Neural coding in retina and lateral geniculate

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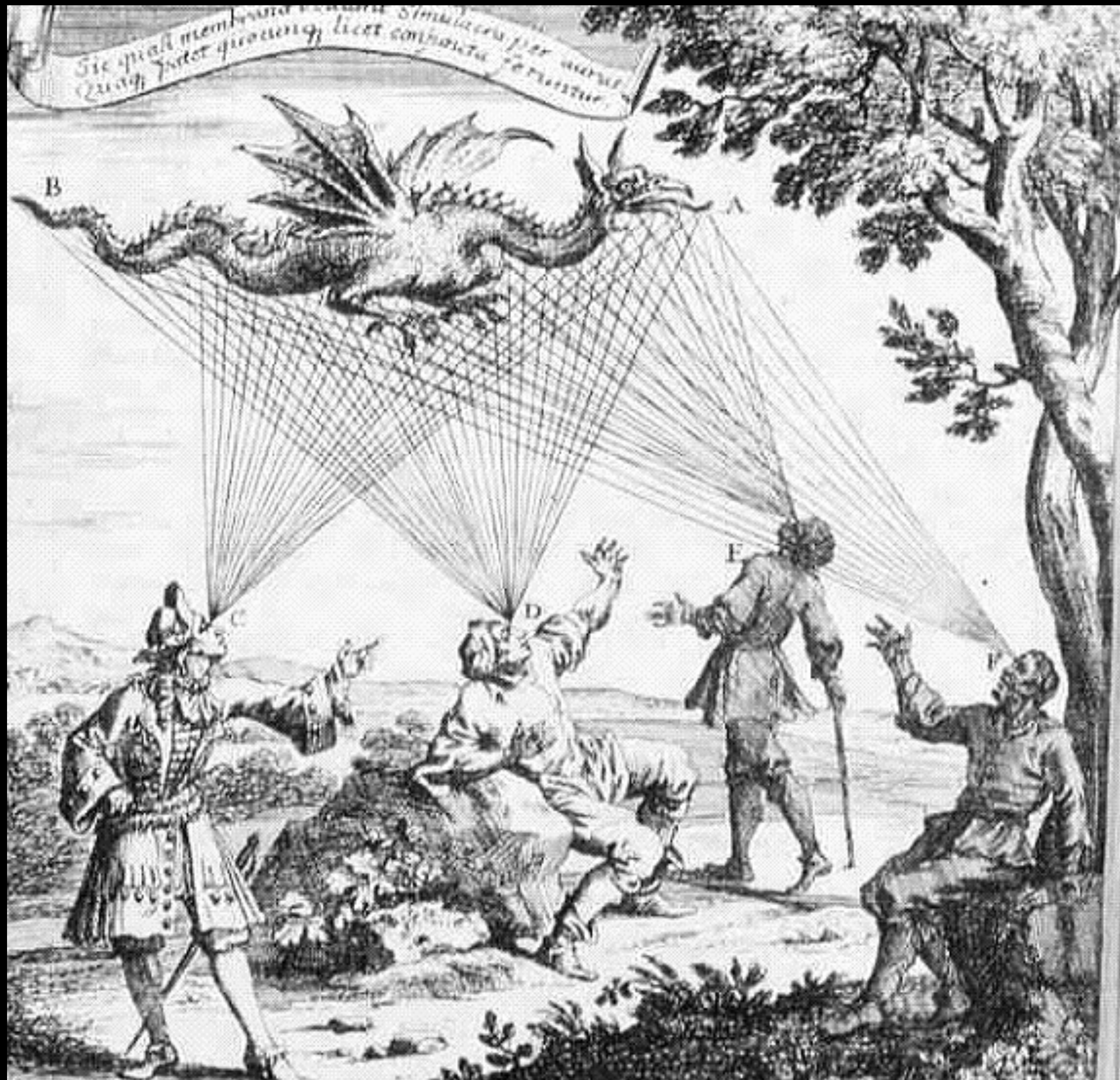
VS-265

Introduction:

- Historic ideas about vision
- Classical physiology and anatomy of retina and LGN
- Is LGN a boring relay between retina and cortex?
- Push-pull, the ubiquitous theme in retina/LGN
- Spiking vs. bursting in LGN cells

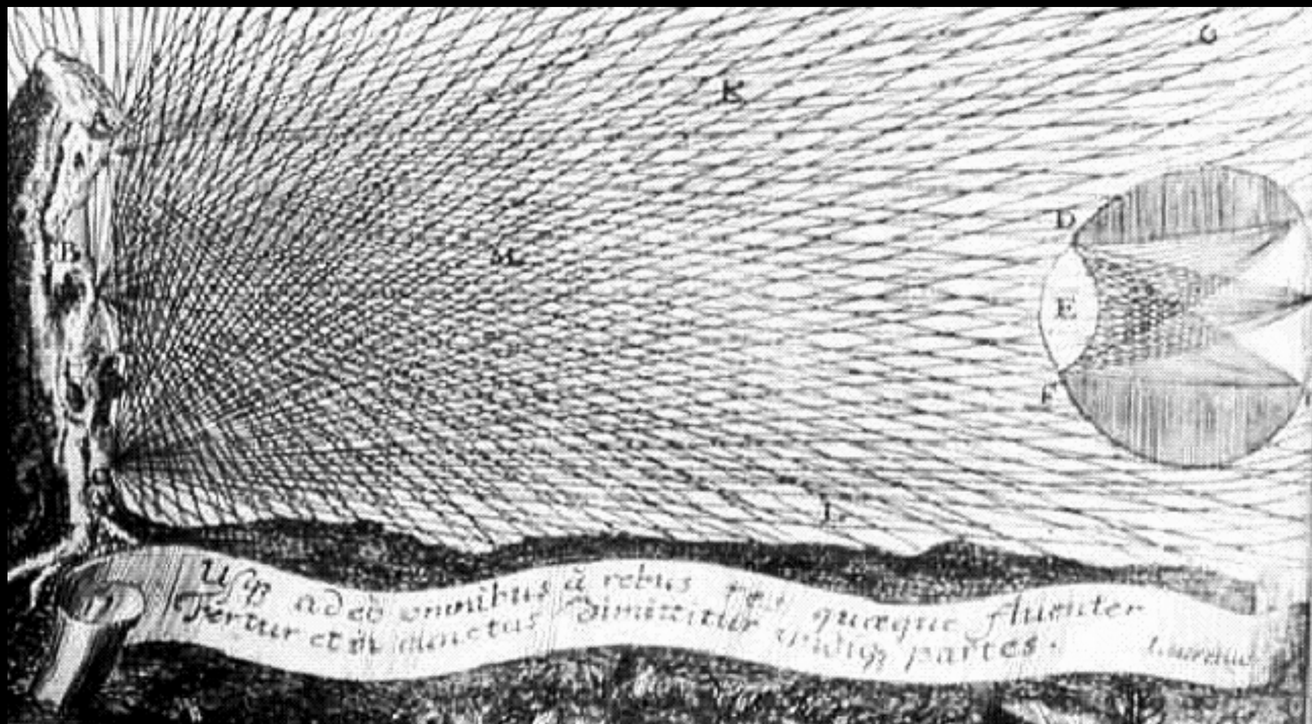
1) Information recoding in LGN relay cells

2) Retinal oscillations and their potential functional role

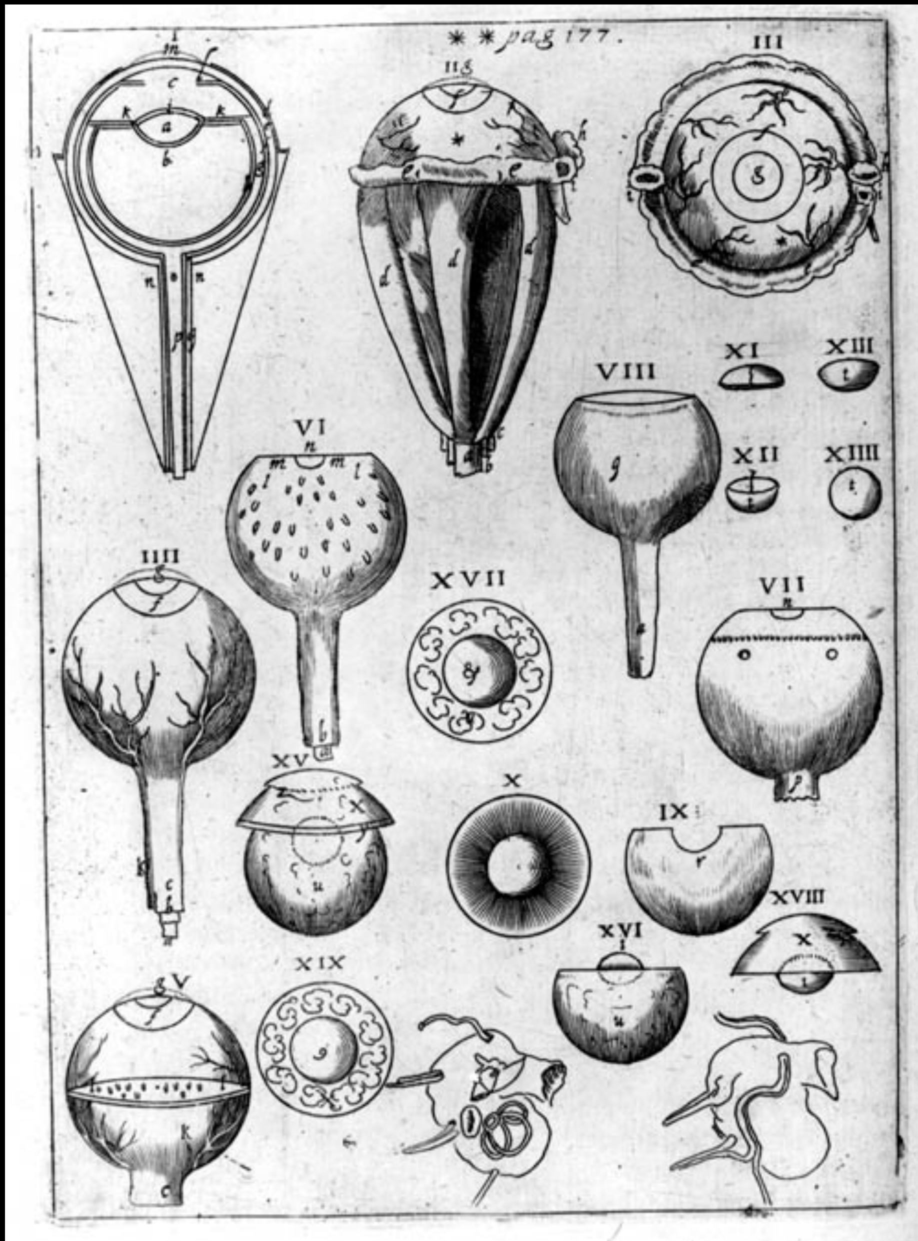


after **Plato** (428-348, B.C.)

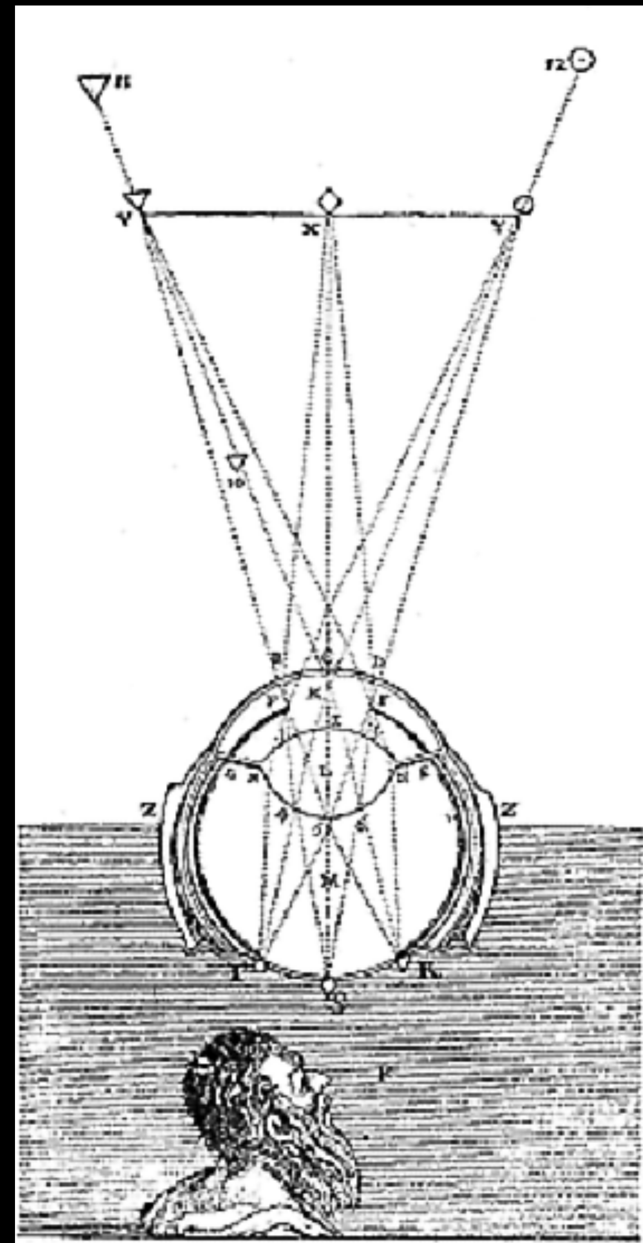
The eye emits rays of fire that coalesce with sunlight and intersect with particles emitted by the object.



after **Abu Ali Al-Hasan Ibn al-Haitham,** (965-1039 AD)
Rays are emitted by external objects and are focused by the optics of eye.

