# Mechanisms of stimulus feature selectivity in sensory systems

1. Orientation and direction selectivity in the visual cortex
2. Selectivity to sound frequency in the auditory cortex
3. Feature selectivity in the somatosensory system.

Orientation selectivity in the primary visual cortex

1. Hubel and Wiesel experiments
2. The H&W model – a simple feedforward model
3. Predictions of the H&W model
4. Mismatches between H&W model and experimental data
5. Recurrent models for orientation selectivity
6. Experiments that support the H&W – intracellular recording data
7. Advanced imaging experiments and the H&W model
8. Optogenetic manipulations of specific types of neurons

Orientation selectivity
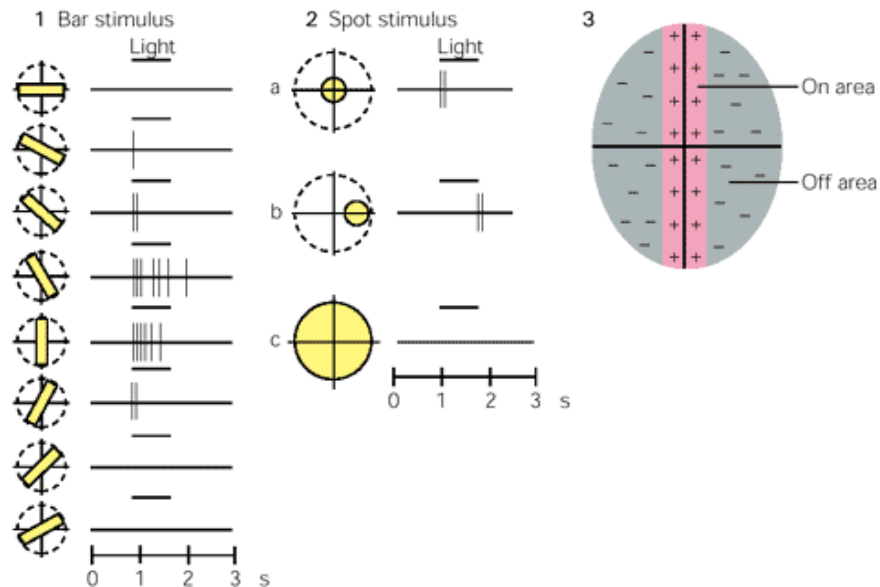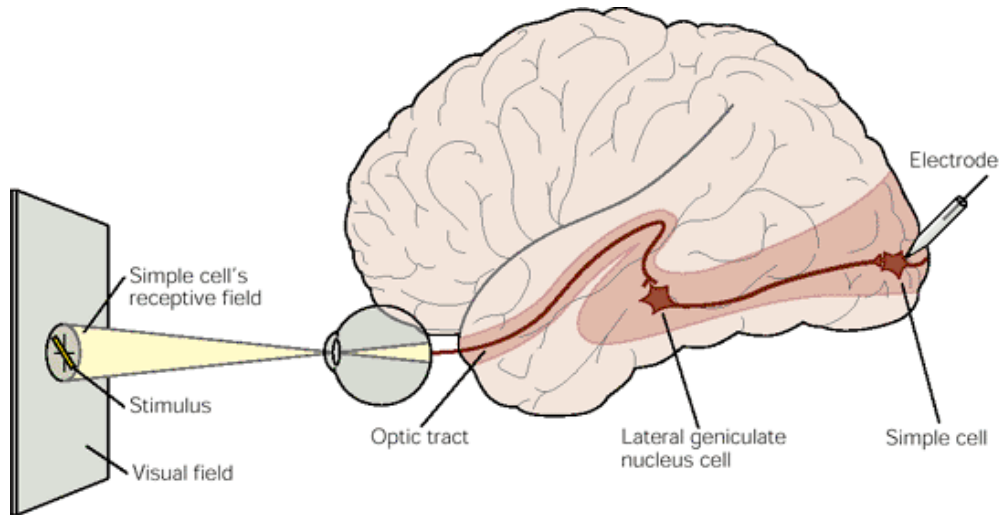
Receptive fields in the retina
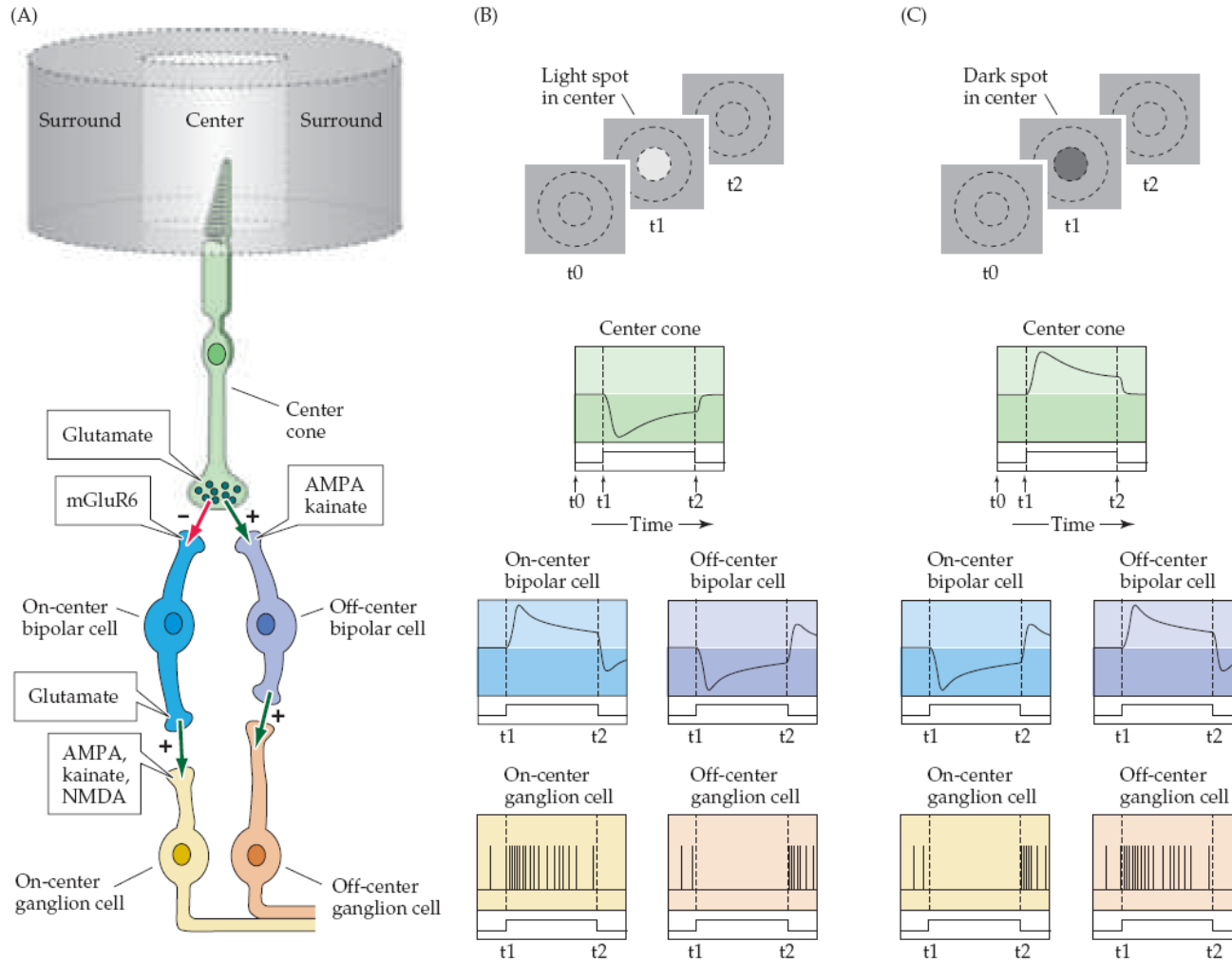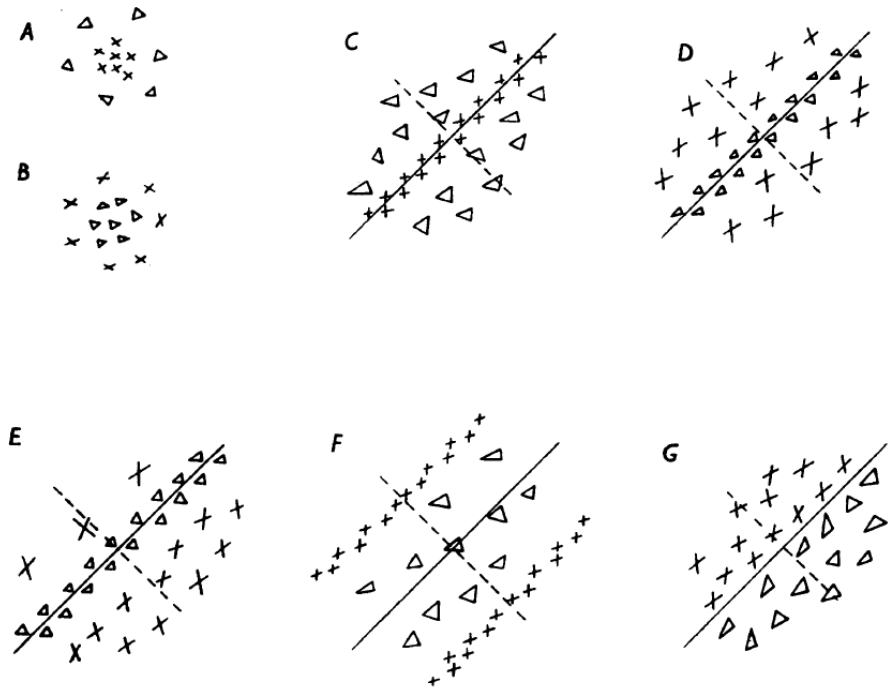
Receptive fields in V1, H&W experiments

RECEPTIVE FIELDS, BINOCULAR INTERACTION AND FUNCTIONAL ARCHITECTURE IN THE CAT'S VISUAL CORTEX

BY D. H. HUBEL AND T. N. WIESEL

From the Neurophysiology Laboratory, Department of Pharmacology
Harvard Medical School, Boston, Massachusetts, U.S.A.

Text-fig. 2. Common arrangements of lateral geniculate and cortical receptive fields. *A*. 'On'-centre geniculate receptive field. *B*. 'Off'-centre geniculate receptive field. *C–G*. Various arrangements of simple cortical receptive fields. ×, areas giving excitatory responses ('on' responses); △, areas giving inhibitory responses ('off' responses). Receptive-field axes are shown by continuous lines through field centres; in the figure these are all oblique, but each arrangement occurs in all orientations.

Data from H&W experiments: flashing bars : "complex cell"
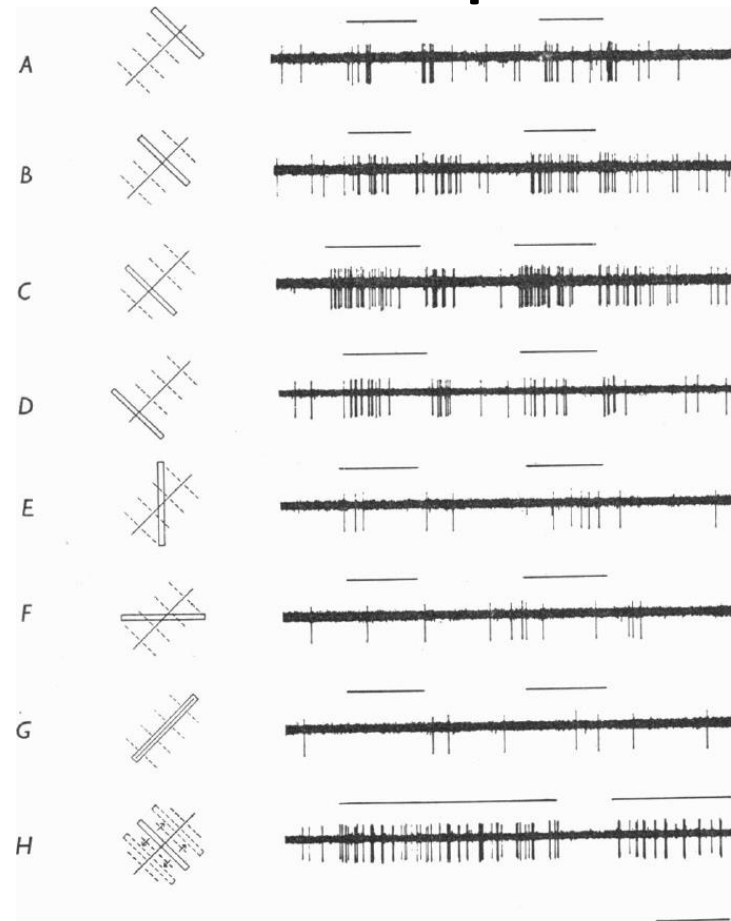
Text-fig. 4. Responses of a cell with a complex field to stimulation of the left (contralateral) eye with a slit $\frac{1}{8} \times 2\frac{1}{2}°$. Receptive field was in the area centralis and was about $2 \times 3°$ in size. A–D, $\frac{1}{8}°$ wide slit oriented parallel to receptive field axis. E–G, slit oriented at 45 and 90° to receptive-field axis. H, slit oriented as in A–D, is on throughout the record and is moved rapidly from side to side where indicated by upper beam. Responses from left eye slightly more marked than those from right (Group 3, see Part II). Time 1 sec.
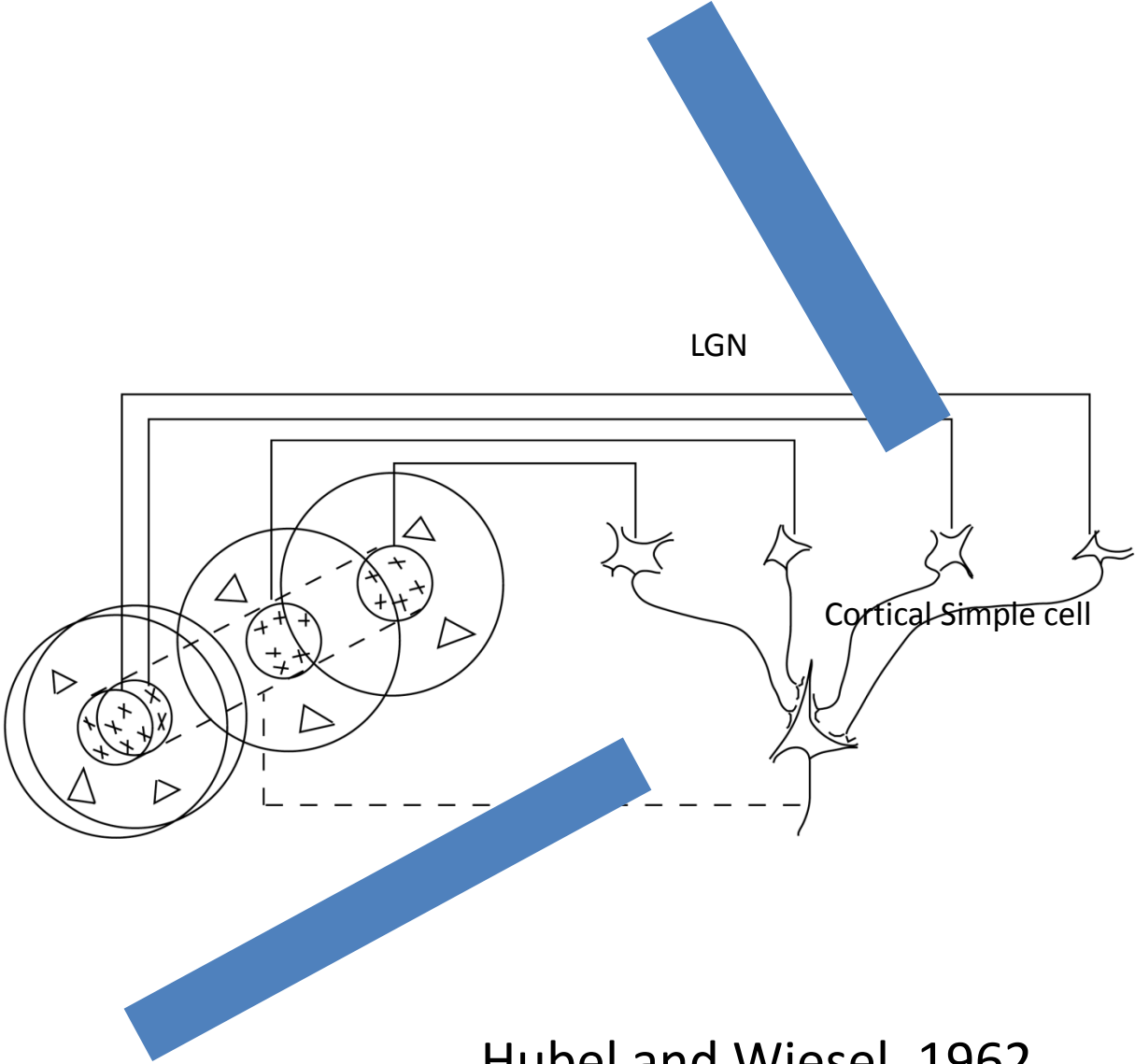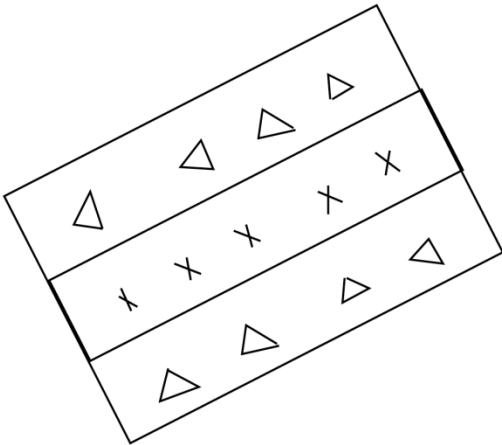
H&W model for simple cells
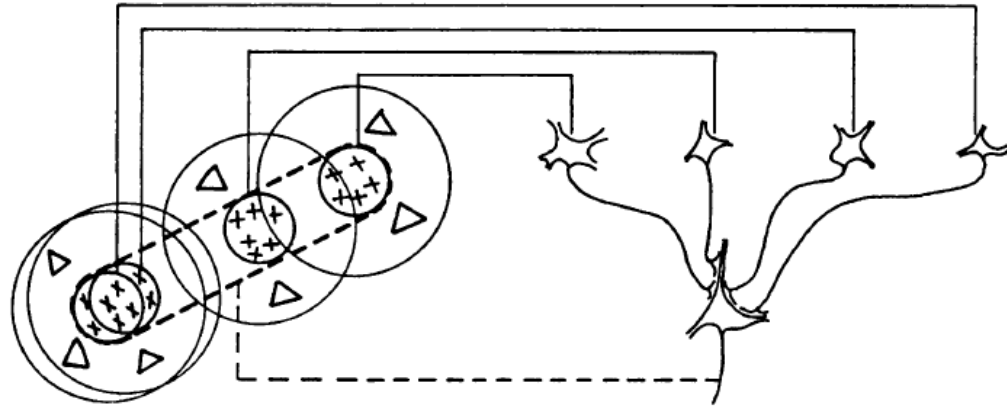
Text-fig. 19. Possible scheme for explaining the organization of simple receptive fields. A large number of lateral geniculate cells, of which four are illustrated in the upper right in the figure, have receptive fields with 'on' centres arranged along a straight line on the retina. All of these project upon a single cortical cell, and the synapses are supposed to be excitatory. The receptive field of the cortical cell will then have an elongated 'on' centre indicated by the interrupted lines in the receptive-field diagram to the left of the figure.
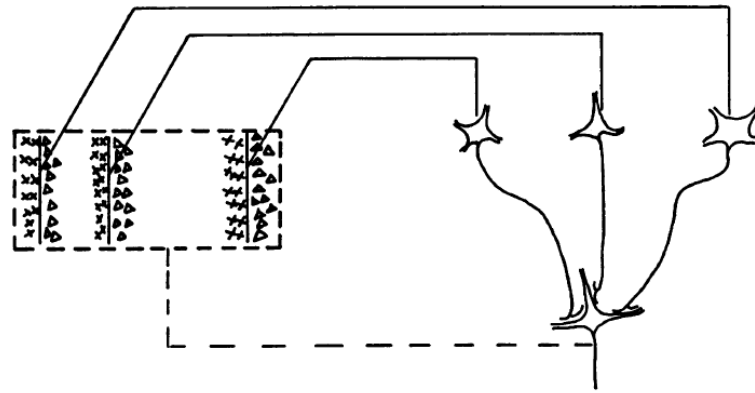
H&W model:

The Feedforward Model

LGN

Cortical Simple cell
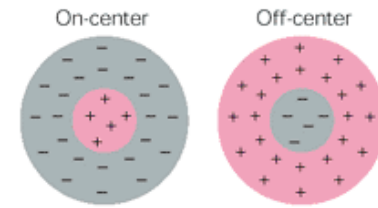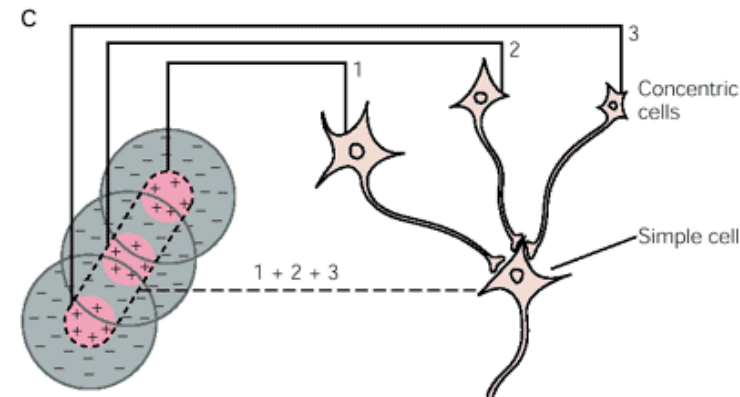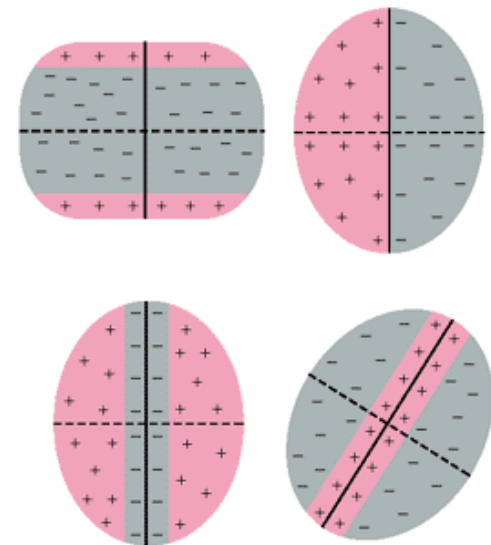
Hubel and Wiesel, 1962

H&W model for complex cells

Text-fig. 20. Possible scheme for explaining the organization of complex receptive fields. A number of cells with simple fields, of which three are shown schematically, are imagined to project to a single cortical cell of higher order. Each projecting neurone has a receptive field arranged as shown to the left: an excitatory region to the left and an inhibitory region to the right of a vertical straight-line boundary. The boundaries of the fields are staggered within an area outlined by the interrupted lines. Any vertical-edge stimulus falling across this rectangle, regardless of its position, will excite some simple-field cells, leading to excitation of the higher-order cell.

H&W model for simple cells

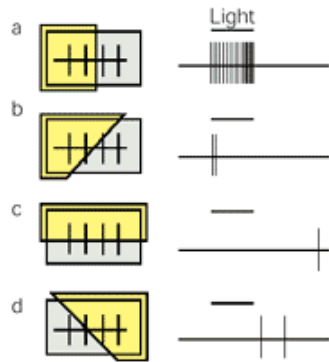A Receptive fields of concentric cells of retina and lateral geniculate nucleus

On-center   Off-center

B Receptive fields of simple cells of primary visual cortex
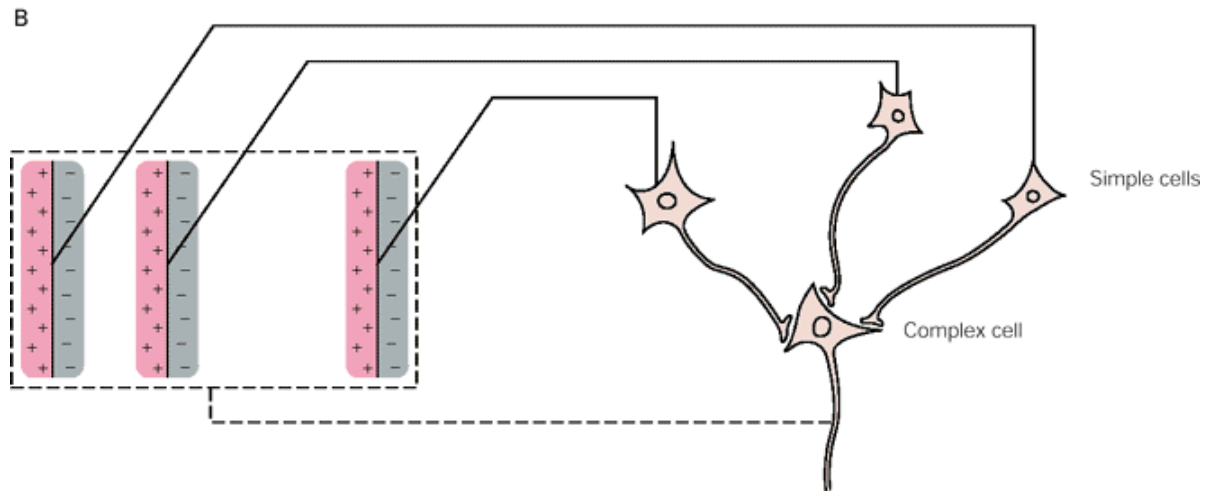
C
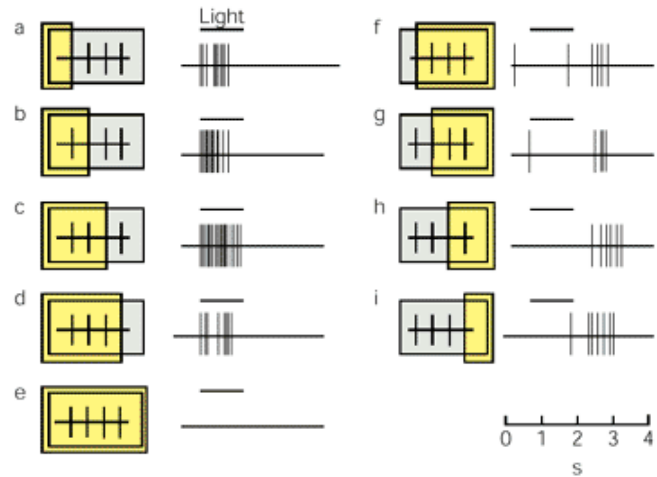
Concentric cells

Simple cell
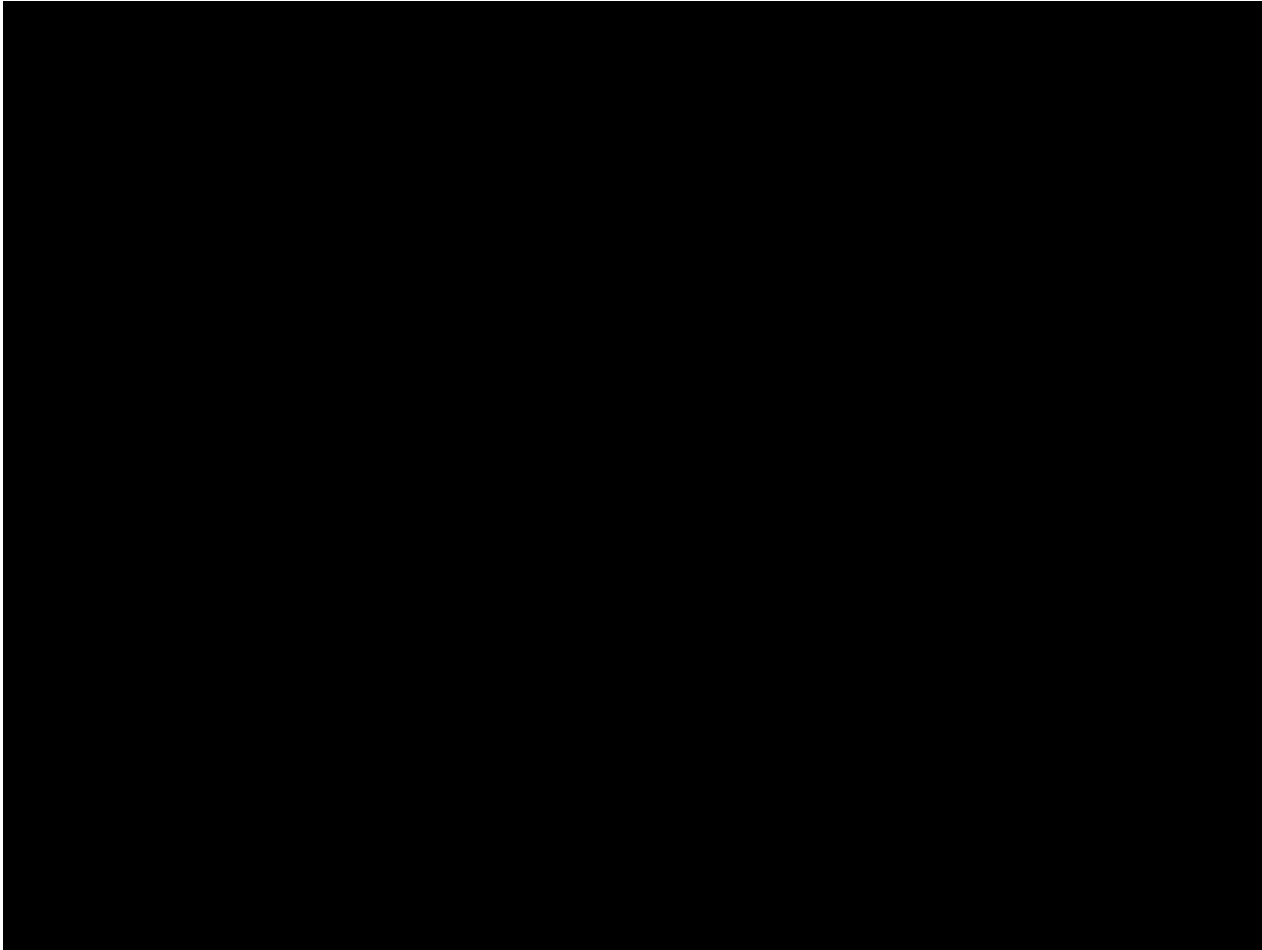
1 + 2 + 3

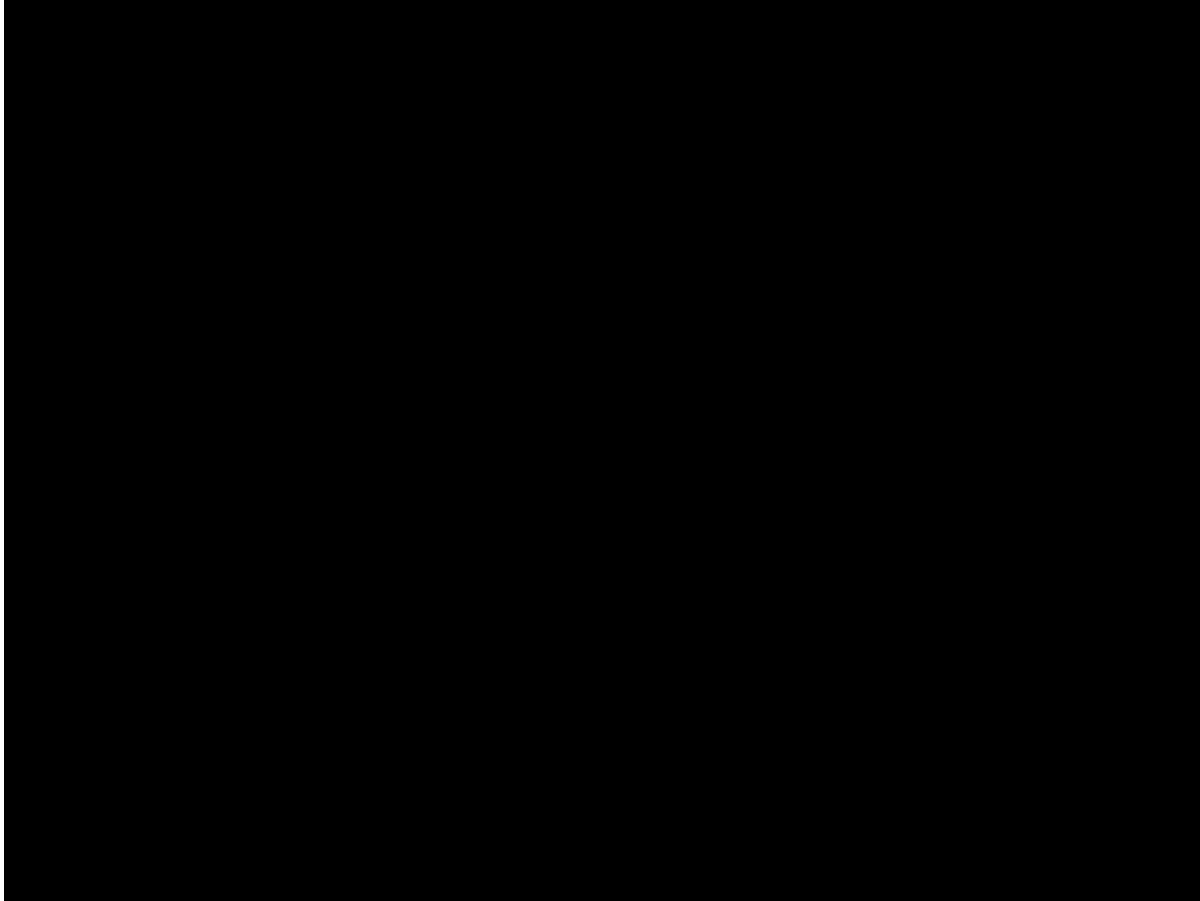# H&W model for complex cells

A₁ Response to orientation of stimulus

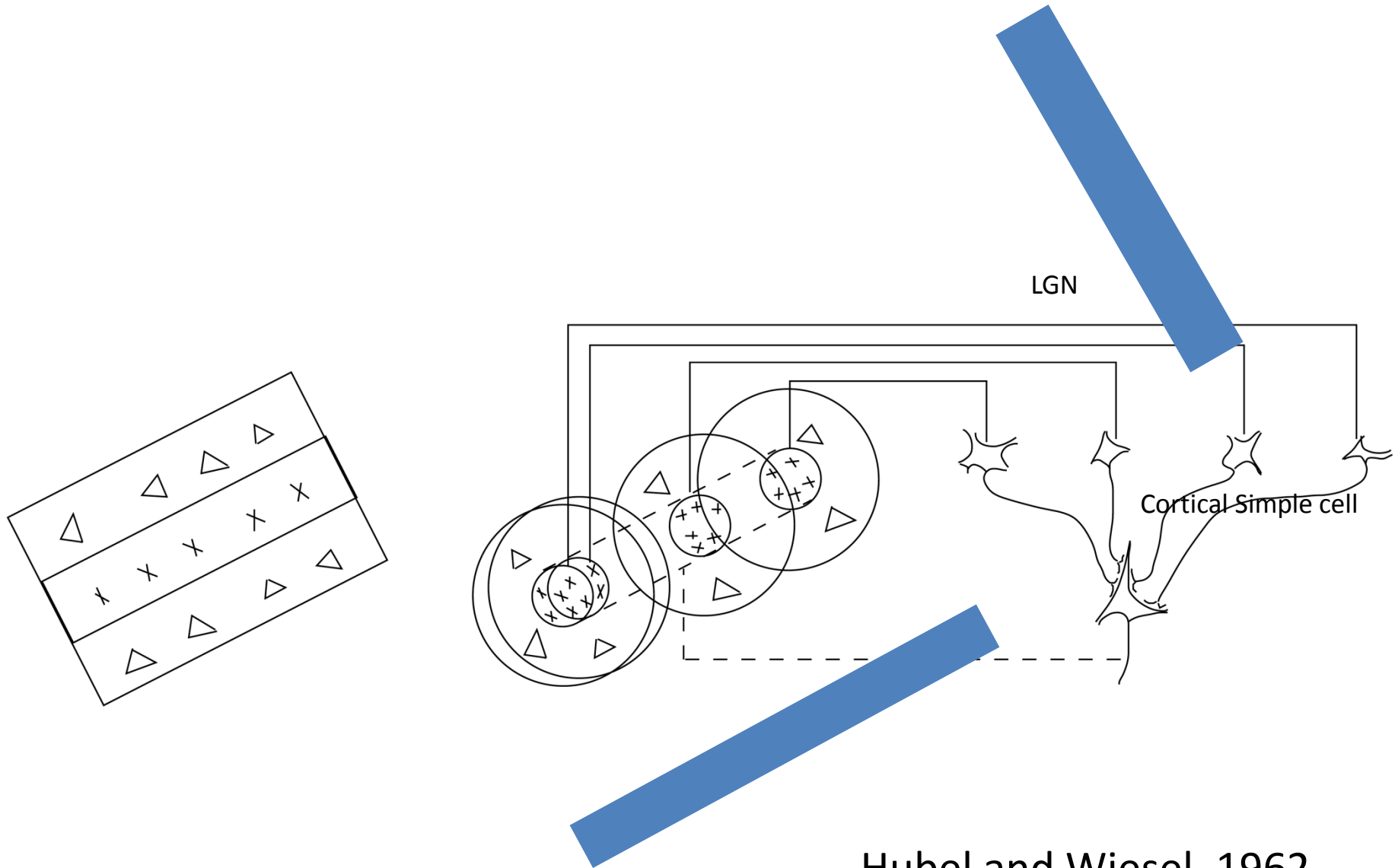A₂ Response to position of stimulus

B

Visual cortex cell

Binacularity

The Feedforward Model

Hubel and Wiesel model

LGN

Cortical Simple cell

Hubel and Wiesel, 1962

Predictions of the H&W model for simple cells do not match the data
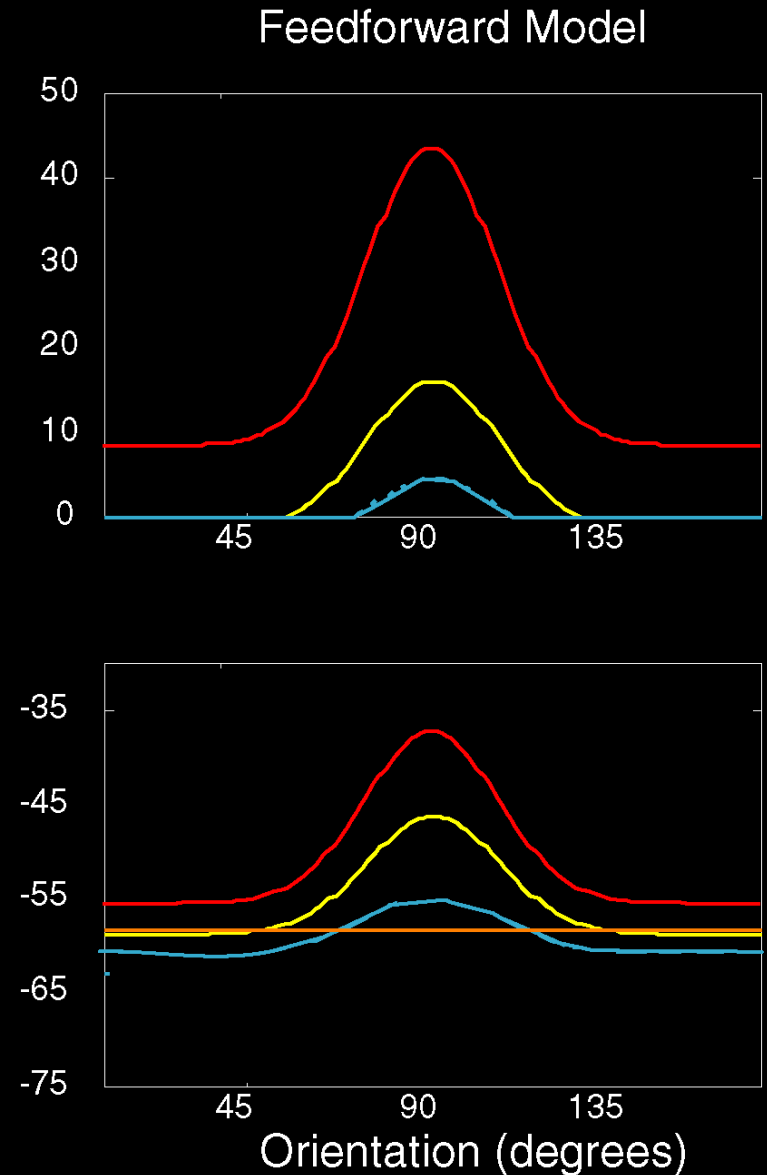
Major Failures of the FF model of H&W:

1. Contrast invariance
2. Cross-orientation suppression
3. Mismatch of receptive field maps and orientation tuning
4. Missing response at the null orientation
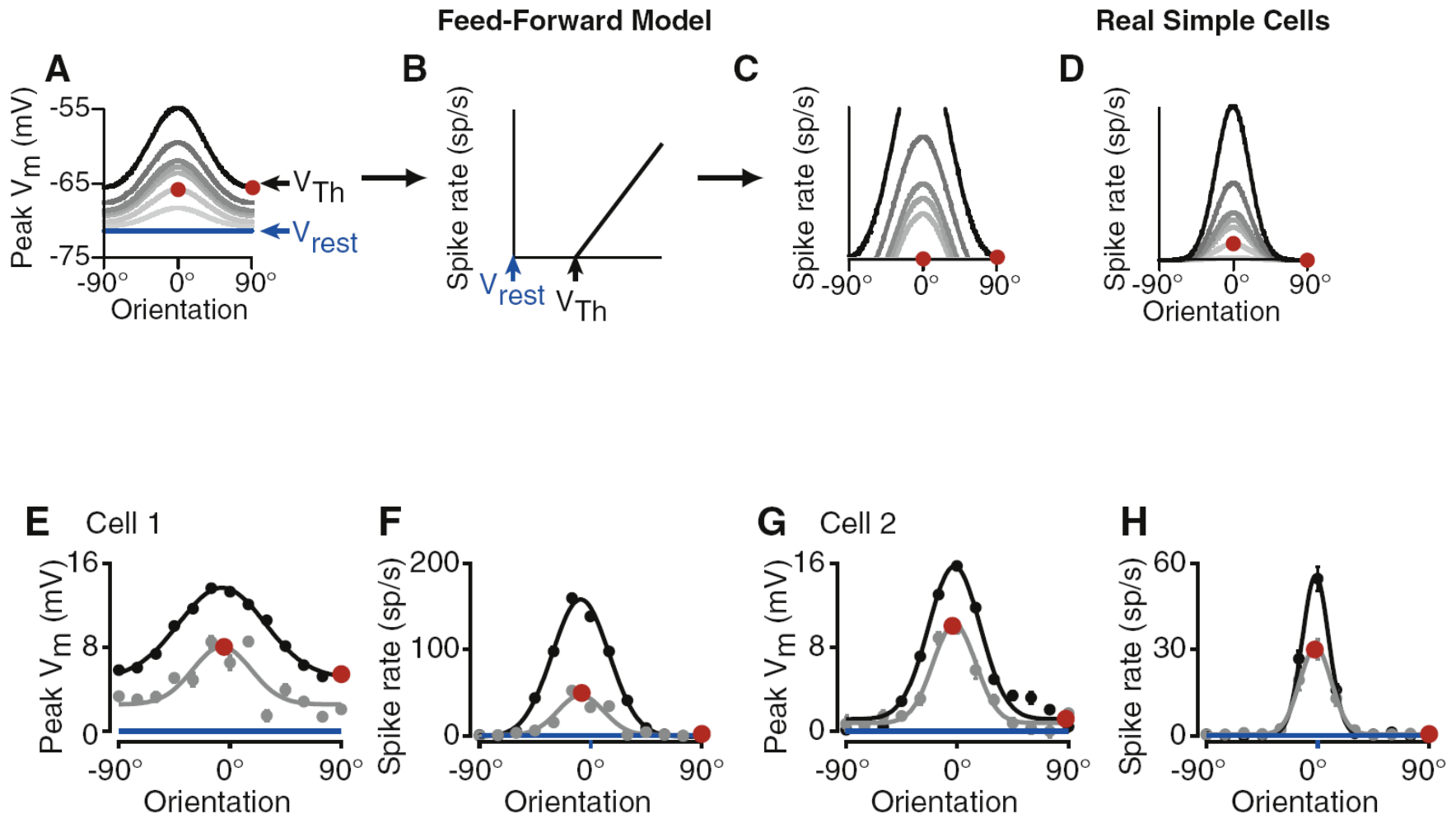5. Pharmacolgy: blocking GABA(a) causes widening of TC.

Feedforward Model Fails to Predict Contrast Invariance

Feedforward Model

80% contrast
20% contrast
5% contrast

Membrane Potential (mV)

Orientation (degrees)

From: Ferster and Miller   Annu. Rev. Neurosci. 2000. 23:441–471
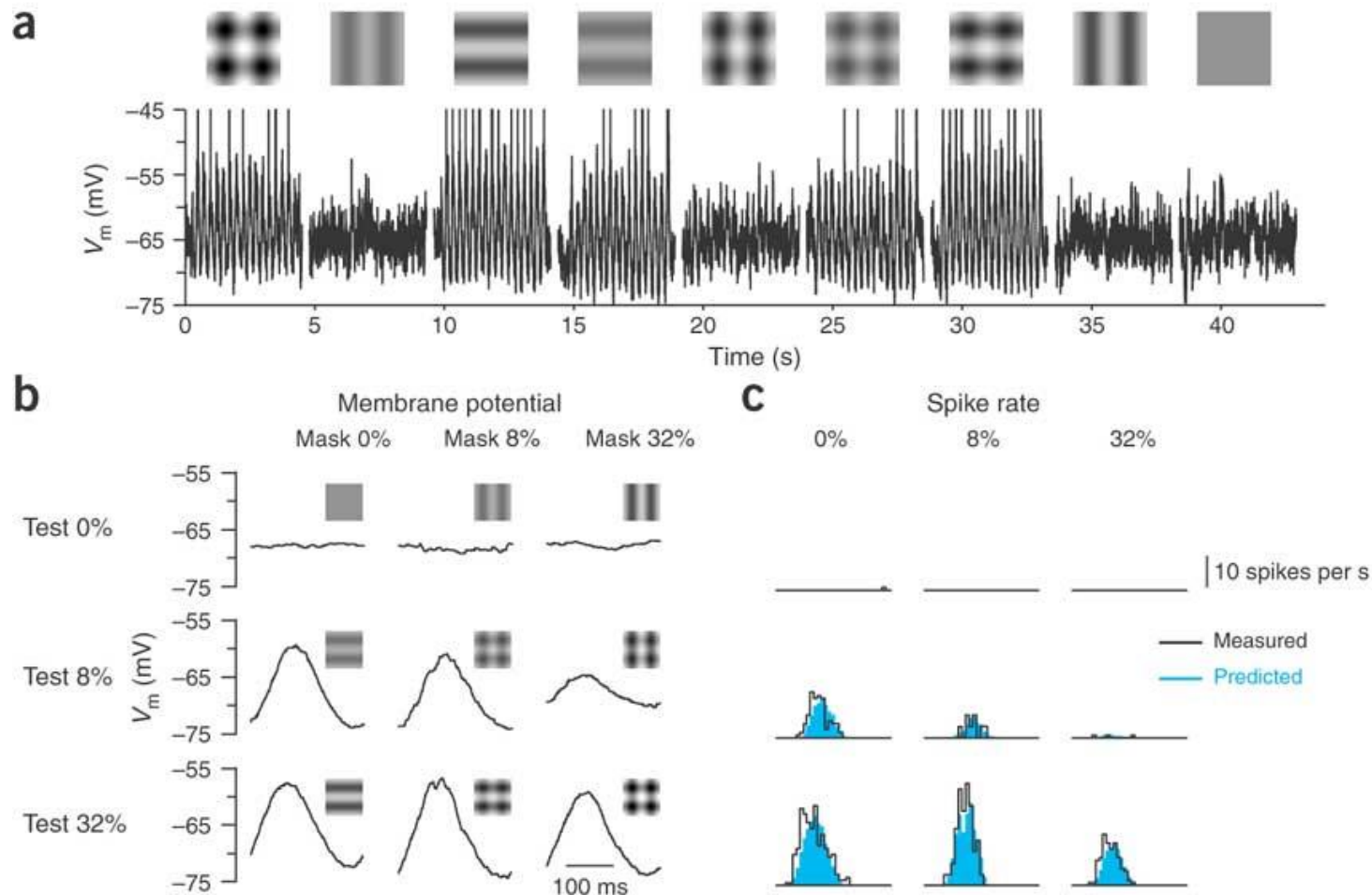
Predictions of the H&W model for simple cells: actual data

Predictions of the H&W model:
Failure 2: cross-orientation suppression

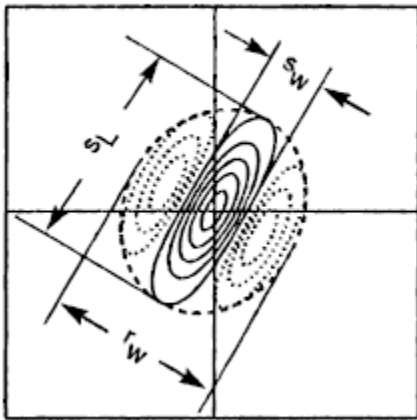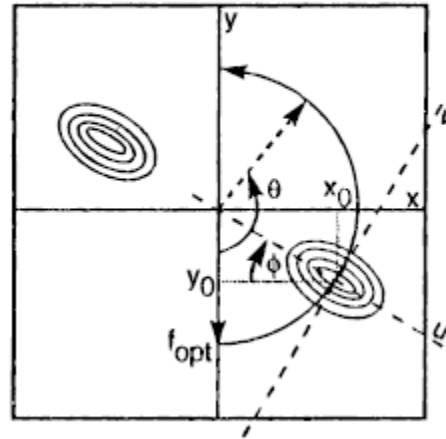# Predictions of the H&W model:
Failure 3:
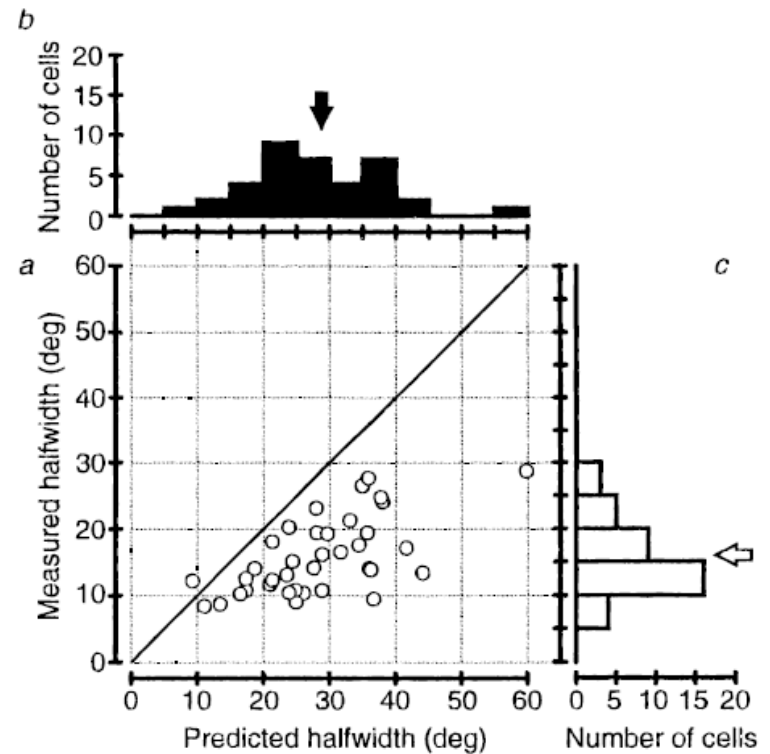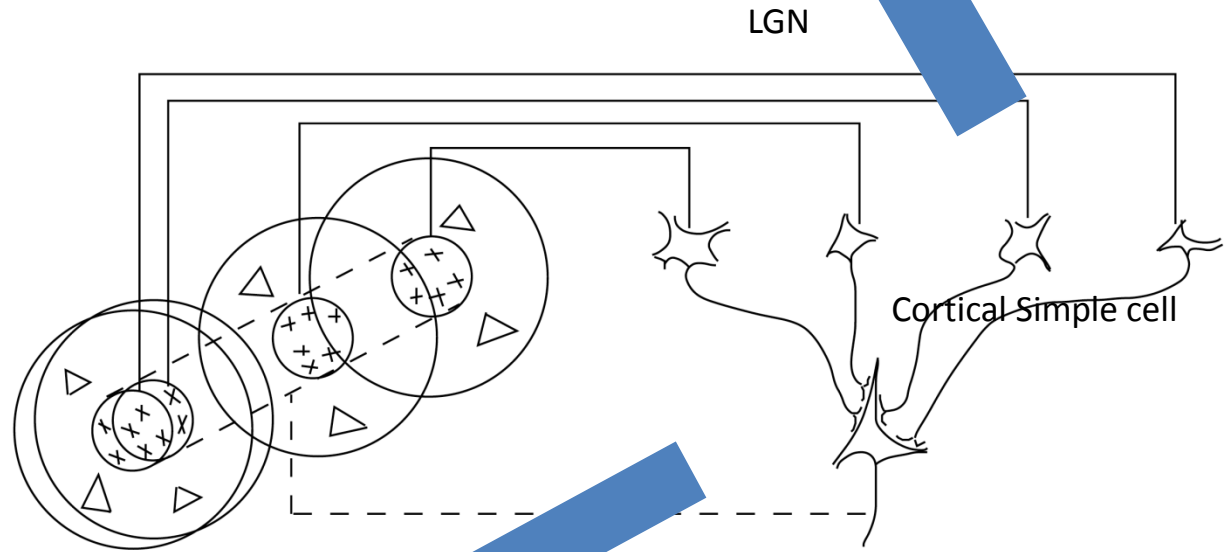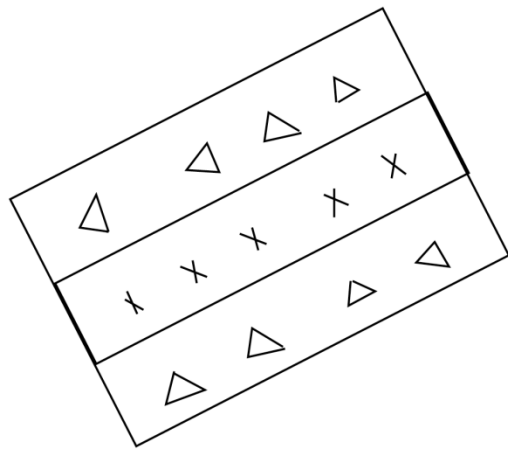## Mismatch of receptive field maps and orientation tuning

Gardner et al. 1999
Extracellular data

Predictions of the H&W model:
Failure 4: Missing response at the null orientation
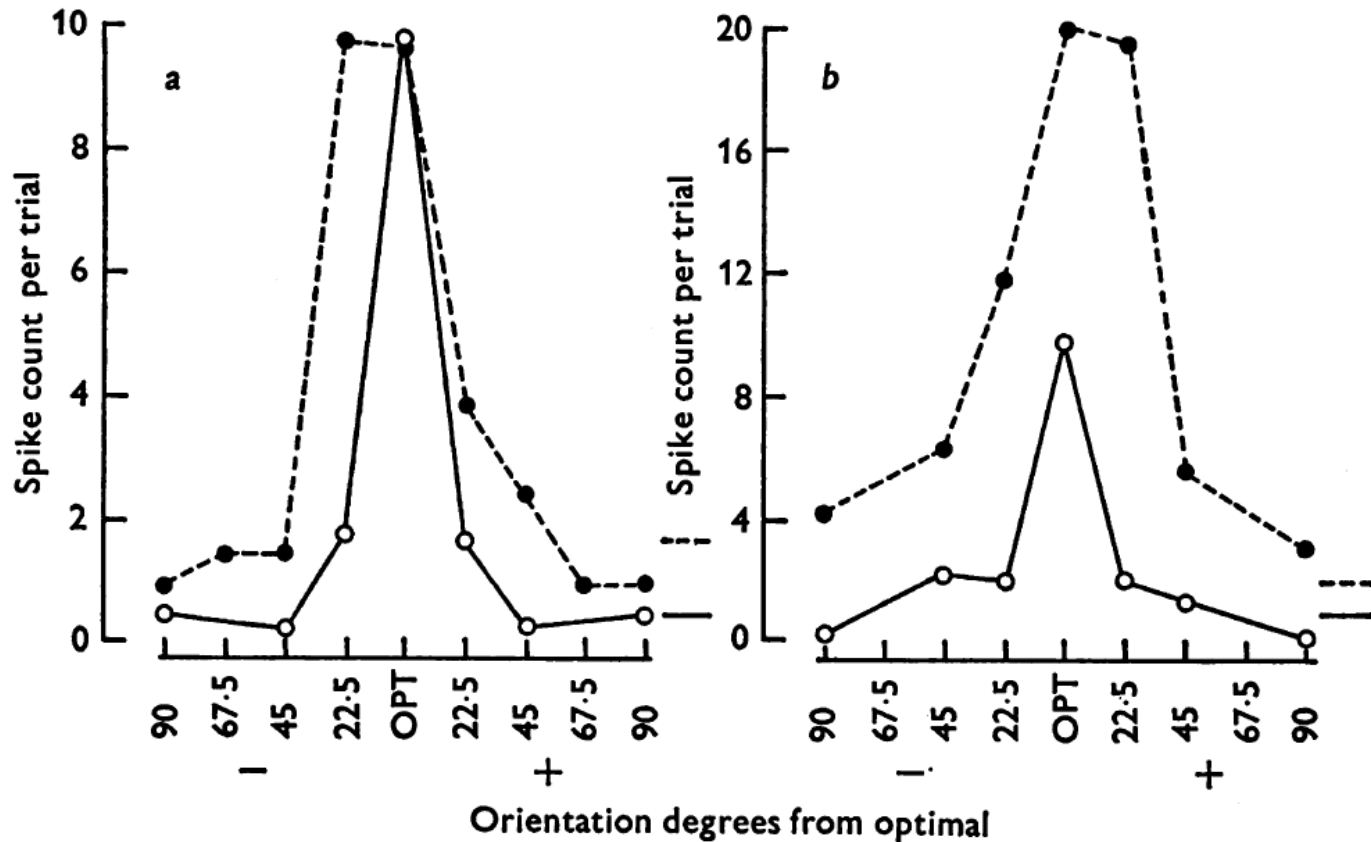
The Feedforward Model

