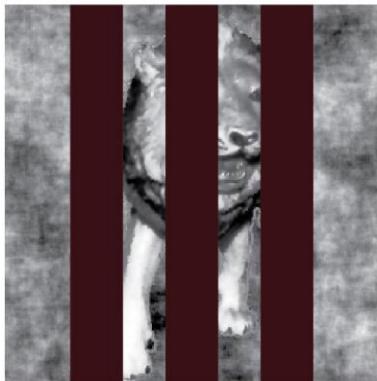
Also:  
**Other sensory modalities**  
**Music**  
**Social interactions**

# Objects can be recognized from partial information

a



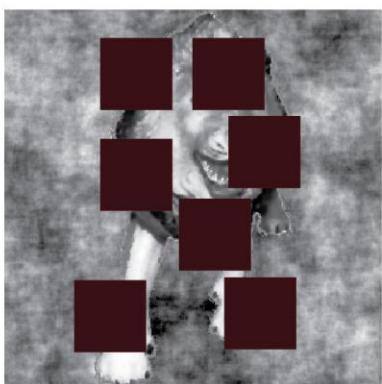
b



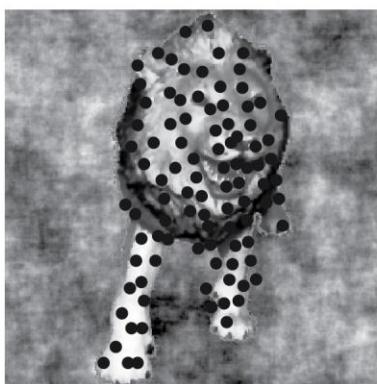
c



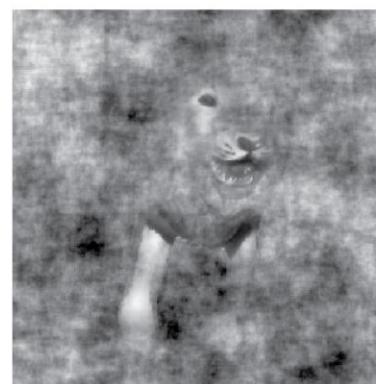
d



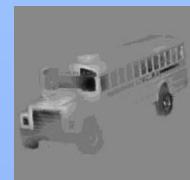
e



f



20 bubbles



10 bubbles



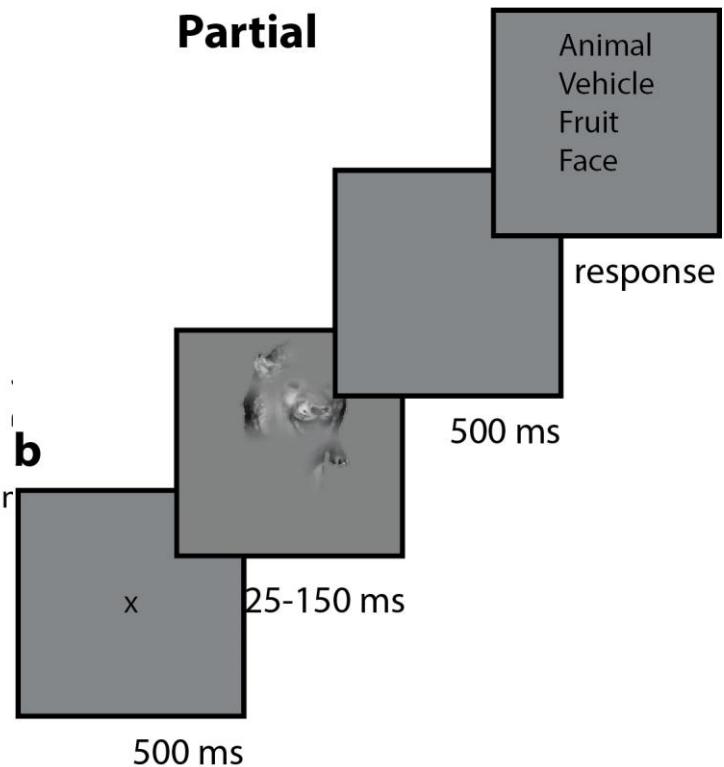
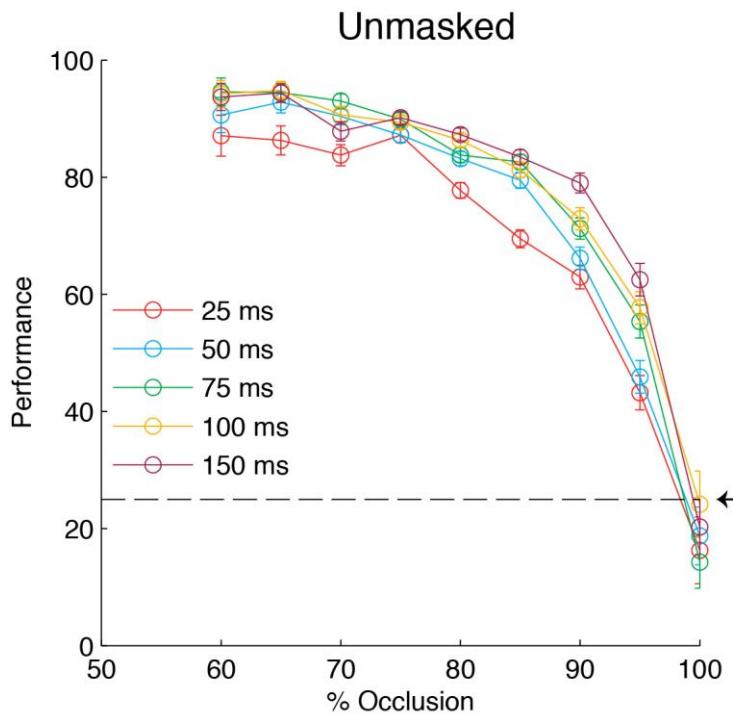
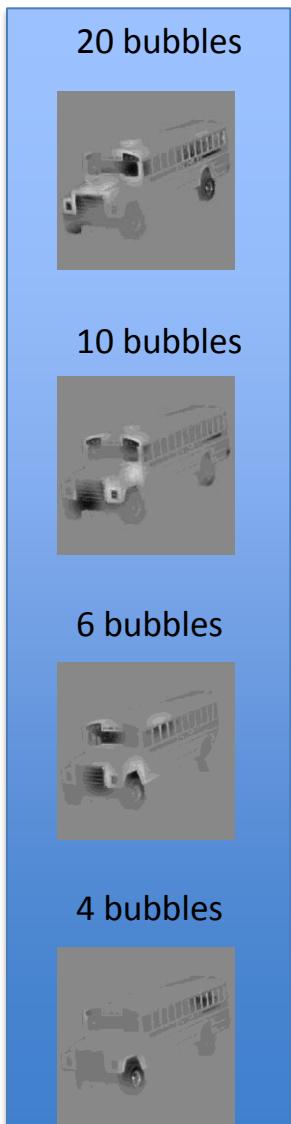
6 bubbles