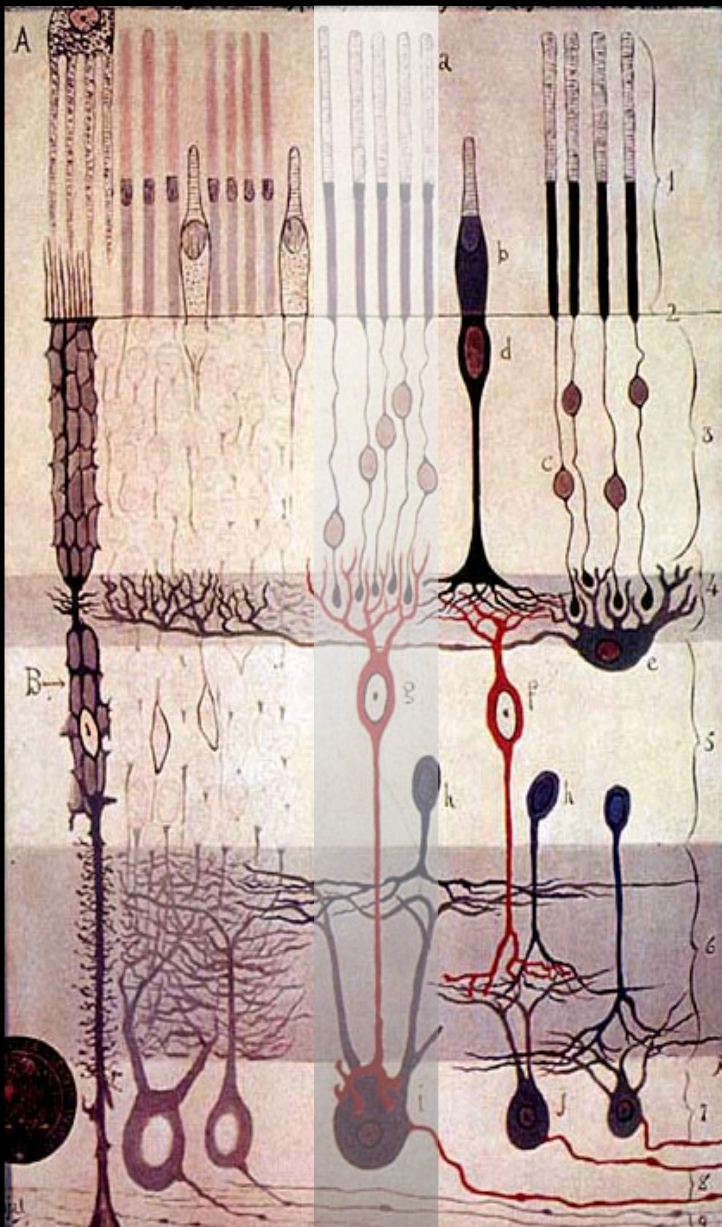


Kepler, *Ad Vitellionem paralipomena, quibus Astronomiae pars optica traditur* 1604, after Platter



Descartes, *Le Dioptrique* 1637, after Kepler

Retina



Photoreceptors
(capture light)

Bipolar Cells
(pool input from
photoreceptors &
contact ganglion cells)

Ganglion Cells
(send signals to the
brain)

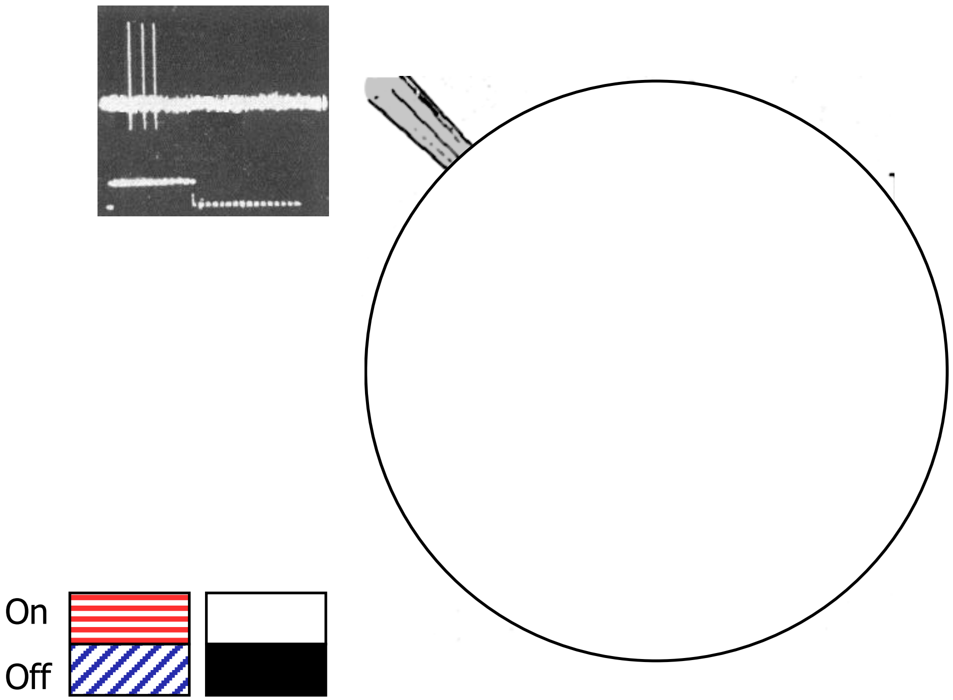
Ramon y Cajal, ~1900

The retinal region occupied by visual sense cells whose connections converge upon a given retinal ganglion cell shall be termed the receptive field of that ganglion cell…

Hartline, *Harvey Lecture*, 1942

Receptive Fields in the Mammalian Retina

Extracellular Recording from an On-Center Ganglion Cell in Cat



Kuffler, *J Neurophys* 1953

Early recordings in LGN

SINGLE UNIT ACTIVITY IN LATERAL GENICULATE BODY AND OPTIC TRACT OF UNRESTRAINED CATS

D. H. HUBEL

J. Physiol. (1960)

"it was clear that receptive field arrangements were qualitatively similar to those of retinal ganglion cells (Kuffler, 1953), that is, they had an 'on' centre and an 'off' periphery, or an 'off' centre and an 'on' periphery."

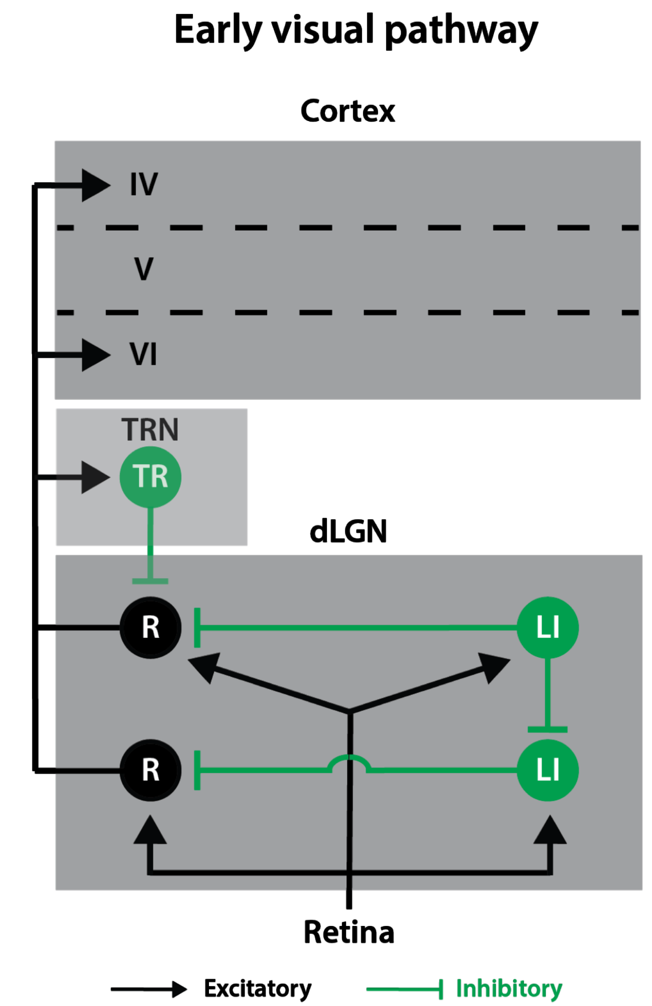
INTEGRATIVE ACTION IN THE CAT'S LATERAL GENICULATE BODY

BY D. H. HUBEL AND T. N. WIESEL
From the Neurophysiology Laboratory, Department of Pharmacology, Harvard Medical School, Boston 15, *Massachusetts, U.S.A.*

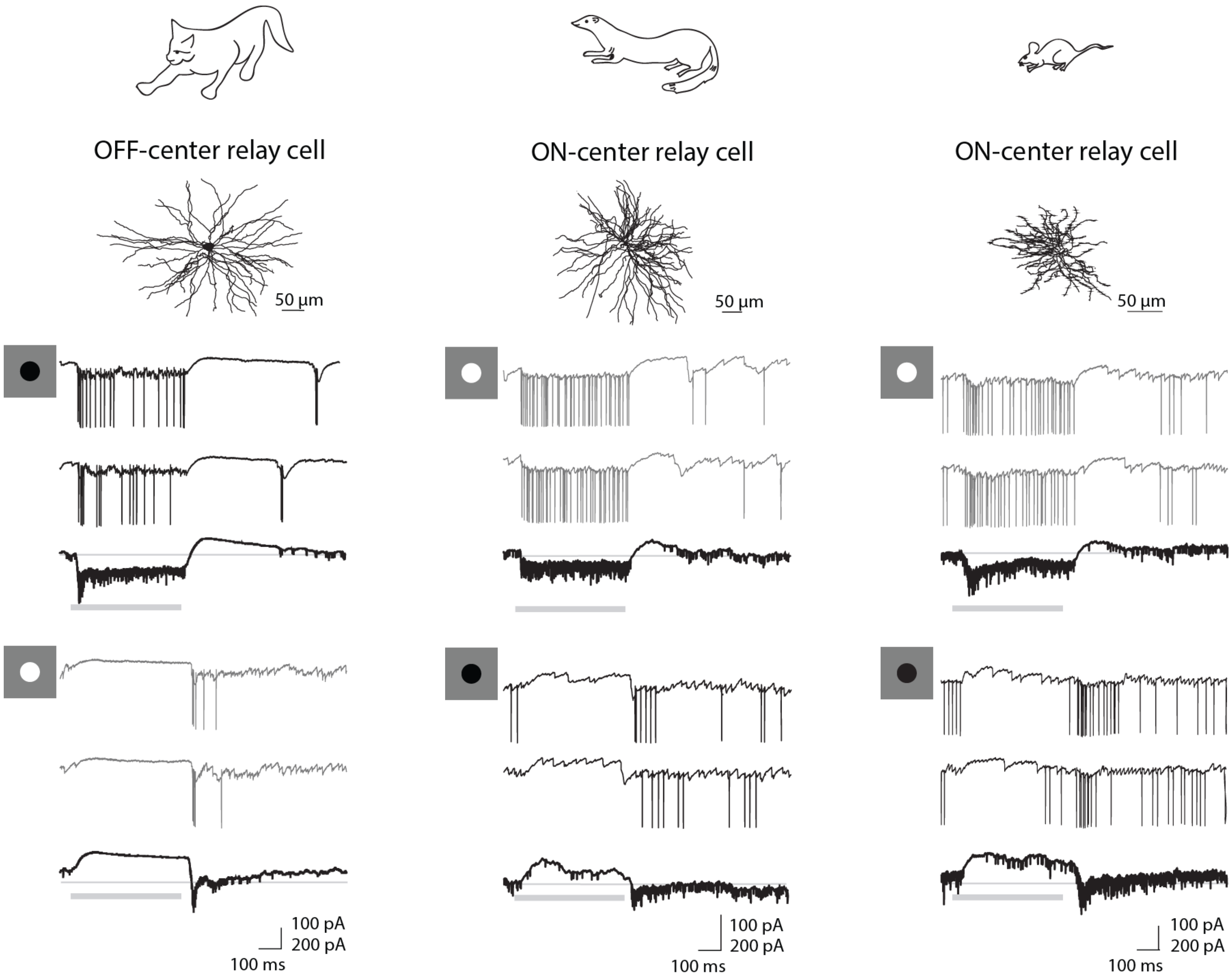
(*Received* 3 *October* 1960)

It has often been asked whether the lateral geniculate body contributes to the integration of incoming visual impulses or is a mere 'way-station' in the pathway from retina to cortex. While perhaps less complex than the retina or cortex, the geniculate is histologically far from the simple structure that the term 'way-station' would imply (O'Leary, 1940; Glees, 1941). The presence of extensive dendritic arborizations, the profuse ramifications of incoming optic-tract fibres, and the existence of short-axon cells, all suggest that there may be something more than a 1:1 transmission of impulses from optic nerve to optic radiations.