LGN

Cortical Simple cell

Hubel and Wiesel, 1962

Predictions of the H&W model:
Failure 5: Pharmacolgy

The effect of bicuculline on tuning curve of simple cells

Sillito 1975

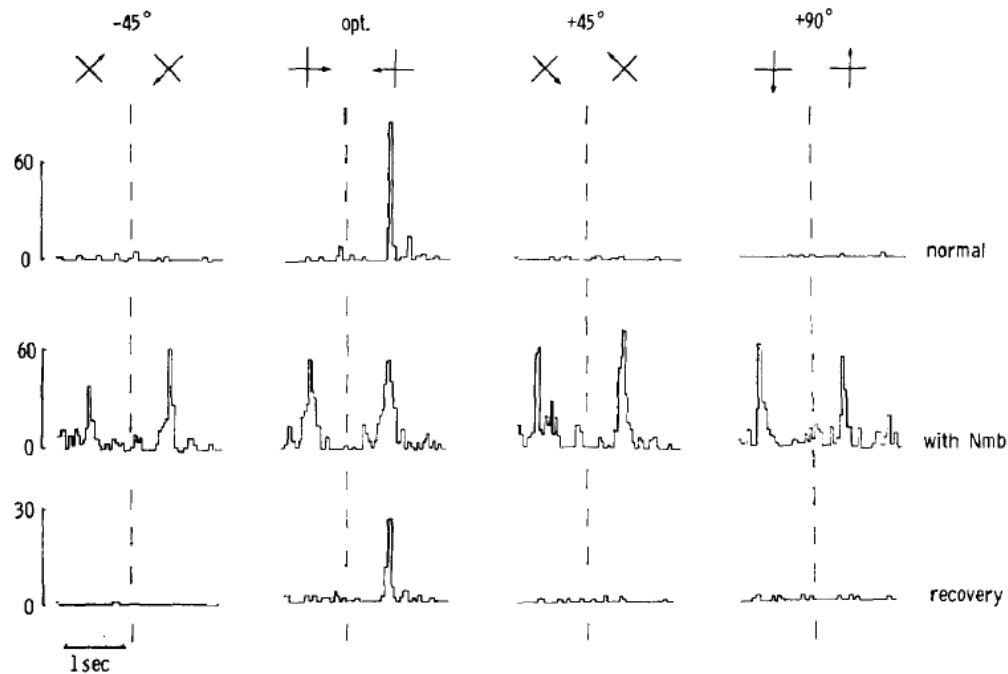# Predictions of the H&W model:
Failure 5: Pharmacolgy

Fig. 1. Action of N-methyl bicuculline (Nmb) on simple cell orientation selectivity. Testing orientation and direction of stimulus motion is indicated above each set of PSTHs. Dotted line subdivides records into zones corresponding to the two directions of motion. Optimal orientation is arbitrarily referred to as zero, —, indicates anti-clockwise rotation from optima, +, clockwise rotation. Each PSTH constructed from 25 trials. Bin size 50 msecs. Vertical calibration indicates number of counts per bin.

Sillito et al. 1980

Recurrent models for orientation selectivity

Feedforward **Inhibitory** **Recurrent**
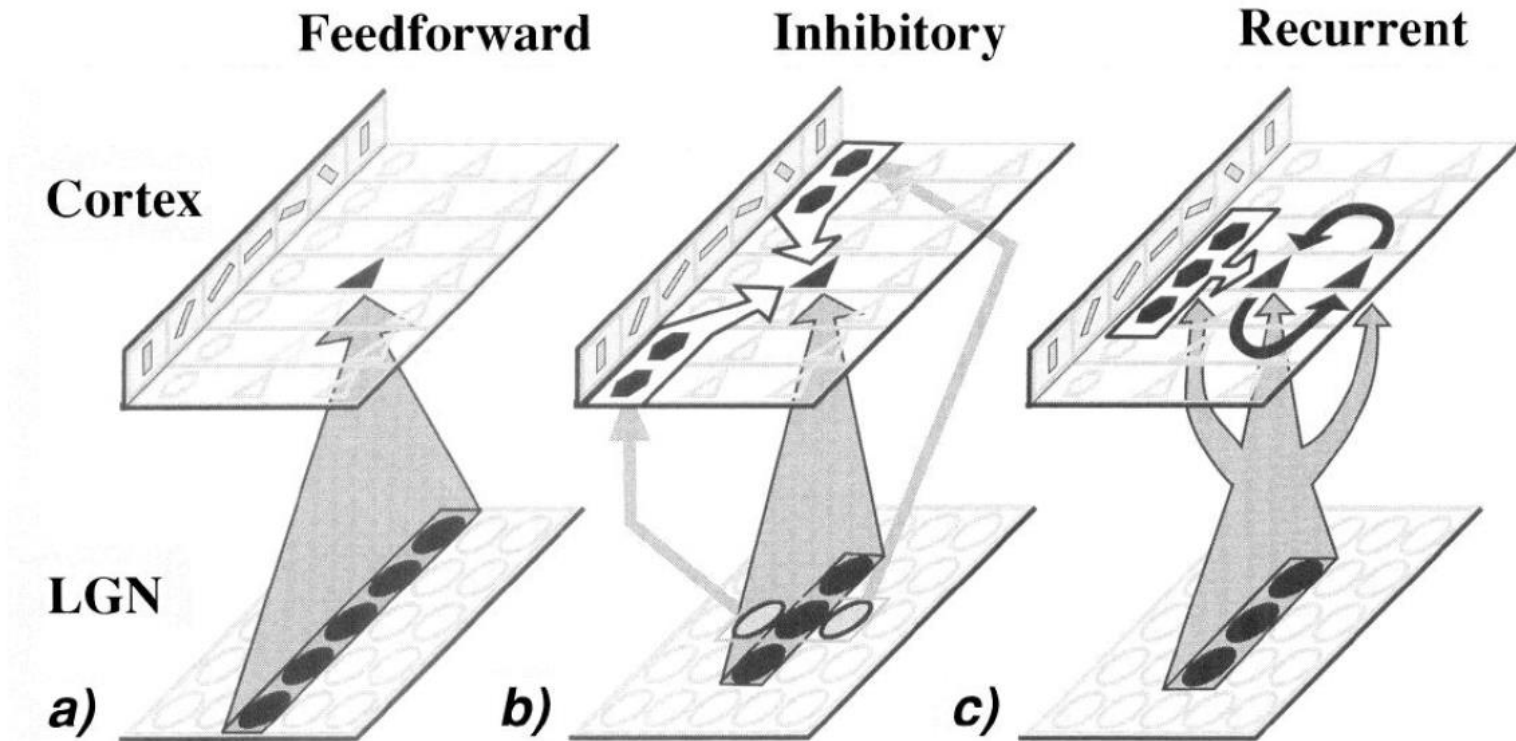
Cortex

LGN

a) b) c)

Figure 1. Models of visual cortical orientation selectivity. *a*, In feedforward models all "first-order" cortical neurons (*triangle,* excitatory; *hexagon,* inhibitory) receive converging input (*gray arrow*) from a population of LGN neurons that cover a strongly oriented region of visual space. The bandwidth or sharpness of a cortical cell's orientation tuning is determined by the aspect ratio of its LGN projection. *b,* Many inhibitory models employ a mild feedforward bias to establish the initial orientation preference of cortical neurons and utilize inhibitory inputs (*white arrows*), from cortical neurons preferring different orientations, to suppress nonpreferred responses. Here, we present a model, *c,* in which recurrent cortical excitation (*black arrows*) among cells preferring similar orientations, combined with iso-orientation inhibition from a broader range of orientations, integrates and amplifies a weak thalamic orientation bias, which is distributed across the cortical columnar population.

Somers et al. 1995

Recurrent models for orientation selectivity
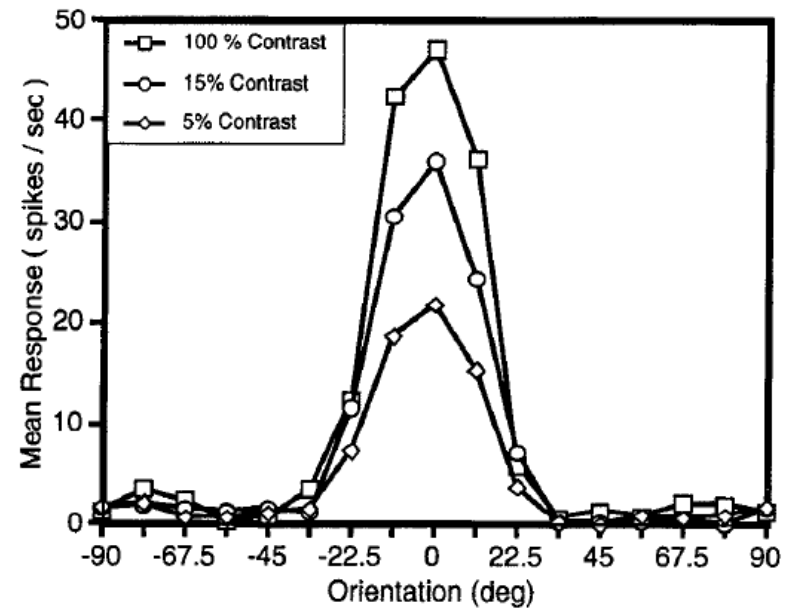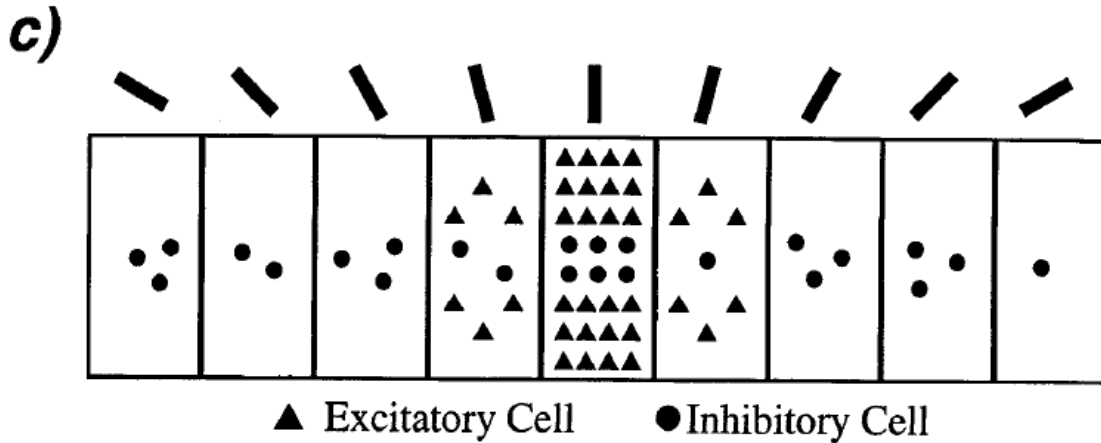
Somers et al. 1995

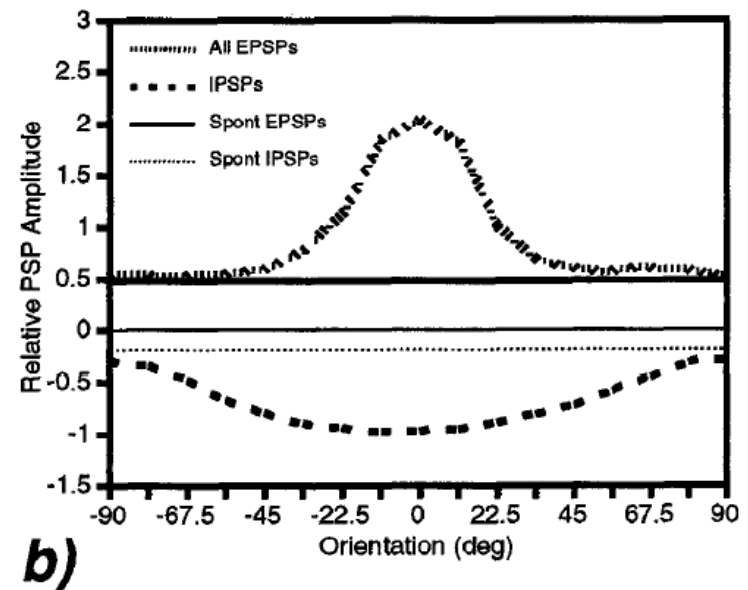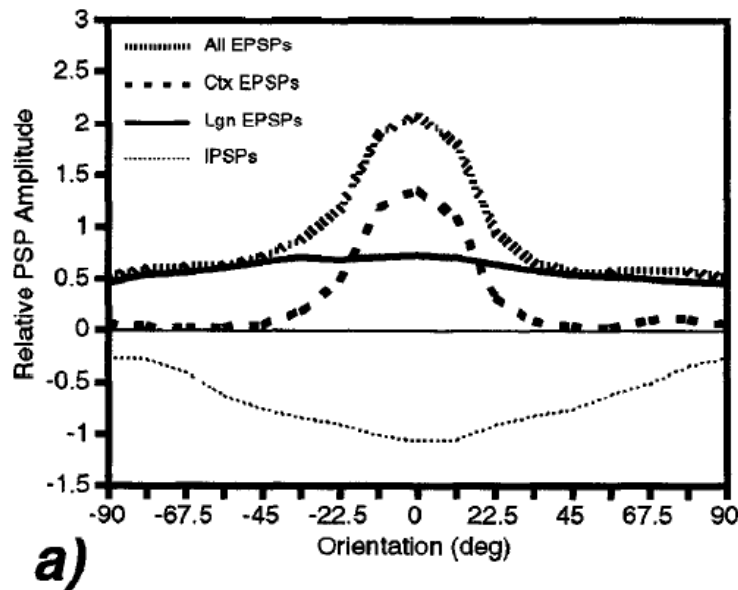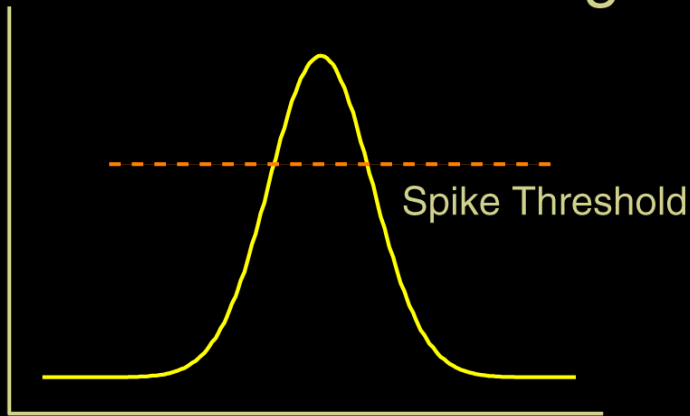# Recurrent models for orientation selectivity

Figure 4. Orientation tuning of postsynaptic potentials. *a*, Postsynaptic potentials evoked in the example cell by thalamic excitatory, cortical excitatory, and cortical inhibitory synaptic inputs. LGN EPSPs were very broadly tuned. IPSPs were strongest at the preferred orientation (0°) and weakest at the cross-orientation (90°). Cortical EPSPs provided the strongest orientation-selective input. Net EPSPs were, therefore, well-tuned for 0° stimuli. *b*, Averaged EPSP and IPSP inputs for all excitatory (*n* = 84) cells in the 0° column. Both EPSPs and IPSPs were largest in response to stimuli of the preferred orientation. Cross-orientation stimuli evoked IPSPs that were only mildly stronger than spontaneously evoked (no stimulus) IPSPs. All PSPs were scaled by $g_{leak}/(1000 \, C_m)$.
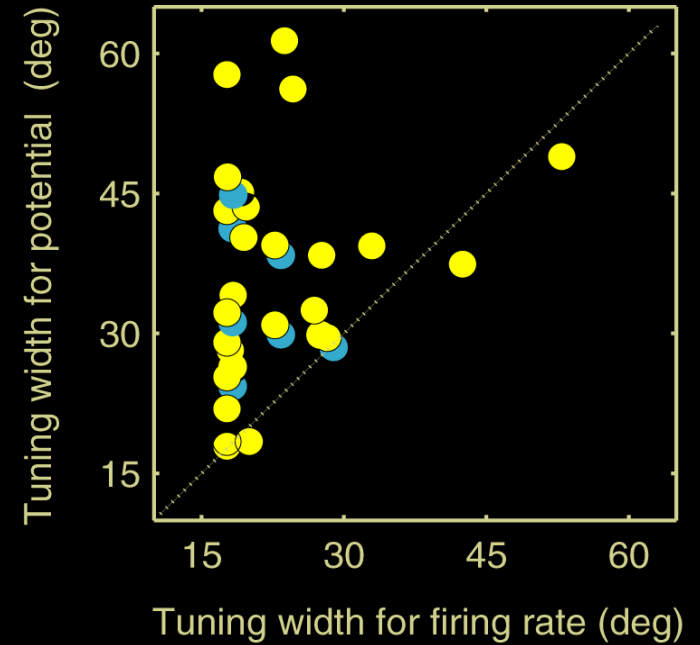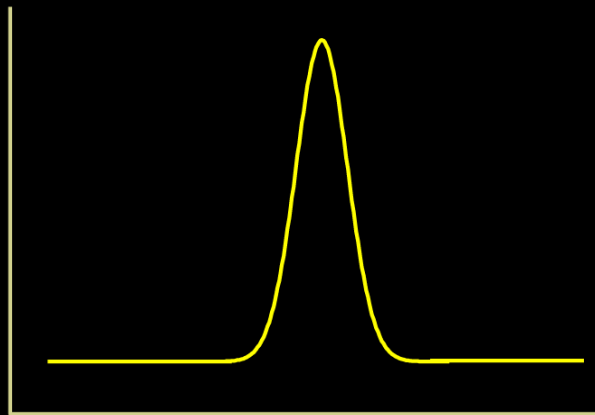
Somers et al. 1995

The Iceberg Effect

Orientation Tuning

Potential

Spikes

Spike Threshold

Tuning width for potential (deg)

