Outline

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

Biologically-inspired computation

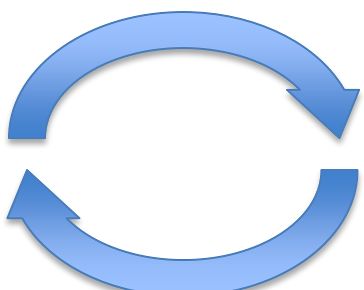
Claim (without proof):
over millions of years of evolution, "interesting" solutions to difficult problems have emerged through changes in neuronal circuits

Theories

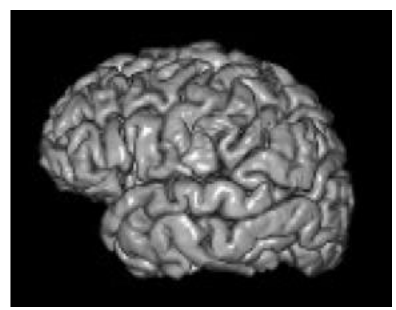
Technology developments

Computational models

Tools, models, hardware



Algorithms, solutions



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Listening to neuronal circuits

Decoding activity

Writing-in information

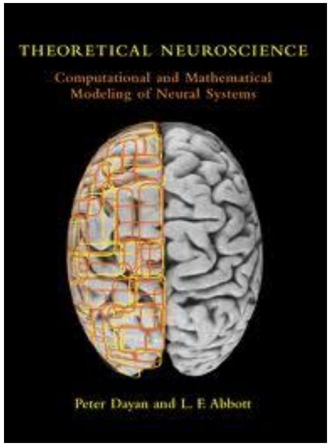
Some features of brain-based computations

- 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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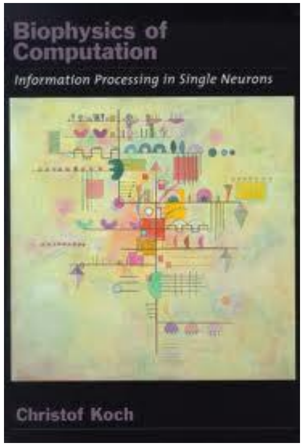

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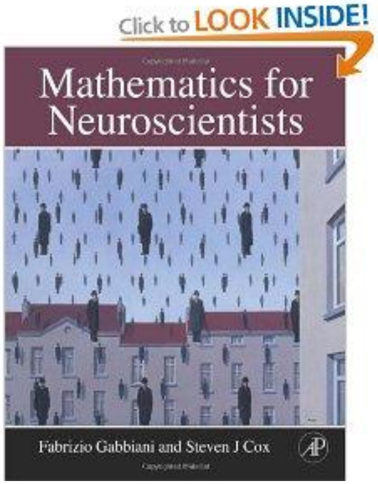

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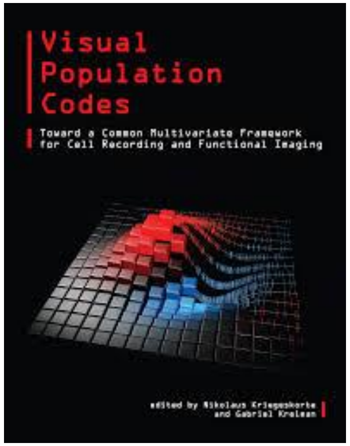

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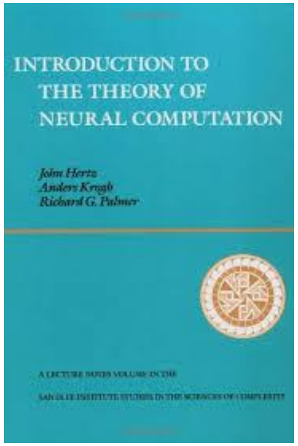

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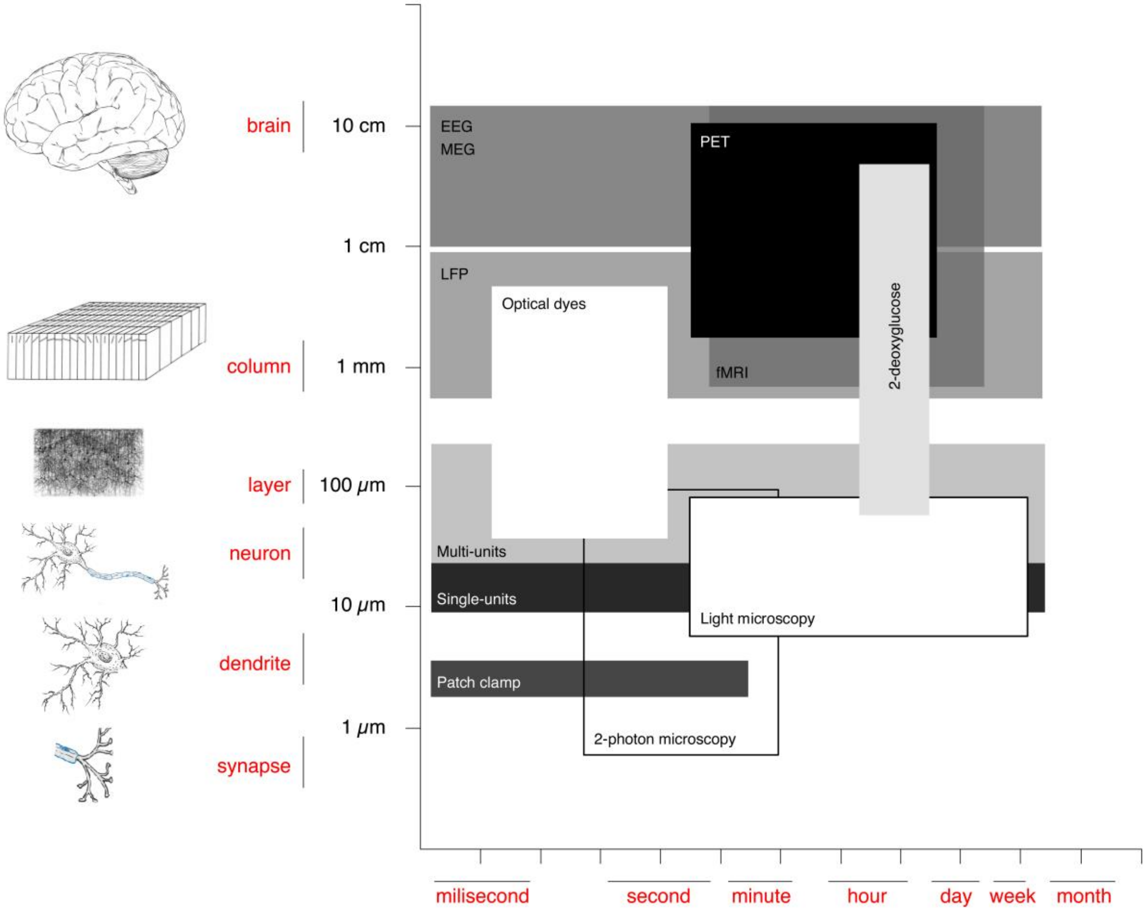
- Abbott and Dayan. Theoretical Neuroscience - Computational and Mathematical Modeling of Neural Systems [2001] (ISBN 0-262-04199-5). MIT Press.
- Koch. Biophysics of Computation [1999] (ISBN 0-19-510491-9). Oxford University Press.
- Gabbiani and Cox. Mathematics for Neuroscientists. [2010] (ISBN 978-0-12-374882-9). 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.

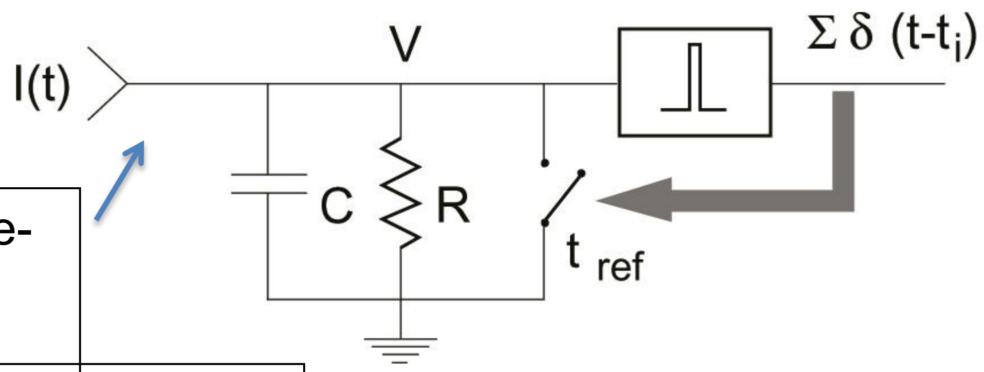
Methods to study the brain at different scales



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.

Kreiman. *Physics of Life Reviews* 2004

Simulating single neurons: A nested family of models



Filter operations

Integrate-and-fire circuit

Hodgkin-Huxley units

Multi-compartmental models

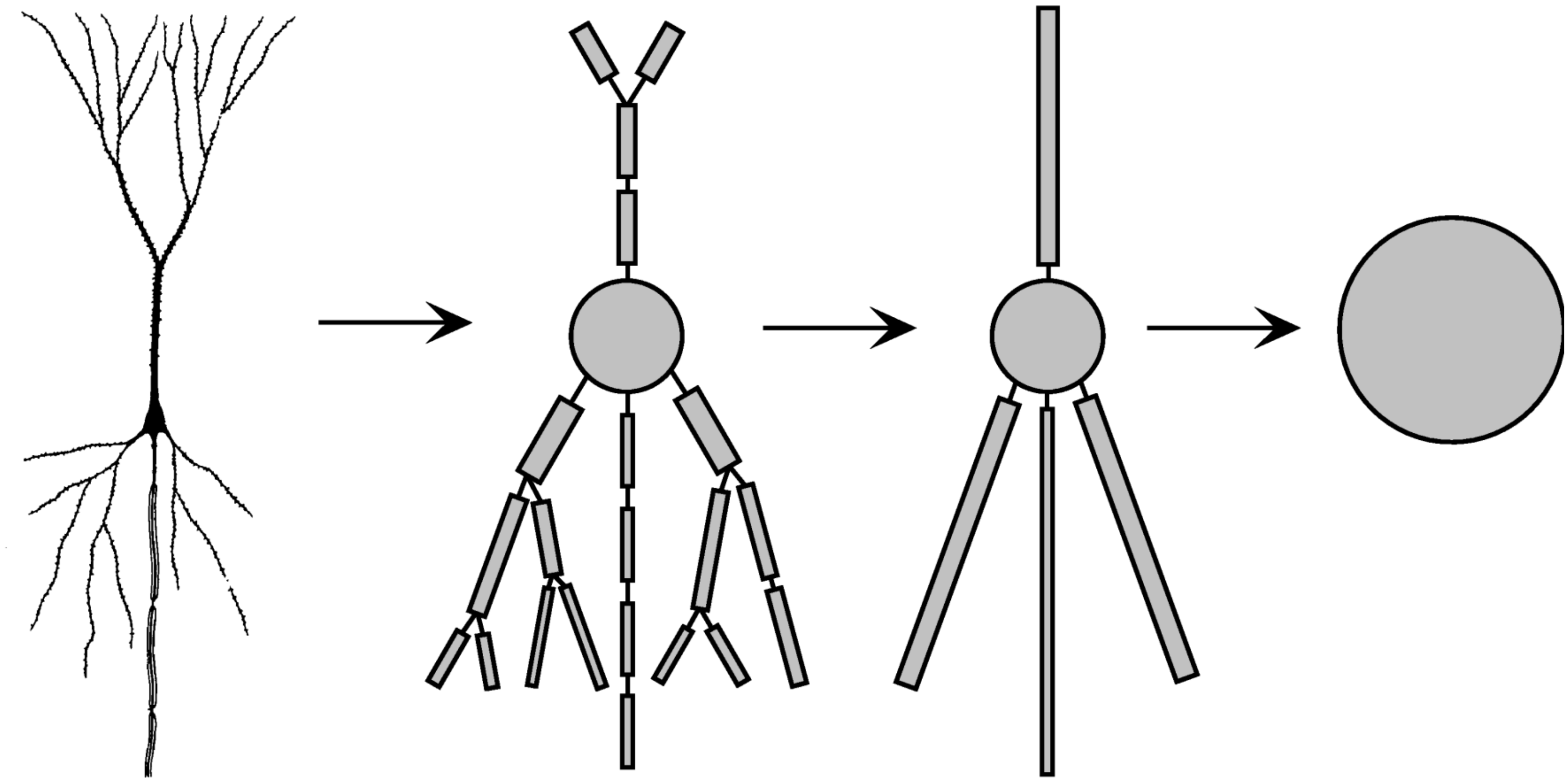
Spines, channels

Biological accuracy

Lack of analytical solutions

Computational complexity

Geometrically accurate models vs. spherical cows with point masses



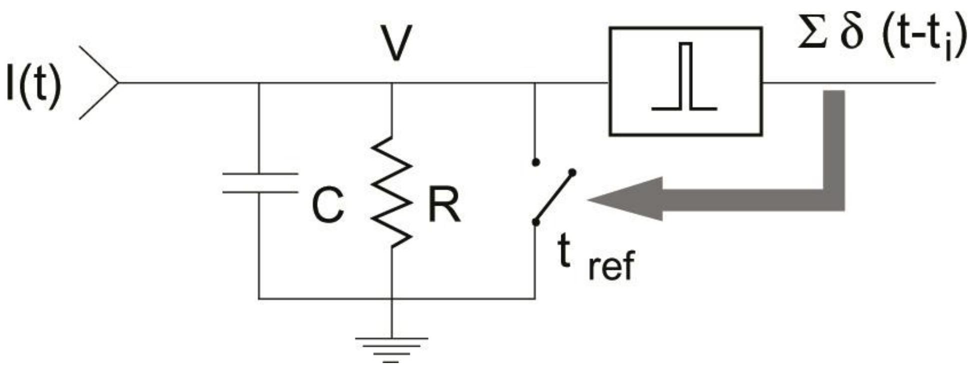
A central question in Theoretical Neuroscience:
What is the “right” level of abstraction?