The classical early visual pathway

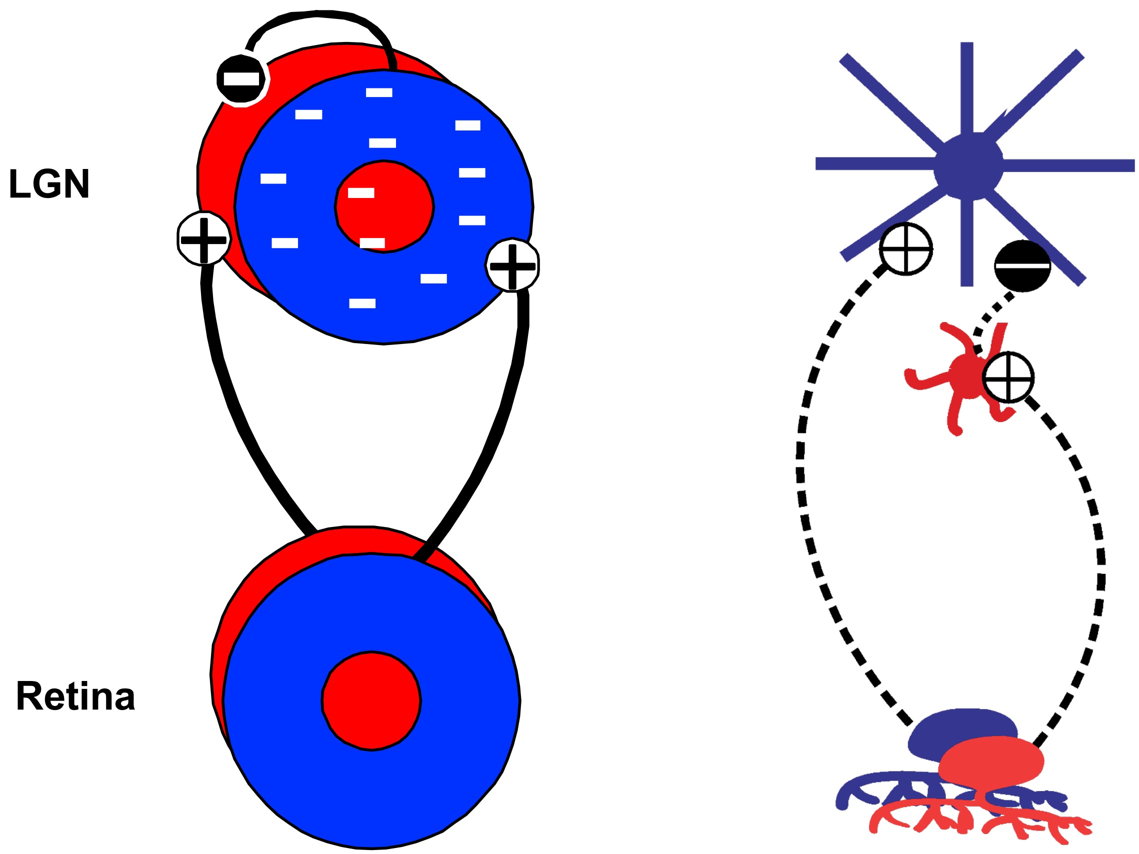


“Push-Pull” found in LGN across Species



Suresh et al., *J Neurosci* 2016

Push-Pull Circuit for Receptive Fields in dLGN

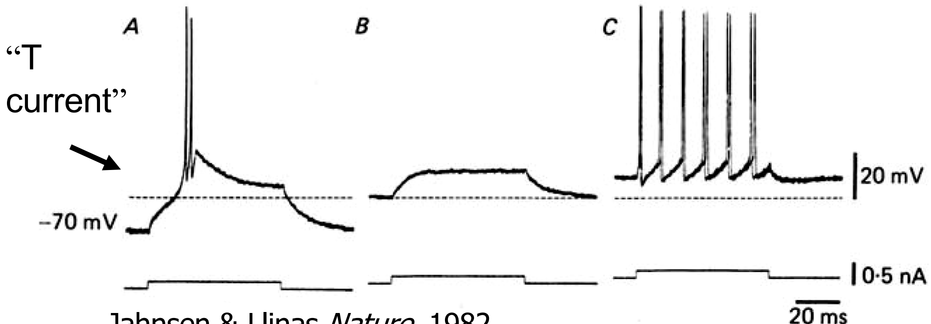


Burst and Tonic Firing Modes in LGN

Dual Models of Firing in Thalamus

Burst

Tonic firing



Jahnsen & Llinas *Nature*, 1982

Encoding of Natural Scene Movies by Tonic and Burst Spikes in the Lateral Geniculate Nucleus
Lesica and Stanley (2004) *J. Neurosci*

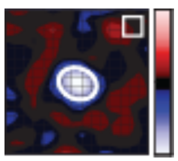
Visual Control of Burst Priming in the Anesthetized Lateral Geniculate Nucleus
Denning & Reinagel (2005) *J. Neurosci.*

Paired-Spike Interactions and Synaptic Efficacy of Retinal Inputs to the Thalamus.
Usrey et al., (1998) *Nature*

Spatial & Temporal Correlations in Natural Images

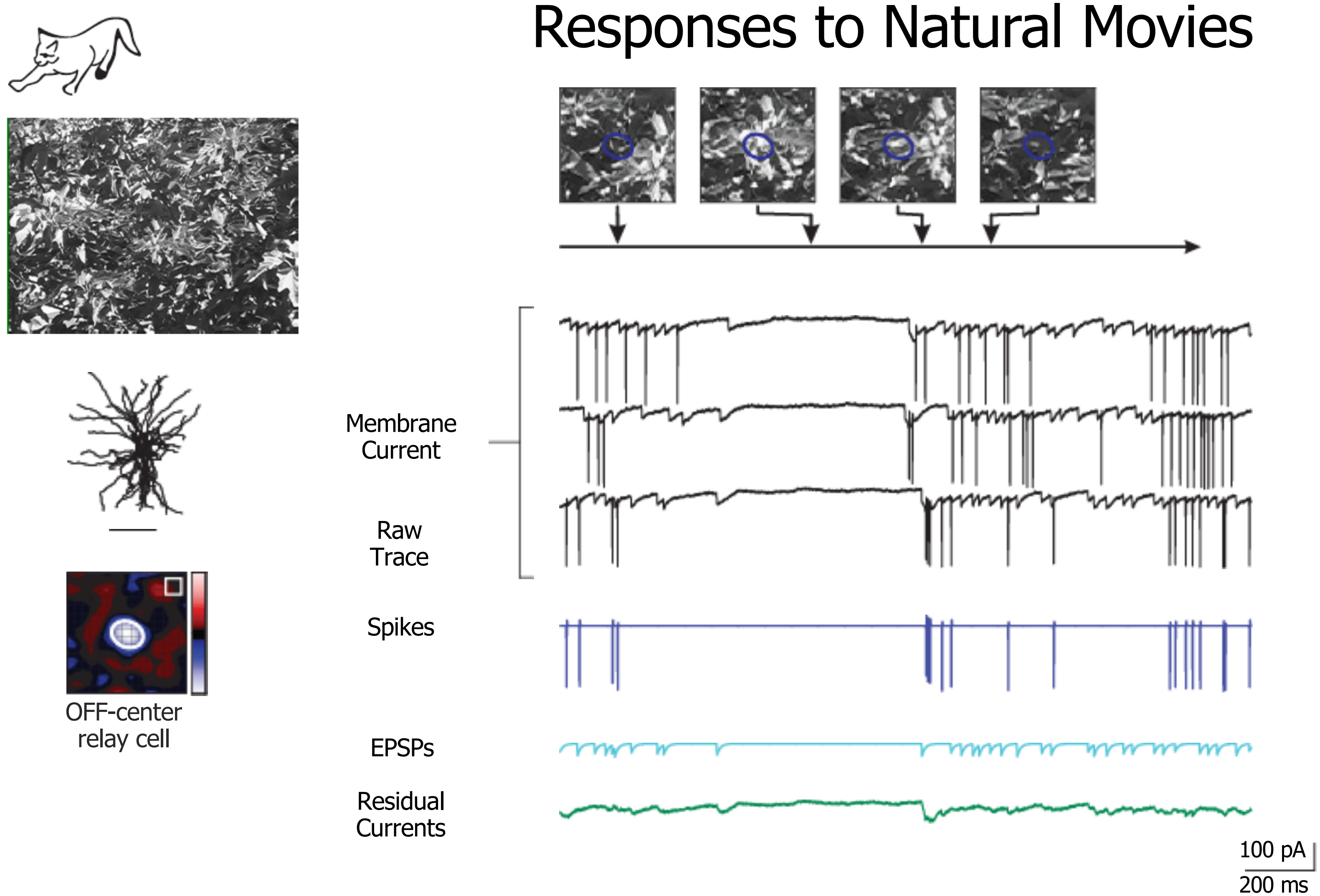
van Hateren & van der Schaaf (1998) *Proc.R.Soc.Lond. B*

Bursty Responses to Natural Movies



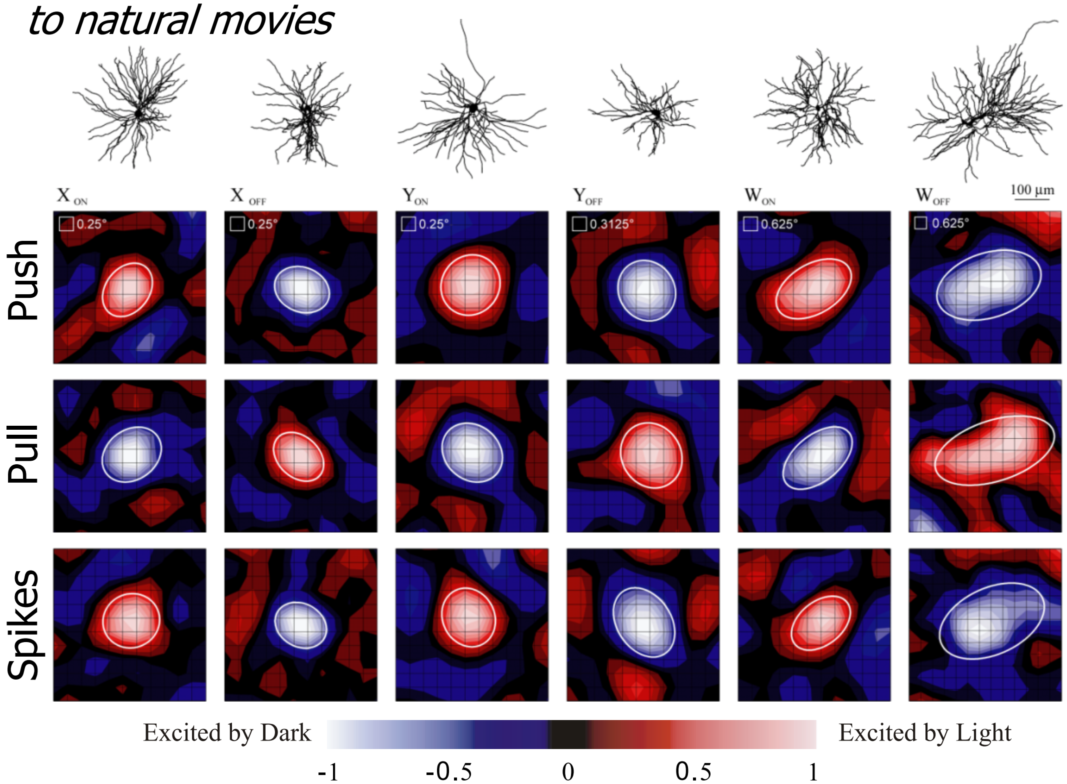
OFF-center
relay cell

Responses to Natural Movies

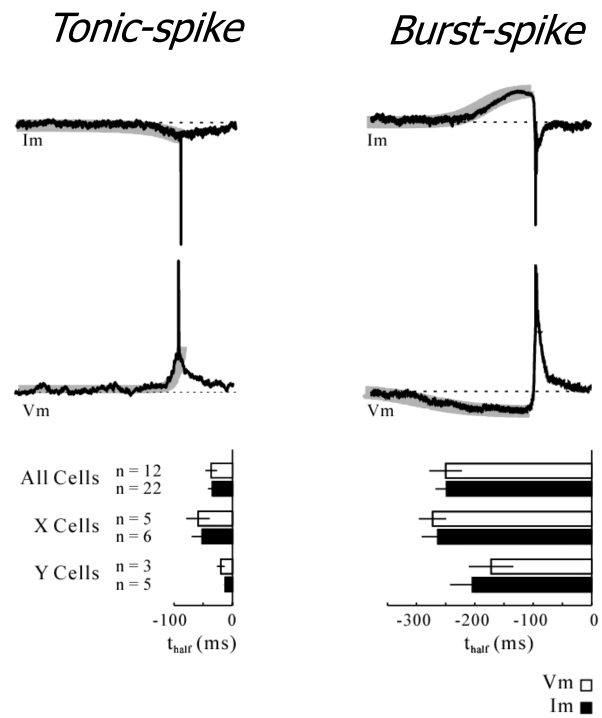


Features That Produce Bursts in LGN

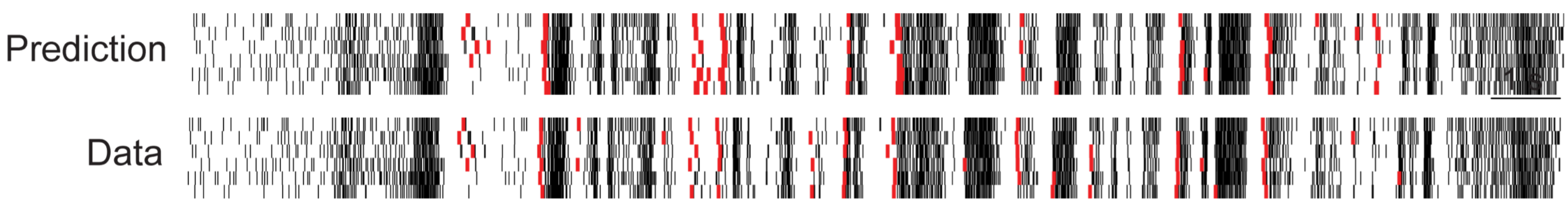
Receptive fields for push, pull and spikes made from responses to natural movies