4 bubbles



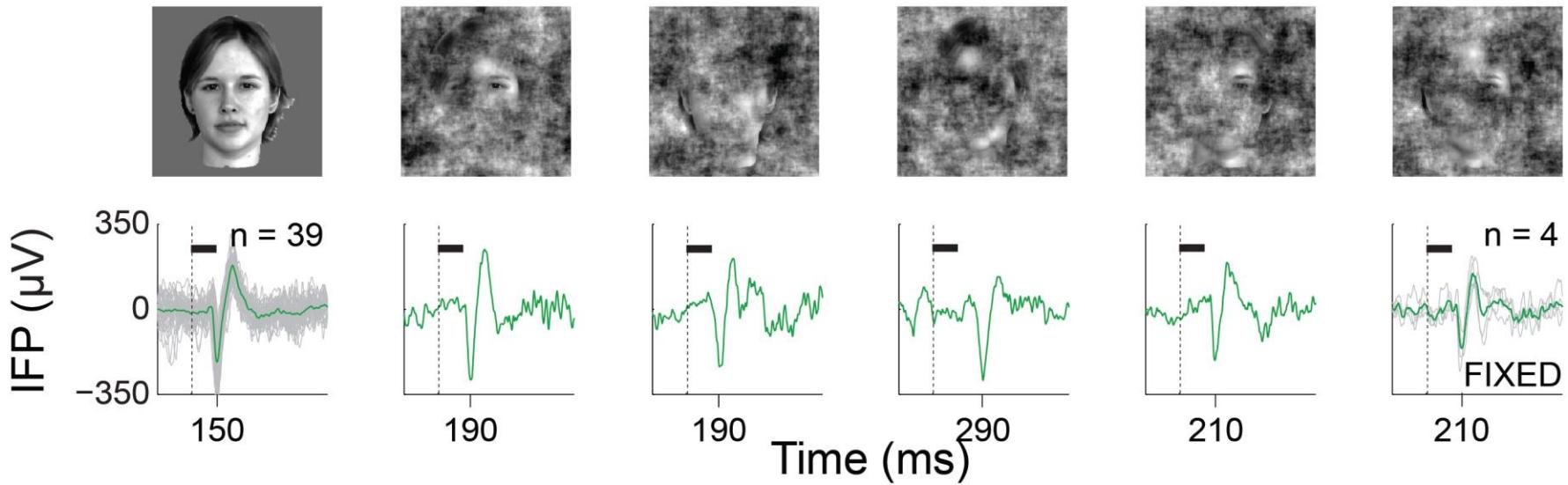
# Behavior: Robustness to presentation of partial image information



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# Example responses during object completion

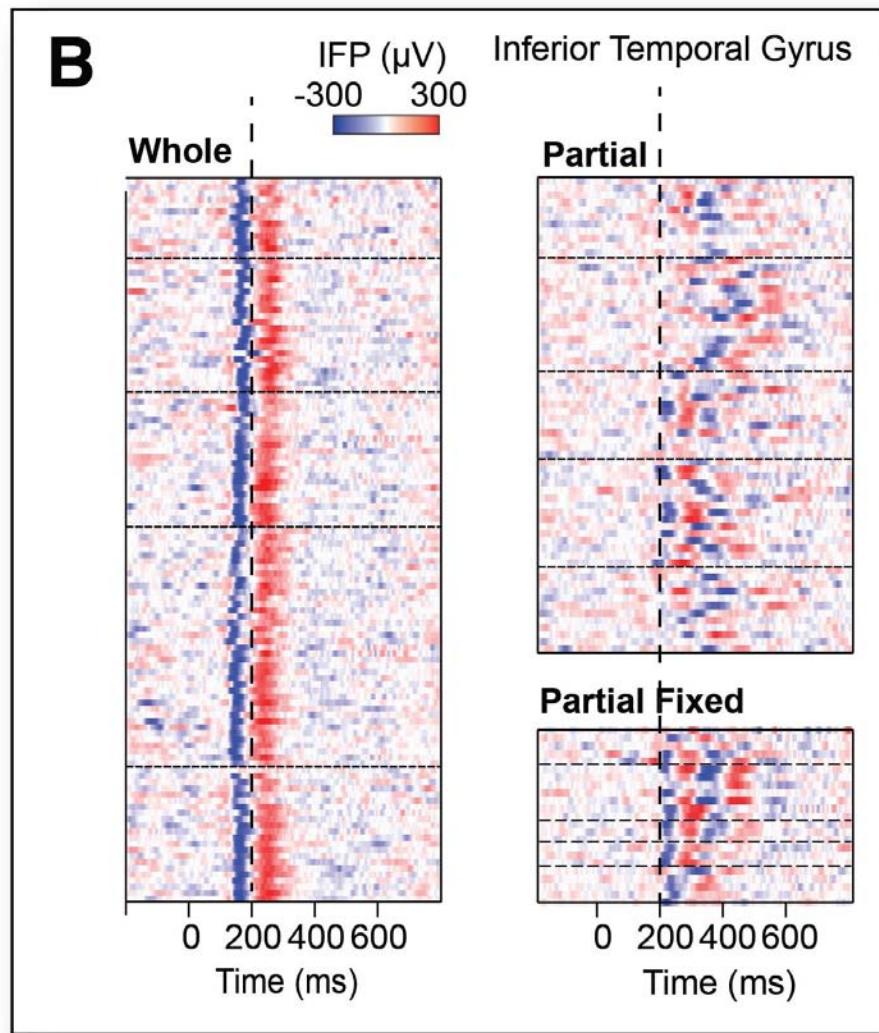
A



Courtesy of Elsevier, Inc., <http://www.sciencedirect.com>. Used with permission.  
Source: Tang, Hanlin, Calin Buia, Radhika Madhavan, Nathan E. Crone, Joseph R. Madsen, William S. Anderson, and Gabriel Kreiman. "Spatiotemporal dynamics underlying object completion in human ventral visual cortex." *Neuron* 83, no. 3 (2014): 736-748.

Tang et al,  
Neuron 2014

# Example responses during object completion



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Source: Tang, Hanlin, Calin Buia, Radhika Madhavan, Nathan E. Crone, Joseph R. Madsen, William S. Anderson, and Gabriel Kreiman. "Spatiotemporal dynamics underlying object completion in human ventral visual cortex." *Neuron* 83, no. 3 (2014): 736-748.

Inferior Temporal Gyrus

Tang et al,  
Neuron 2014

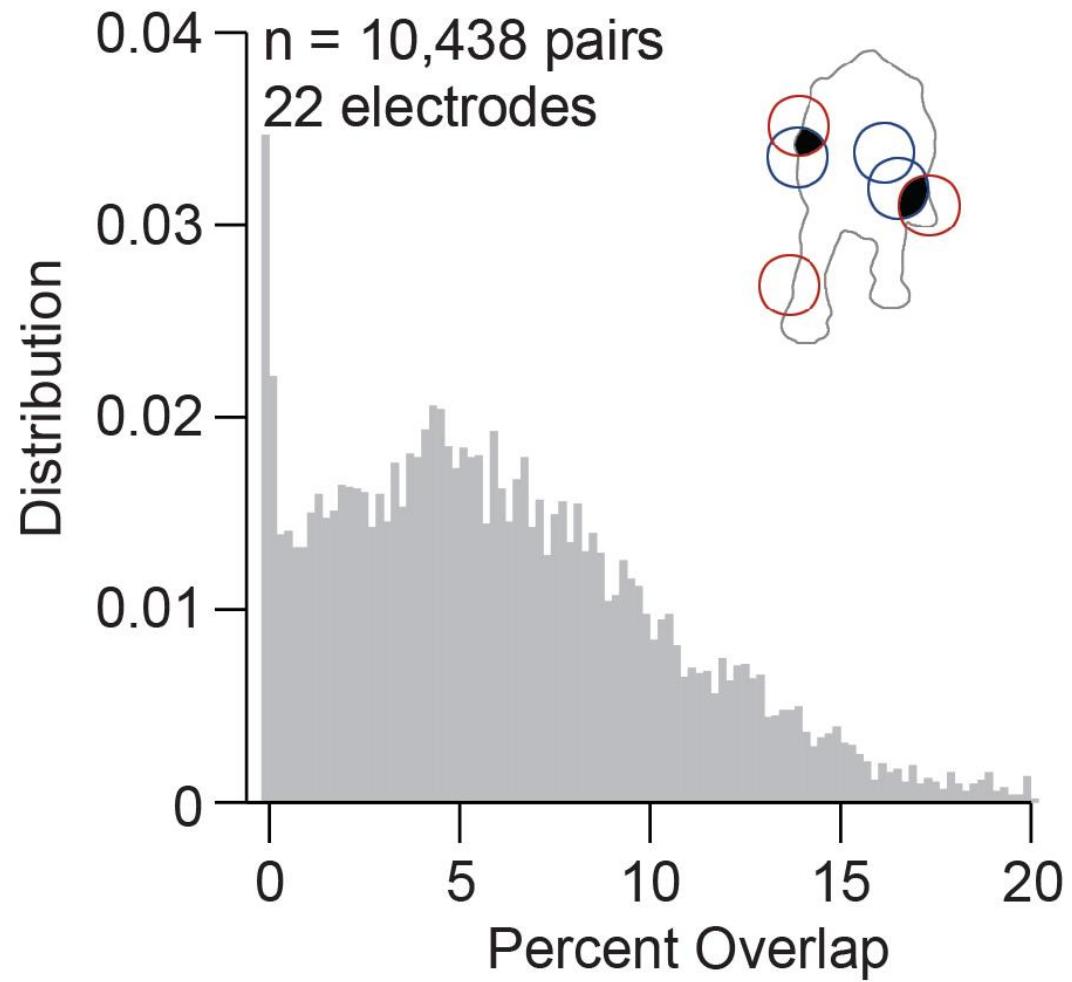
# Limited object completion in feed-forward model

Figure removed due to copyright restrictions. Please see the video.  
Source: Figure 29, Kreiman, Gabriel. "Computational models of visual object recognition." *Principles of Neural Coding 1* (2013): 0.