60

45

30

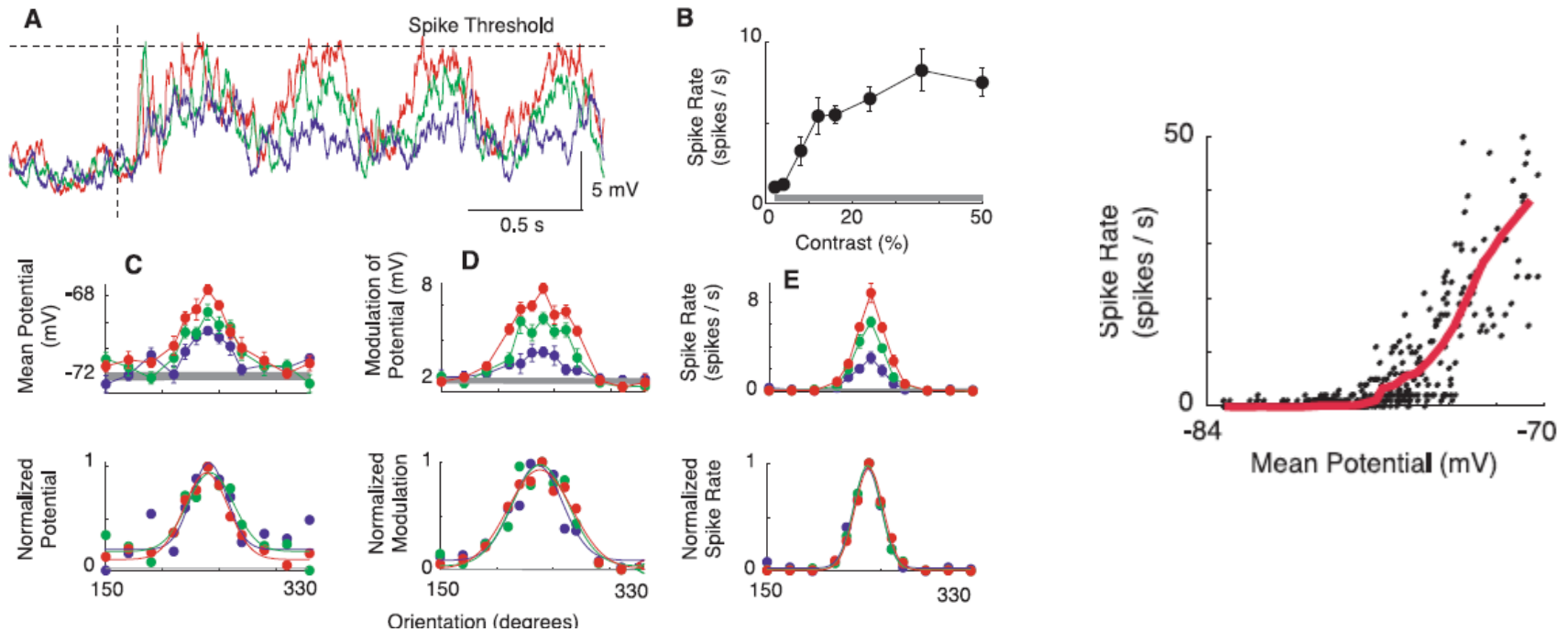15

Tuning width for firing rate (deg)

15   30   45   60

- Simple Cell
- Complex Cell

Experiments that support the H&W – intracellular recording data. The role of noise in contrast invariance

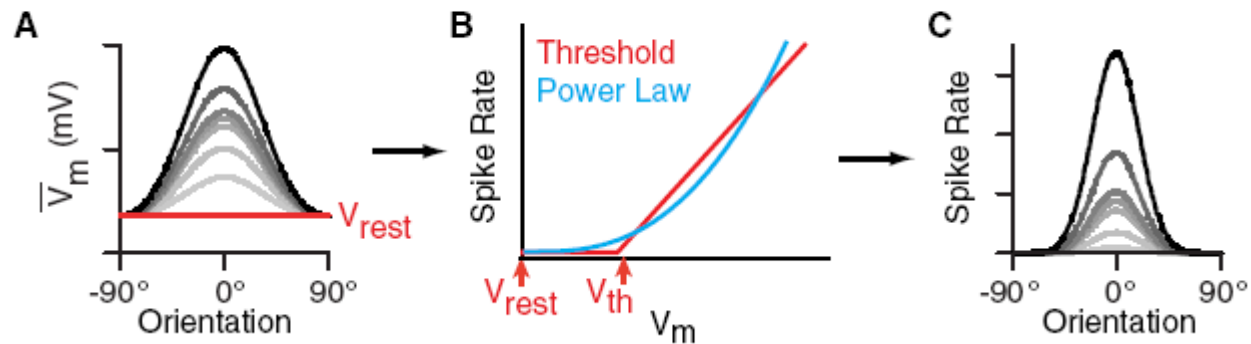1. Contrast invariance

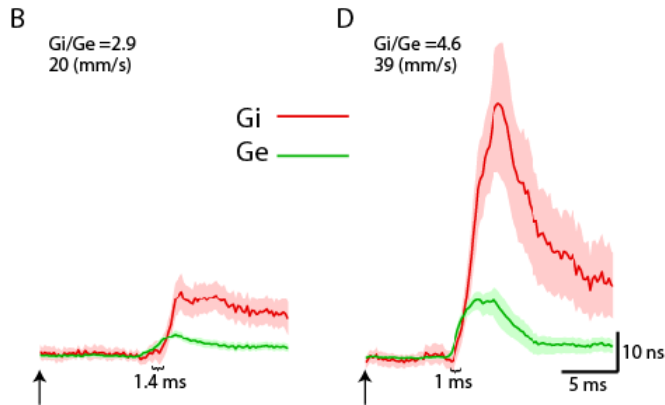Anderson et al. 2000

Experiments that support the H&W – intracellular recording data. The role of noise in contrast invariance

1. Contrast invariance
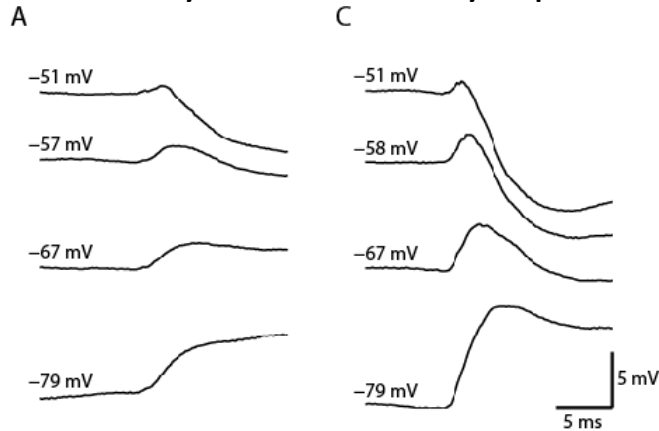

Priebe and Ferster 2012

Experiments that support the H&W :
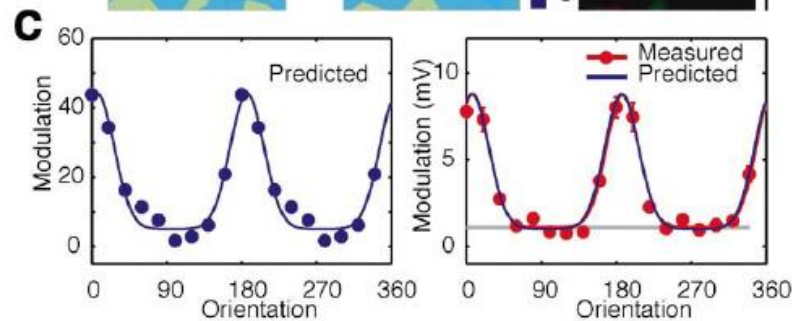# The role of noise in contrast invariance
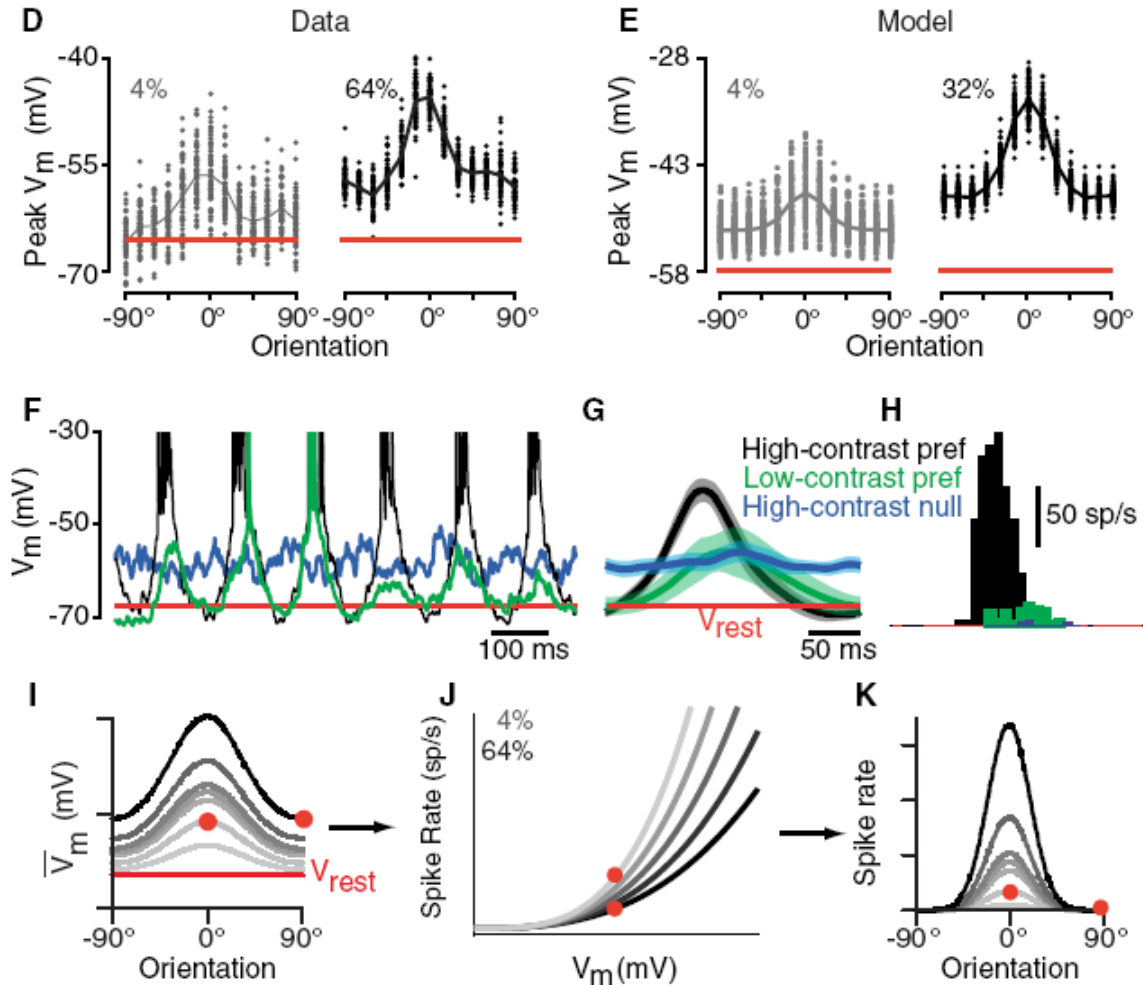
1. Contrast invariance

Priebe and Ferster 2012

2. TC of excitatory and inhibitory inputs

A

−51 mV

−57 mV

−67 mV

−79 mV

C

−51 mV

−58 mV

−67 mV

−79 mV

5 mV

5 ms

$$c\frac{dV}{dt} = -G_l(V - E_{rest}) - G_i(V - E_i) - G_e(V - E_e) + I$$

Synaptic current

B

Gi/Ge =2.9
20 (mm/s)

Gi ——
Ge ——

D

Gi/Ge =4.6
39 (mm/s)

10 ns

1.4 ms

1 ms

5 ms

Ei ~= -80 mV

Ee~ = 0 mV

Heiss et al. 2008

Experiments that support the H&W – Excitatory and inhibitory inputs have similar TC

2. TC of excitatory and inhibitory inputs

orientation

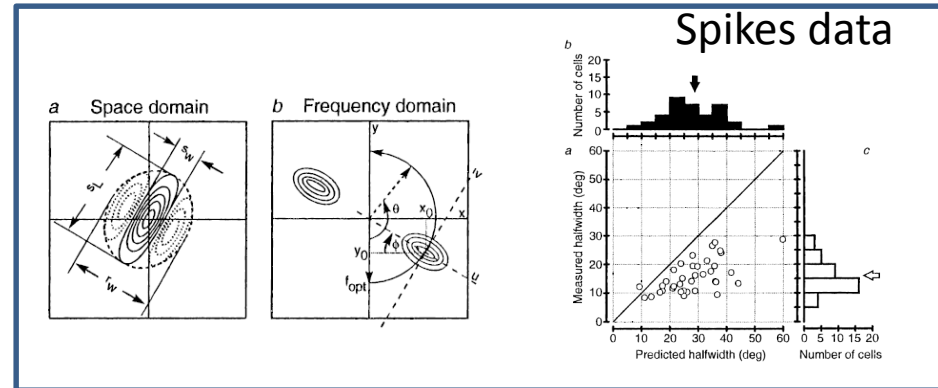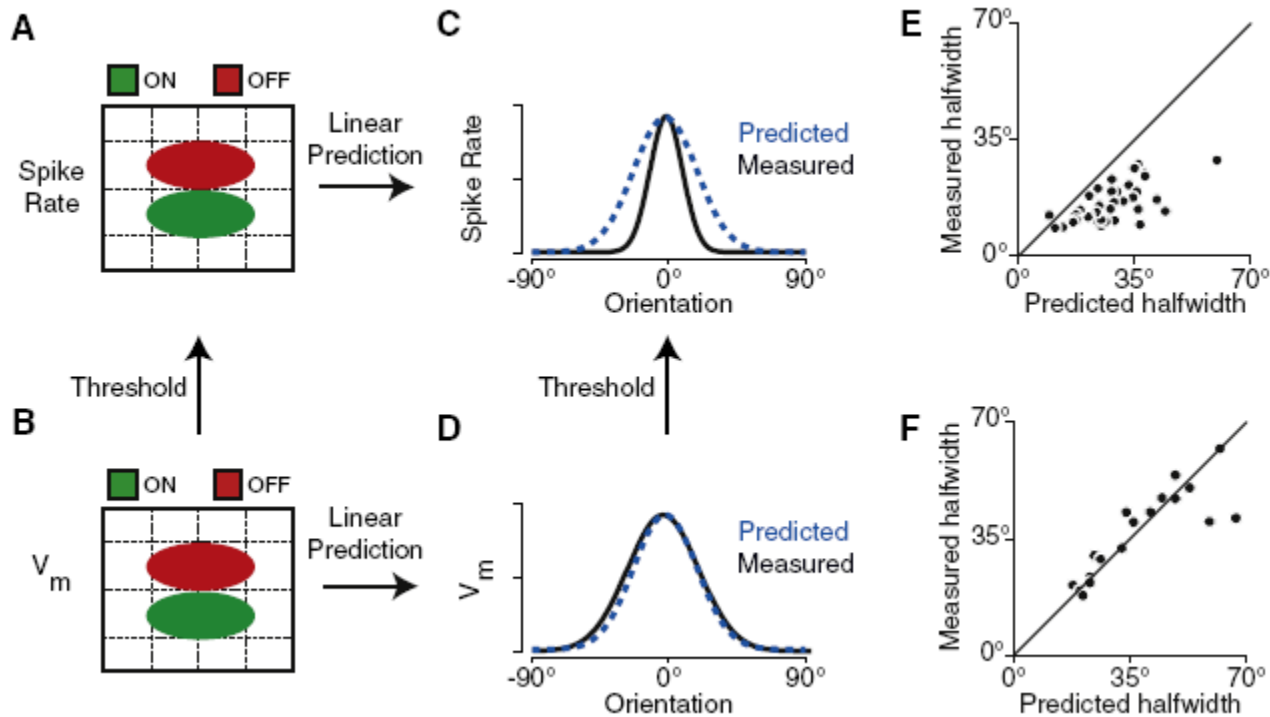Anderson et al. 2000

Experiments that support the H&W – Mismatch of receptive field maps and orientation tuning.
Intra cellular data show why TC and RF do not match at spikes level because of the iceberg effect

Spikes data

Vm data

Lampl et al. 2001

Experiments that support the H&W – Mismatch of receptive field maps and orientation tuning.
Intra cellular data show why TC and RF do not match at spikes level because of the iceberg effect

Priebe and Ferster 2012

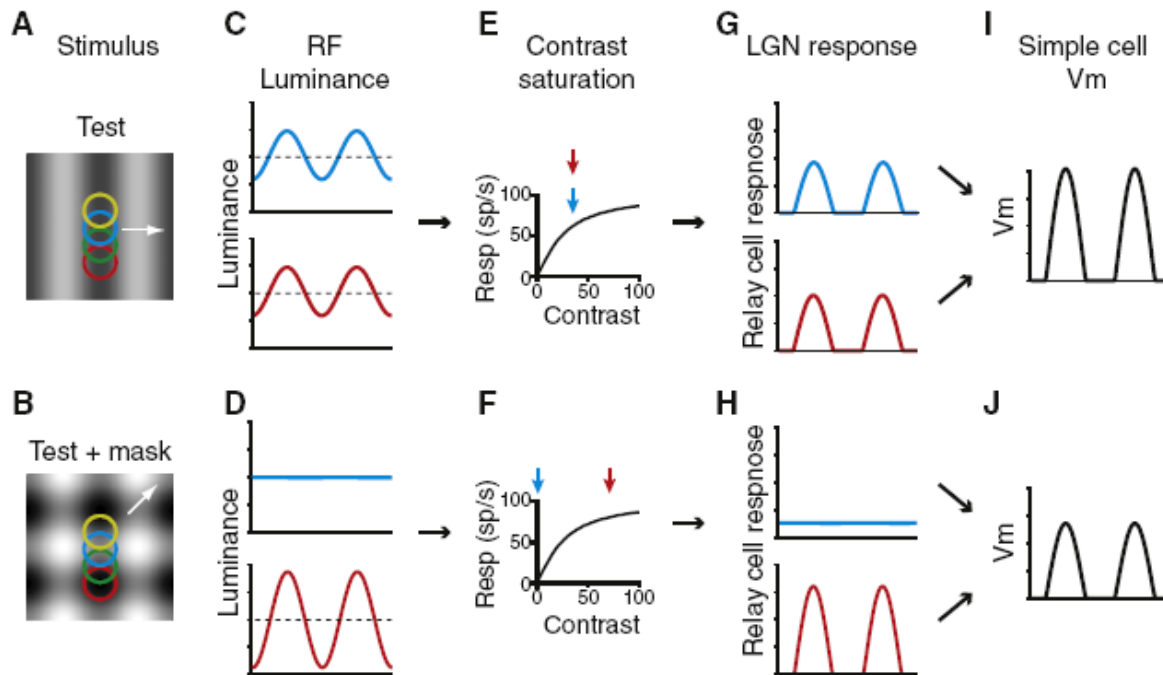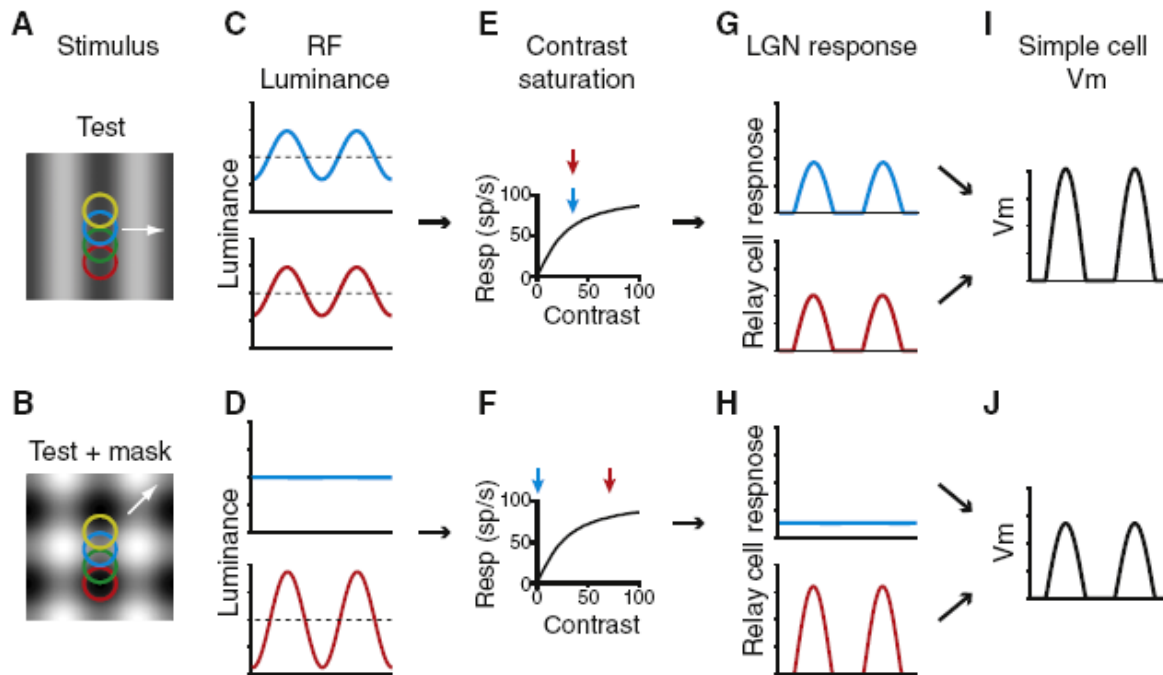# Experiments that support the H&W – Cross-orientation suppression