Spike-triggered averages using burst or tonic spikes



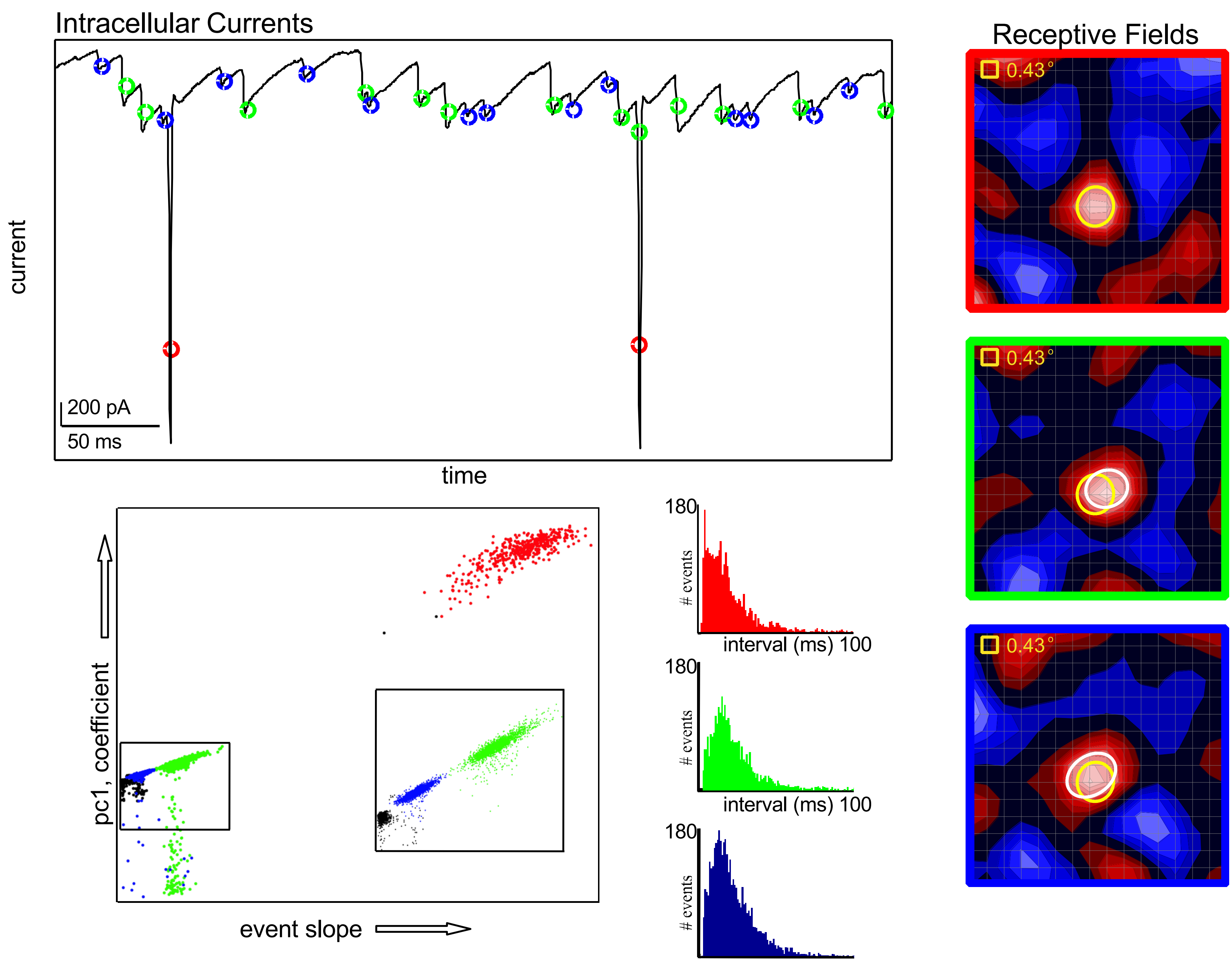
Predicting the occurrence of bursts during natural stimulation



Conclusion: *Feedforward inhibition (via local interneurons) promotes bursts during vision.*

Wang et al. *Neuron*, 2007

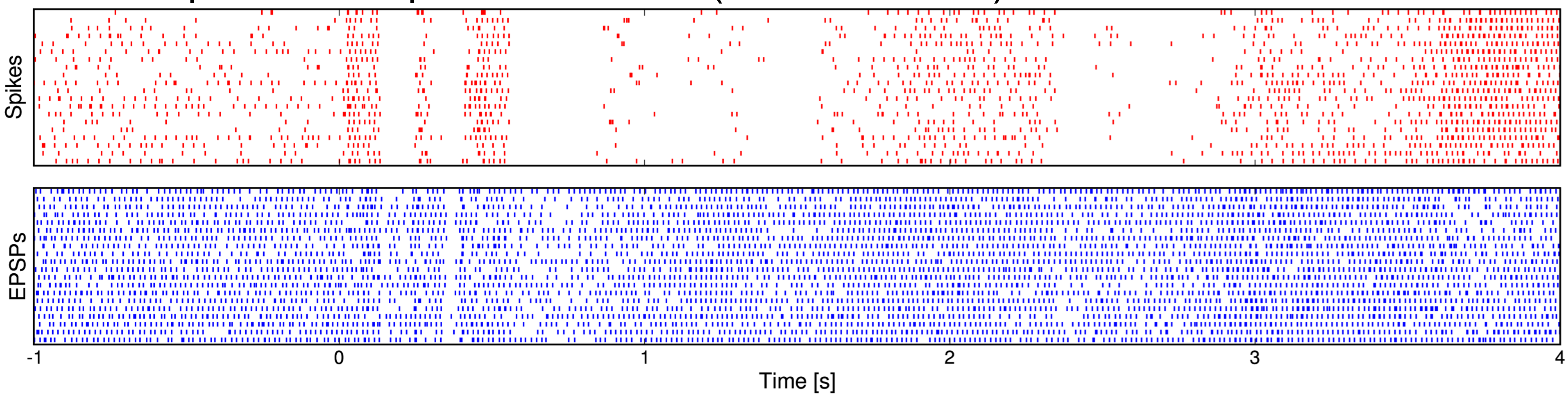
Extracting input and output spikes from whole-cell recording in a relay cell



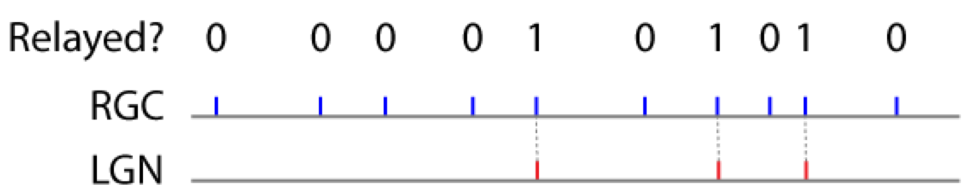
Vishal Vaingankar

1) Recoding of retinal input in LGN cells

Raster plots: 20 repeats of movie (5 sec window)



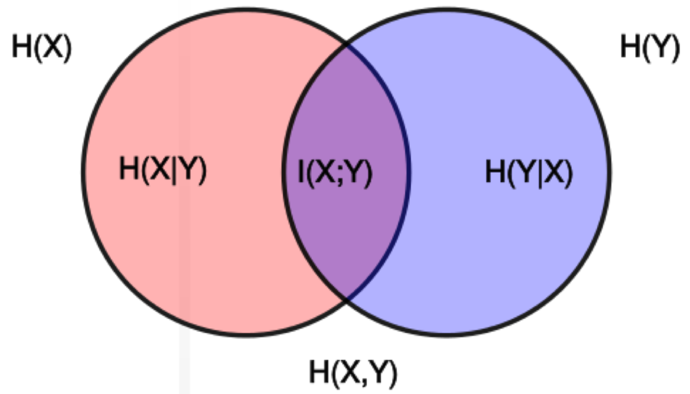
Transmission through an LGN relay cell, “a spike editing” process:



What visual information is transmitted and how is it encoded?

(Wang, Hirsch, Sommer, J Neurosci. 2010)

Mutual Information



$$\begin{aligned}\mathrm{I}(X;Y) &\equiv \mathrm{H}(X) - \mathrm{H}(X|Y) \\ &\equiv \mathrm{H}(Y) - \mathrm{H}(Y|X)\end{aligned}$$

$$\mathrm{I}(X;Y) = \sum_{y\in\mathcal{Y}} \sum_{x\in\mathcal{X}} p_{(X,Y)}(x,y) \log\left(\frac{p_{(X,Y)}(x,y)}{p_X(x)\,p_Y(y)}\right),$$

$$\mathrm{I}(X;Y) = \int_{\mathcal{Y}} \int_{\mathcal{X}} p_{(X,Y)}(x,y) \log\left(\frac{p_{(X,Y)}(x,y)}{p_X(x)\,p_Y(y)}\right) dx\,dy,$$

$$I(X;Y) = D_{\mathrm{KL}}\left(P_{(X,Y)} \| P_X \otimes P_Y\right)$$

Wikipedia

Information Rates in Sensory Neurons

$p(r_i)$	Probability that neural response takes the value r_i
$p(s_j)$	Probability that stimulus condition takes the value s_j
$p(r_i \mid s_j)$	Probability that neural response takes the value r_i when stimulus condition s_j is presented (conditional probability)

Information about stimulus condition s_x:

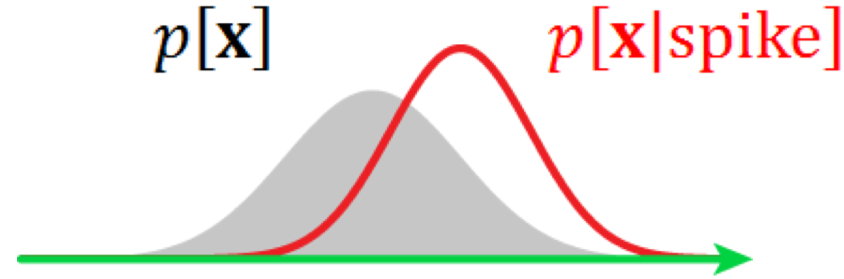
$$I(R, s_x) = \sum_i p(r_i \mid s_x) \log_2 \frac{p(r_i \mid s_x)}{p(r_i)}$$

Average information obtained from all stimulus conditions:

$$I(R, S) = \sum_i \sum_j p(s_j) p(r_i \mid s_j) \log_2 \frac{p(r_i \mid s_j)}{p(r_i)}$$

Theunissen & Borst, 1999

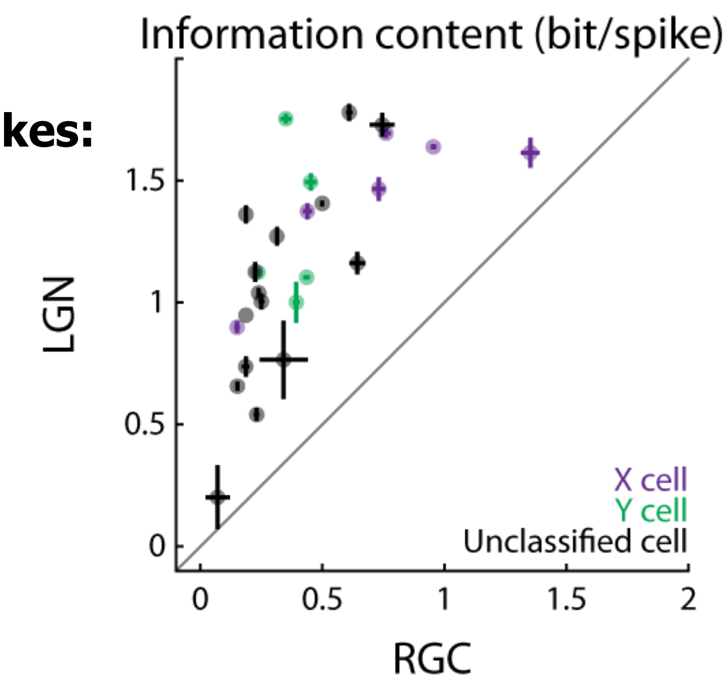
Information encoded by single spikes



$$I_{\mathbf{B}}[\text{spike}; \mathbf{s}] = \left\langle \frac{p[\mathbf{x}|\text{spike}]}{p[\mathbf{x}]} \log_2 \frac{p[\mathbf{x}|\text{spike}]}{p[\mathbf{x}]} \right\rangle_{\mathbf{x}}$$

$$\mathbf{x}(t) = \mathbf{s}(t)\mathbf{B}$$

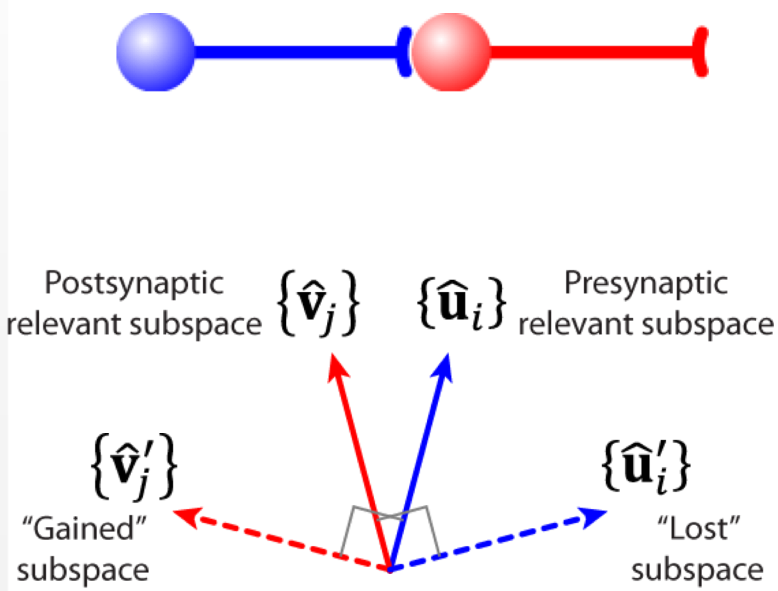
LGN spikes carry more information than retinal spikes:

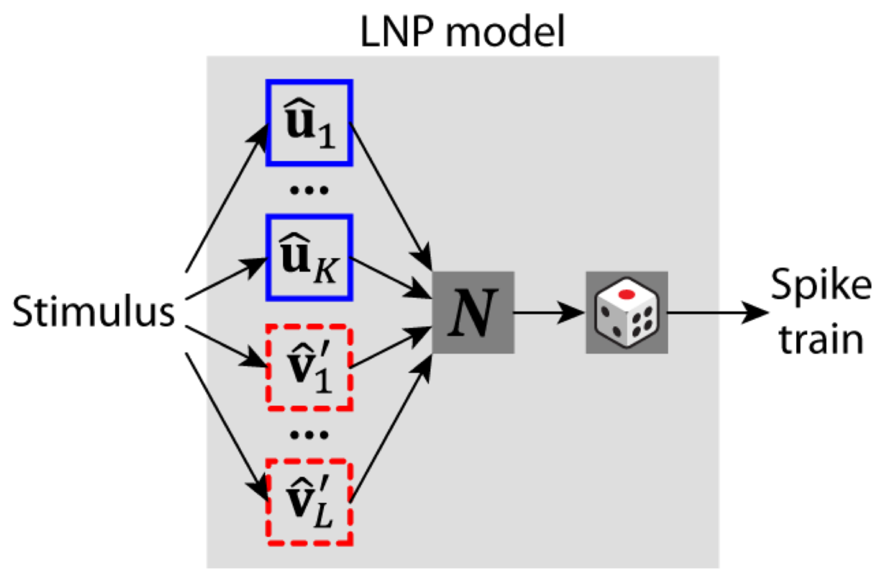


see also:

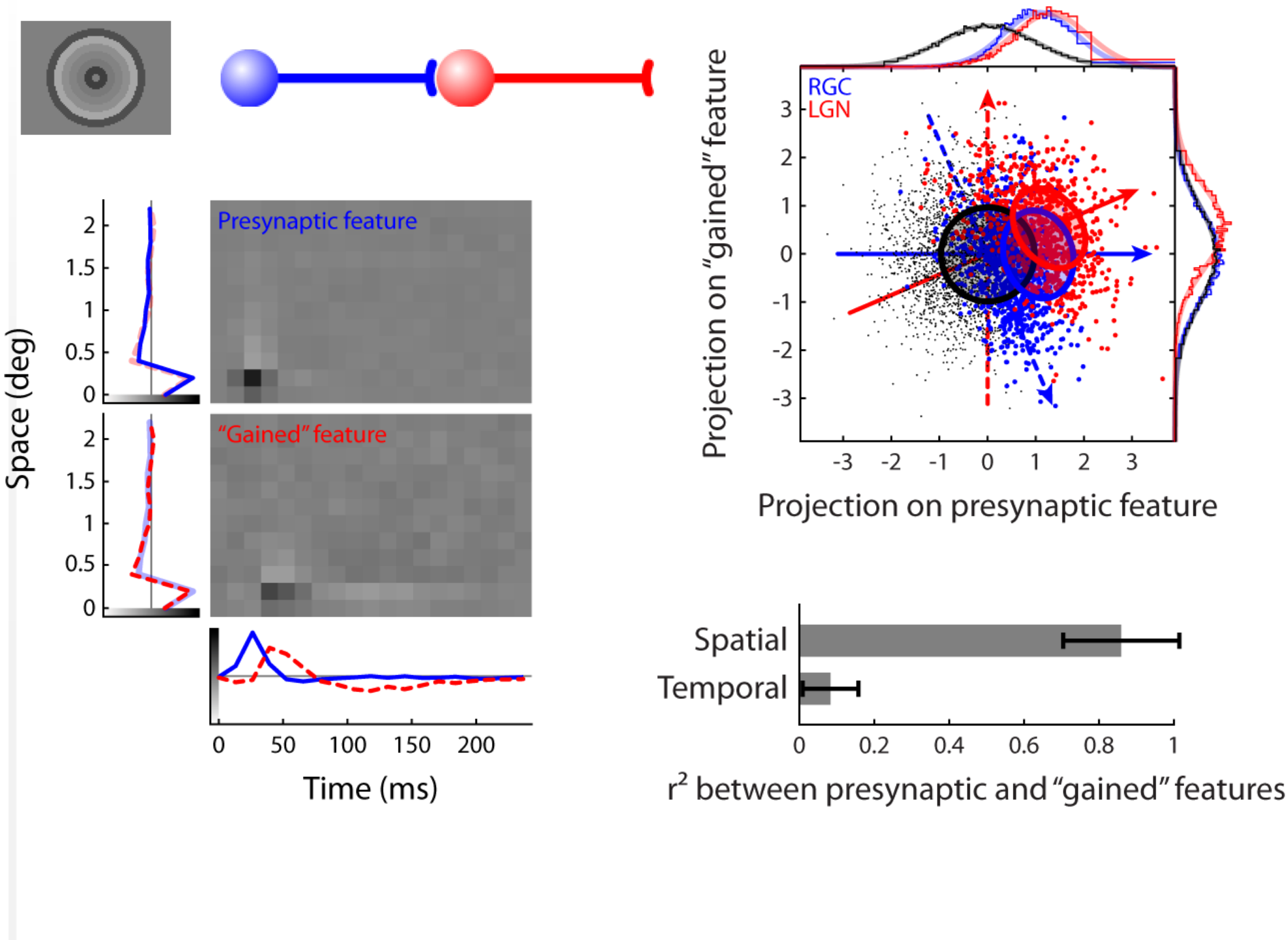
Sincich, Horton, Sharpee, 2009
Rathbun, Warland, Usrey, 2010
Uglesich, Casti, Hayot, Kaplan, 2009

Joint feature space / joint encoding model

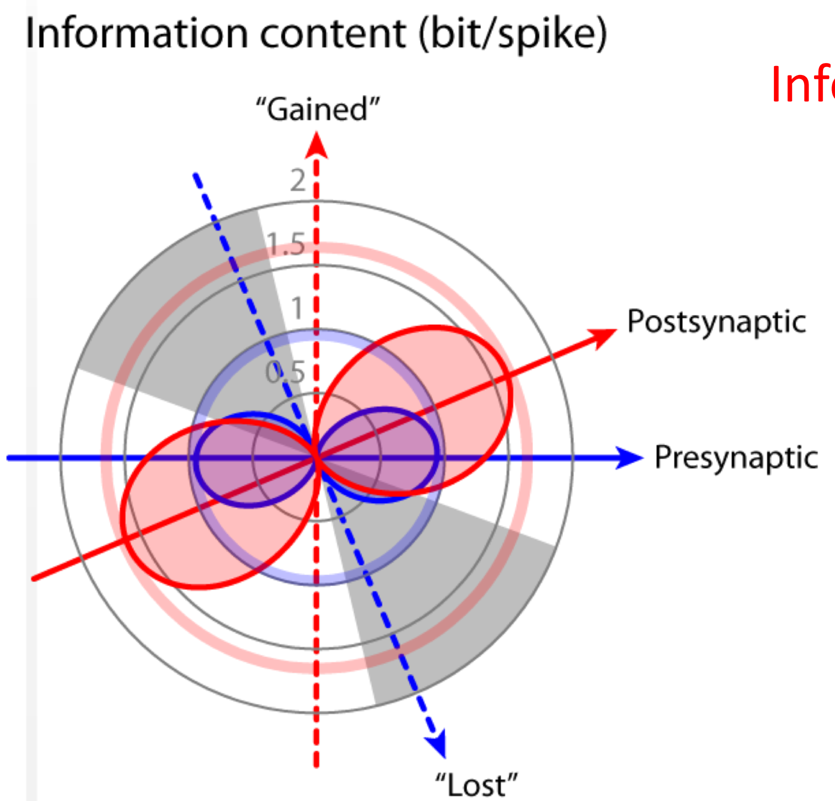




Joint spatio-temporal feature space



Information content resolved by feature

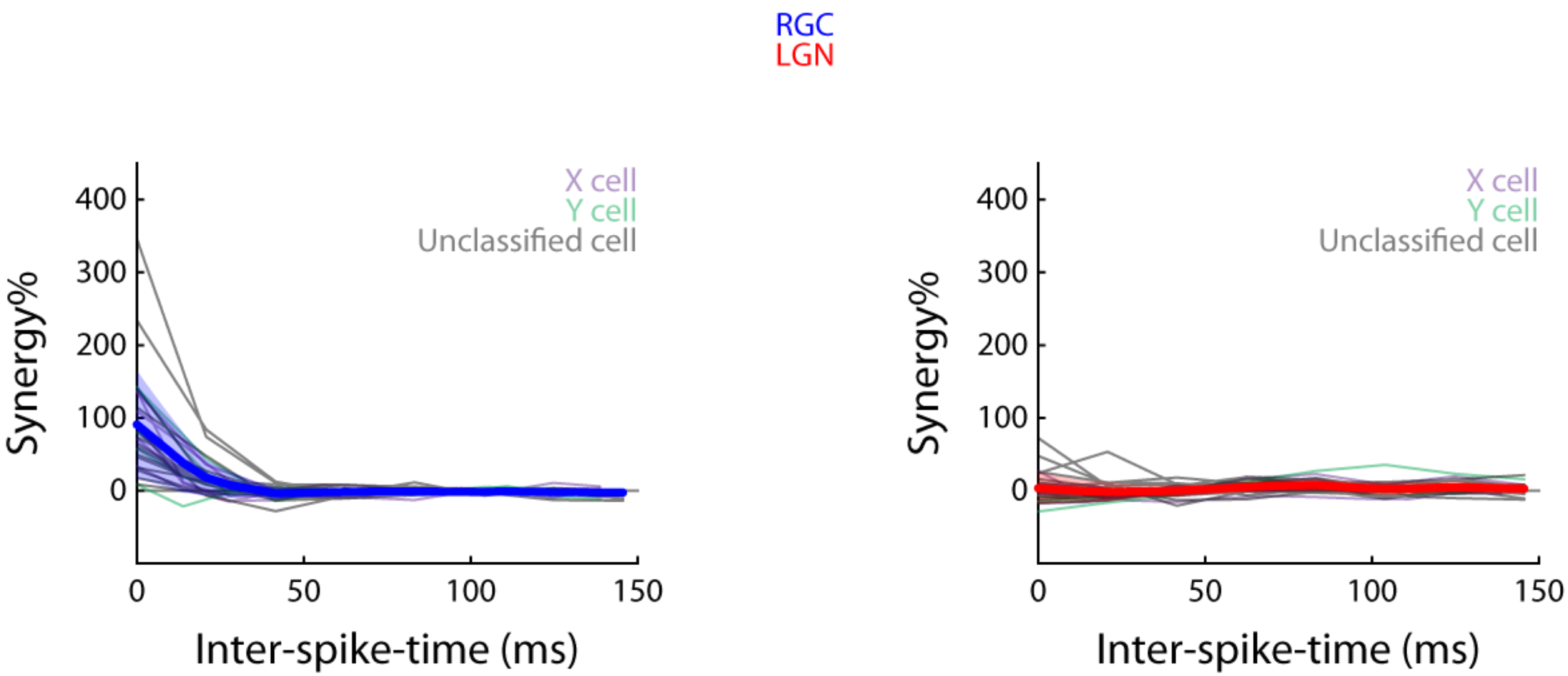


Information channel cannot add information!
What is going on?

- **Evaluate Synergy**:
  - **positive**, if the spike pair encodes additional information;
  - **zero**, if the two spikes in the pair are independent;
  - **negative**, if the two spikes in the pair are redundant.

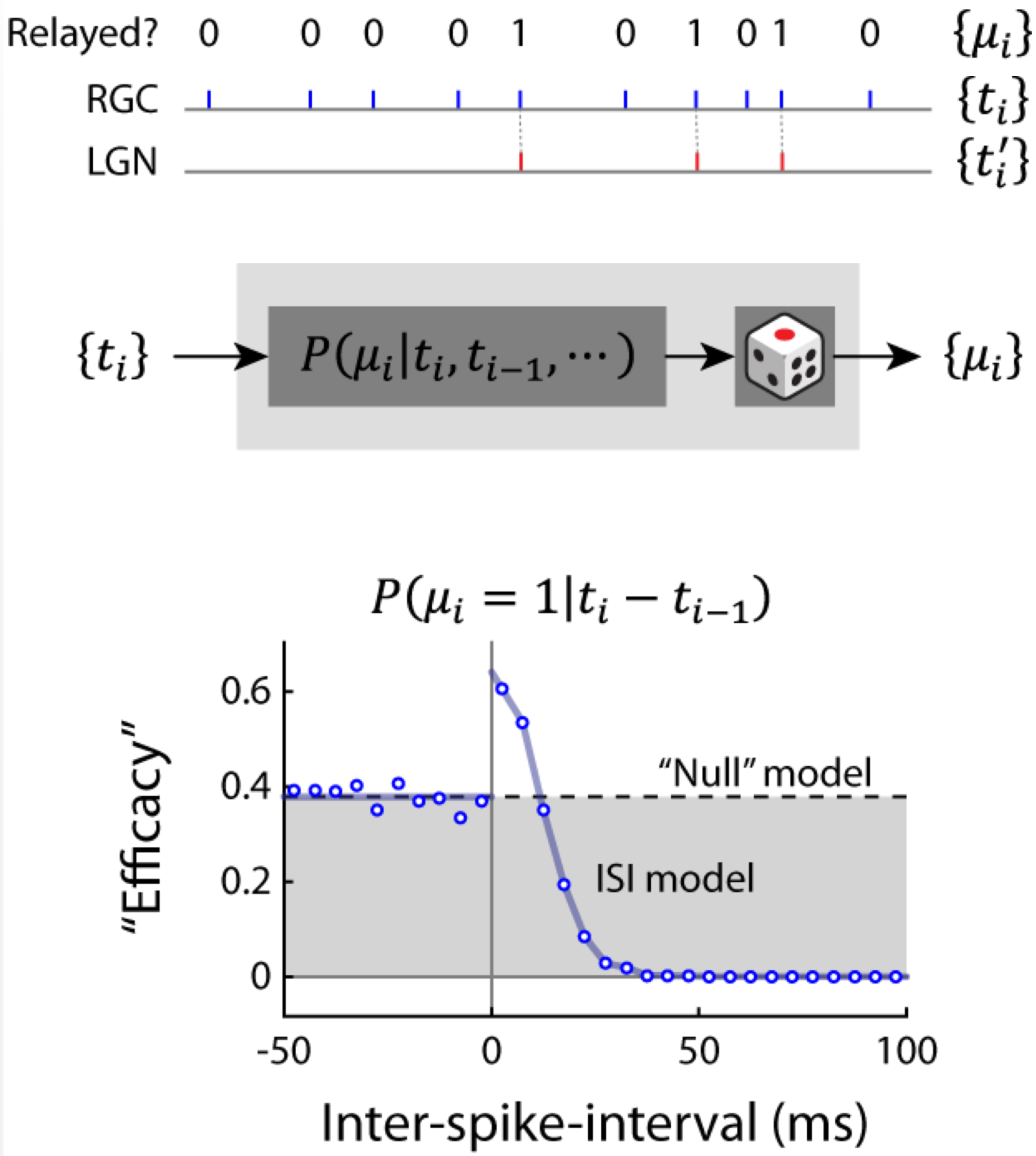
Brenner et al, 2000: Synergy in a neural code