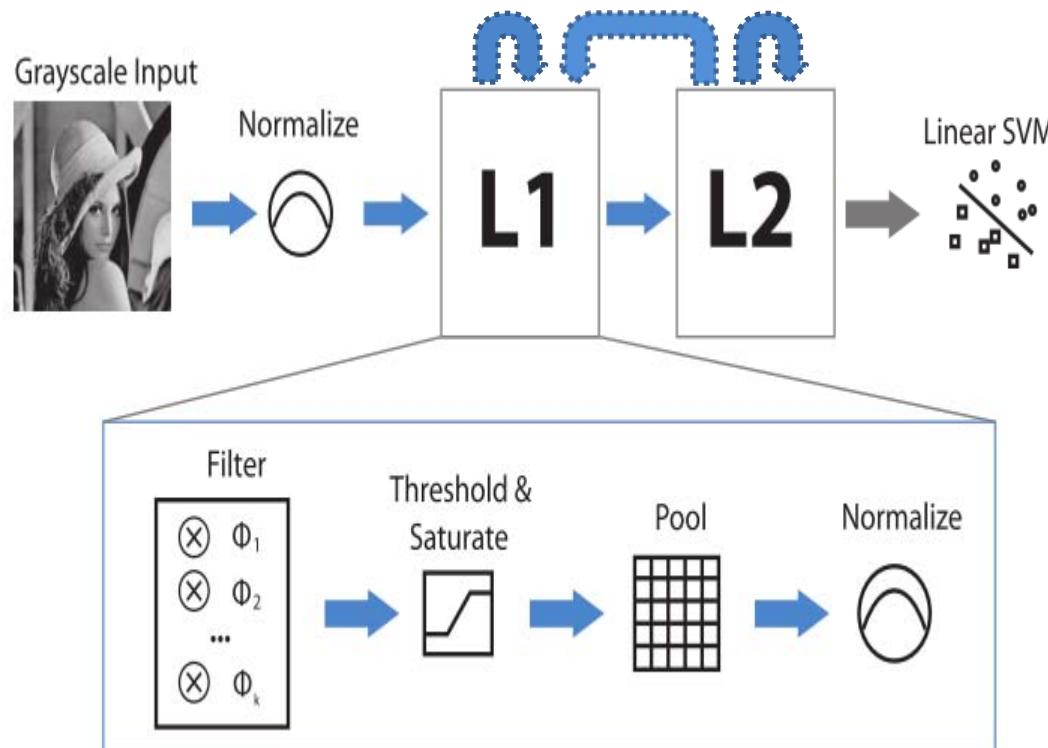
2000 "C2" units in the model  
Model responses to 25 exemplar objects  
Consider 20 units with high SNR (training data)  
500 repetitions with different bubble locations  
Train classifier with 70% of the repetitions  
Test classifier on remaining 30% of the repetitions  
Identification task (chance=4%)