Figure 2. Cross-orientation Suppression in a Feedforward Model of Visual Cortex
(A and B) The spatial receptive fields of LGN relay cells (colored circles) are superimposed on top of a 32% contrast vertical grating (A) or a plaid composed of 32% horizontal and vertical gratings (B).
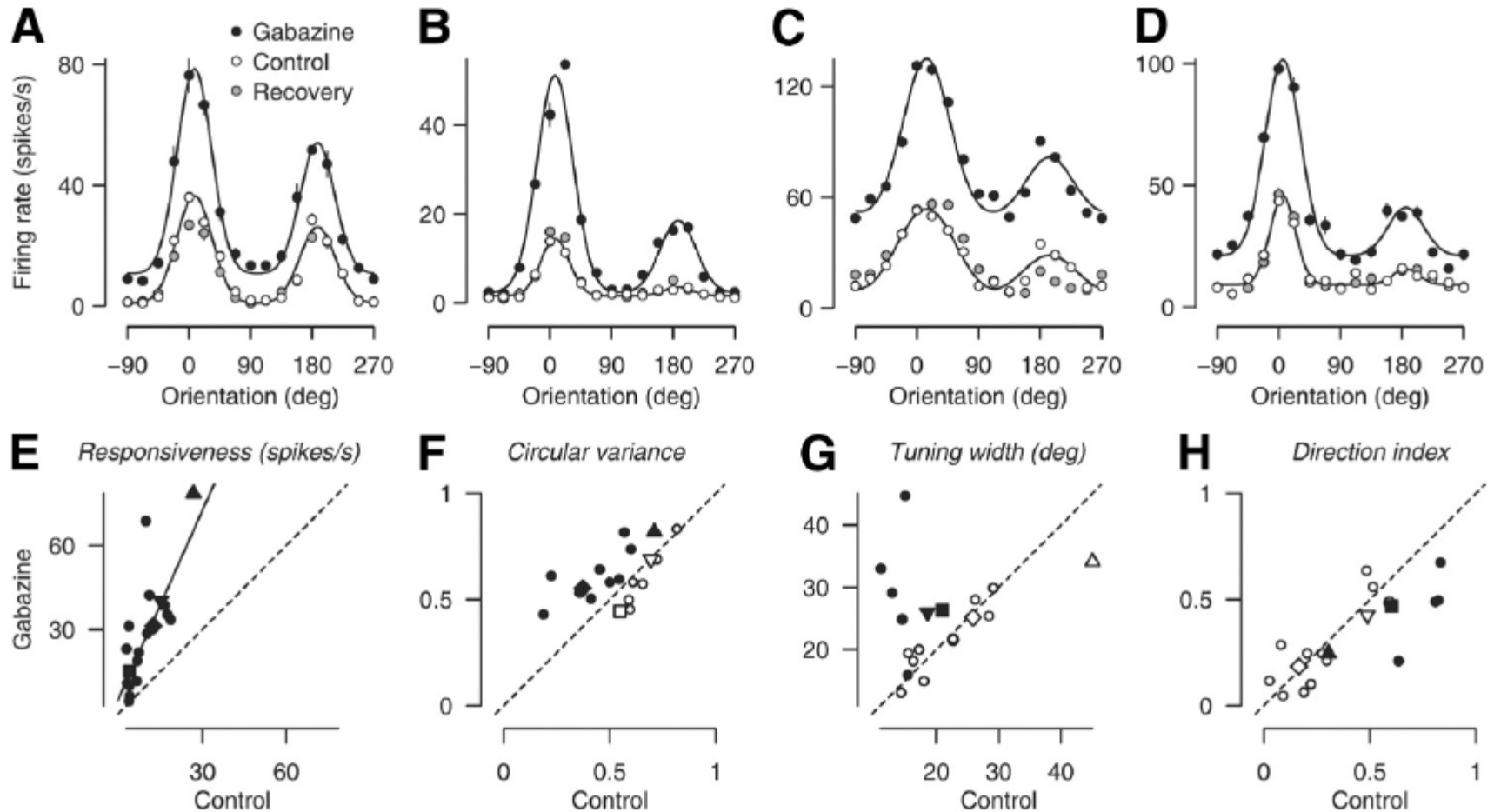(C and D) Stimulus luminance is plotted as a function of time for two LGN relay cells, indicated by color (C, grating; D, plaid).
(E and F) The contrast response curve of LGN relay cells. The arrows indicate the contrast passing over each relay cell's receptive field (E, grating; F, plaid).
(G and H) The modeled responses of the relay cells based on the contrast passing over their receptive fields include both saturation and rectification (G, grating; H, plaid).
(I and J) The average input to a target V1 simple cell. The average relay cell input is about 10% less for the plaid stimulus (I) than for the grating stimulus (J).

Priebe and Ferster 2012

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Priebe and Ferster 2012

Experiments that support the H&W:
New insights on the pharmacological effects on TC

Katzner et al. 2011

Experiments that support the H&W:
New insights on the pharmacological effects on TC – the iceberg effect

Control | Gabazine

A Firing rate

E

B Membrane potential

F

C Synaptic excitation

G

D Synaptic inhibition

H

Orientation (deg)
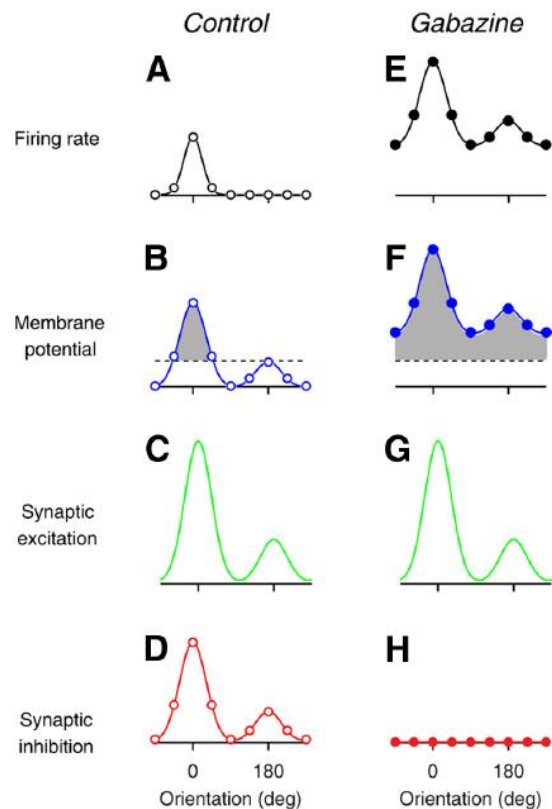
Figure 7. A simple cellular model. *A*, Tuning of firing rate in control condition. *B*, Corresponding tuning of membrane potential responses. Dashed line indicates threshold. Shaded area indicates responses that elicit nonzero firing rates. *C*, Tuning of excitation. *D*, Tuning of inhibition, under the simplified assumption that inhibition has the same tuning as excitation (matching inhibition). In the untuned inhibition version of the model, this curve would be flat. *E–H*, Same, under gabazine.

Katzner et al. 2011

Recurrent models for orientation selectivity
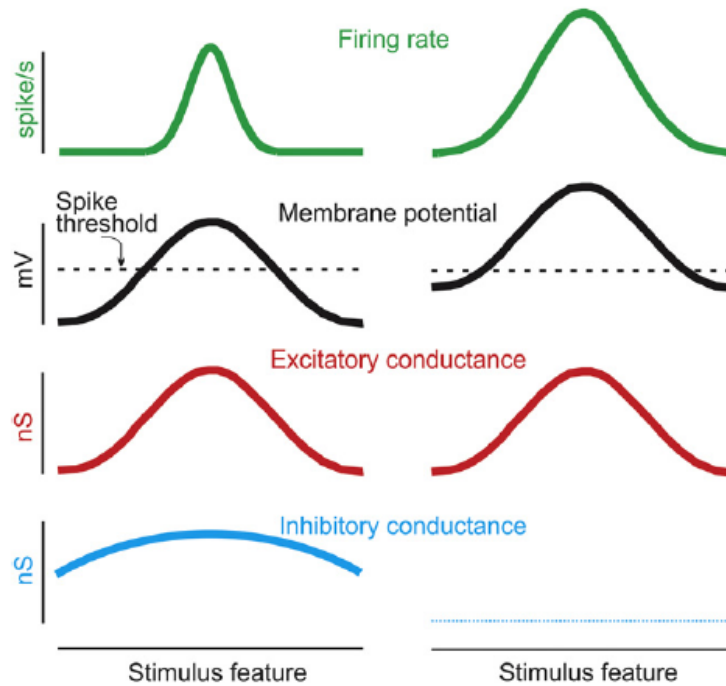
Figure 4. Inhibition Sharpens Stimulus Selective Spike Output via the "Iceberg Effect"

Schematic illustrates hypothetical tuning curves for firing rate (green), membrane potential (black), excitatory (red), and inhibitory (blue) conductances of a cortical neuron to stimulus features (e.g., orientation). Action potential firing occurs only when membrane potential exceeds a fixed spike threshold (dotted line). Responses are shown in the presence (left) and absence (right) of a weakly tuned inhibitory conductance. Inhibition leads to more narrowly tuned spike output by allowing only the strongest (preferred) excitatory stimuli to drive the membrane potential above spike threshold.

Issacoson and Scanziani 2011

Two Photon (2P) Imaging studies of the visual cortex
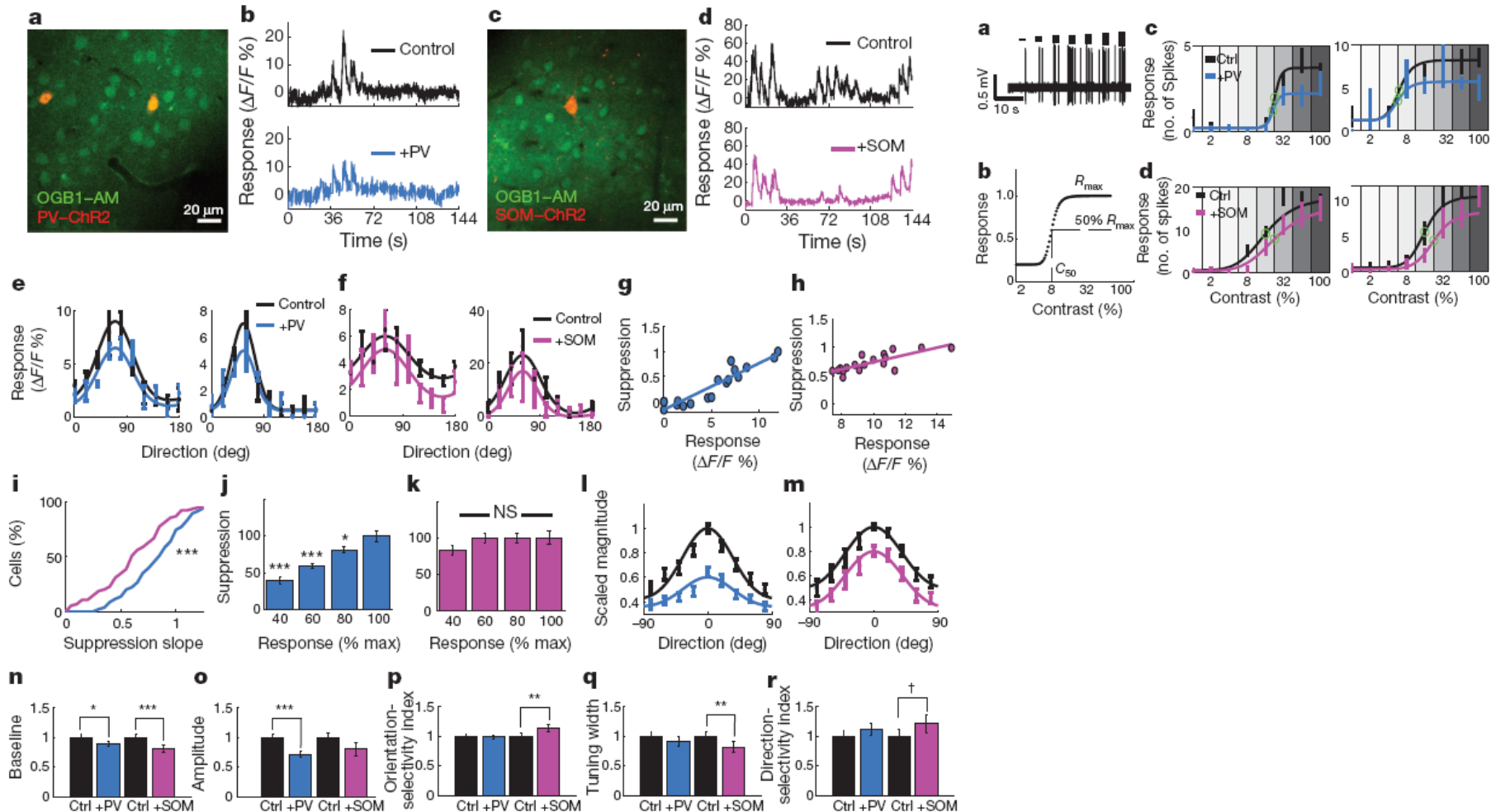
1. Contrast invariance

Wilson et al. 2012

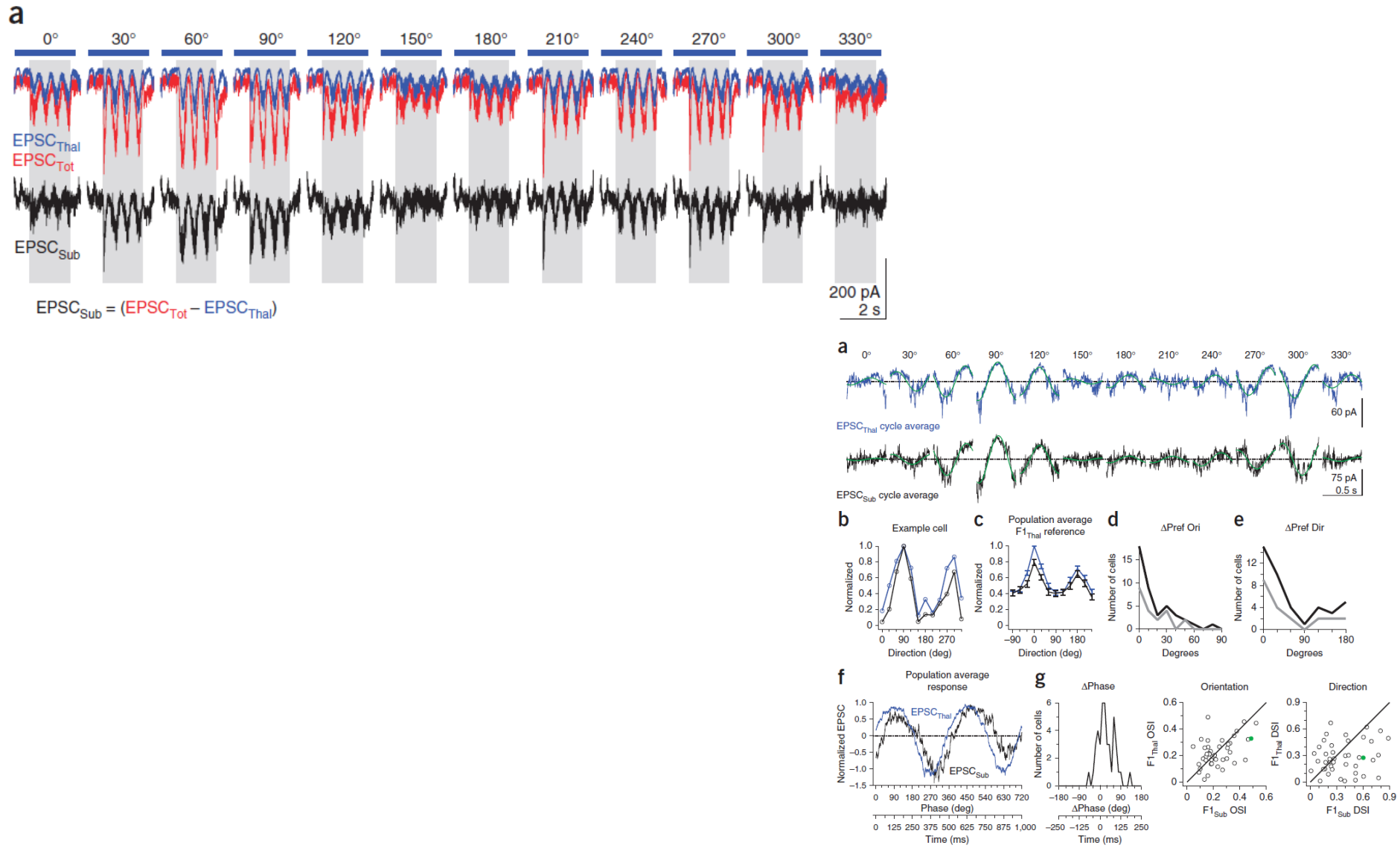# Optogenetic studies of the visual cortex