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

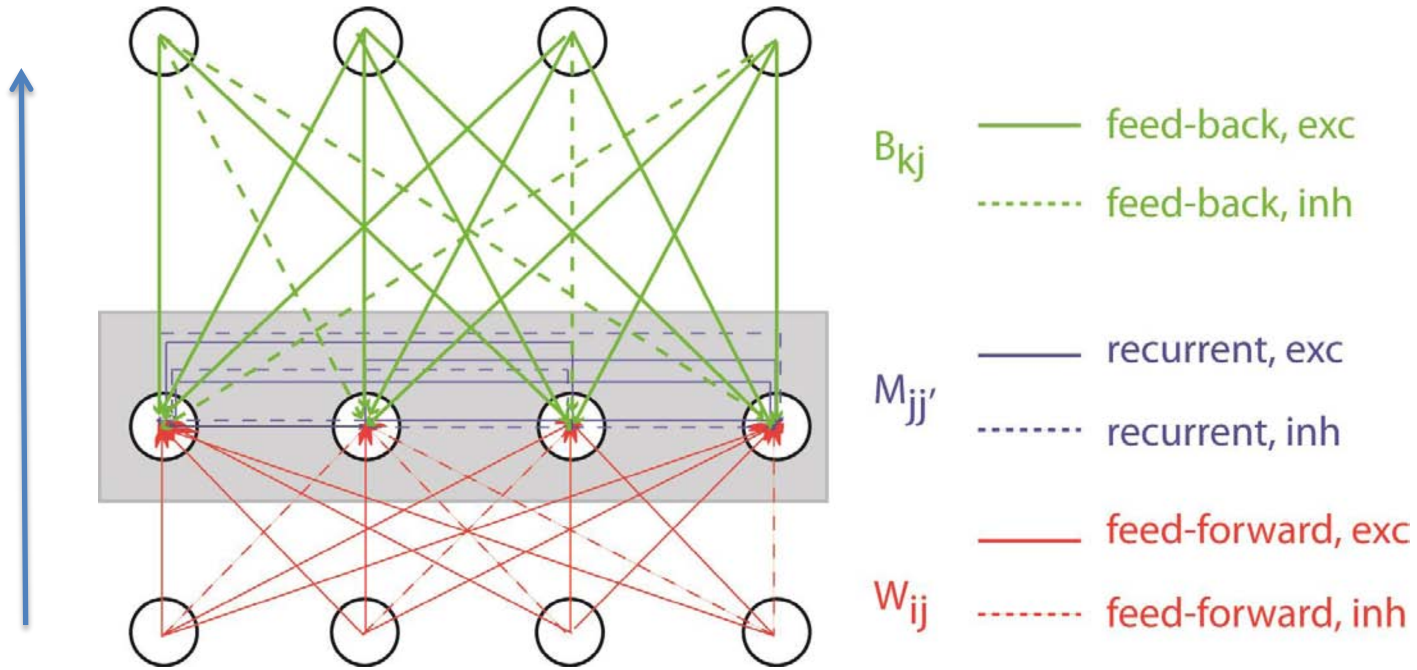
$$C\frac{dV(t)}{dt} = -\frac{V(t)}{R} + I(t)$$

```
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 MOhm]
% 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)                      % Emit a spike if V is above threshold
      V(t)=V_res;                      % And reset the voltage
      spk(t)=1;
   end
end
```

All of these lines are comments

This is the key line integrating the differential equation

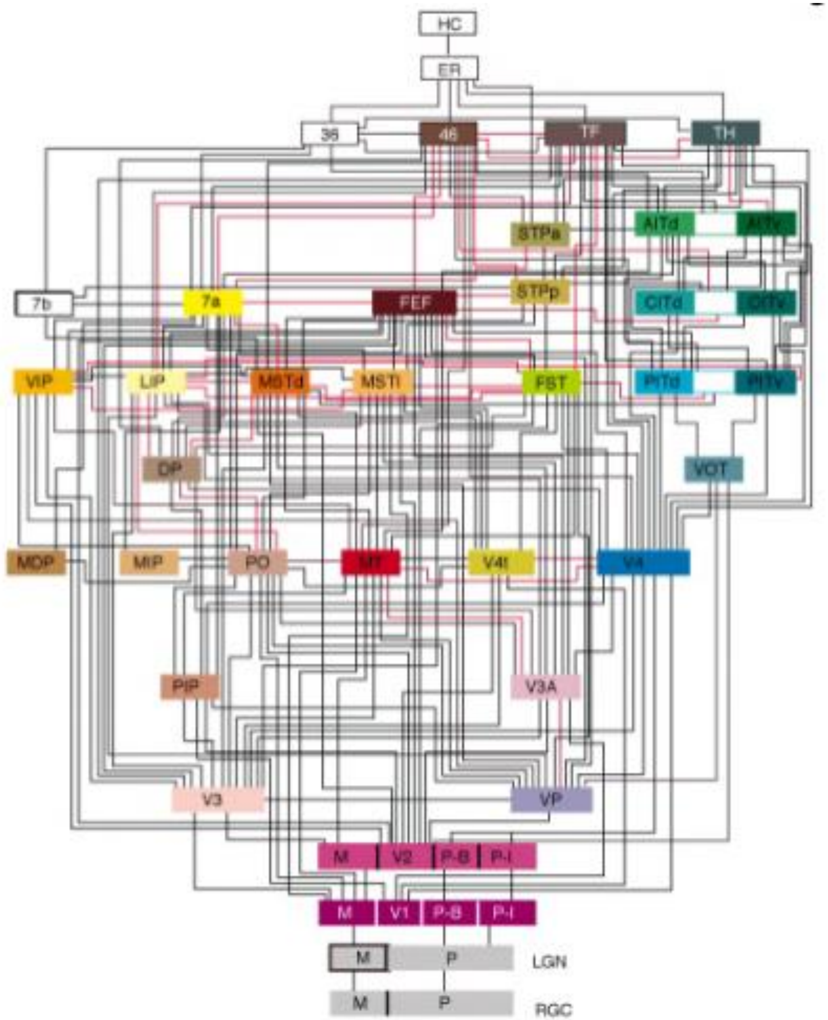
Circuits – some basic definitions



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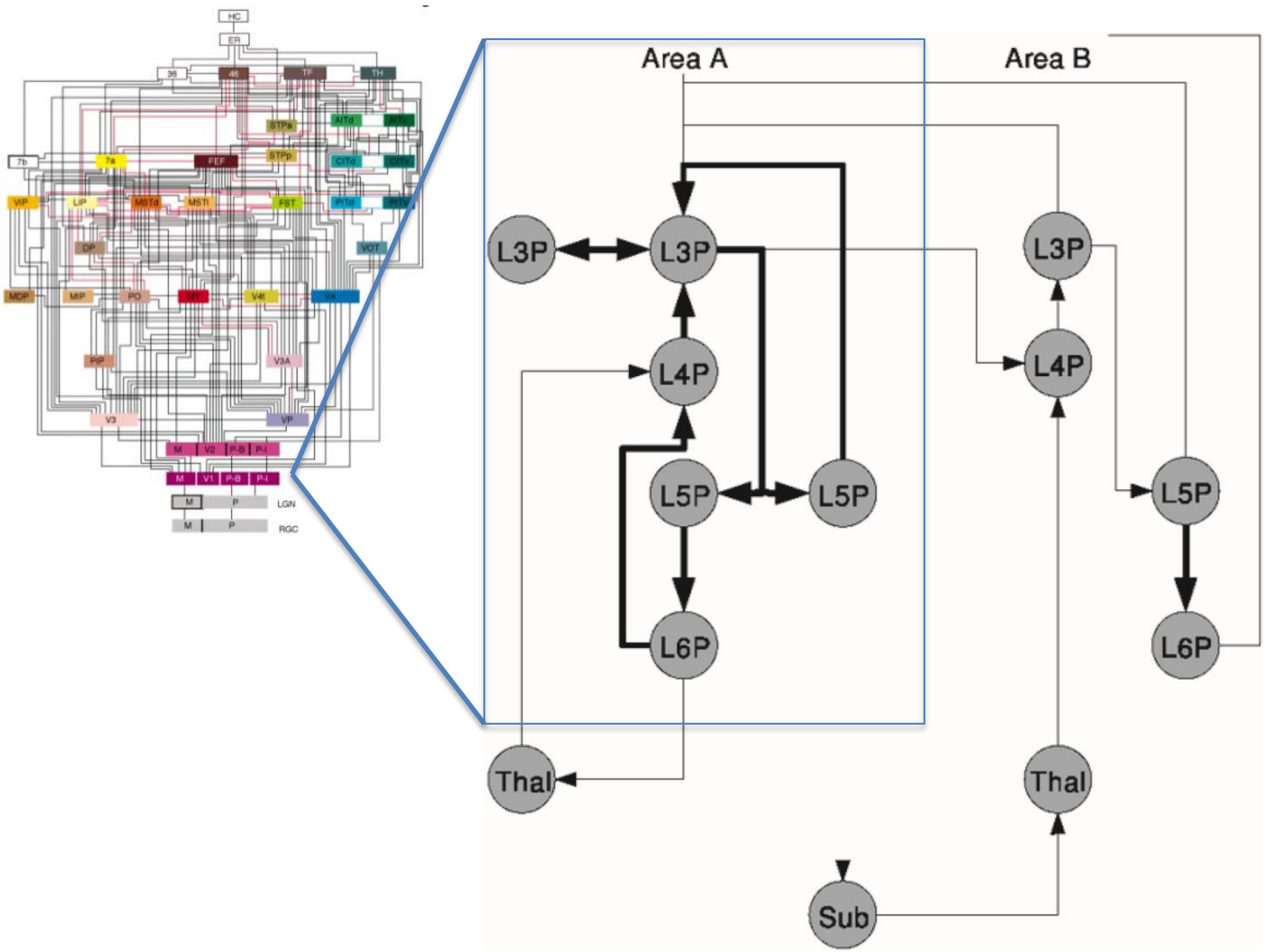
Source: Felleman, Daniel J., and David C. Van Essen. "Distributed hierarchical processing in the primate cerebral cortex. " Cerebral cortex 1, no. 1 (1991): 1-47.

And a canonical microcircuit structure within each area



Douglas and Martin 2004

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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

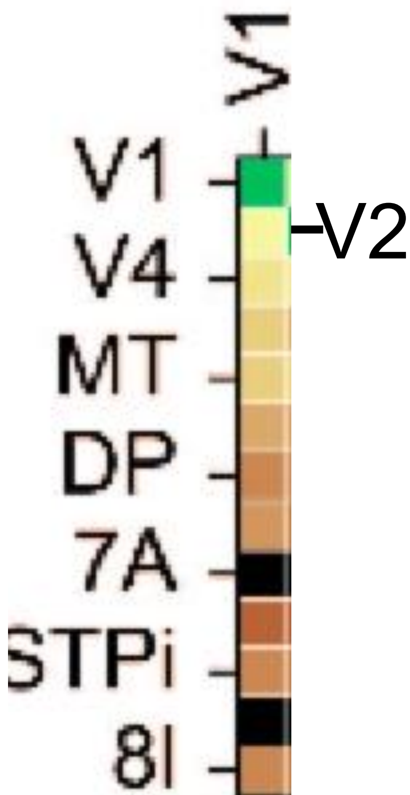
1. Behavior: We can recognize objects within ~150ms (e.g. Potter et al 1969, Thorpe et al 1996)

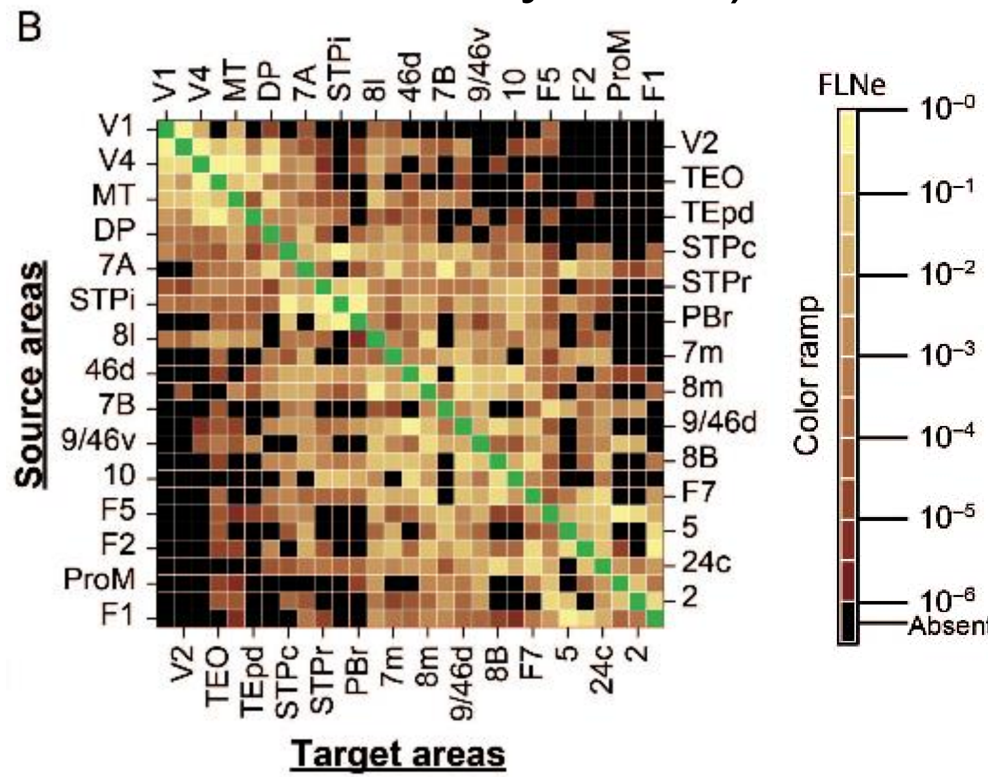
2. Physiology: Visually selective responses to complex shapes arise within ~150 ms (e.g. Keysers et al 2001, Hung et al 2005, Liu et al 2009)

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)





Markov et al 2012

What are feedback signals doing?
When?
Why?
How?