# Holistic responses (?)

D

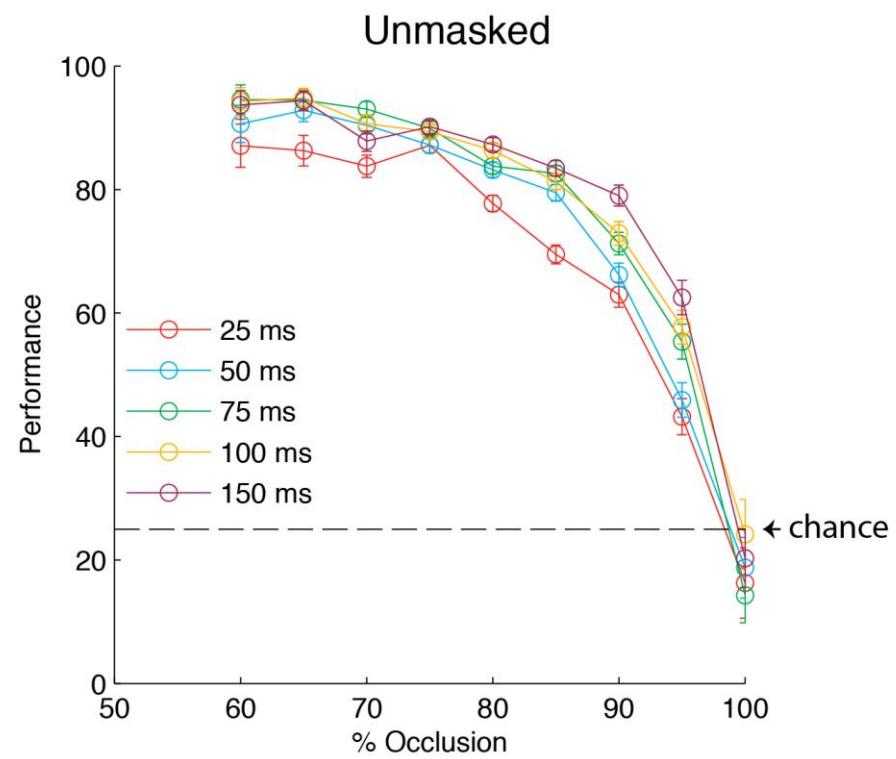


# Adding recurrency to deep network models

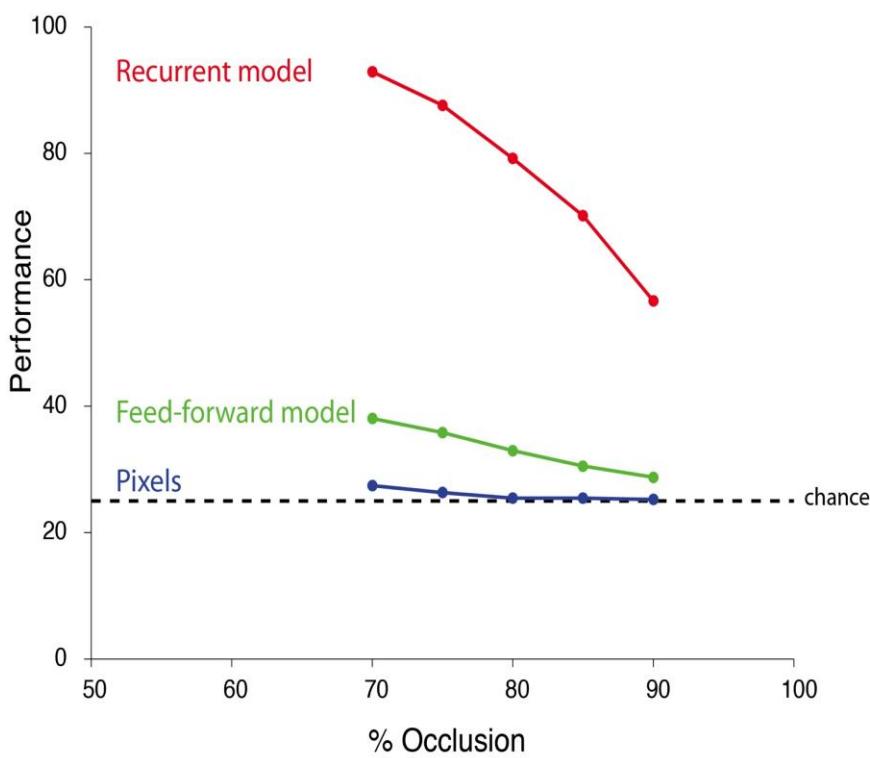


# Preliminary results: Recurrent connections can improve recognition of occluded objects

Behavior

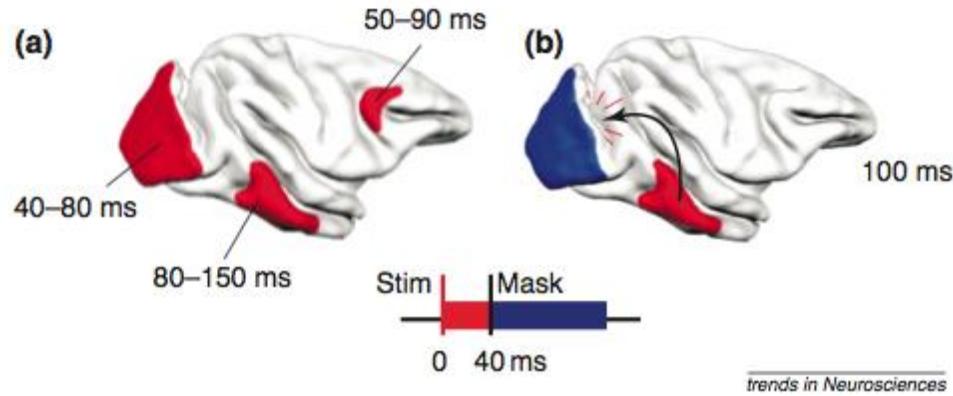


Recurrent model  
Trained on whole images

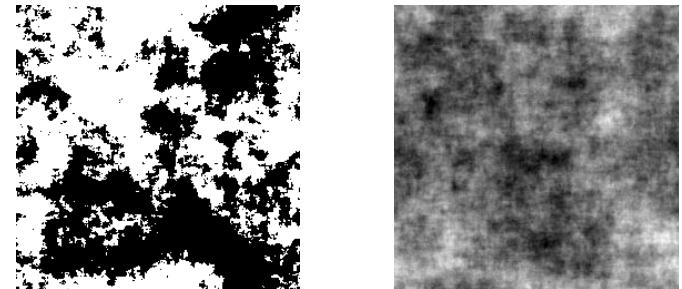


# Backward masking has been proposed to reduce the effects of feedback

## Models:



## Masks:

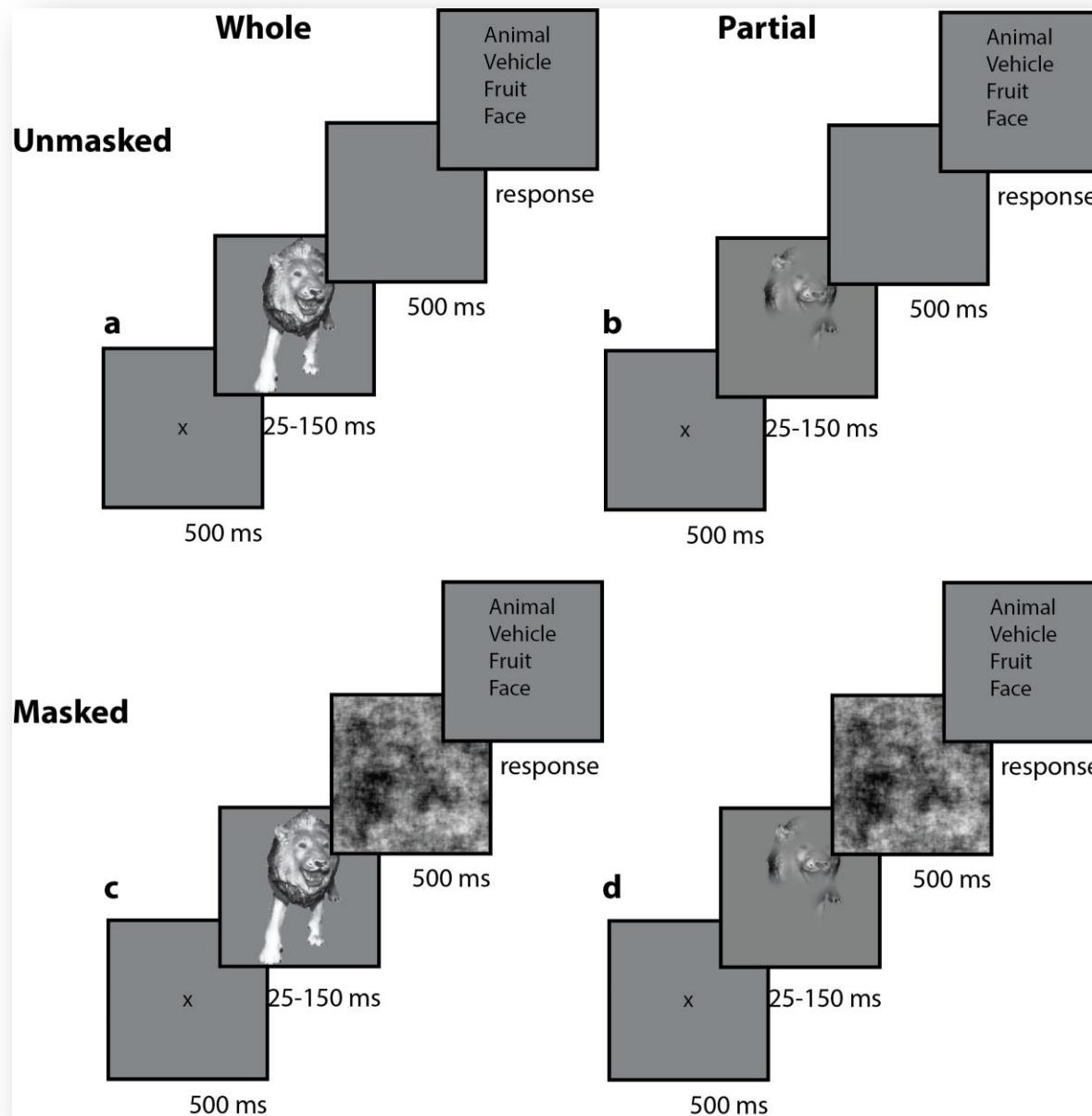


Lamme V, Roelfsema P (2000)

Courtesy of Elsevier, Inc., <http://www.sciencedirect.com>. Used with permission.  
Source: Lamme, Victor AF, and Pieter R. Roelfsema. "The distinct modes of vision offered by feedforward and recurrent processing." *Trends in neurosciences* 23, no. 11 (2000): 571-579.

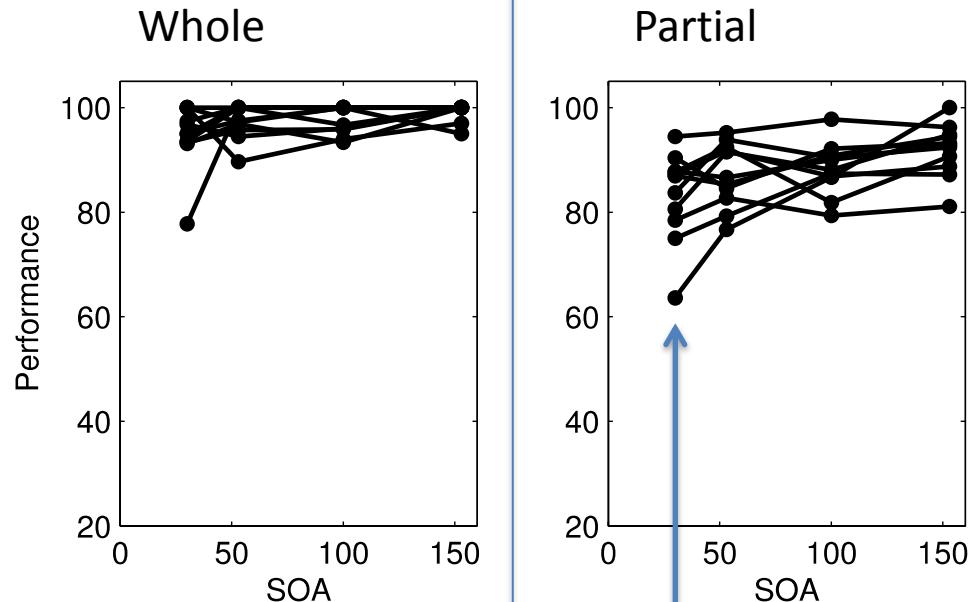
- For short delays (SOA<20ms), the mask reduces visibility of the first stimulus.
- For longer delays, the mask disrupts top-down processing.