LGN spike is more independent than RGC

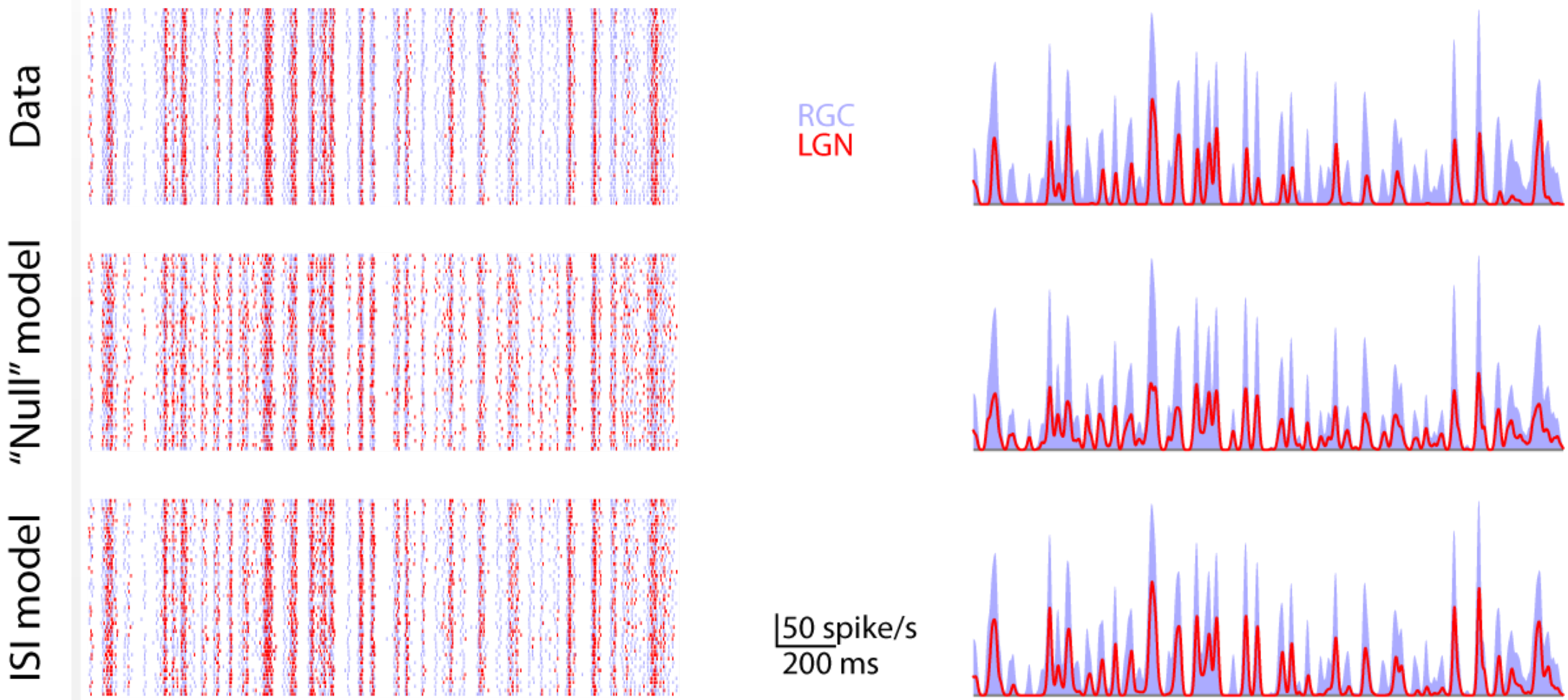


Brenner et al, 2000: Synergy in a neural code

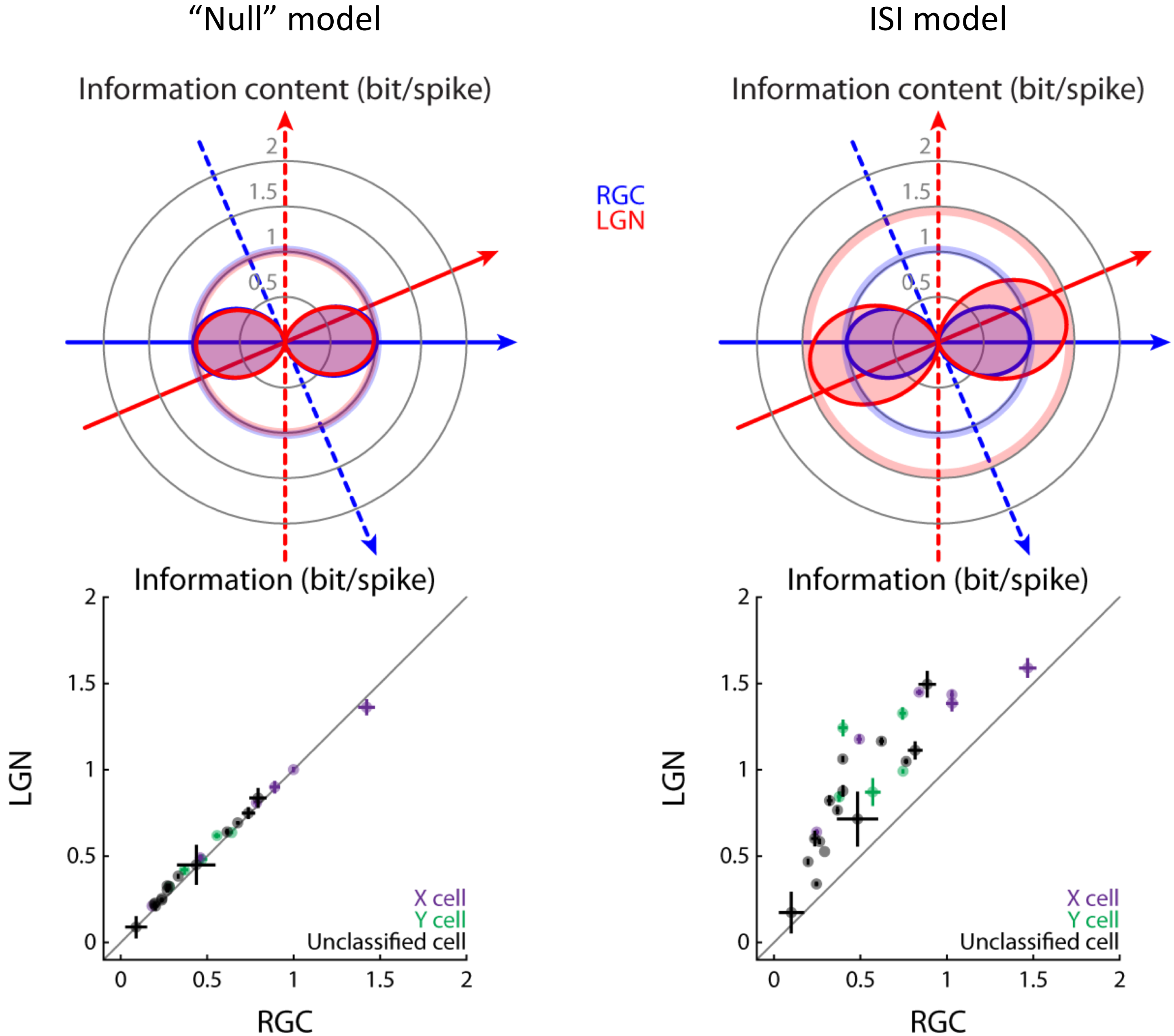
“Null” model and summation (ISI) model



Model performance (1)

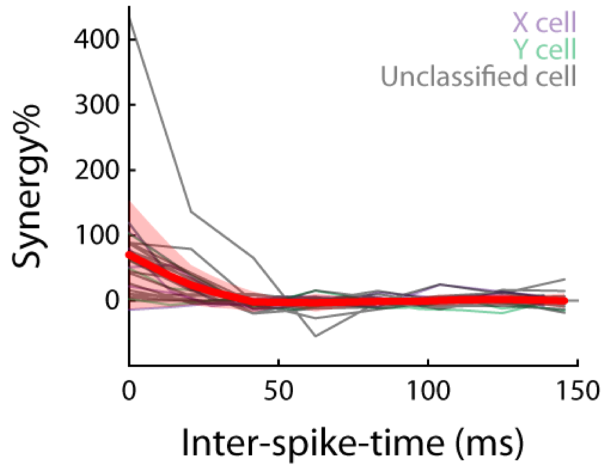


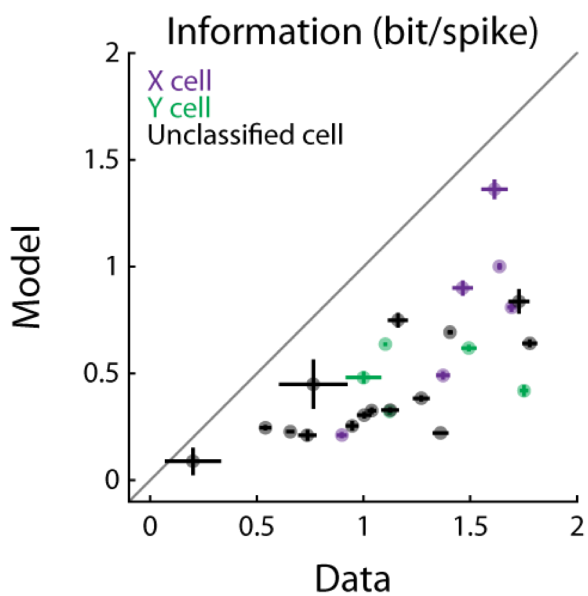
Model performance (2)



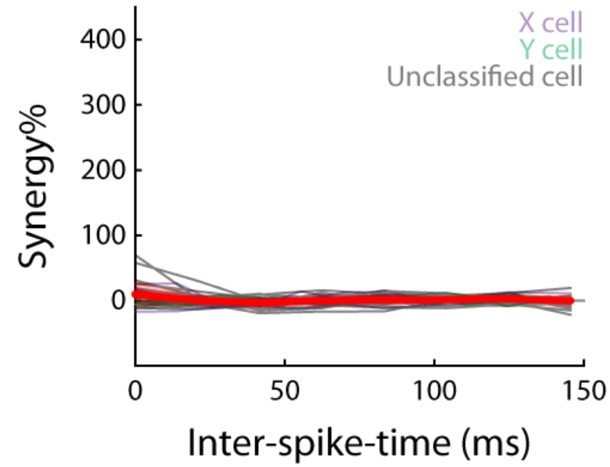
Model performance (3)