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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

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

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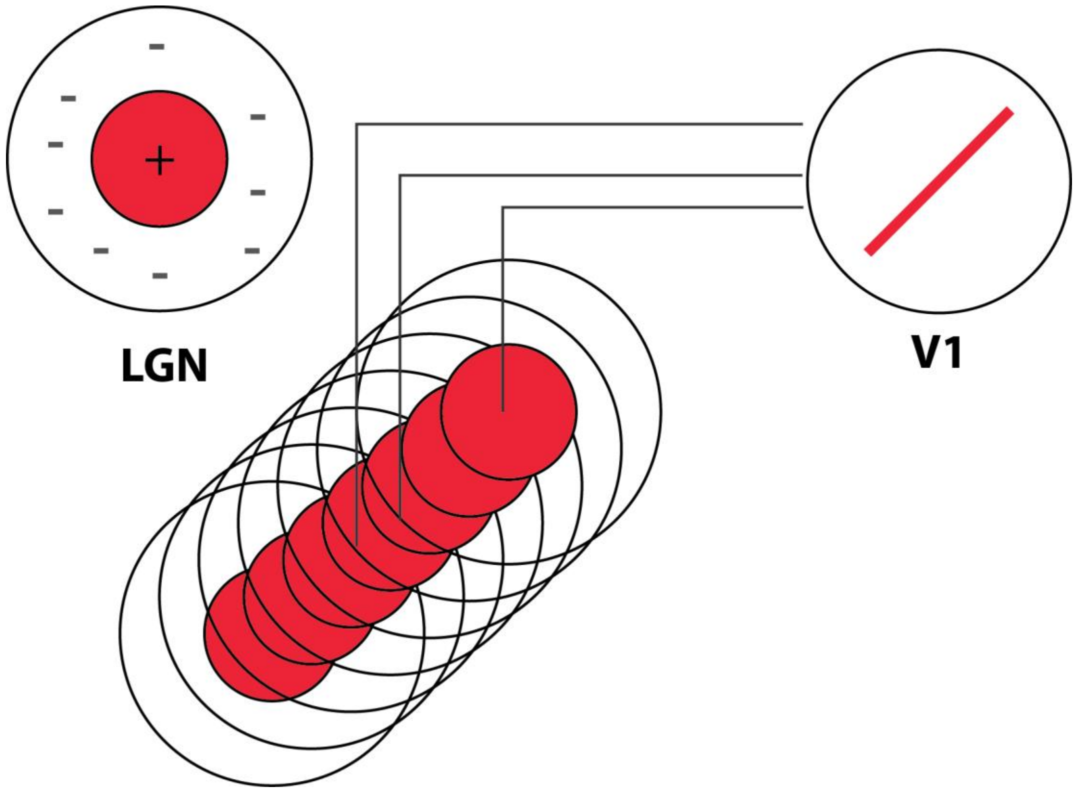
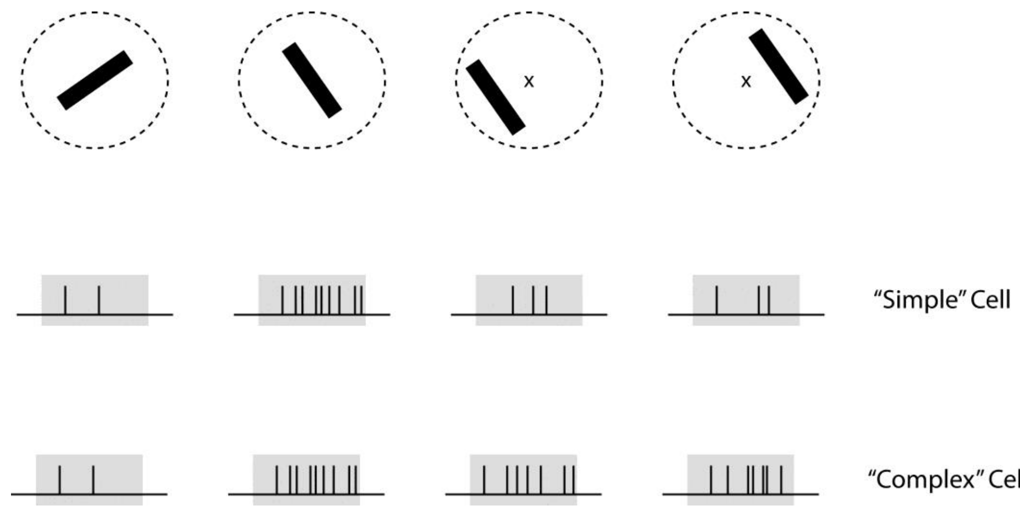
Source: Eye, Brain, and Vision. David H. Hubel. New York : Scientific American Library : Distributed by W.H. Freeman, c1988. ISBN: 0716750201.

A simple model for simple cells

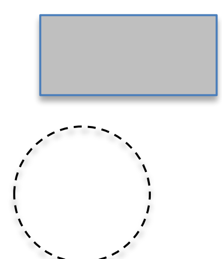


A feed-forward model for orientation selectivity in V1
(by no means the only model)

Complex cells show position tolerance



Stimulus: black bar



Stimulus presentation time

Receptive field

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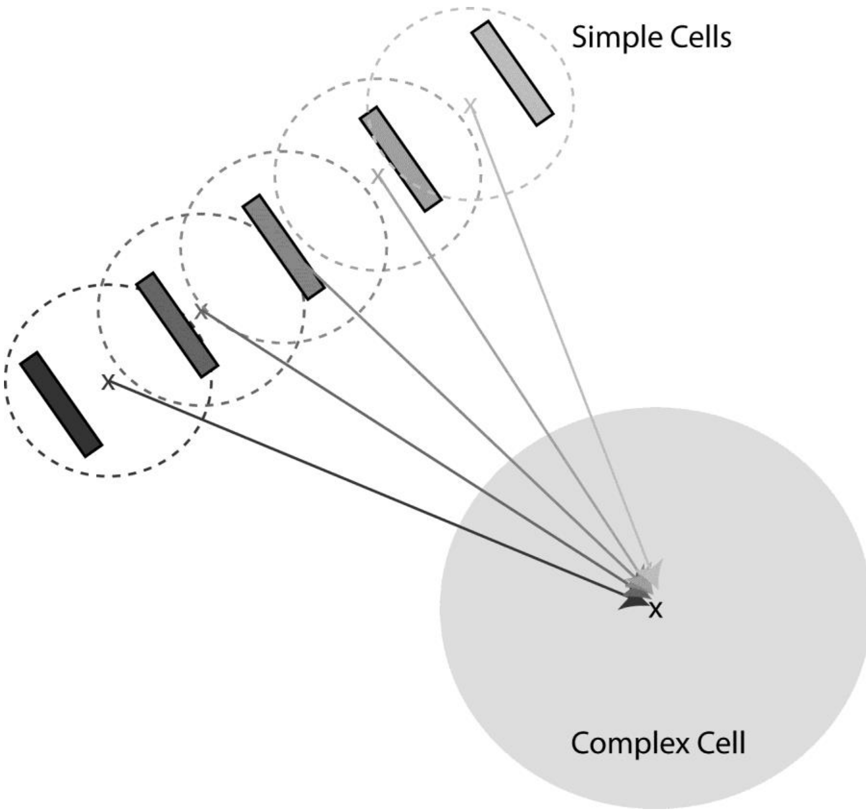
Source: Hubel, David H., and Torsten N. Wiesel. "Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. "The Journal of physiology 160, no. 1 (1962): 106-154.

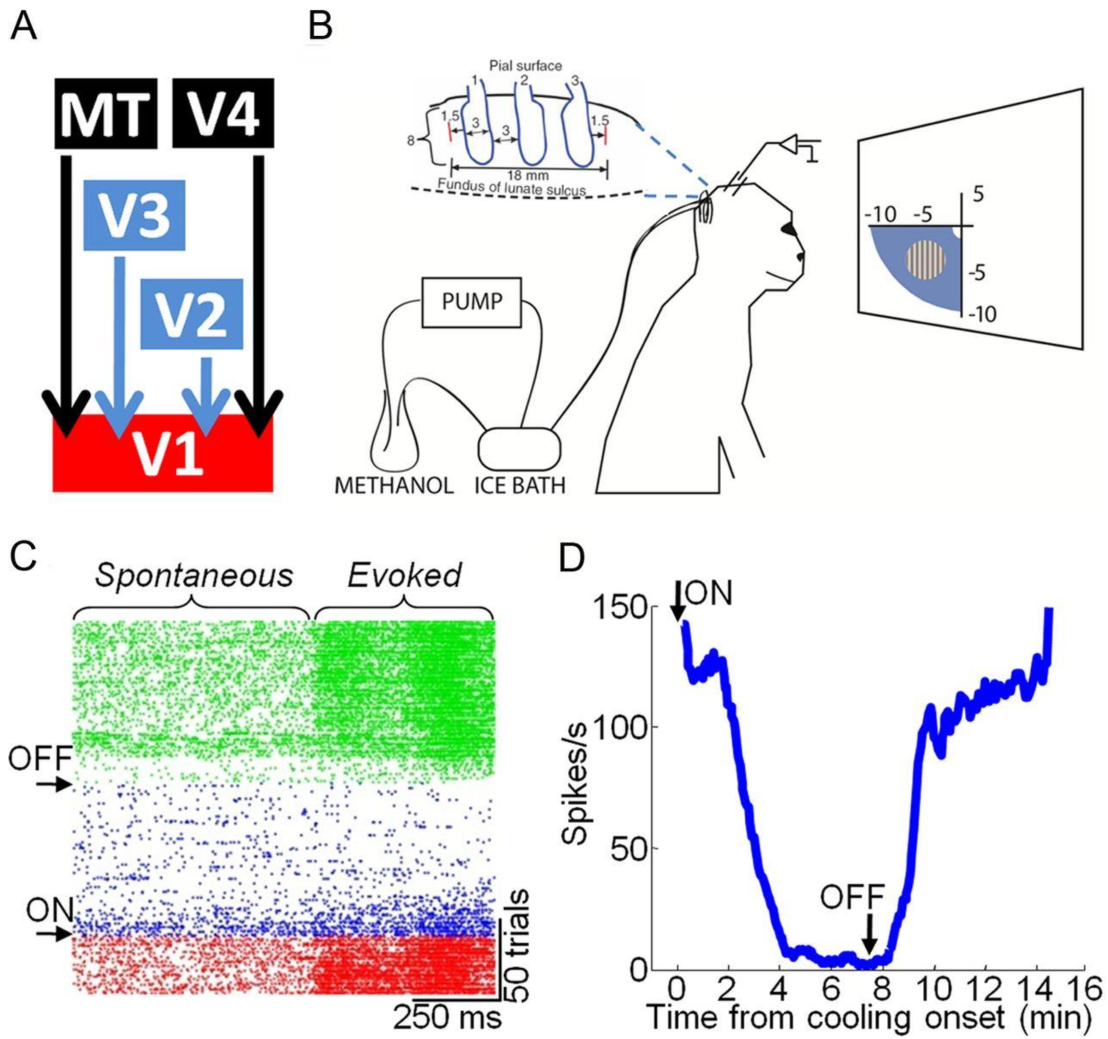
A model to describe tolerance in complex cells



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



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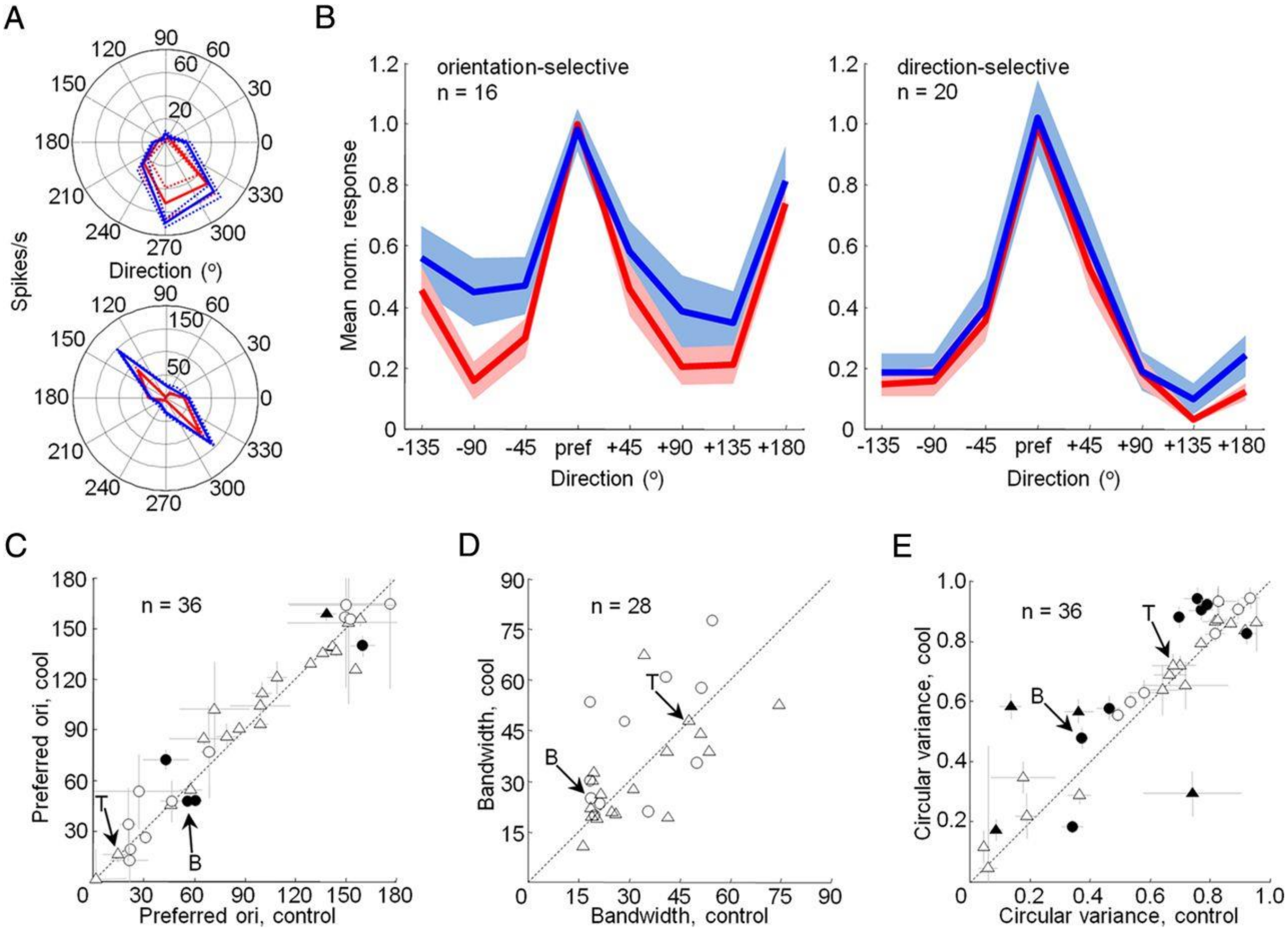
Source: Nassi, Jonathan J., Stephen G. Lomber, and Richard T. Born. "Corticocortical feedback contributes to surround suppression in V1 of the alert primate. "Journal of Neuroscience 33, no. 19 (2013): 85048517.

JoJo Nassi and Richard Born

Feedback inactivation does not change orientation or direction selectivity



Cooling V2/V3

Control

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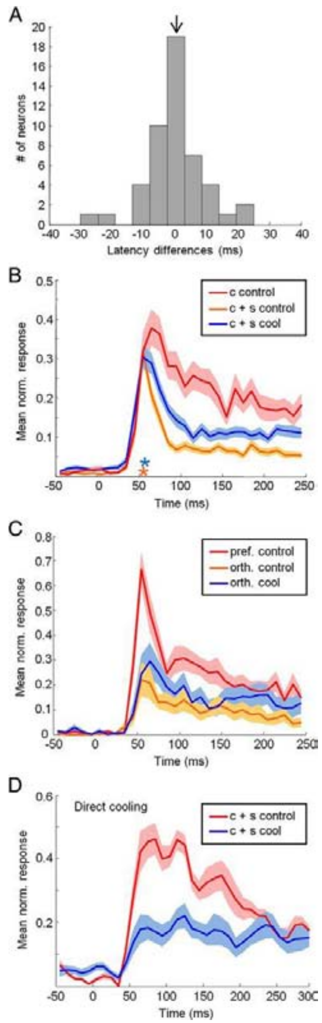
Source: Nassi, Jonathan J., Stephen G. Lomber, and Richard T. Born. "Corticocortical feedback contributes to surround suppression in V1 of the alert primate. "Journal of Neuroscience 33, no. 19 (2013): 85048517.