# Object completion task (psychophysics)

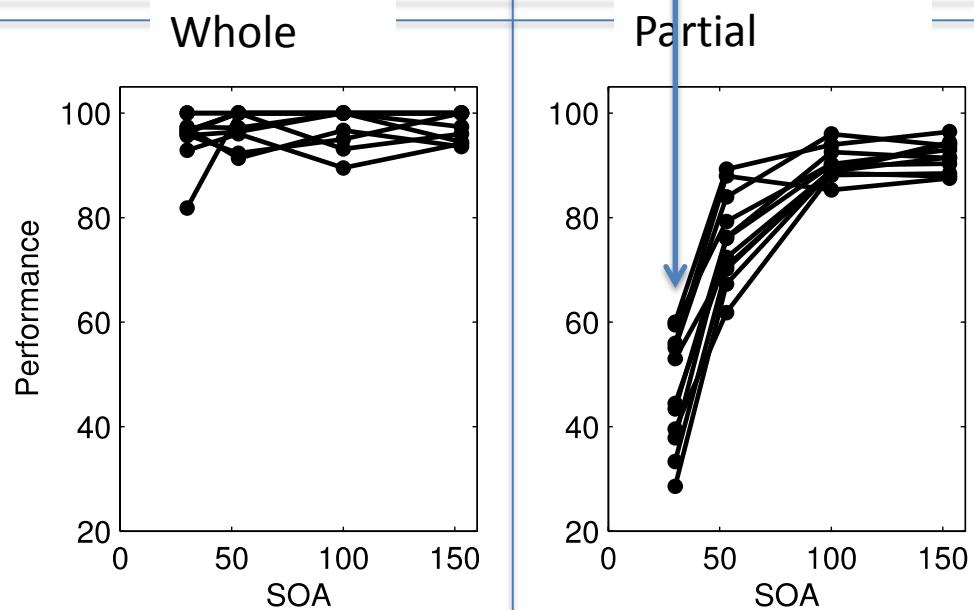


# Backward masking impairs recognition of partial objects at short SOAs

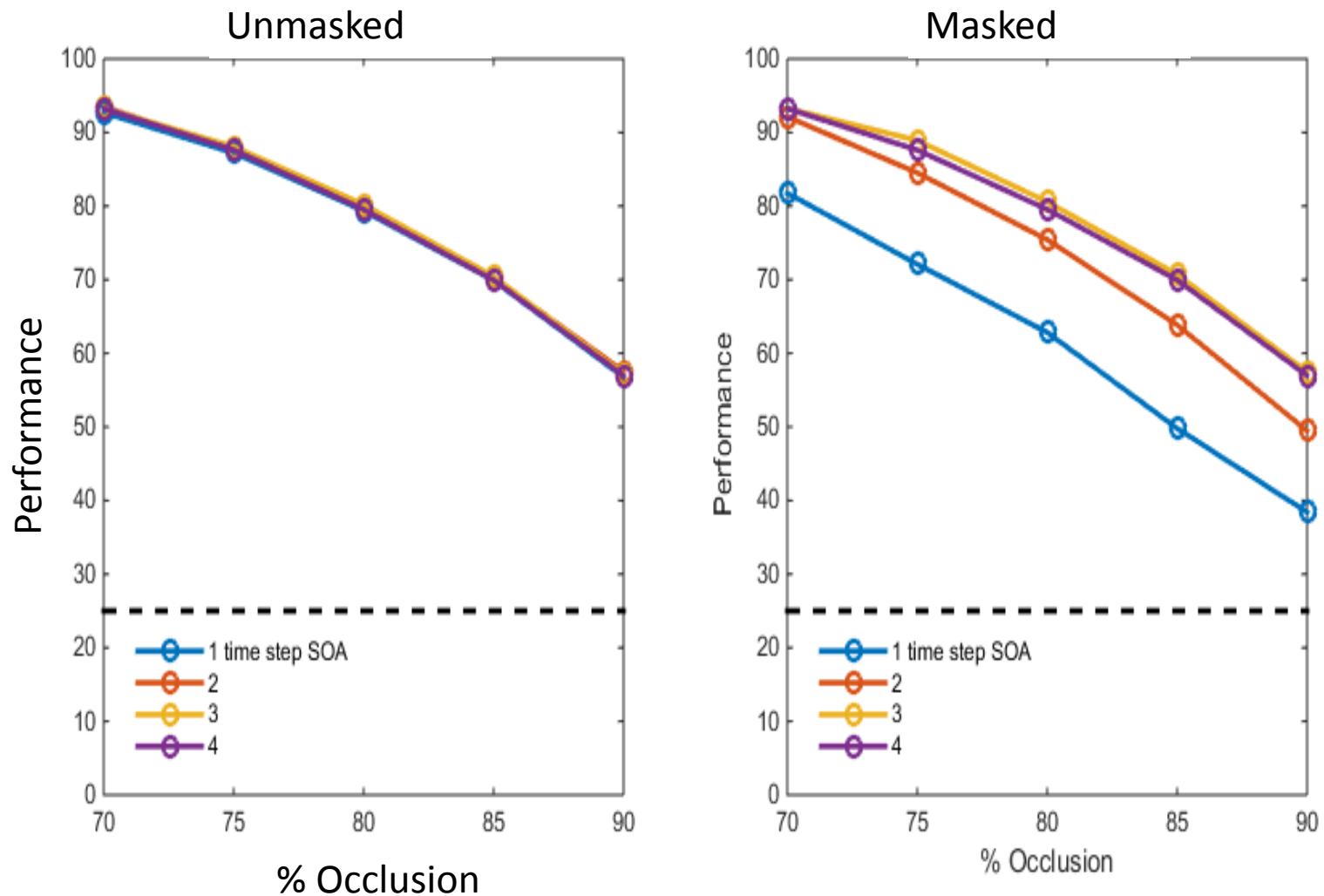
Unmasked



Masked

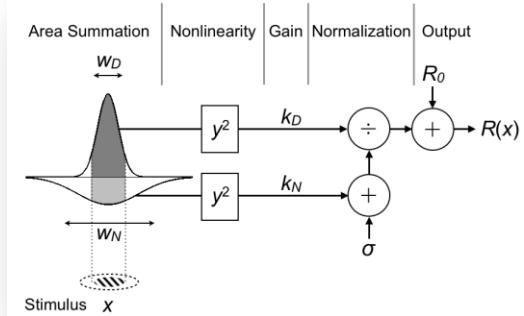


# Model performance in masking experiment

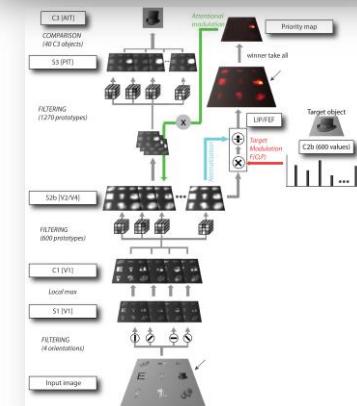


# Summary

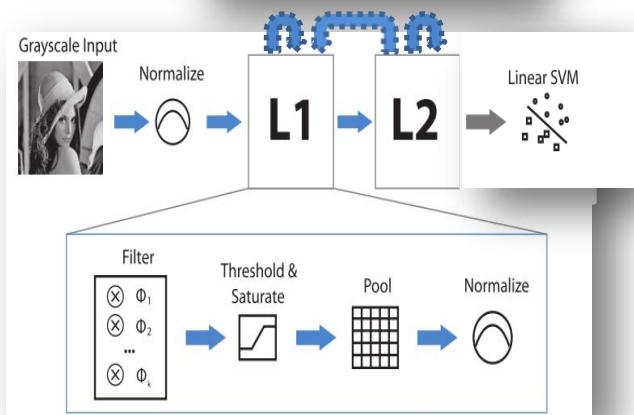
- Basic mechanisms in V1: Feedback signals enhance surround suppression



- Visual search: Tuned feedback signals can instantiate visual search (and feature-based attention)  
(Turing question: what will happen next?)