1. Contrast invariance

Attalah et al. 2012
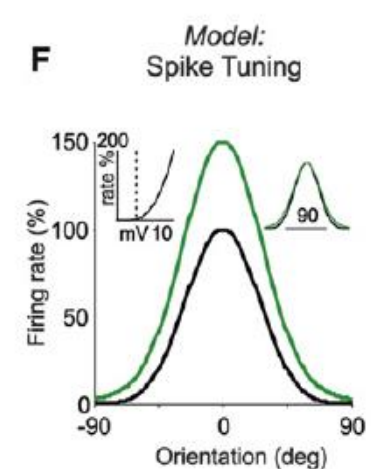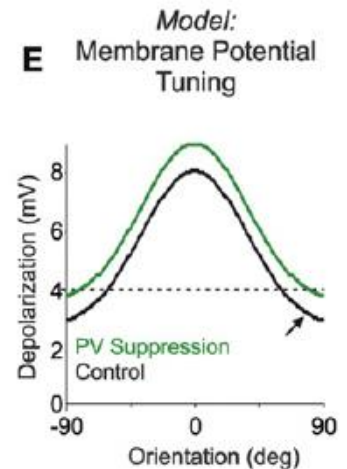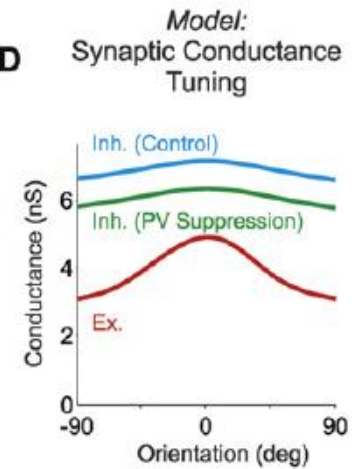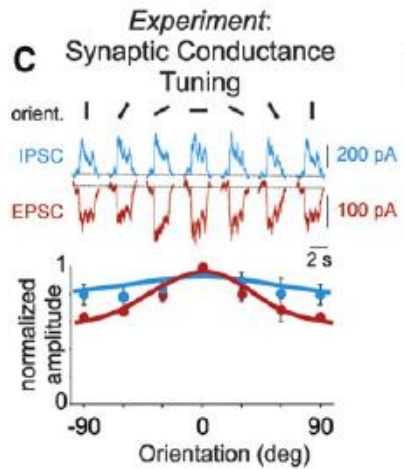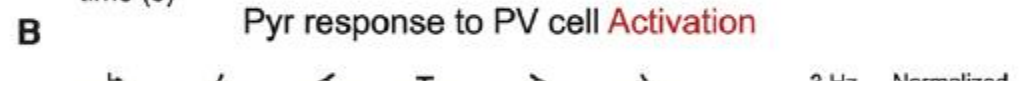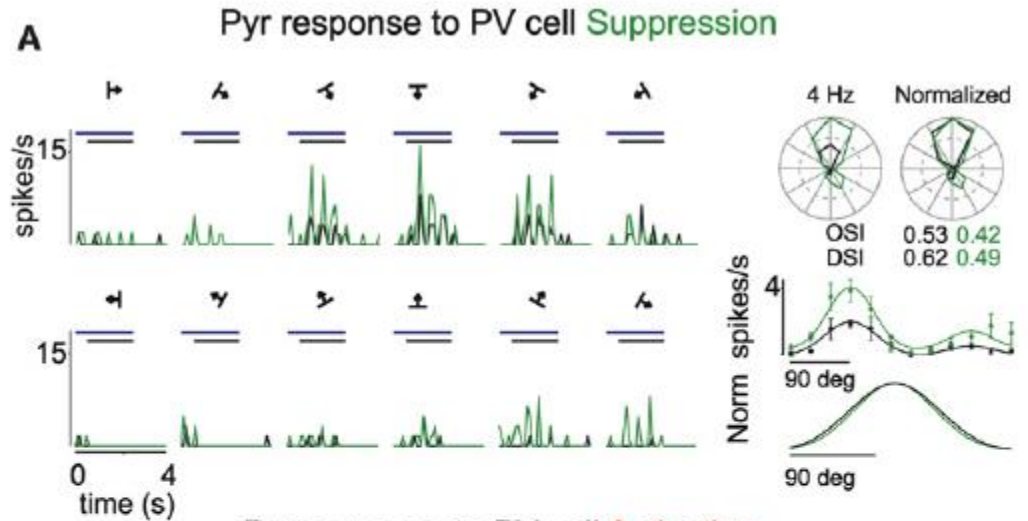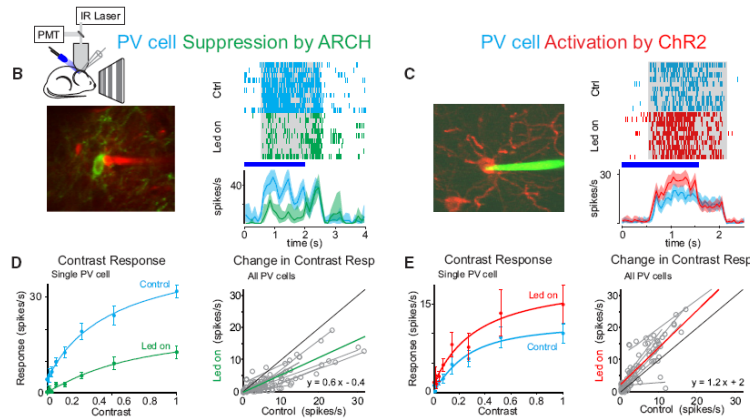
Optogenetic studies of the visual cortex
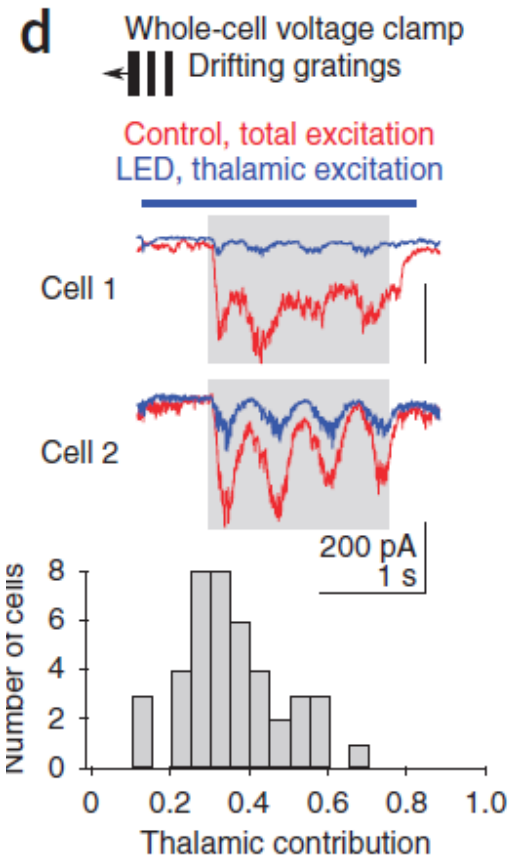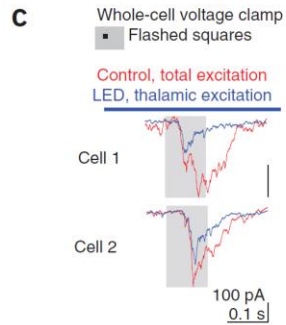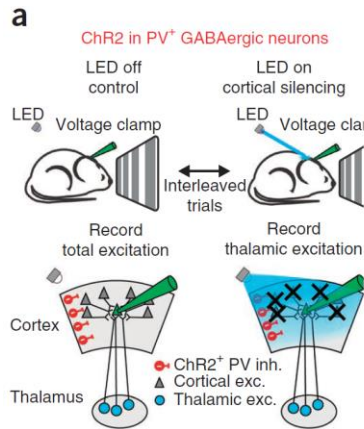
Cortical circuits amplify tuned thalamic inputs without altering orientation selectivity

$EPSC_{Sub} = (EPSC_{Tot} - EPSC_{Thal})$

# Auditory cortex – lateral suppression

1. Inhibition?

SUTTER, SCHREINER, McLEAN, O'CONNOR, AND LOFTUS

A Single-tone FRA   B Two-tone FRA

10 kHz@40 dB + 7kHz@90dB
10 kHz@40 dB + 12 kHz@80dB
10 kHz@40 dB + 5kHz@20dB

Level (dB SPL)

A

Broad Inhibition +   Excitation   = "lateral" inhibition
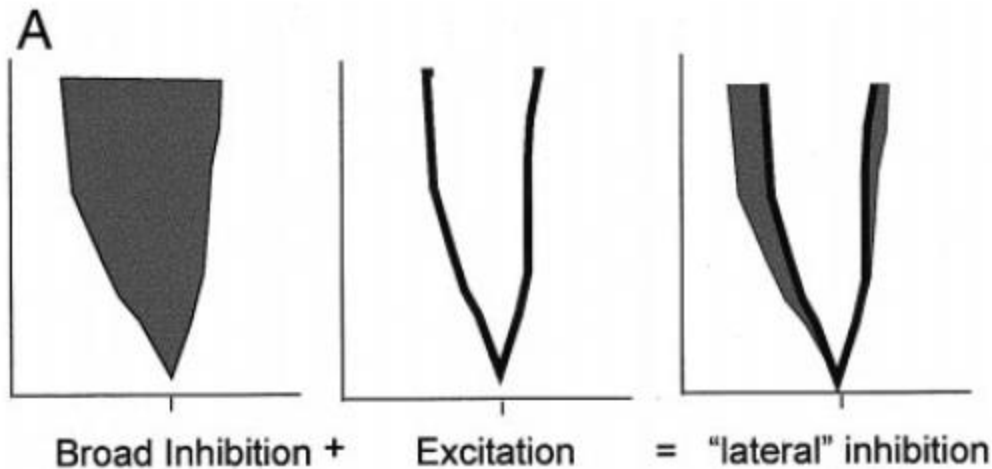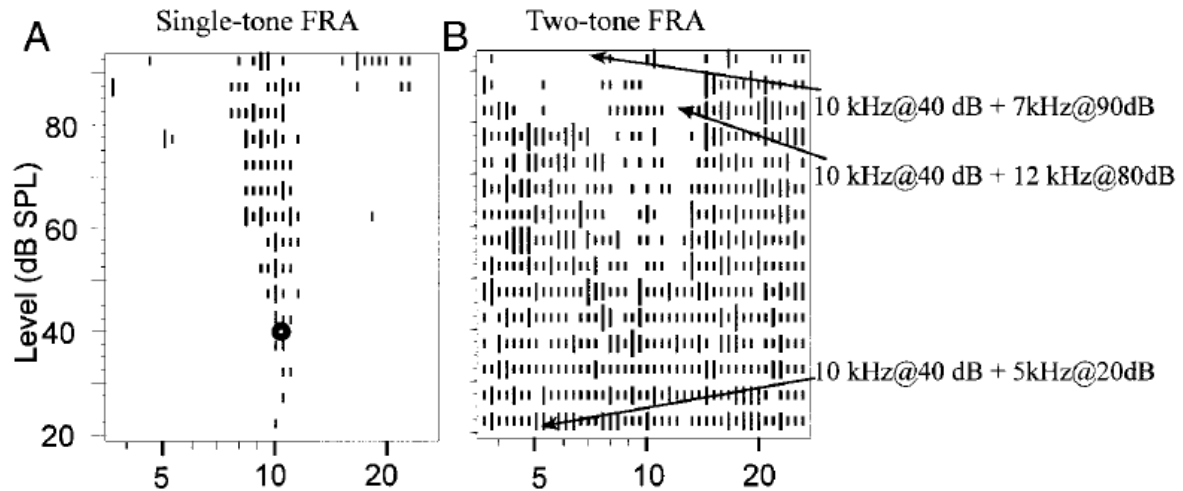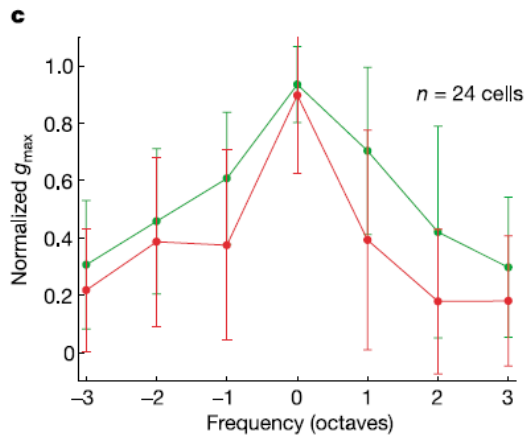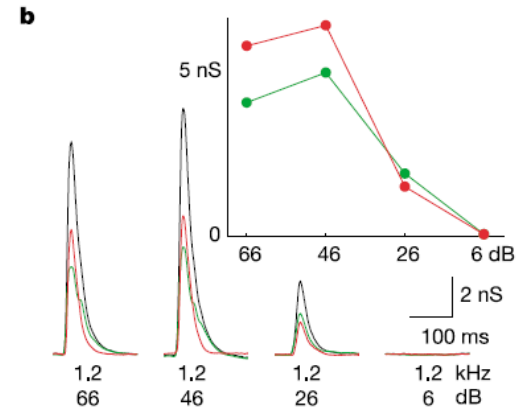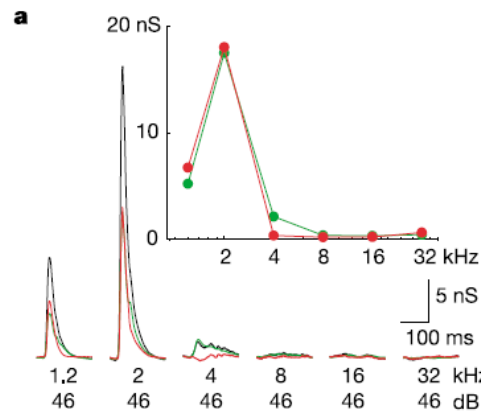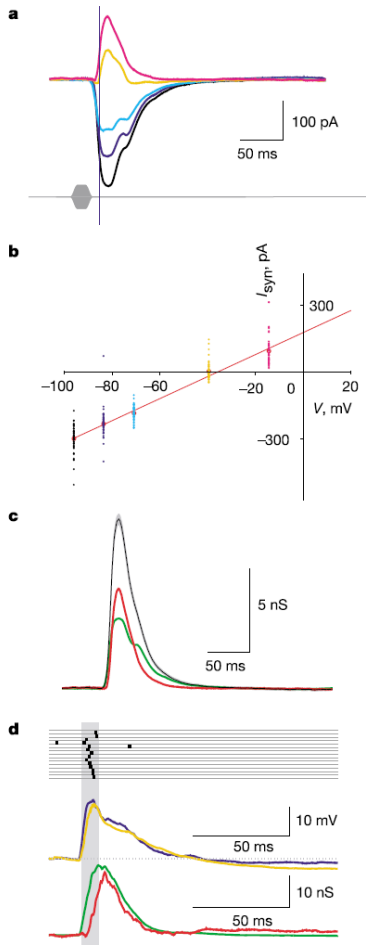
Sutter et al. 1999

Auditory cortex – Excitation and inhibition are co-tuned to sound intensity and frequency
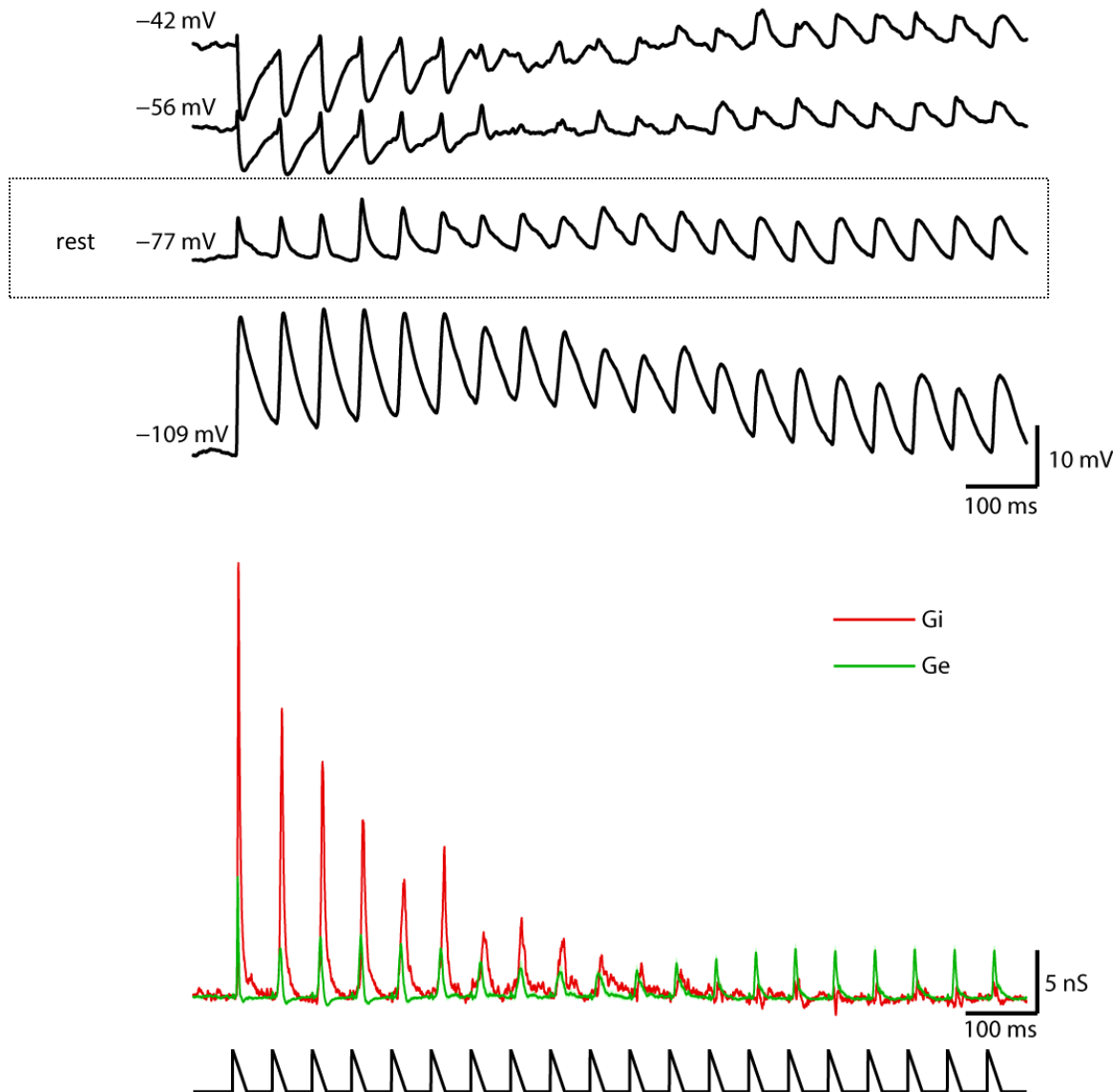
1. Inhibition?