Nassi et al 2013

Temporal dynamics of feedback inactivation effects



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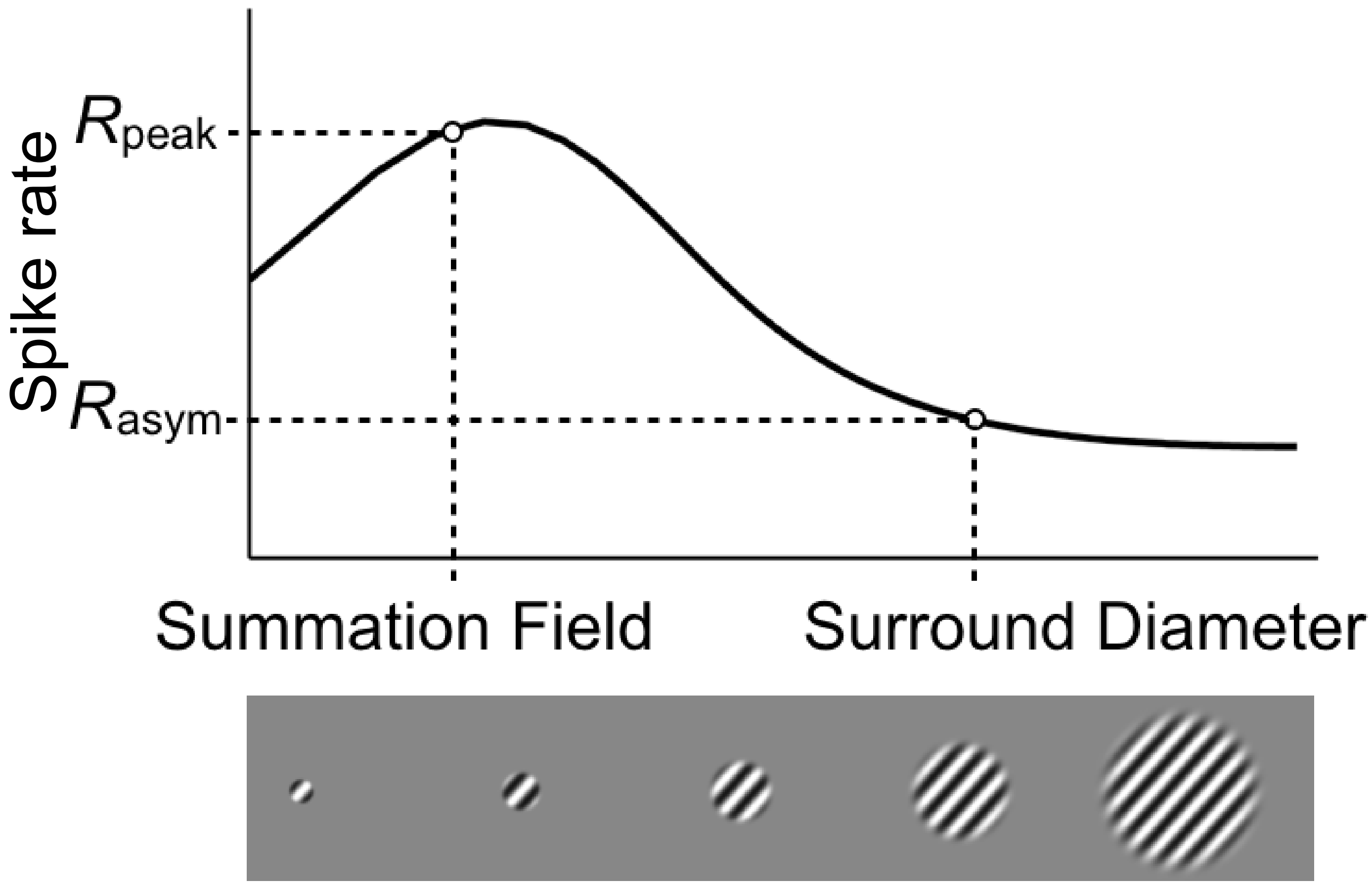
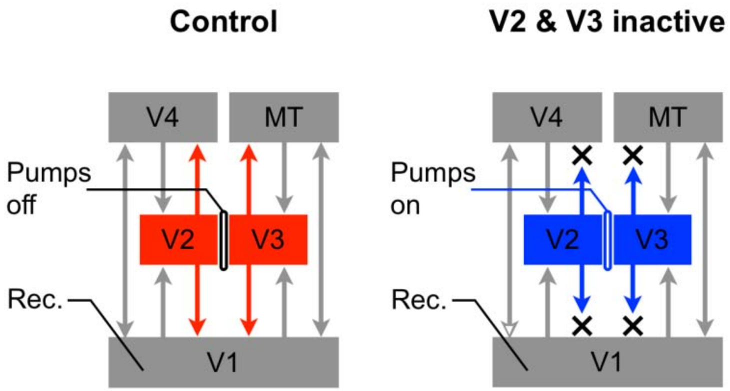
Source: Nassi, Jonathan J., Stephen G. Lomber, and Richard T. Born. "Corticocortical feedback contributes to surround suppression in V1 of the alert primate. "Journal of Neuroscience 33, no. 19 (2013): 85048517.

Area summation curve in V1

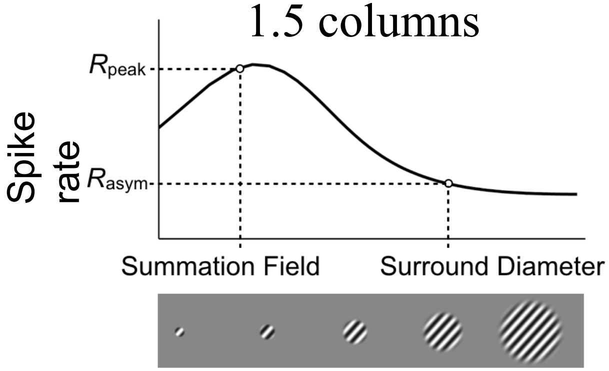


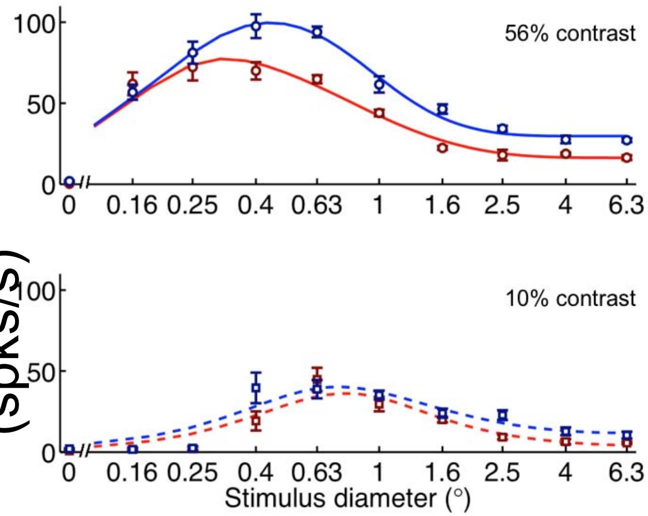
Courtesy of Frontiers in Systems Neuroscience. Used with permission.
Source: Nassi, Jonathan J., Camille Gómez-Laberge, Gabriel Kreiman, and Richard T. Born. "Corticocortical feedback increases the spatial extent of normalization. "Frontiers in systems neuroscience 8 (2014): 105.

Feedback inactivation leads to reduced surround suppression



Composite
1.5 columns





Spike rate (spks/s)

Stimulus diameter (degrees)

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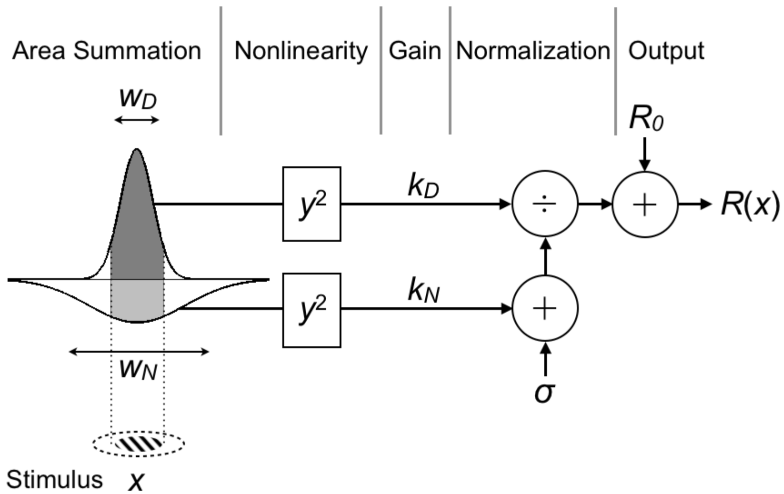
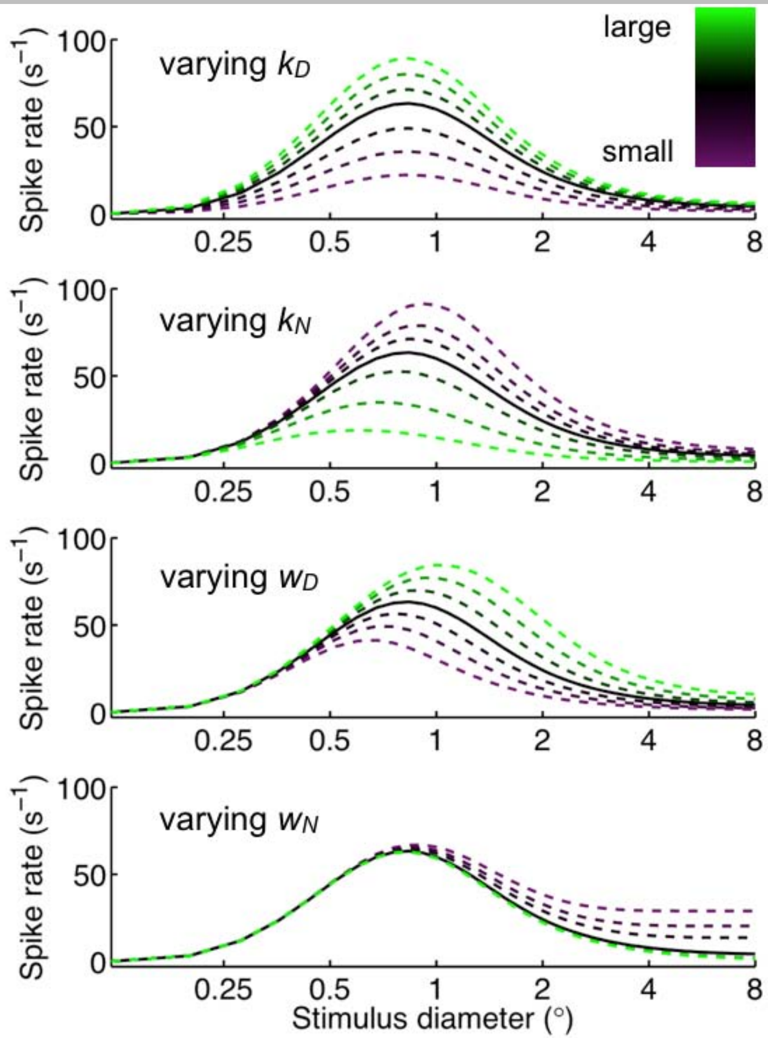
Source: Nassi, Jonathan J., Camille Gómez-Laberge, Gabriel Kreiman, and Richard T. Born. "Corticocortical feedback increases the spatial extent of normalization. "Frontiers in systems neuroscience 8 (2014): 105.

A simple normalization model to explain area summation curves



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

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



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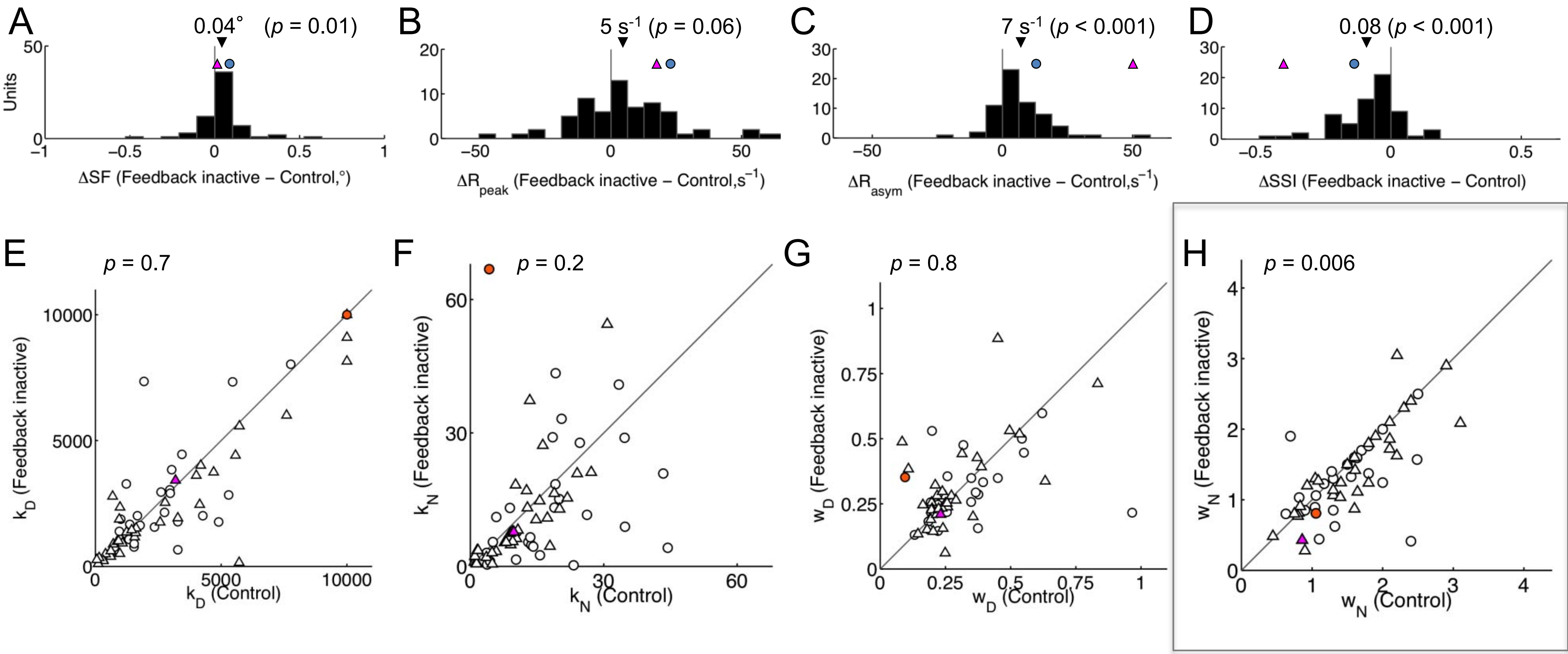
Feedback increases the normalization width: w_N



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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): bhv129.