- Pattern completion: Feedback and/or recurrent connections can help recognize heavily occluded objects  
(Turing question: what is there?)



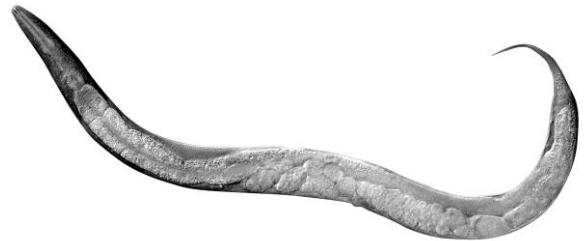
# Outline

1. Introduction to neural circuits and computational models
2. Computational roles of feedback signals
3. **Open questions, challenges, opportunities**

# Reasons for optimism

- **Wiring diagram**: Rapid progress tracing circuits in humans (low resolution) and animal models (high resolution)
- **Strength in numbers**: Rapid progress recording and mathematically analyzing neurophysiological activity from large ensembles in humans and animal models
- **Source code**: We can manipulate neural circuits (rodents, macaques) to examine necessary and sufficient computational elements

# Wiring diagrams



Courtesy of Professor Sander van den Heuvel and Dr. Mike Boxem. Used with permission.

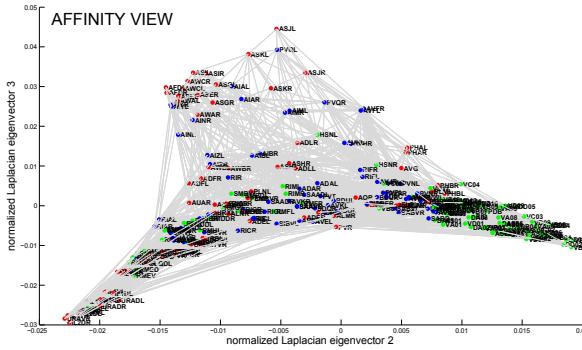
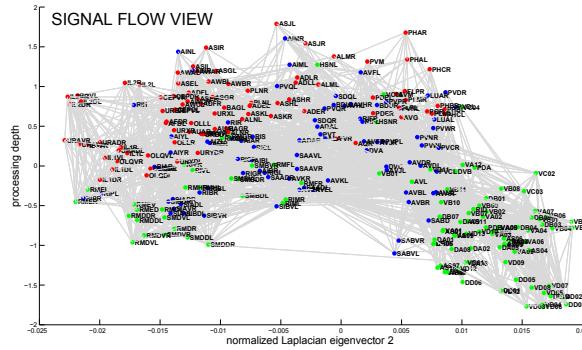
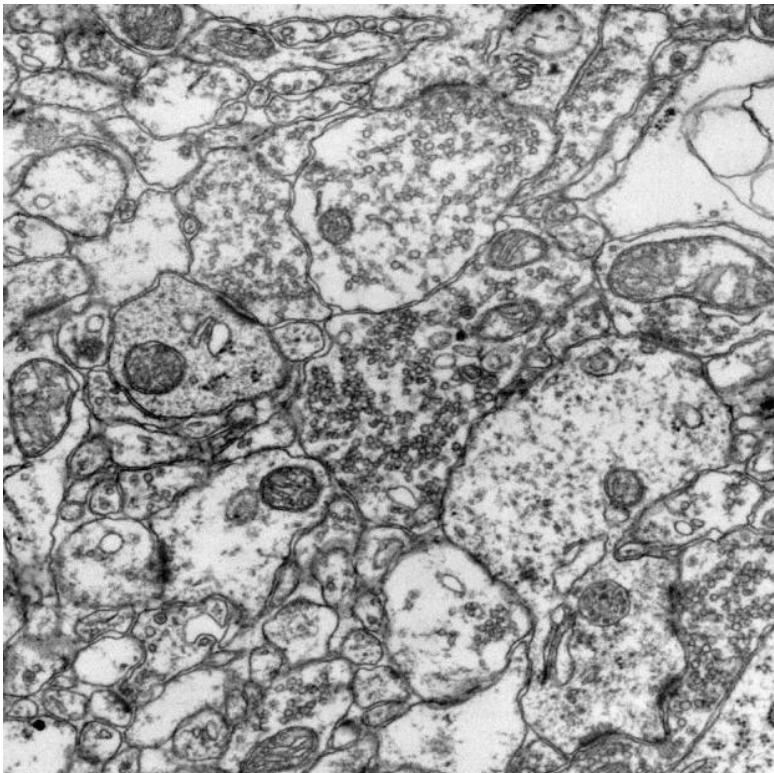
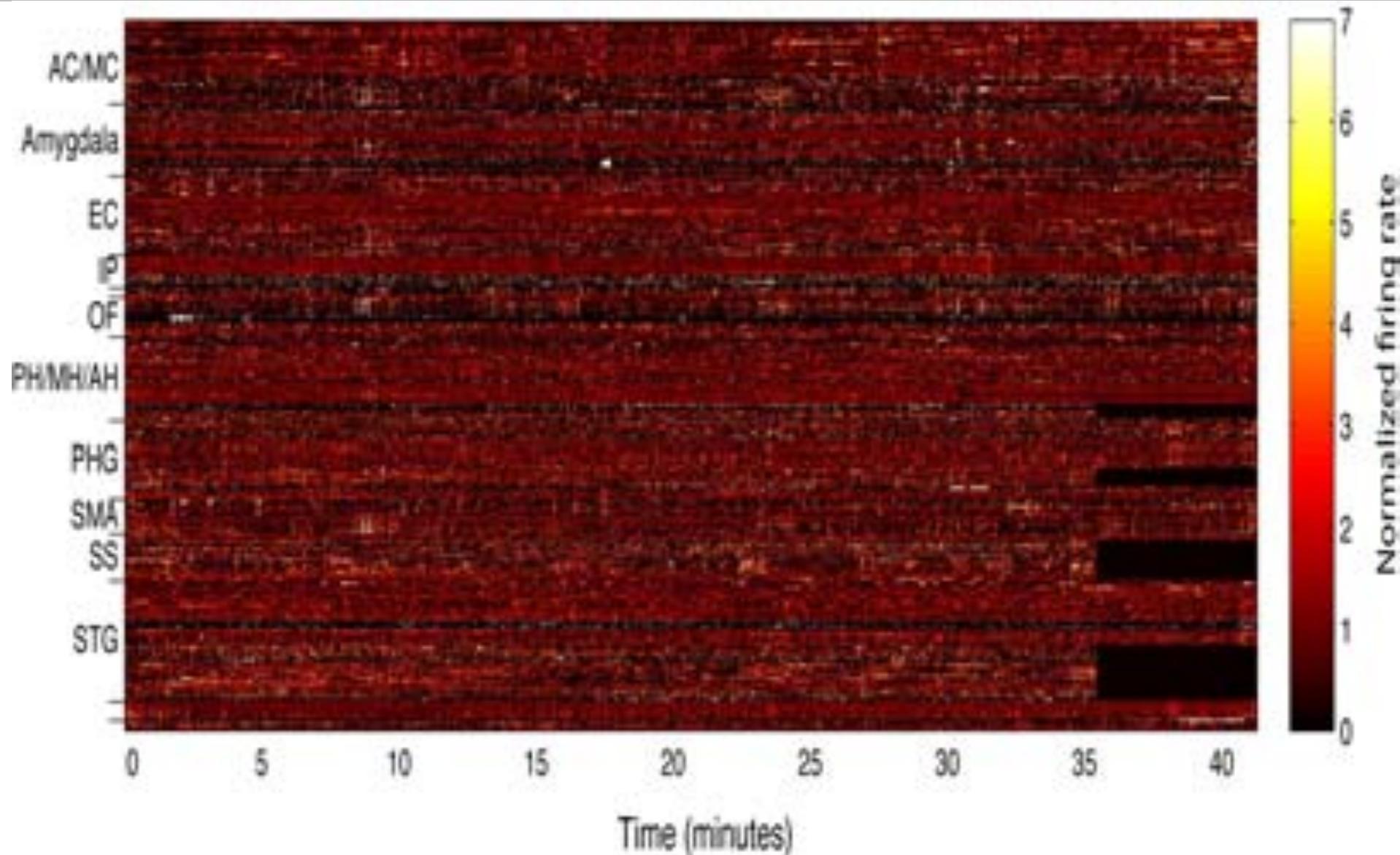