Wehr and Zador 2003

# Auditory cortex – Excitation and inhibition are co-tuned to sound intensity and frequency

1. Inhibition?

Wehr and Zador 2003

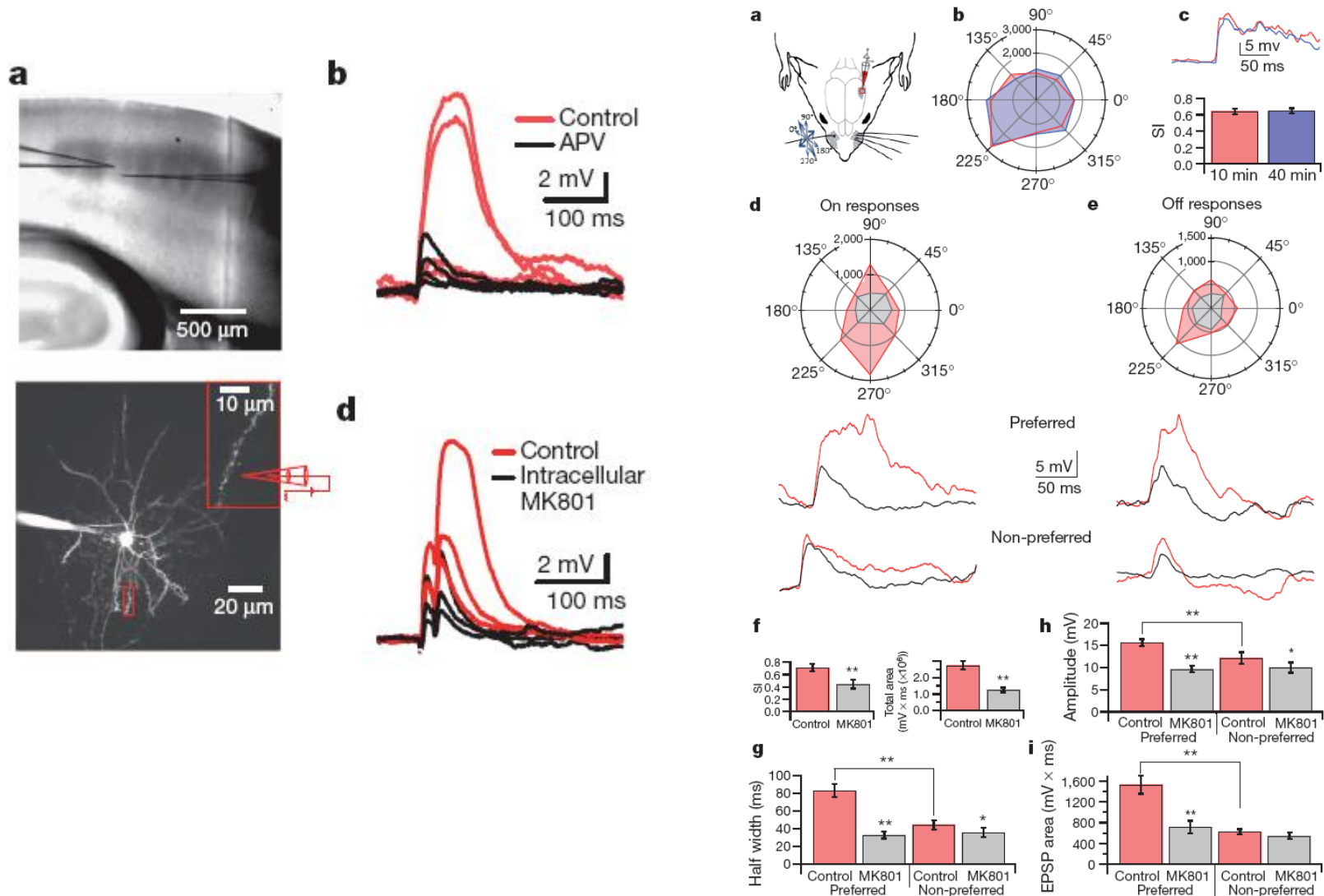# Auditory cortex – Excitation and inhibition are co-tuned to sound intensity and frequency
AWAKE

1. Inhibition?

Li et al, 2014
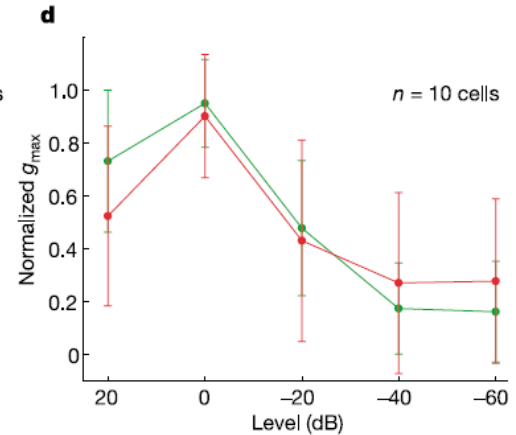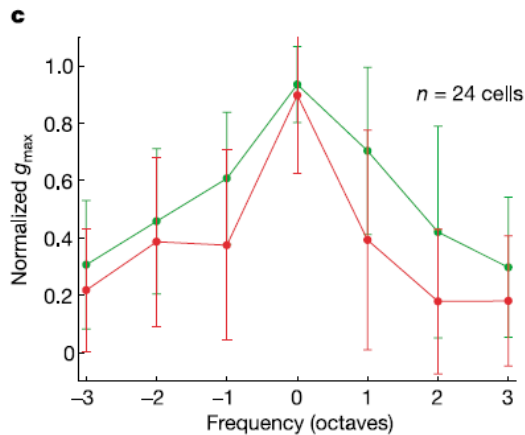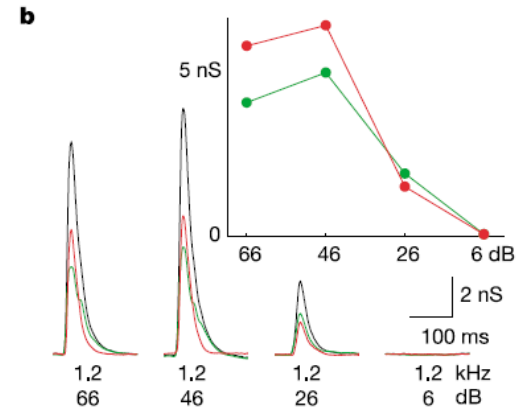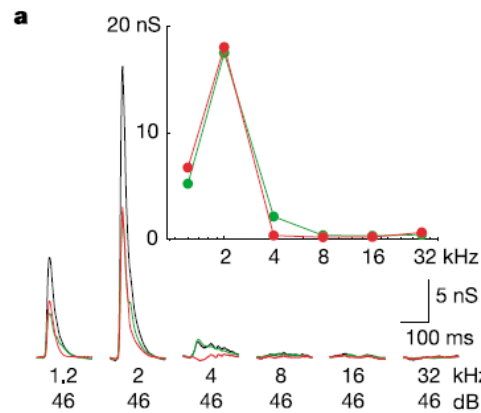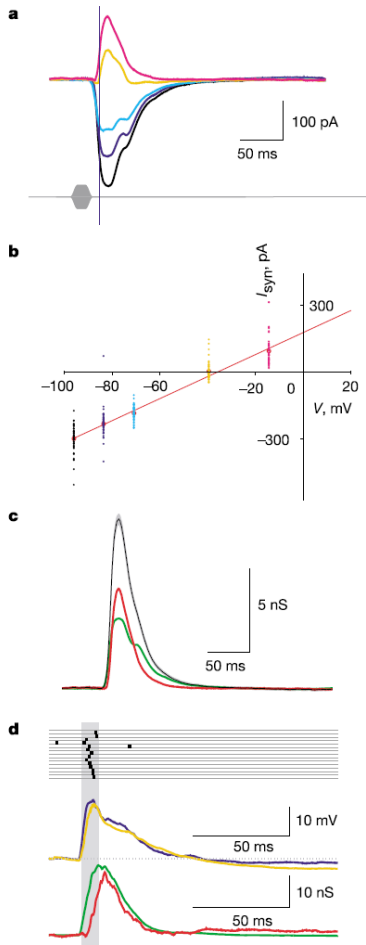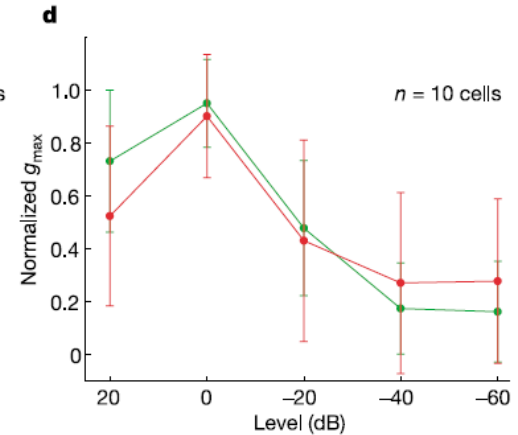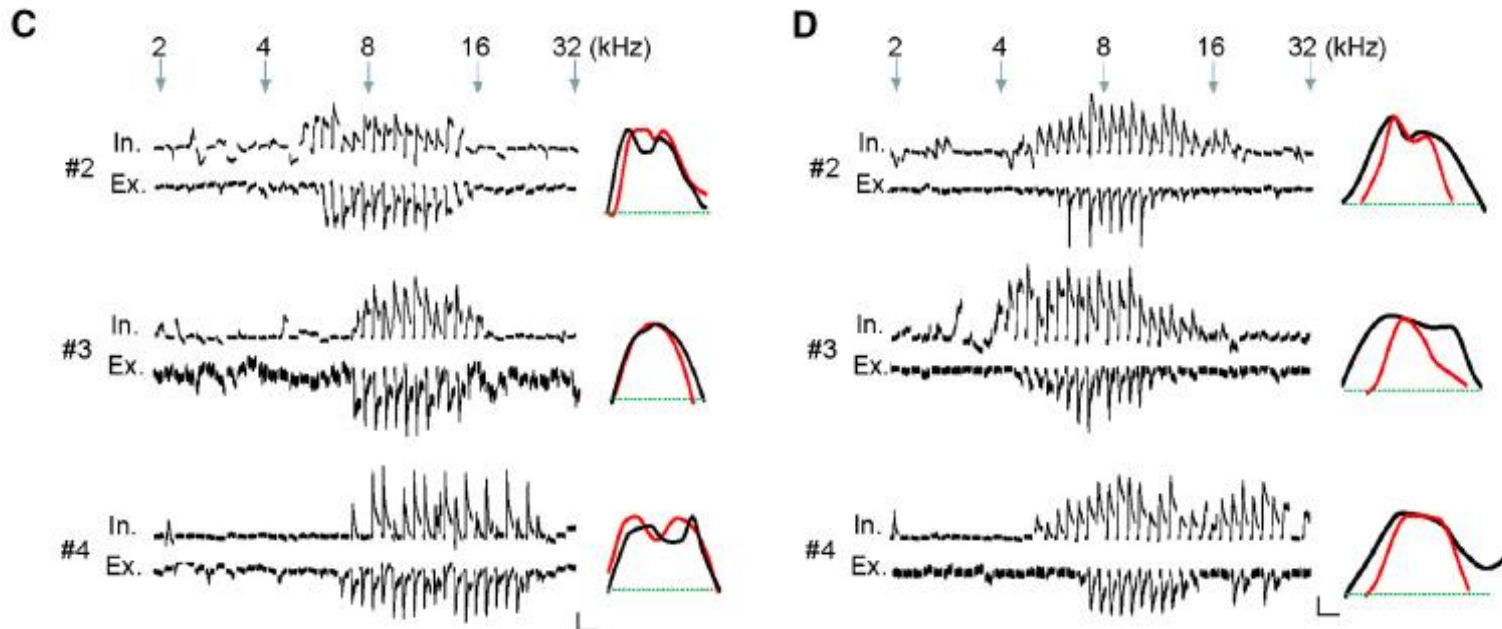
Inhibition Adapts More than Excitation

Heiss et al. 2008

Selectivity to direction of whisker deflection
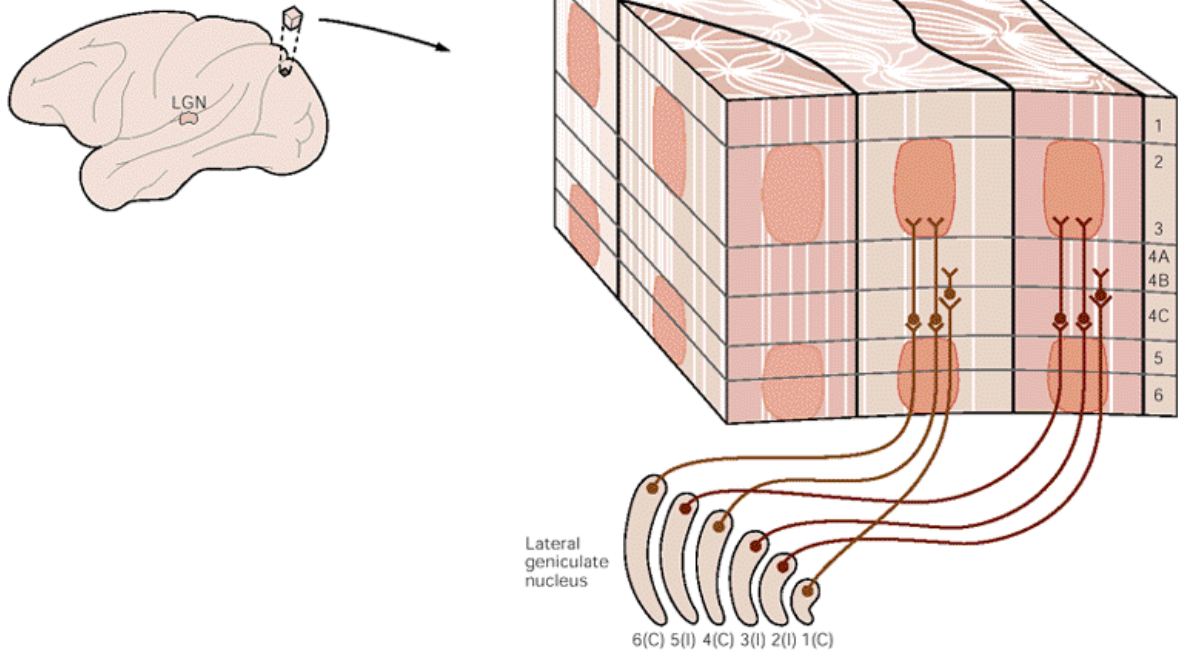

Wilent and Contreras 2005
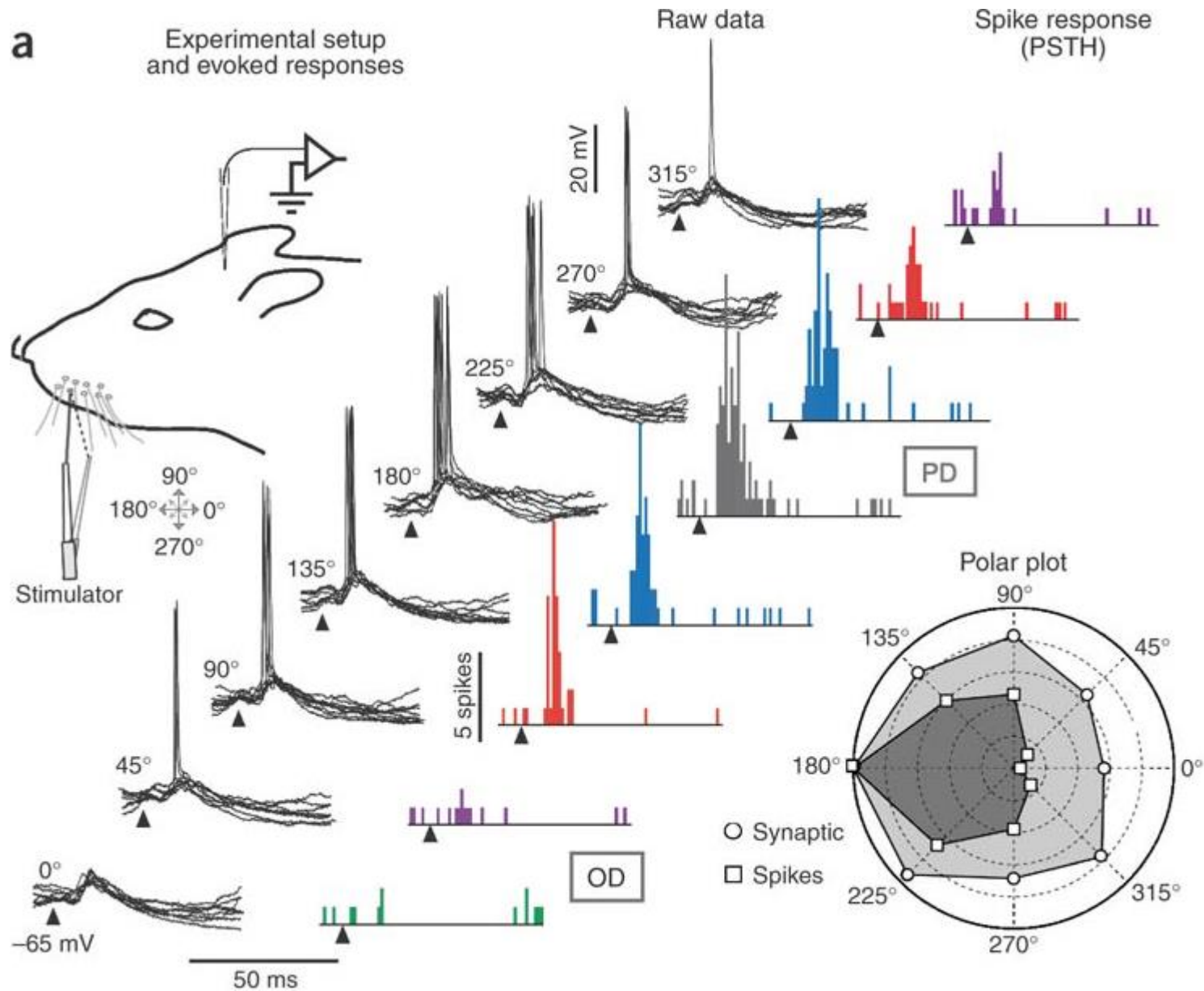
Selectivity to direction of whisker deflection: Excitation but not inhibition is selective
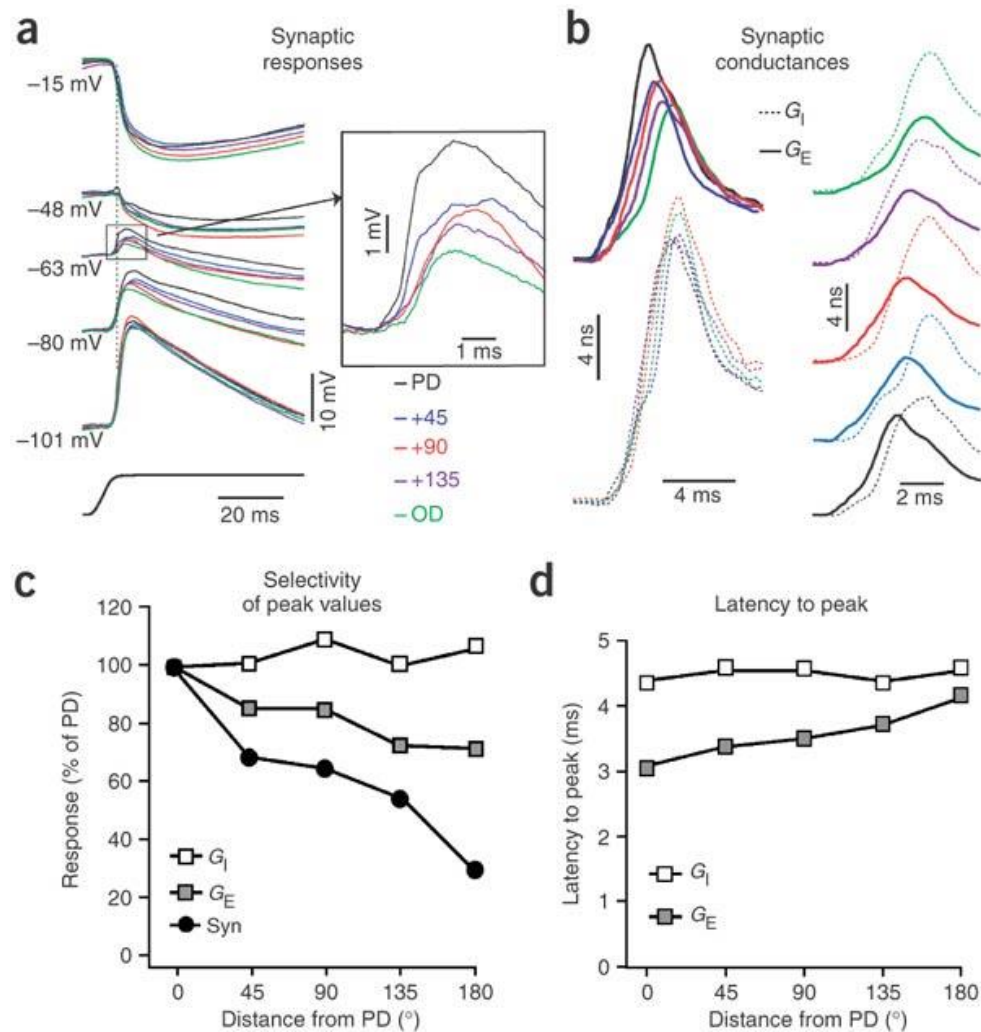
Selectivity to direction of whisker deflection: Response to preferred direction is NMDA dependent
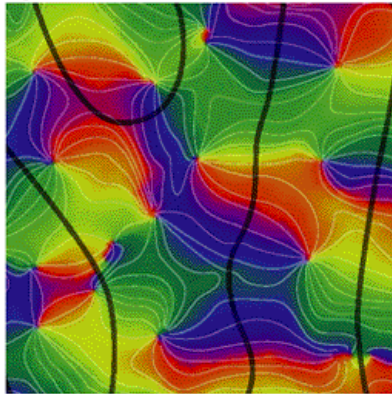

Lavzin et al. 2012

A

C   I   C   I

1
2
3
4A
4B
4C
5
6

Lateral
geniculate
nucleus

6(C) 5(I) 4(C) 3(I) 2(I) 1(C)

LGN

B₁   **B₂**   **B₃**