Computational roles of feedback signals

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

Image by Hanlin Tang

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Inference and pattern completion as a hallmark of intelligence

A, C, E, G, → **I**

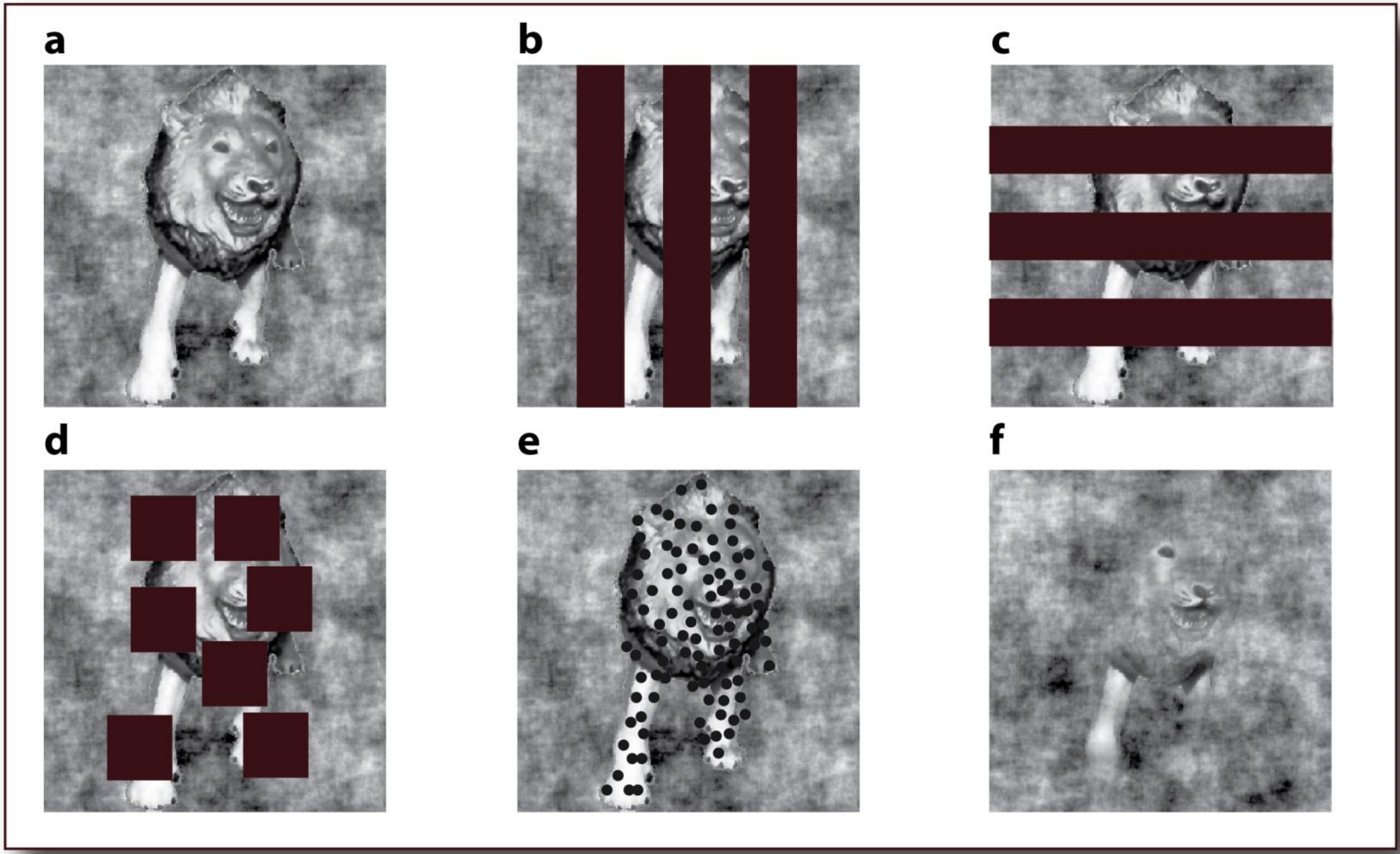
1, 2, 3, 5, 7, 11, → **13**

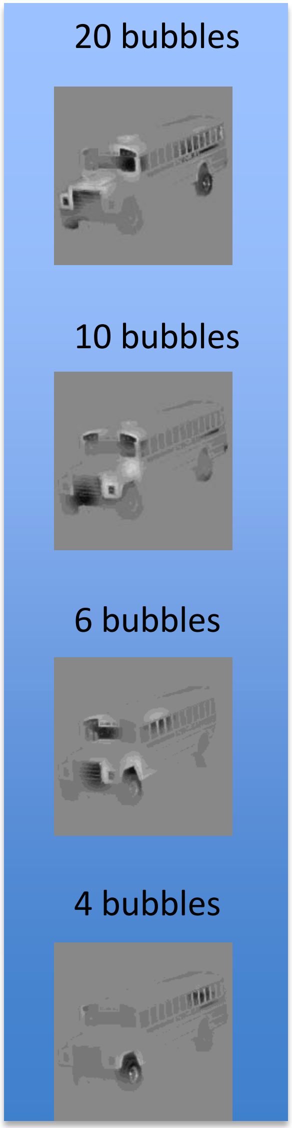
V-s-a- R-c-g-i-i-n → **Visual Recognition**

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





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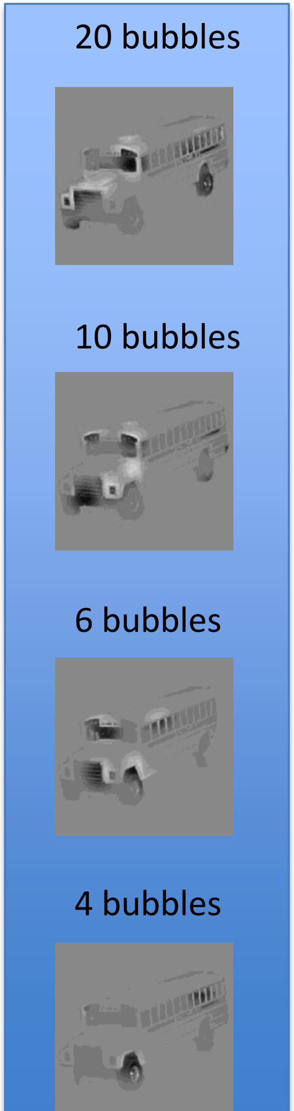
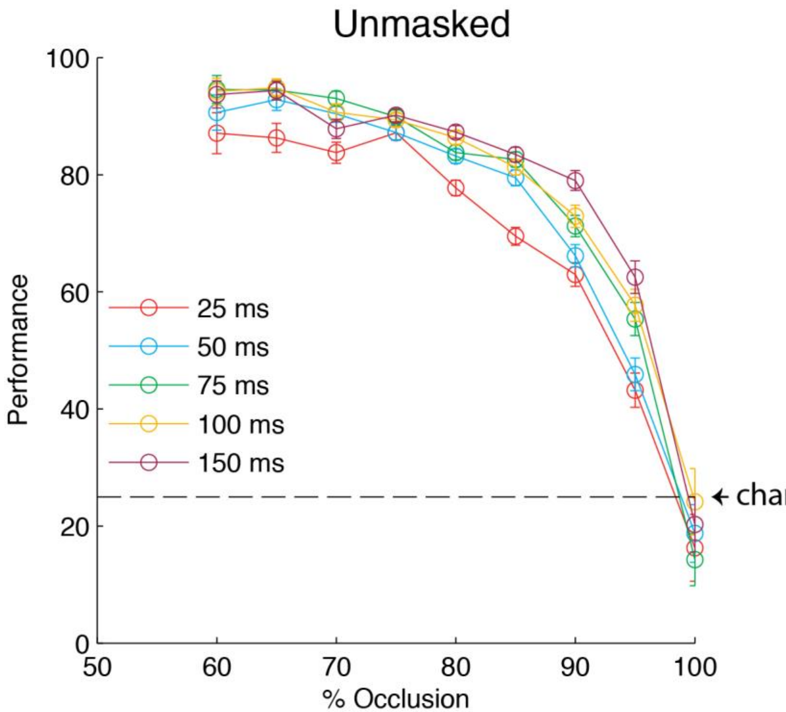
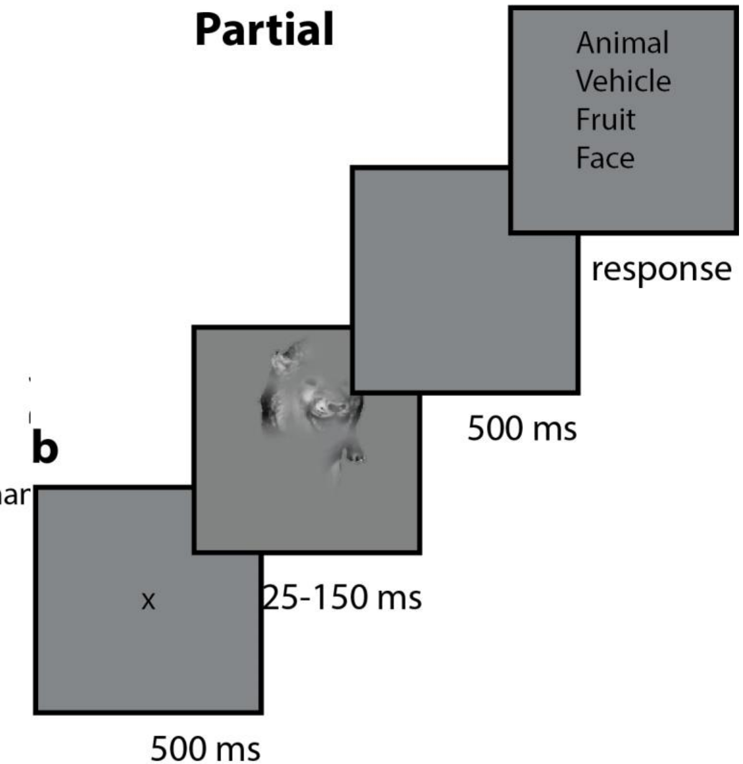
Behavior: Robustness to presentation of partial image information







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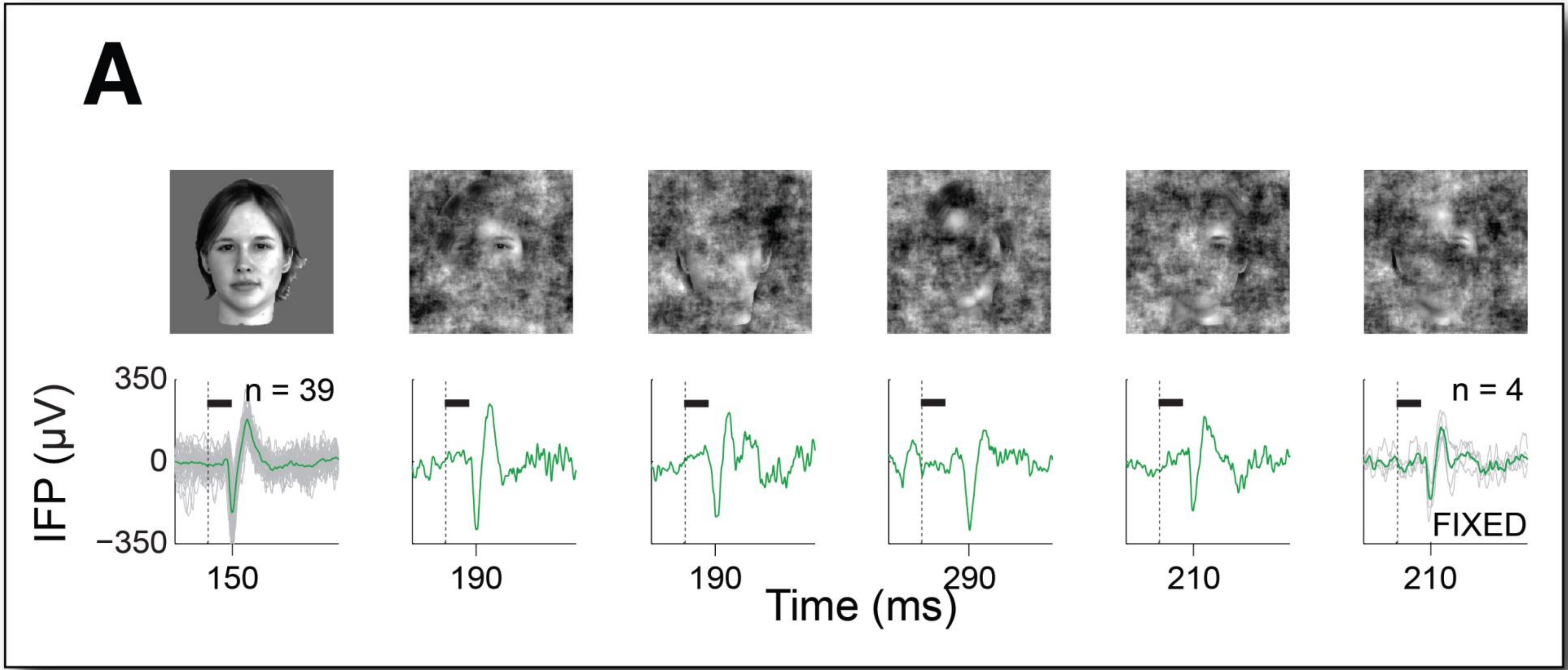
Example responses during object completion



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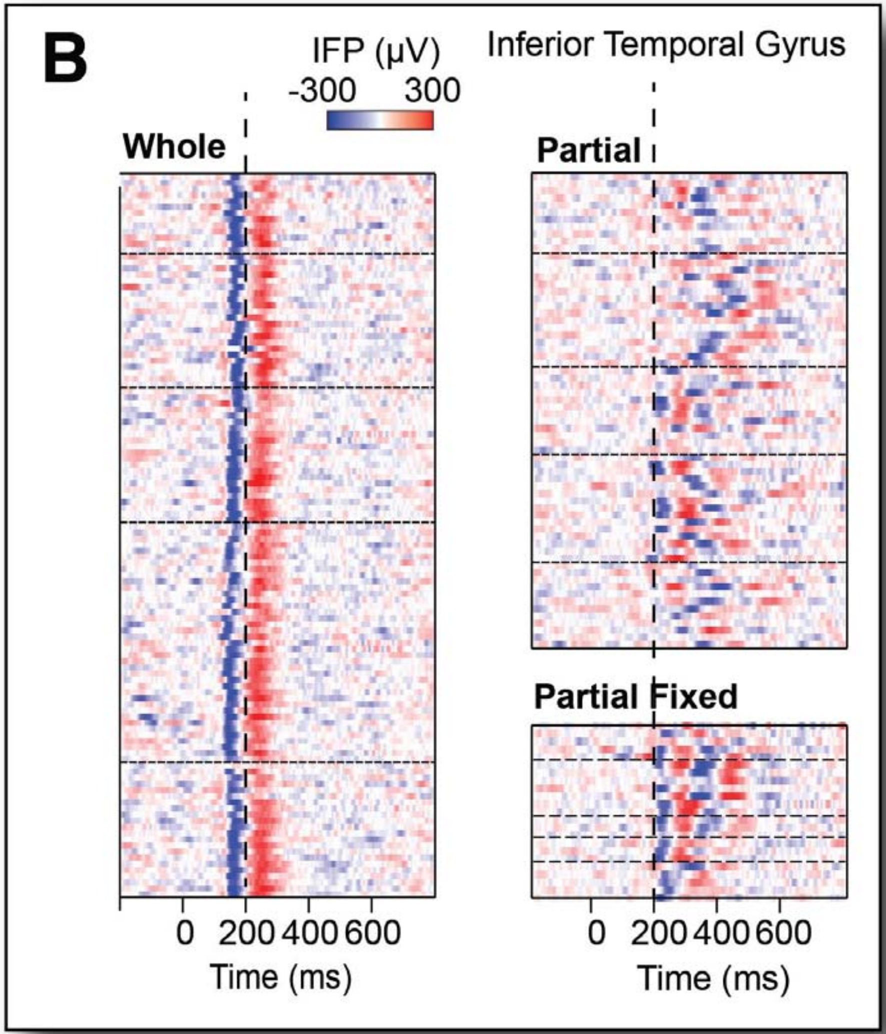
Source: Tang, Hanlin, Calin Buia, Radhika Madhavan, Nathan E. Crone, Joseph R. Madsen, William S. Anderson, and Gabriel Kreiman. "Spatiotemporal dynamics underlying object completion in human ventral visual cortex." Neuron 83, no. 3 (2014): 736-748.