Fig. 2. The *C. elegans* wiring diagram is a network of identifiable, labeled neurons connected by chemical and electrical synapses. Red, sensory neurons; blue, interneurons; green, motorneurons. (a) Signal flow view shows neurons arranged so that the direction of signal flow is mostly downward. (b) Affinity view shows structure in the horizontal plane reflecting weighted non-directional adjacency of neurons in the network.

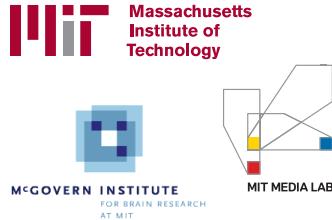
Original work: Sydney Brenner  
Image: Doctoral Dissertation Thesis by  
Beth Chen, 2007

Varshney, Lav R., Beth L. Chen, Eric Paniagua, David H. Hall, and Dmitri B. Chklovskii. "Structural properties of the *Caenorhabditis elegans* neuronal network." *PLoS Comput Biol* 7, no. 2 (2011): e1001066. DOI: 10.1371/journal.pcbi.1001066. License CC BY.

# Strength in numbers



# Strength in numbers: electrode arrays (e.g. Boyden)

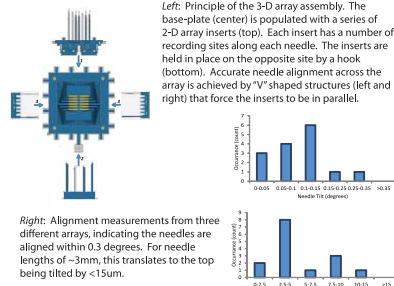


## Introduction

Optogenetics is commonly used for precision modulation of the activity of specific neurons within neural circuits, but assessing the impact of optogenetic neuromodulation on the neural activity of local and global circuits remains difficult. Our collaborative team recently initiated a project (Scholvin et al., SFN 2011) to design and implement 3-D silicon-micromachined electrode arrays with customizable electrode locations, targetable to defined neural substrates distributed in a 3-D pattern throughout a neural network in the mammalian brain, and compatible with simultaneous use of a diversity of existing light delivery devices.

We here describe a series of innovations we have pursued aimed at facilitating the scalability aspect of these probes—that is, aspects of probe design that should enable them to scale up to 1000's of channels of neural recording or more. First, we have developed streamlined electrode fabrication methodologies that enable micromachined probes to be first fabricated using conventional silicon micromachining, then rapidly assembled onto a base plate using 3-D assembly techniques, instead of the necessary wire-electrode connection and mechanical constraints. Second, we have developed a set of surgical and insertion technologies towards the goal of enabling the insertion of electrode arrays with a high number of electrode shanks into the brain, while minimizing probe insertion damage. Finally, in order to facilitate scaling of the channel count beyond what is feasible with external amplifiers, we are exploring new approaches for integration of amplifier circuitry directly on the probe arrays themselves, to remove bottlenecks associated with connecting of probes to the outside world.

## Design Components



## Scalable 3-D Microelectrode Recording Architectures for Characterization of Optogenetically Modulated Neural Dynamics

J. Scholvin<sup>1</sup>, S.K. Arfin<sup>1</sup>, J. Bernstein<sup>1</sup>, J. Kinney<sup>1</sup>, C. Moore-Kochlacs<sup>1,2</sup>, P.E. Monaghan<sup>1</sup>, A.N. Zorzos<sup>1</sup>, N. Kopell<sup>2</sup>, C.G. Fonstad<sup>1</sup>, E.S. Boyden<sup>1</sup>

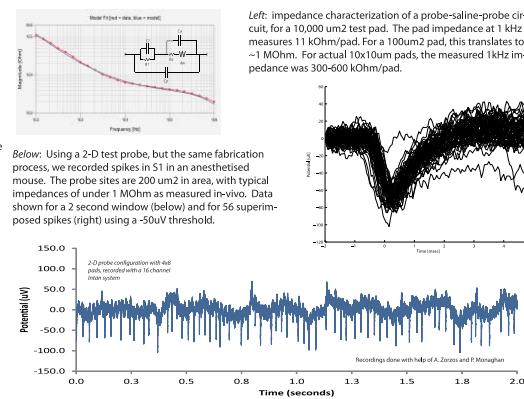
<sup>1</sup> Synthetic Neurobiology Group, MIT Media Lab and MIT McGovern Institute, Departments of Biological Engineering and Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, MA, <sup>2</sup> Boston University, Boston, MA

## 3-D Array Construction



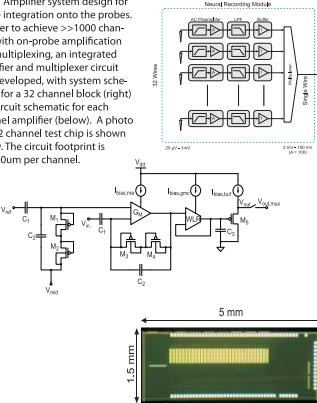
Below: Schematic design for a 1000 channel 3-D probe that is capable of recording uniformly throughout the brain. Recording sites are spaced 300  $\mu\text{m}$  in the plane and 110  $\mu\text{m}$  in the vertical. Pad arrangement: 10x10. Volume covered: 2.7  $\times$  2.8  $\times$  1 mm. Recording site area: 100  $\mu\text{m}^2$ . Recordings per electrode: 110  $\mu\text{m}$ , 300  $\mu\text{m}$ , 310  $\mu\text{m}$ . Needle geometry: 1600  $\mu\text{m}$ , 1100  $\mu\text{m}$ , 40  $\mu\text{m}$ . Length with recording sites: 15, 30, or 50  $\mu\text{m}$ . Width: 1.5% for 30  $\mu\text{m}$  thickness: 600  $\Omega$ / $\text{cm}^2$ . Tissue displacement ratio: Expected recording site impedance: 600  $\Omega$ .

## Electrical Connections and Testing



## Future Amplifier Integration

Right: Amplifier system design for future integration onto the probes. In order to achieve >>1000 channels with on-probe amplification and multiplexing, an integrated amplifier and multiplexer circuit was developed, with system schematic for a 32 channel probe (right) and circuit schematic for each channel amplifier (below). A photo of a 32 channel test chip is shown below. The circuit footprint is 90x500  $\mu\text{m}$ .