Tang et al, Neuron 2014

Inferior Temporal Gyrus

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

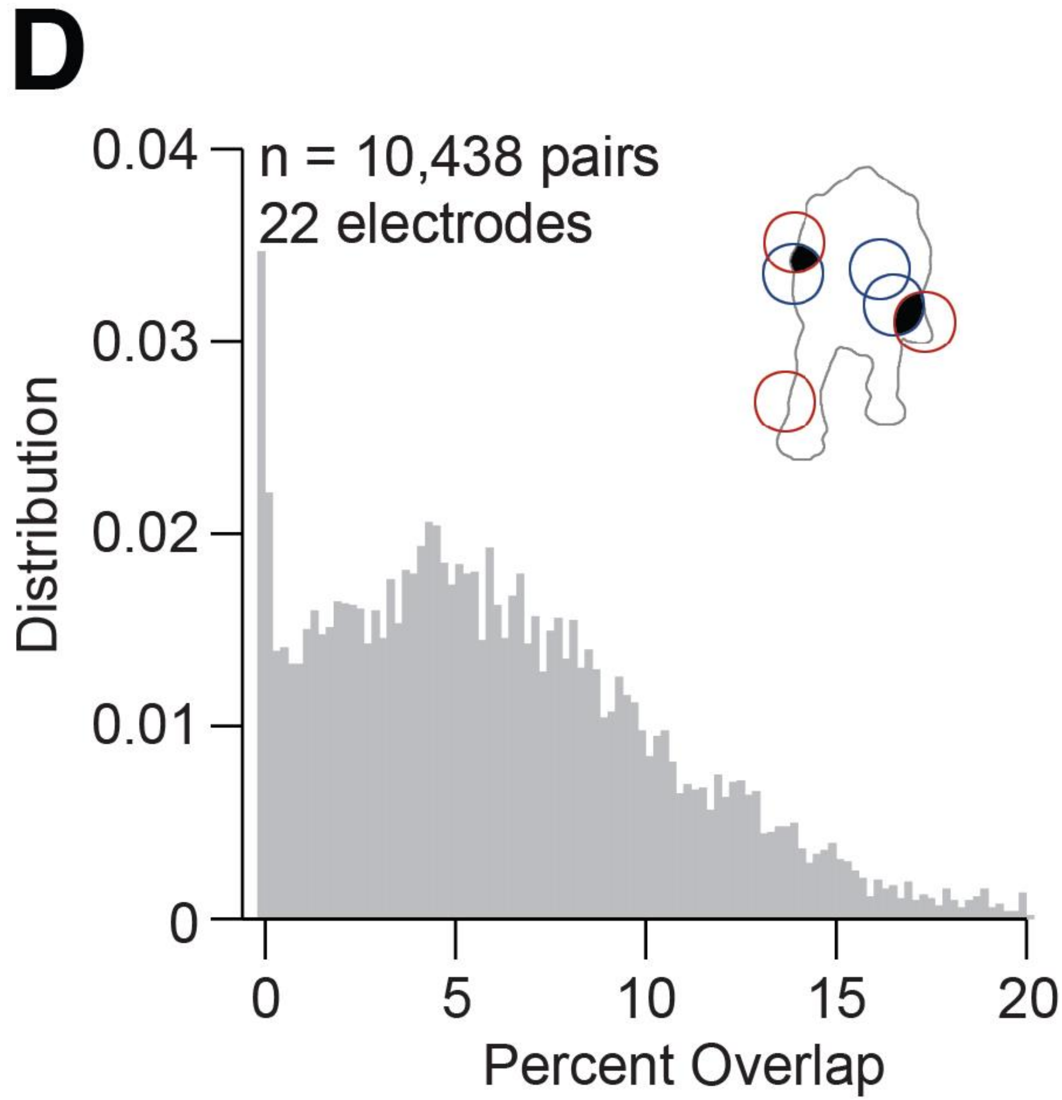
Tang et al, Neuron 2014

Limited object completion in feed-forward model

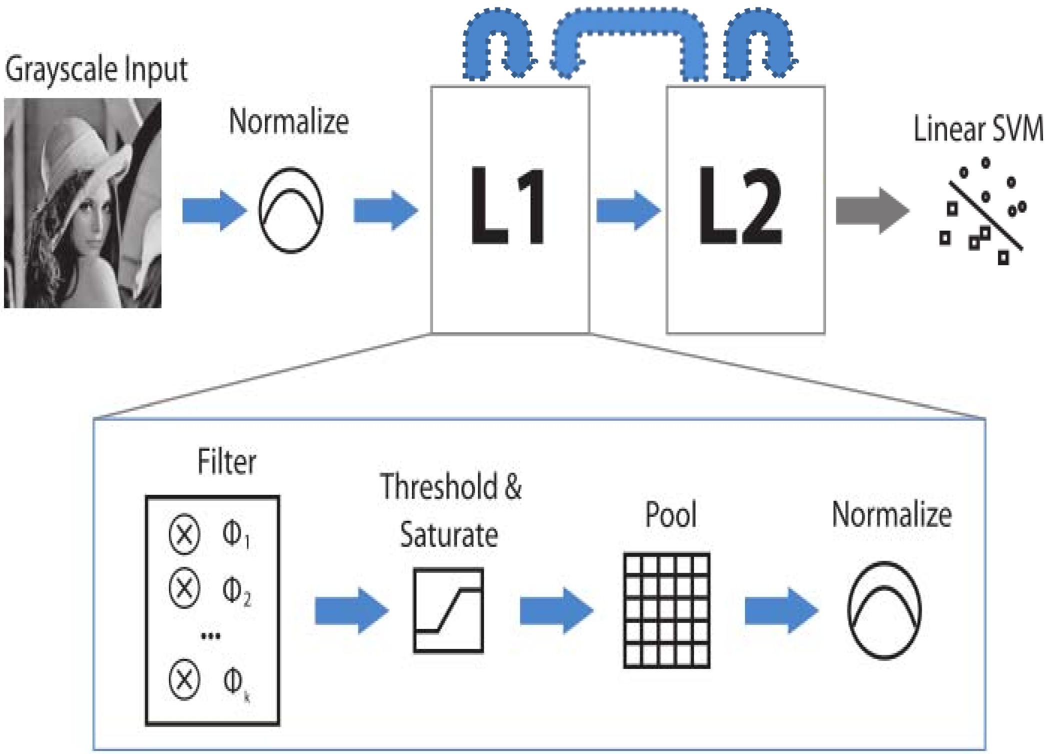
Figure removed due to copyright restrictions. Please see the video.
Source: Figure 29, Kreiman, Gabriel. "Computational models of visual object recognition. "Principles of Neural Coding 1 (2013): 0.

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 (?)



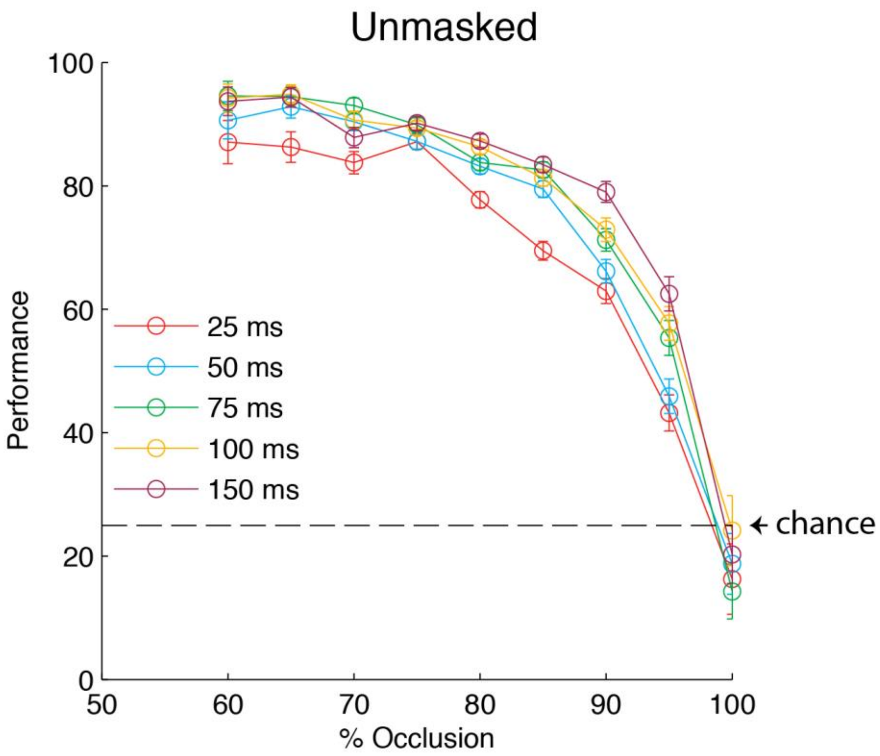
Adding recurrency to deep network models



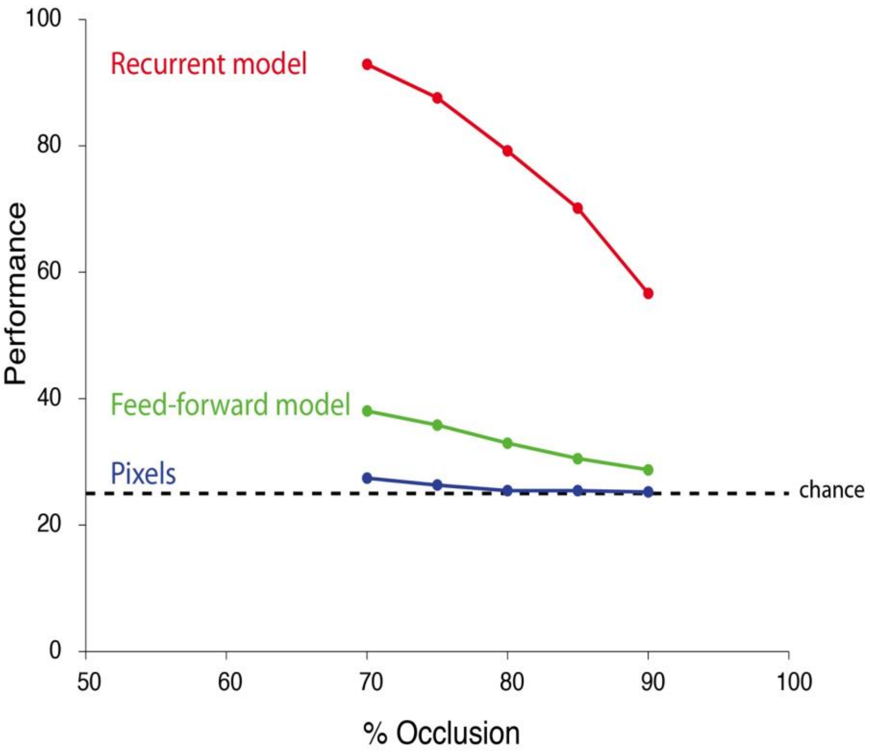
Bill Lotter, Hanlin Tang

Preliminary results: Recurrent connections can improve recognition of occluded objects

Behavior

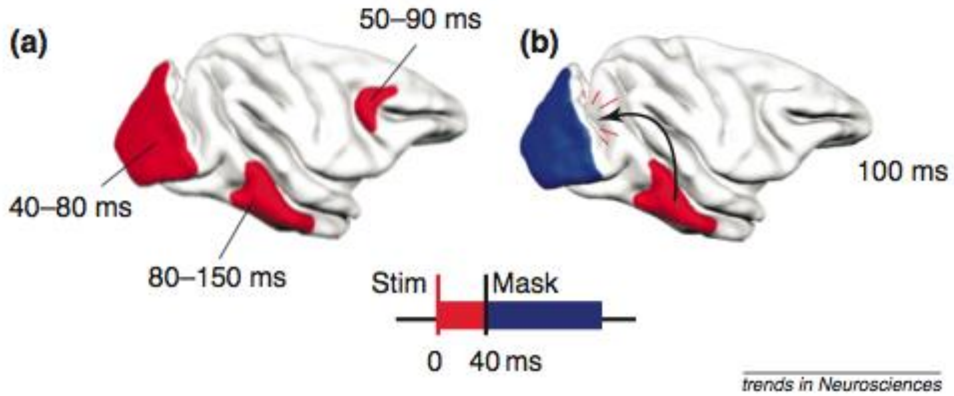


Recurrent model
Trained on whole images



Backward masking has been proposed to reduce the effects of feedback

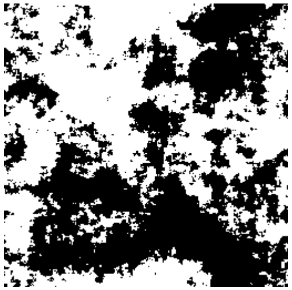
<u>Models</u>:

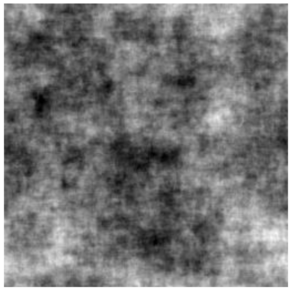


Lamme V, Roelfsema P (2000)

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.