## Acknowledgments

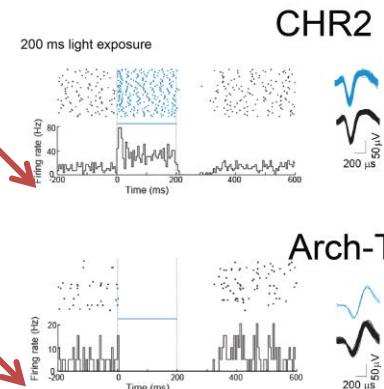
E.S.B. acknowledges funding by Benes Foundation; Jerry and Marge Burnett; DARPA Living Foundries Program; Department of Defense CDMRP PTSD Program; Google; Harvard/MIT Joint Grants Program in Basic Neuroscience; Human Frontiers Science Program; IET A. Harvey Prize; Lincoln Labs Capstone College Award; MIT Alumni Class Funds; MIT Intelligence Initiative; MIT McGovern Institute and McGovern Institute for Brain Research; McGovern Media Lab and Media Lab Consortia; including State Farm and A2Z (Amazon); MIT Mind-Machine Project; MIT Neurotechnology Fund (& its generous donors); NARSAD; New York Stem Cell Foundation-Robertson Investigator Award; NIH Director's New Innovator Award (1DP2OD002002); NIH EUREKA Award (1R01NS075423); NIH Translational R01 (R01GM104948-01, and NIH Grants 1R01DA202939, 1R43NS070453, 1RC2DE020519, 1RC1MH088182, and 1R01NS067199; NSF CAREER Award (CMMI-1054537); AFOSR Young Investigator Award (FA9550-11-1-0144 (the Cognitive Prostheses Collaborative); Office of the Assistant Secretary of Defense for Research and Engineering; Paul Allen Distinguished Investigator in Neuroscience Award; SkTech; Alfred P. Sloan Foundation; Society for Neuroscience Research Award for Innovation in Neuroscience (RAIN); Synthetic Intelligence Project; Wallace H. Coulter Foundation.



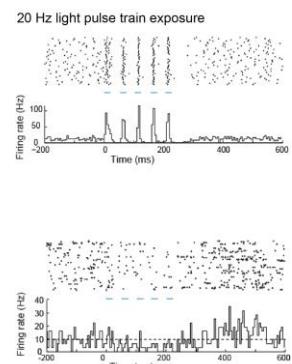
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# Playing with the source code: Using light to modulate neural with high specificity

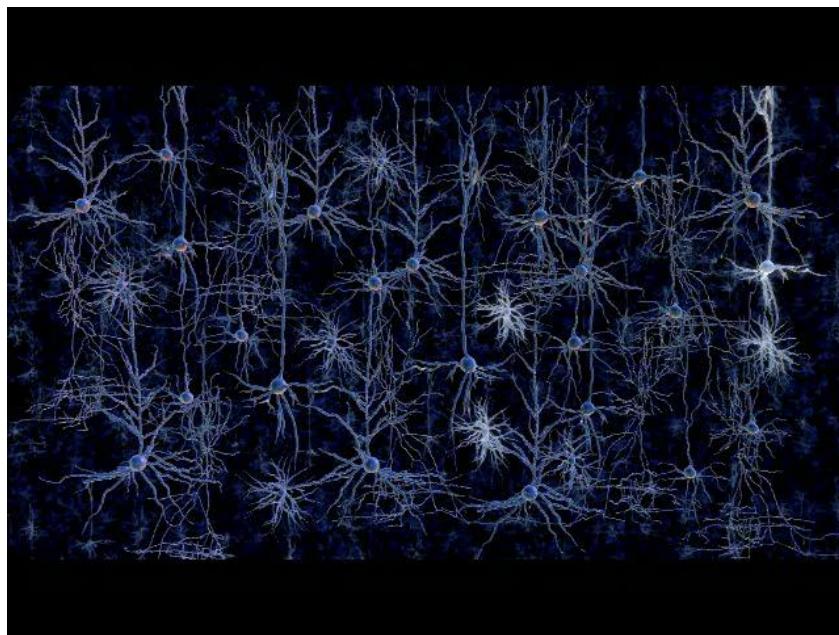
activate



silence



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Source: Han, Xue, Xiaofeng Qian, Jacob G. Bernstein, Hui-hui Zhou, Giovanni Talei Franzesi, Patrick Stern, Roderick T. Bronson, Ann M. Graybiel, Robert Desimone, and Edward S. Boyden. "Millisecond-timescale optical control of neural dynamics in the nonhuman primate brain." *Neuron* 62, no. 2 (2009): 191-198.



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Boyden-Desimone

# Biological codes to computational codes

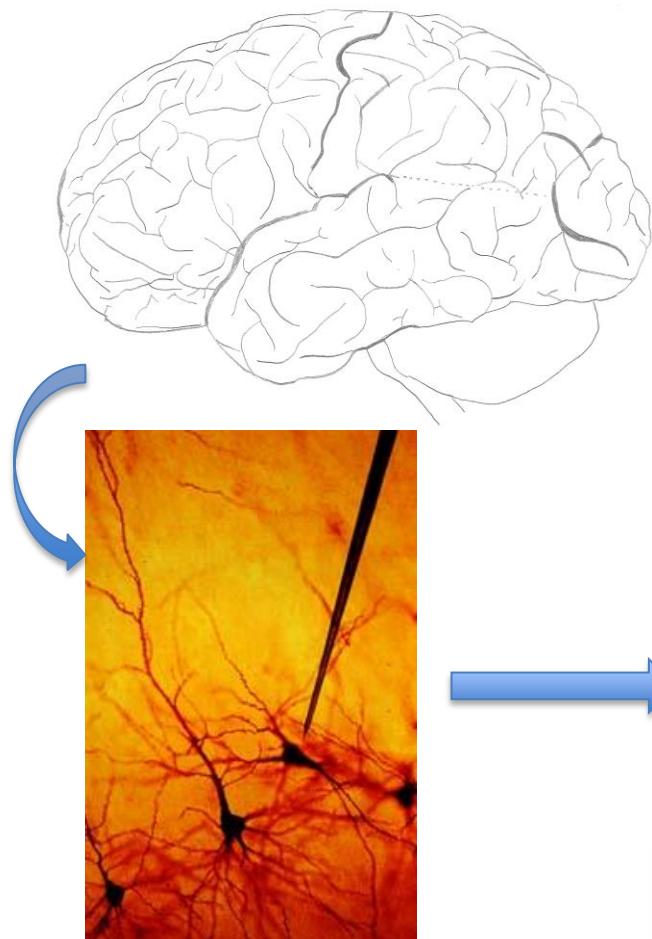
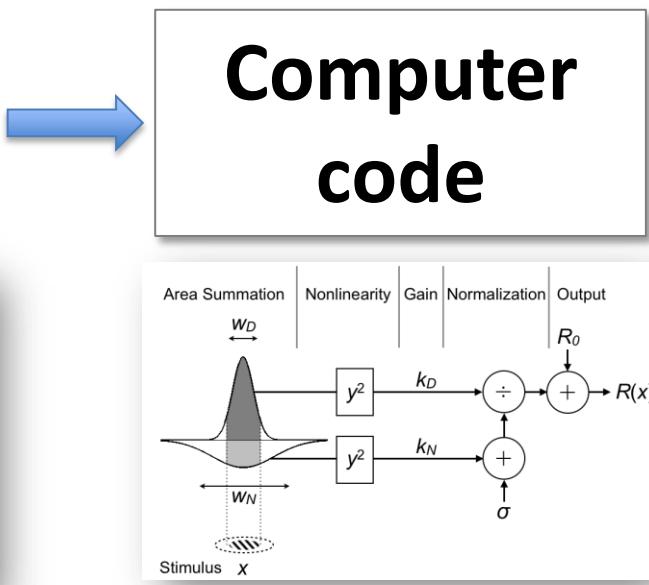
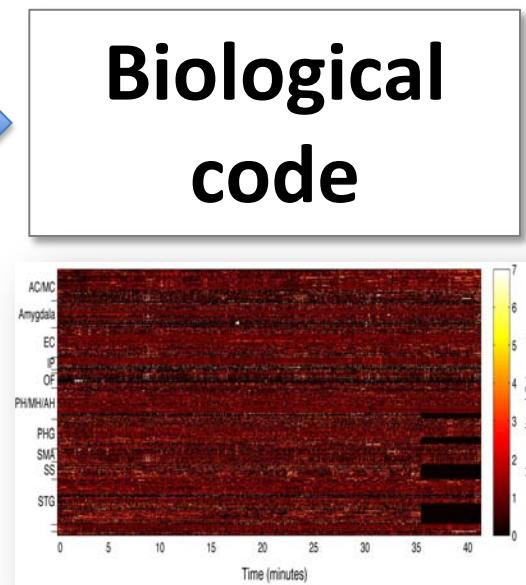


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