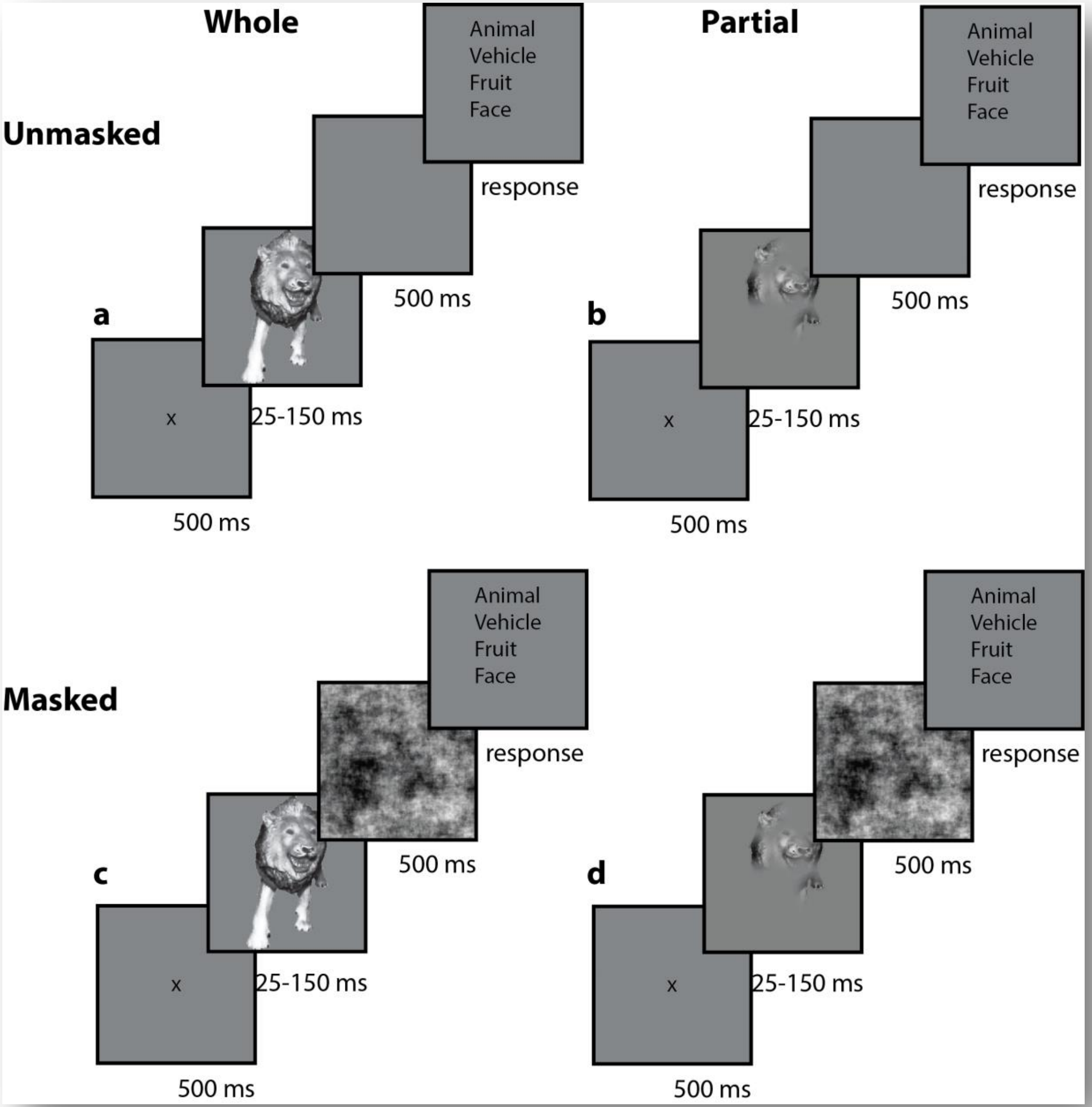
<u>Masks</u>:





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

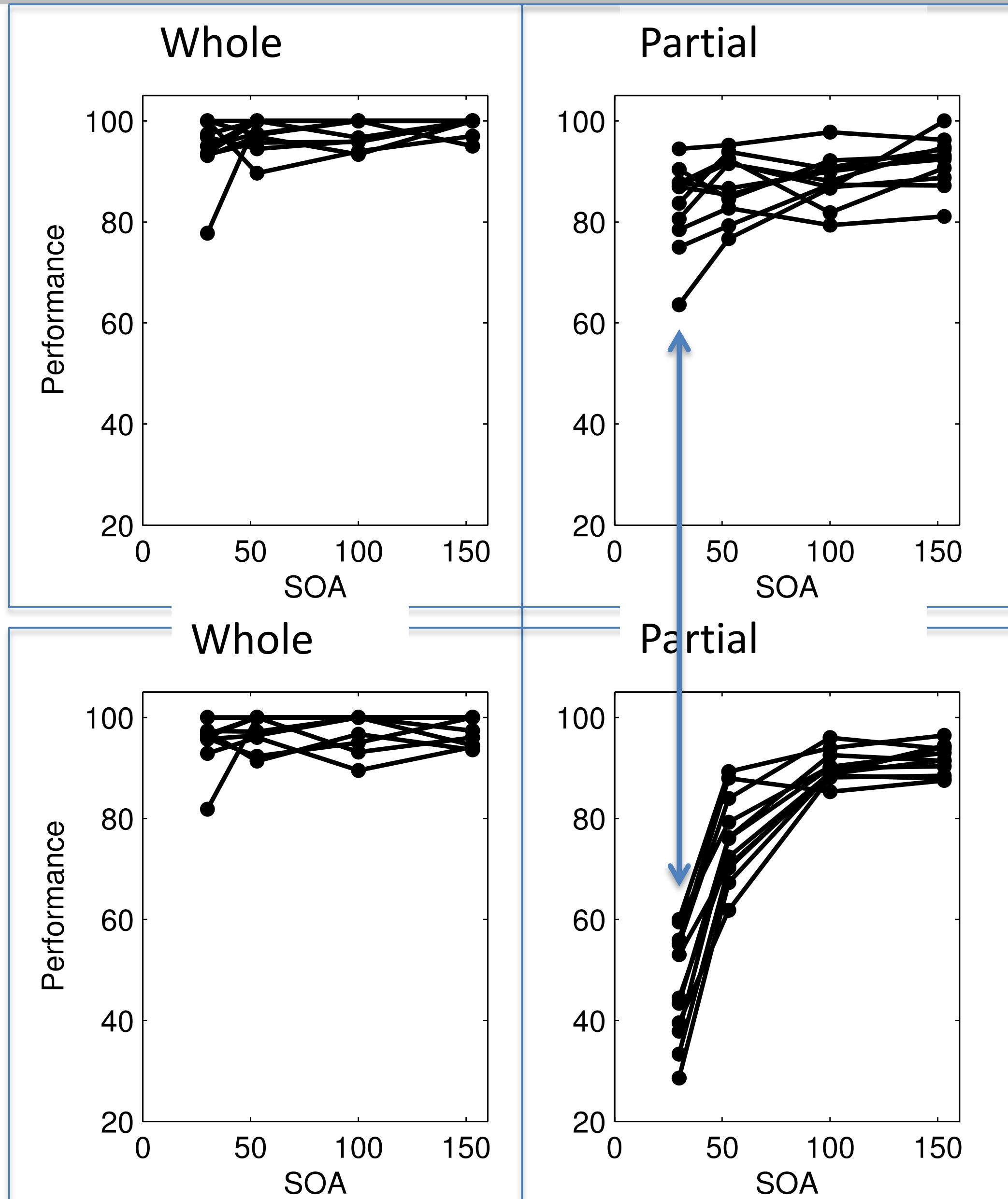
Object completion task (psychophysics)



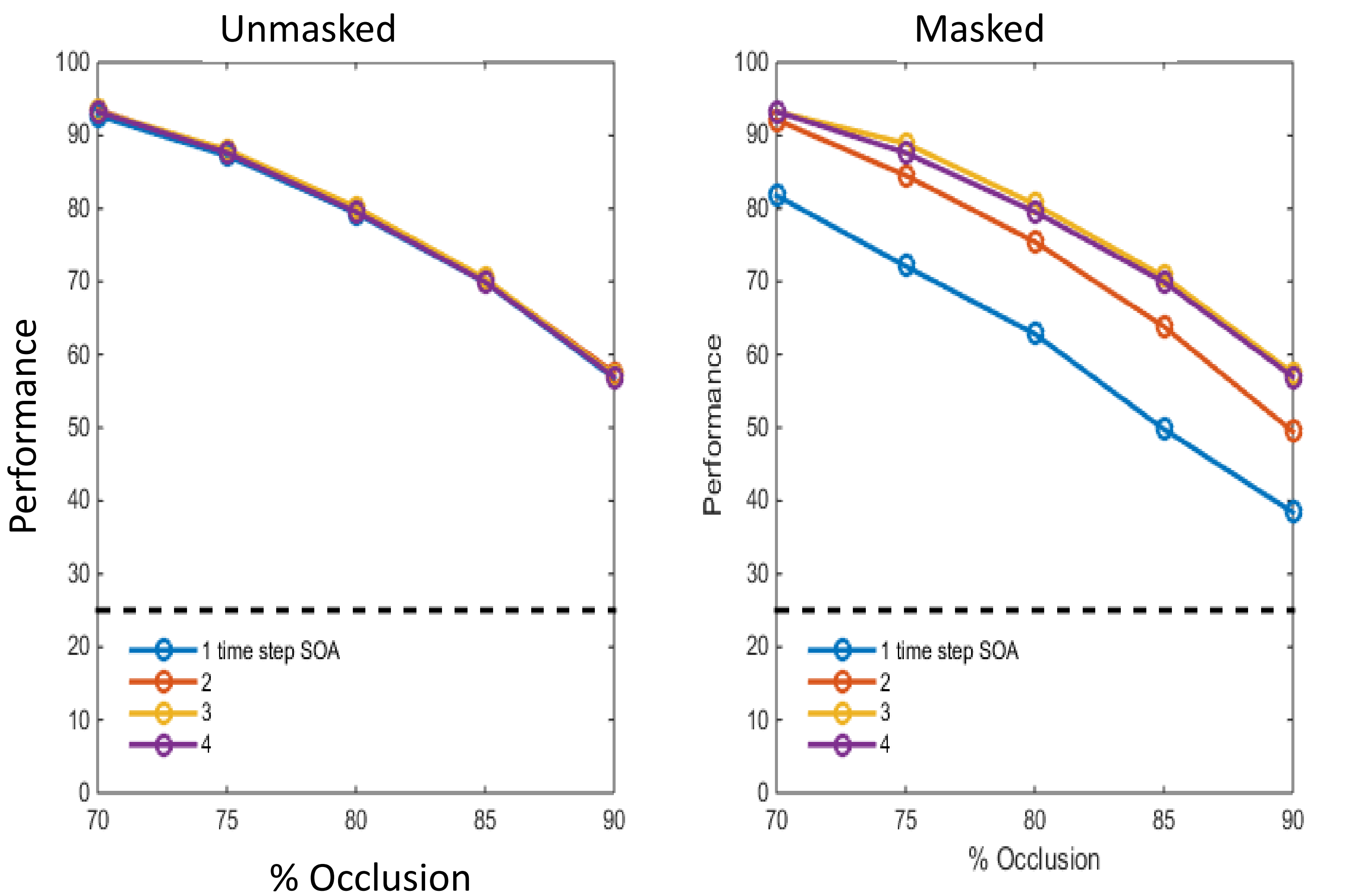
Backward masking impairs recognition of partial objects at short SOAs

Unmasked

Masked

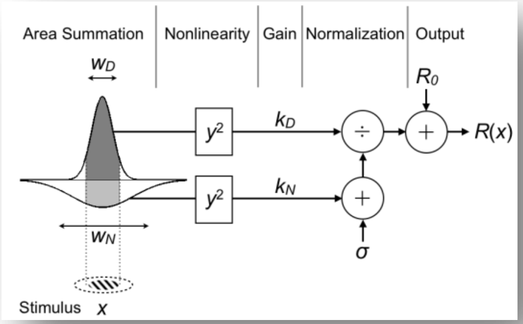


Model performance in masking experiment

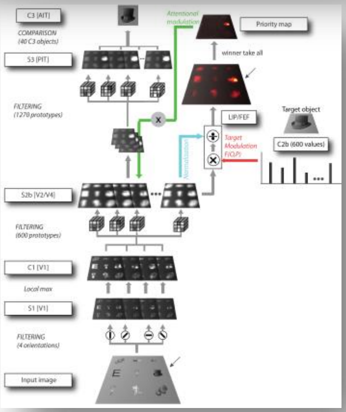


Summary

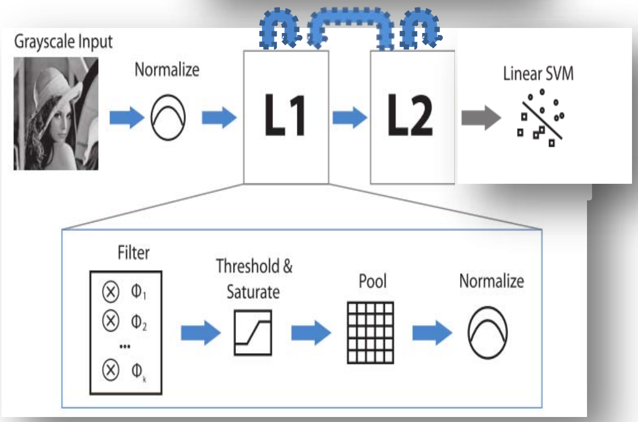
- Basic mechanisms in V1: Feedback signals enhance surround suppression



- 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

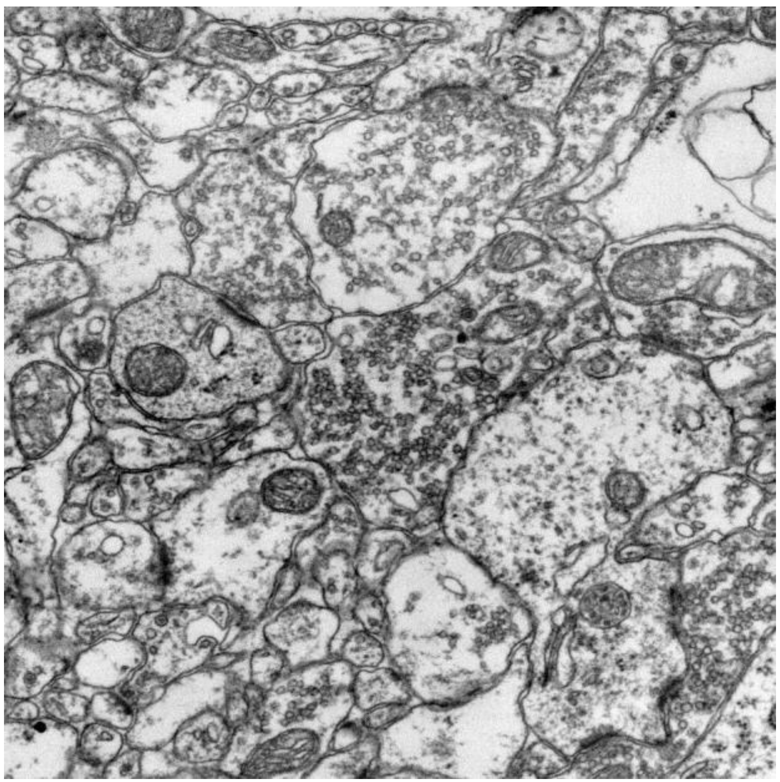
- **Wiring diagram**: Rapid progress tracing circuits in humans (low resolution) and animal models (high resolution)

- **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.



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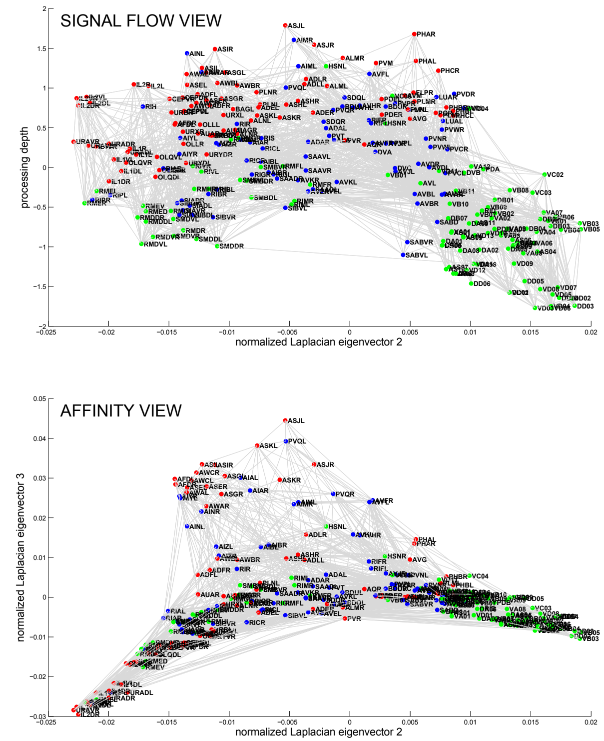
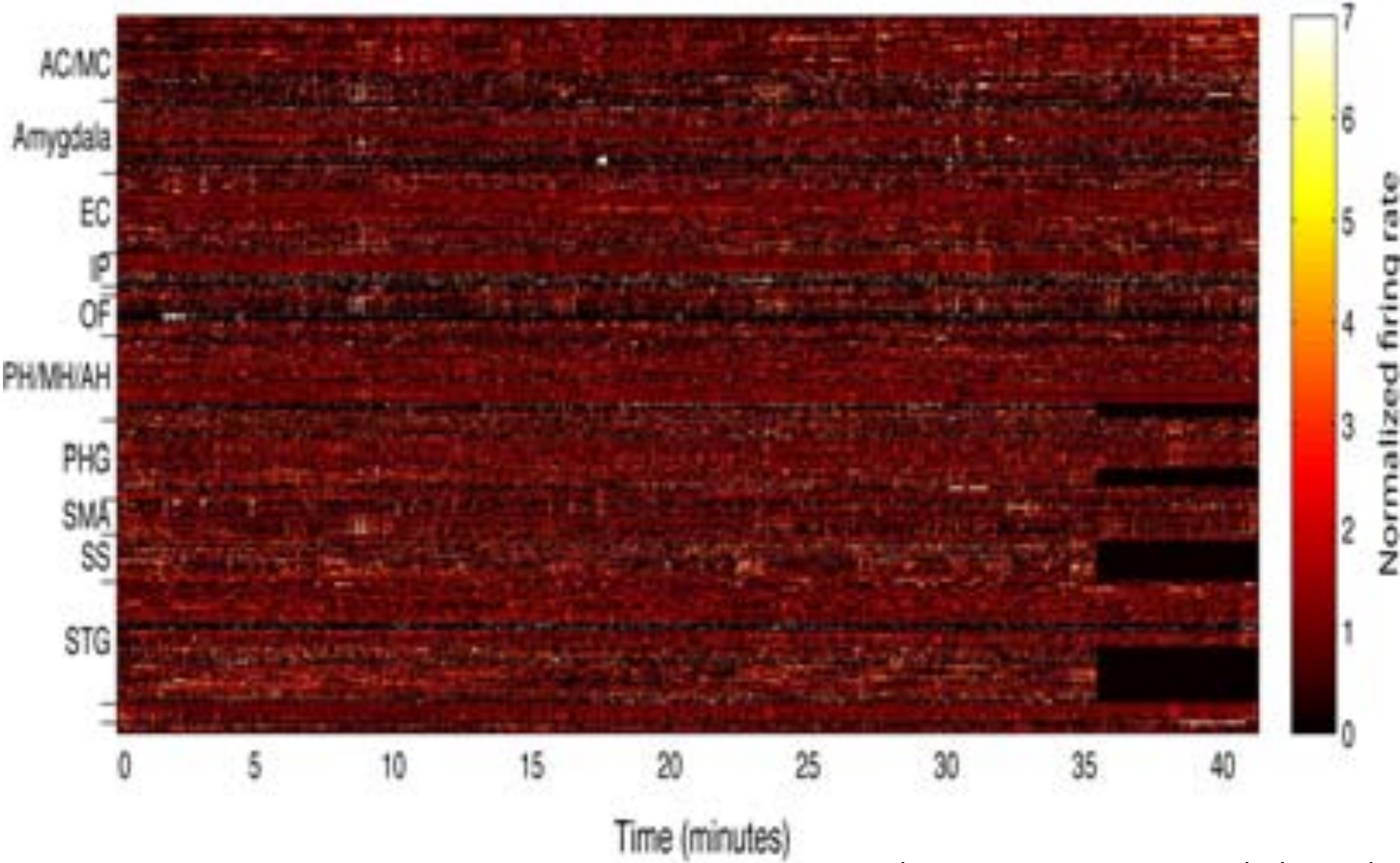


Fig. 2. The *C. elegans* wiring diagram is a network of identifiable, labeled neurons connected by chemical and electrical synapses. Red, sensory neurons; blue, interneurons; green, motorneurons. (a). Signal flow view shows neurons arranged so that the direction of signal flow is mostly downward. (b).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

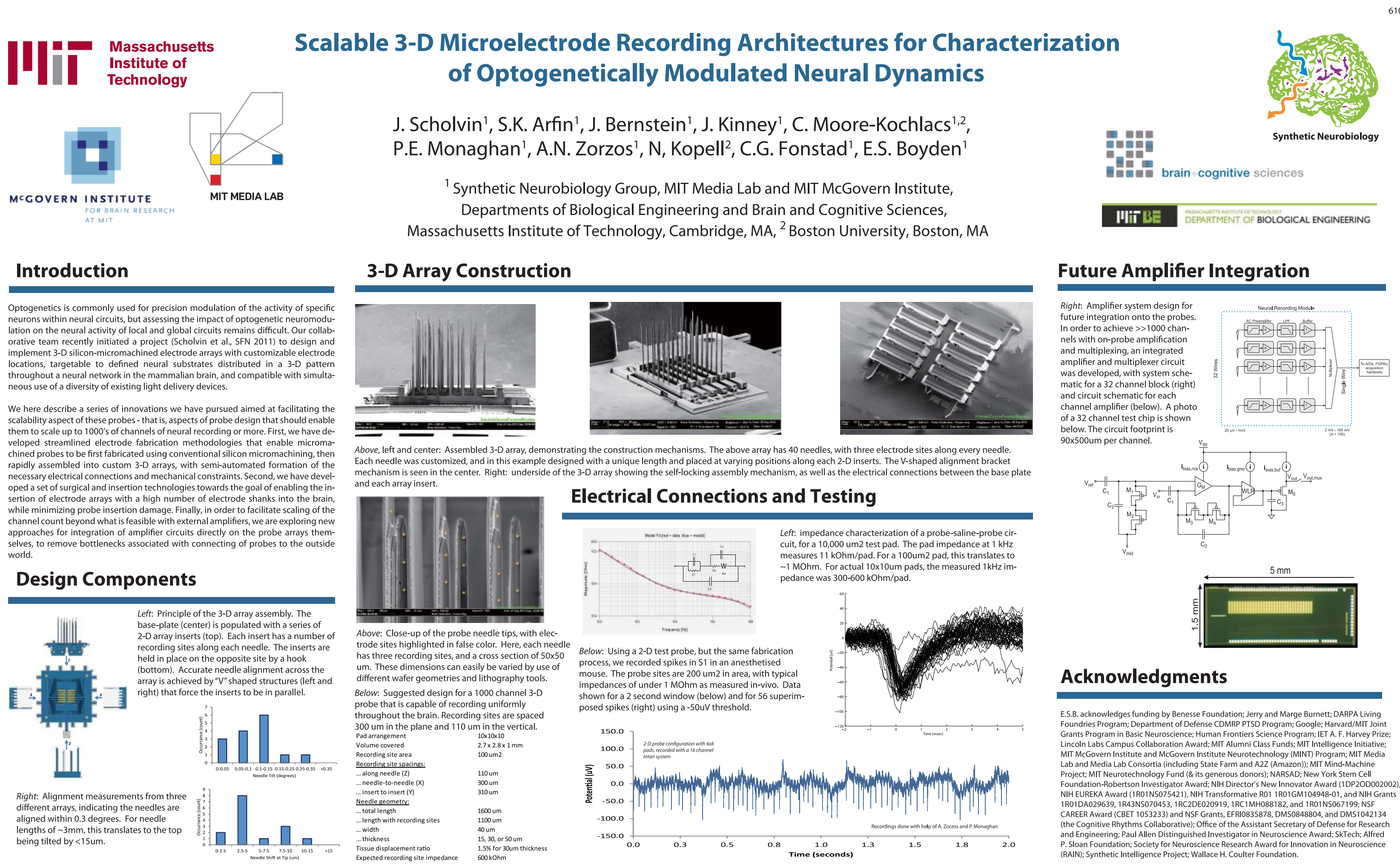
Strength in numbers



Pseudopopulation: 318 units

Hanlin Tang, Matias Ison, Itzhak Fried

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



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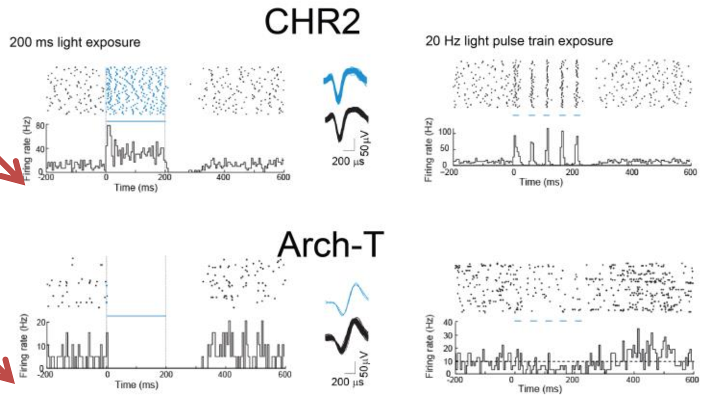
Playing with the source code: Using light to modulate neural with high specificity

activate

silence



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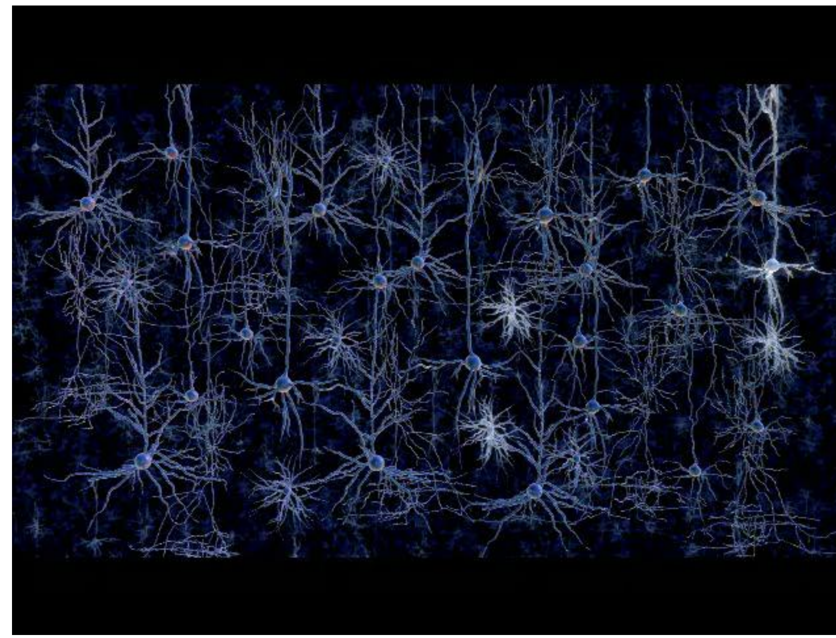
Source: Han, Xue, Xiaofeng Qian, Jacob G. Bernstein, Hui-hui Zhou, Giovanni Talei Franzesi, Patrick Stern, Roderick T. Bronson, Ann M. Graybiel, Robert Desimone, and Edward S. Boyden. "Millisecond-timescale optical control of neural dynamics in the nonhuman primate brain." Neuron 62, no. 2 (2009): 191-198.



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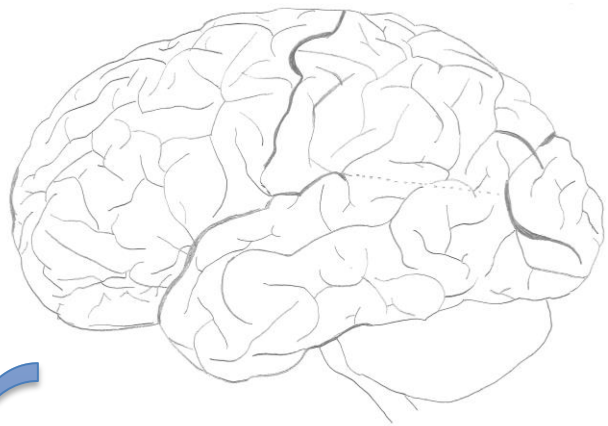
Boyden-Desimone

Biological codes to computational codes



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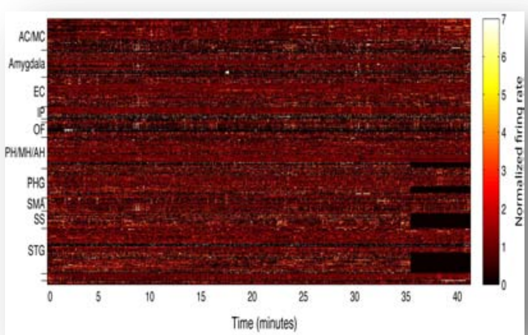
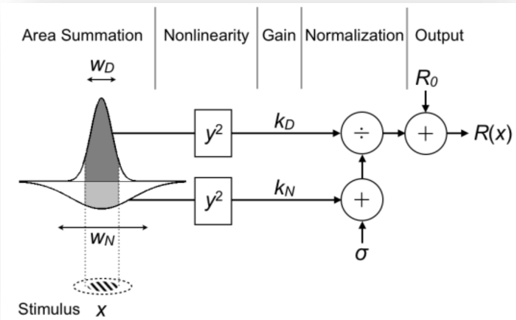
Biological code



Computer code



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Resource: Brains, Minds and Machines Summer Course
Tomaso Poggio and Gabriel Kreiman

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