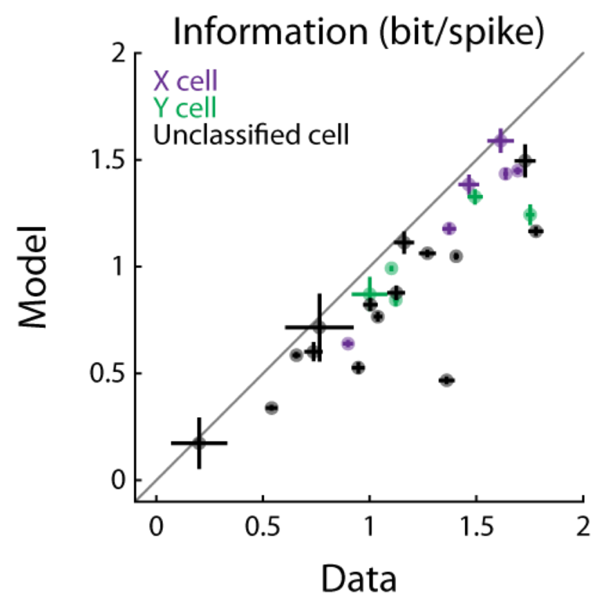
“Null” model





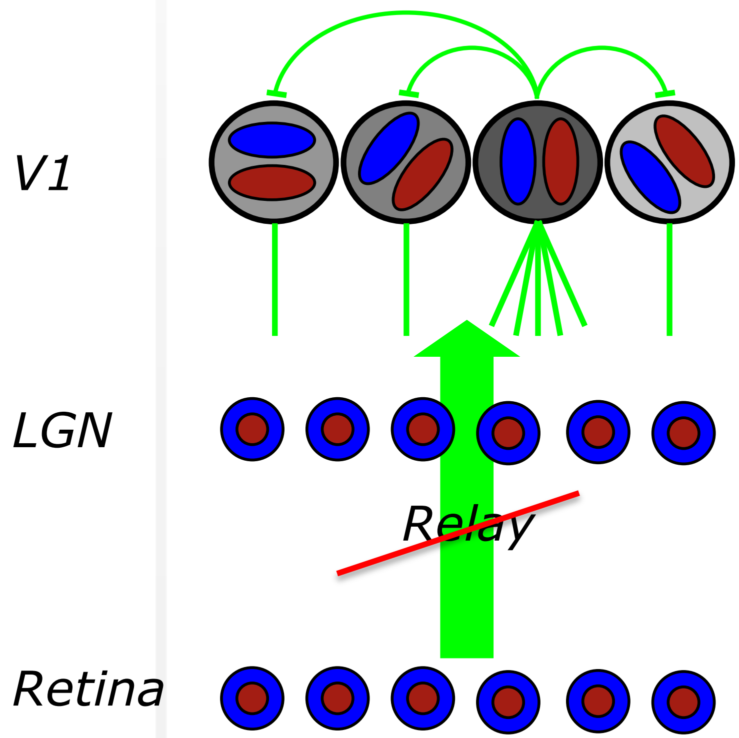
ISI model





Summary 1

Traditional cartoon of LGN function

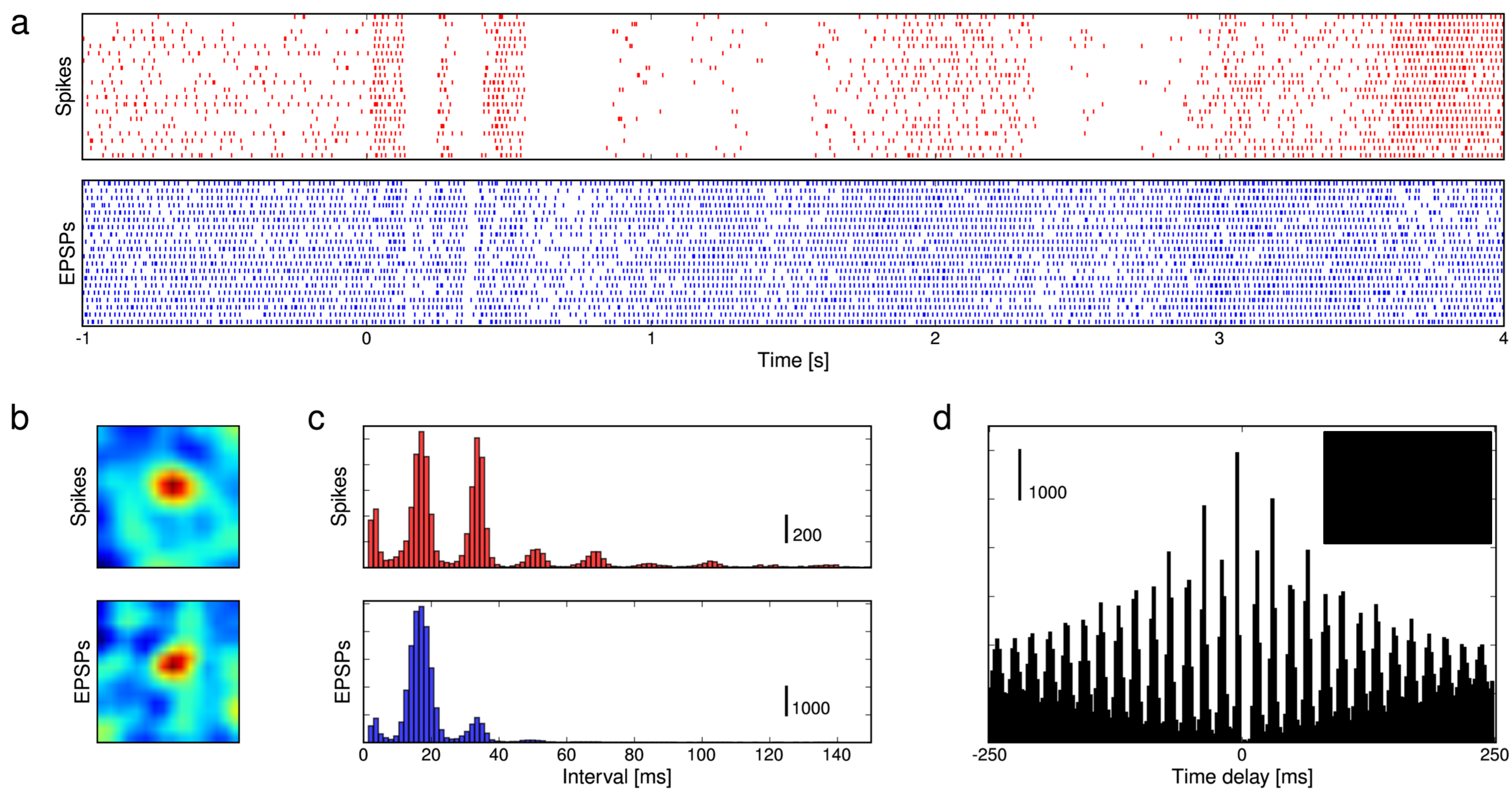


- LGN encodes visual information by independent spikes – in contrast, RGC spike trains are synergistic
- Postsynaptic temporal summation accounts for this transformation

(Wang, Hirsch & Sommer, 2010)

2) Information carried by retinal oscillations

Raster plots: 20 repeats of movie (5 sec window)



Receptive fields

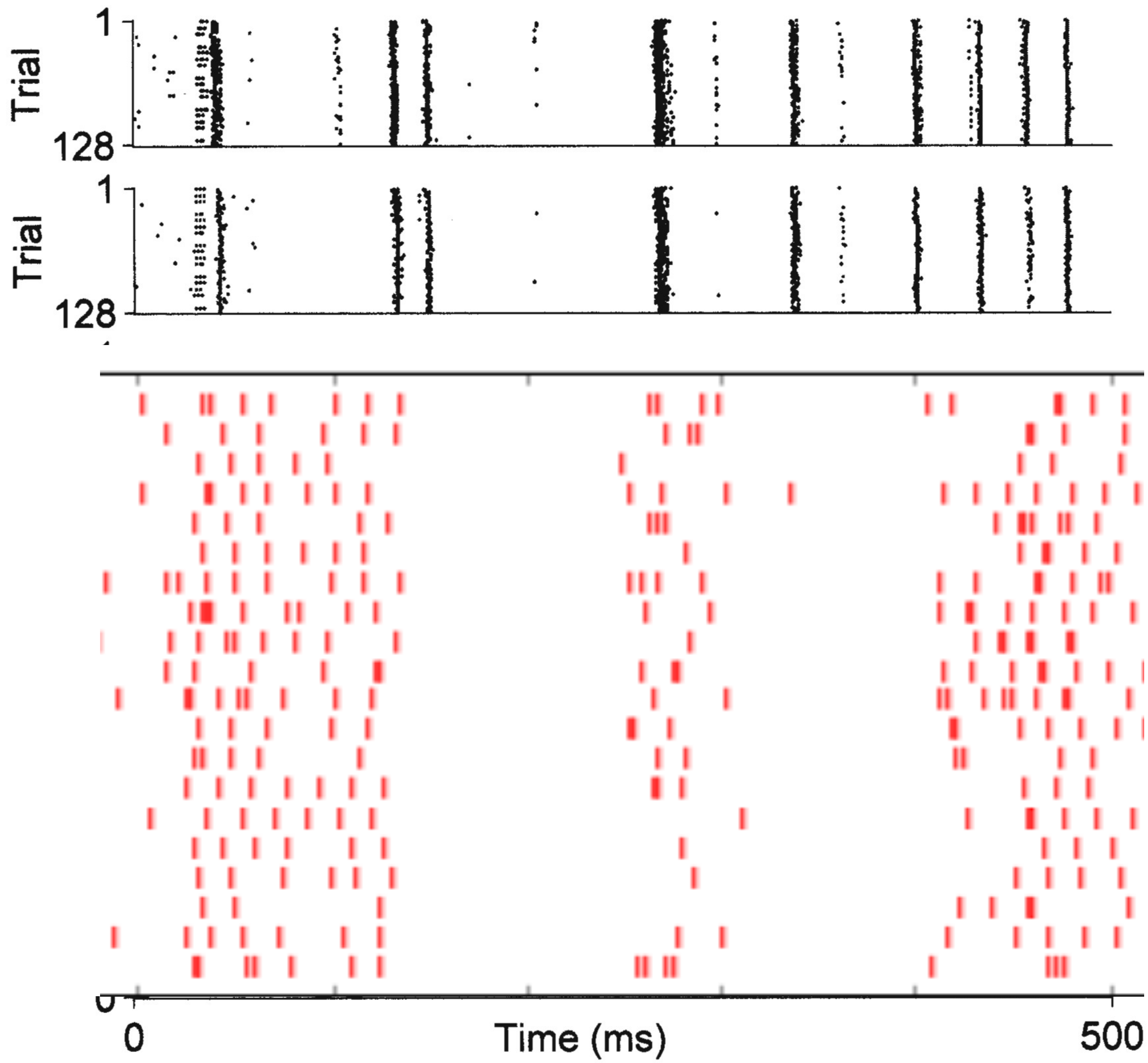
ISI histograms

Crosscorellogram (spike at t=0)

Temporal precision w/r to stimulus

Full field
Stimulus
(Reinagel)

Natural
movie



Reliable low-frequency modulation but higher variability as with full-field stimulus

Quantification of intrinsic oscillations

Oscillation score: uses Fourier transform of the auto-correlogram (Muresan et al. 2007)

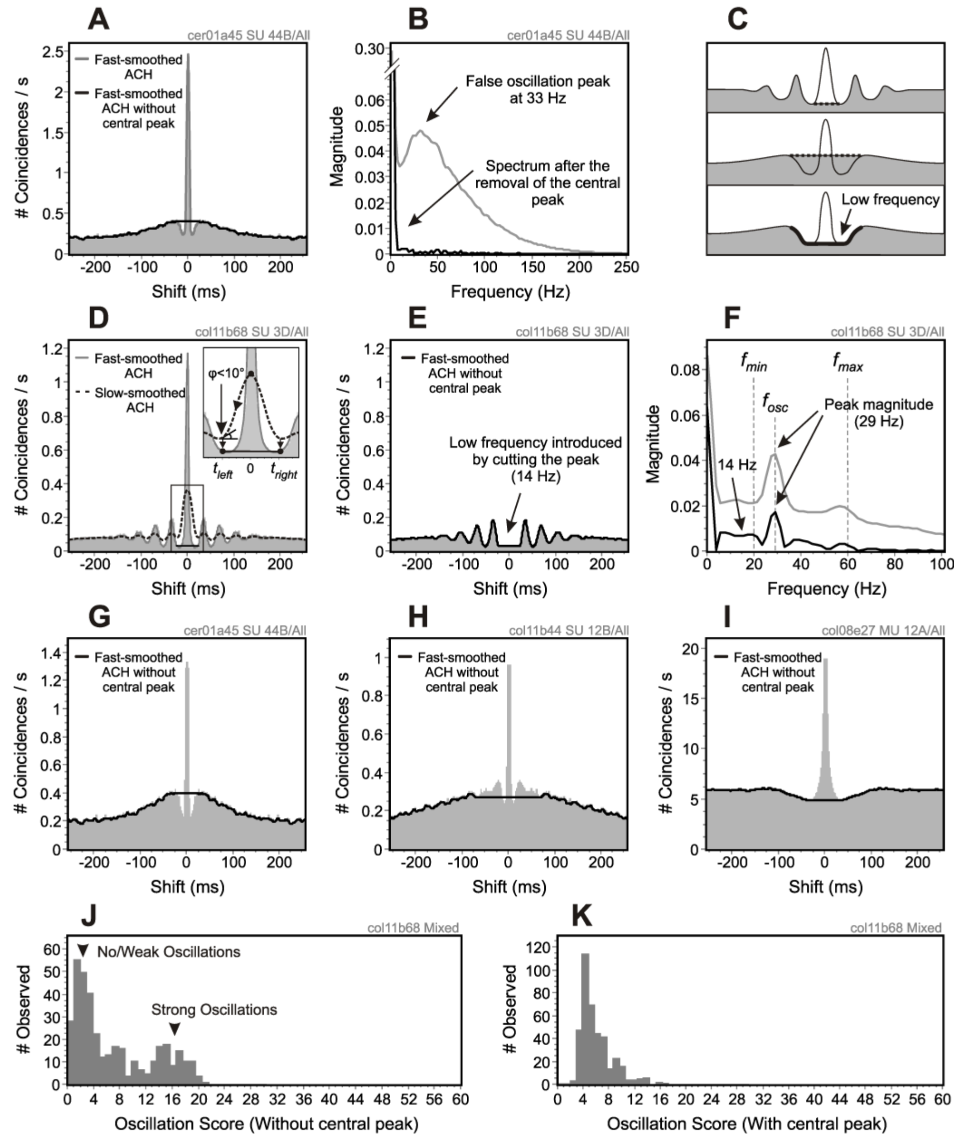
1: High low-pass for eliminating noise

2: Low low-pass for detecting central peak boundaries

3: Remove central peak

4: Fourier transform

5: Oscillation score
OS = ratio between peak hight and baseline



Oscillations in cell populations

Gamma oscillations (40-80 Hz):

Current clamp, Hirsch lab:

- *7/17   LGN outputs*
- *13/17 LGN inputs*

Controls:

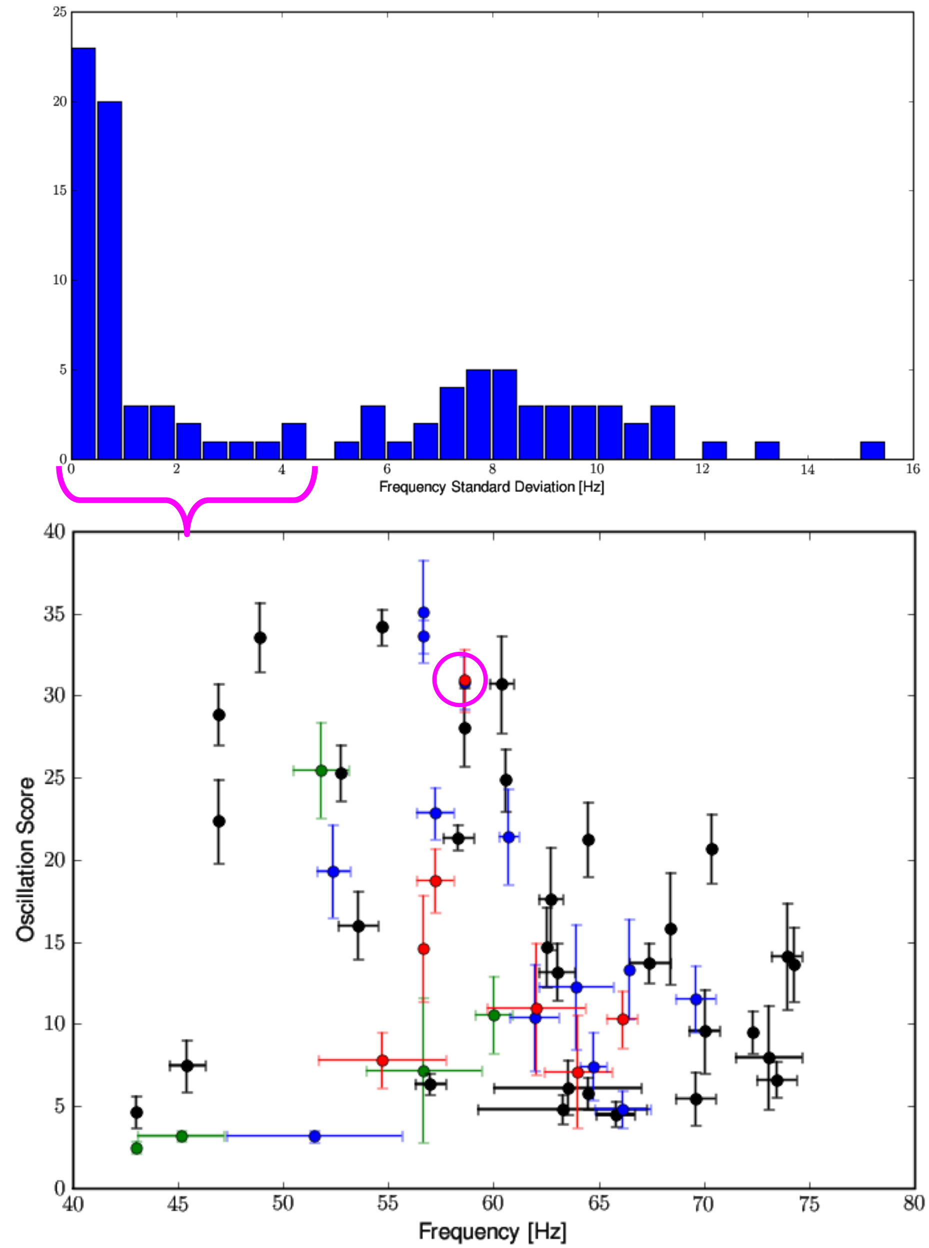
Voltage clamp, Hirsch lab:

- *31/43 LGN inputs*

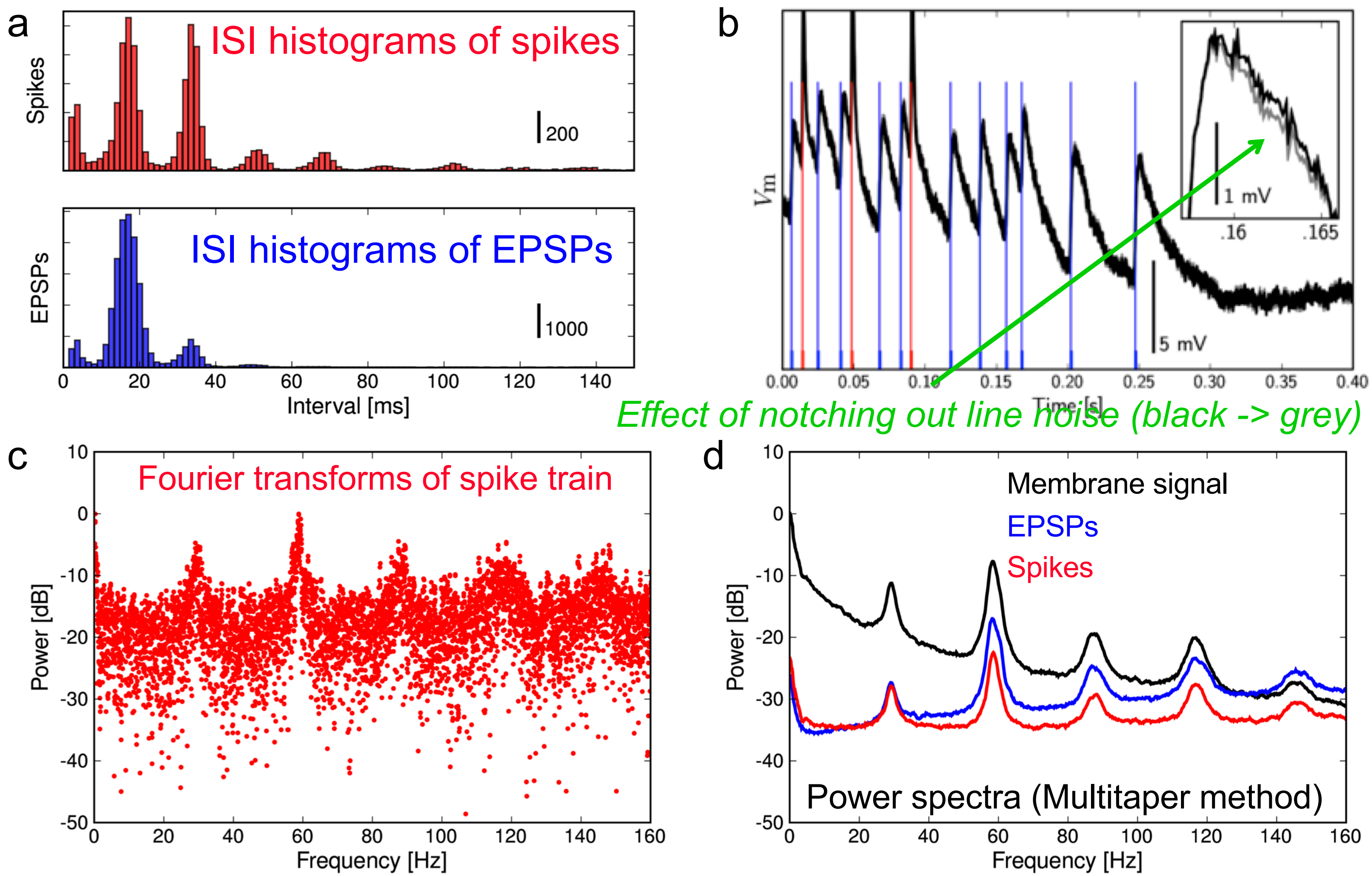
Extracellular optic tract, Usrey lab:

- *5/20 Ganglion cells*

[Heiss & Bornschein, 1966:
10/43 Ganglion cells]



Example cell



(current clamp recording) Input OS=33, Output OS=32

Demodulating instantaneous phase

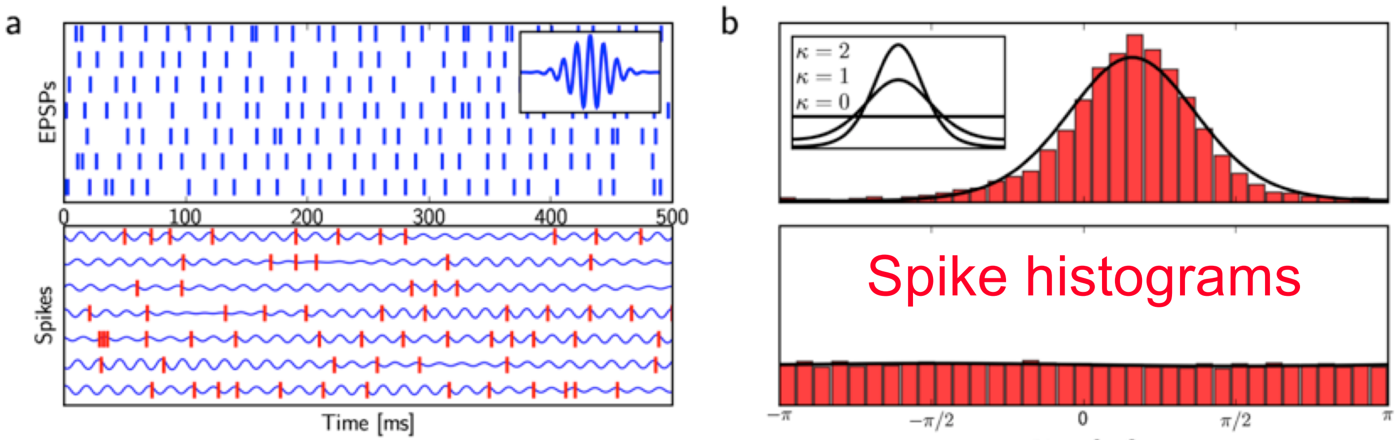
$$cos(\omega t) = \frac{1}{2}\left(e^{i\omega t} + e^{-i\omega t}\right)$$

Complex signal that removes redundancy of real signal: Analytic signal

$$a(t) = e^{i\omega t} = cos(\omega t) + i\mathcal{H}[cos(\omega t)]$$

Instantaneous phase is the phase of analytic signal in complex polar coord.

Spike phase histogram



within trial

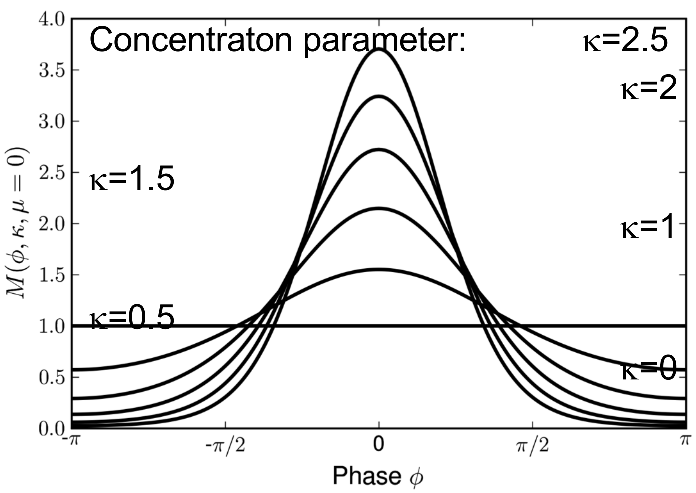
between trials

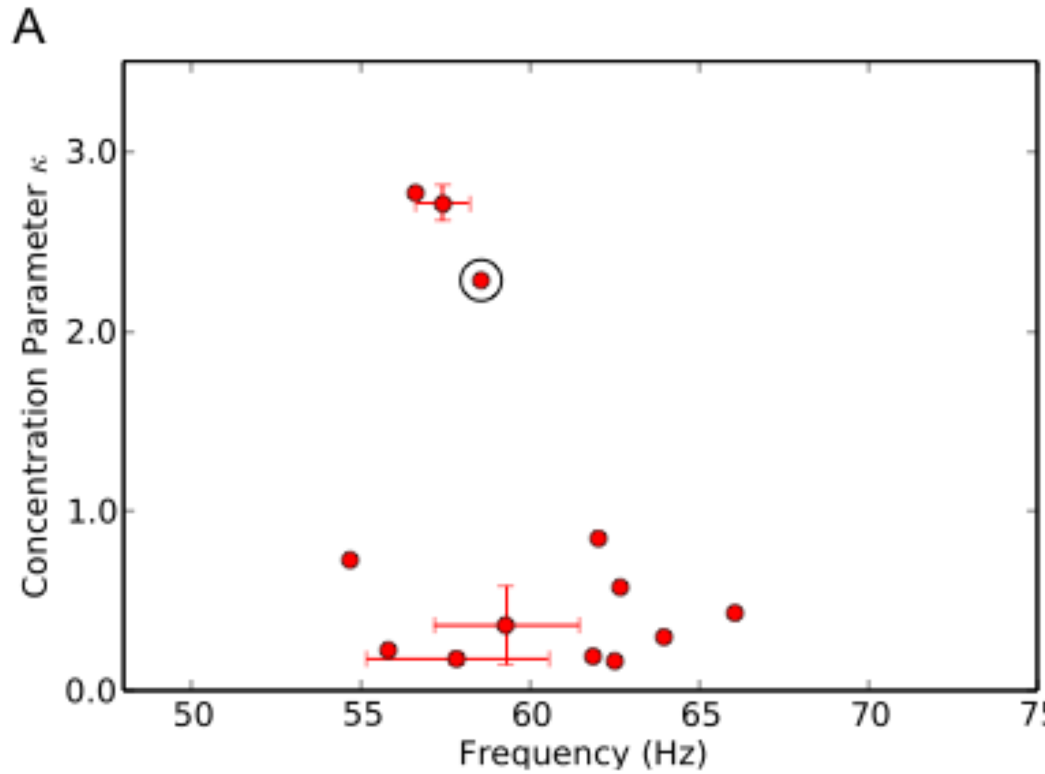
Peak hight in spike phase histogram: measure of phase response accuracy

Phase accuracy of LGN response

Fit spike histogram with Von Mises distribution:

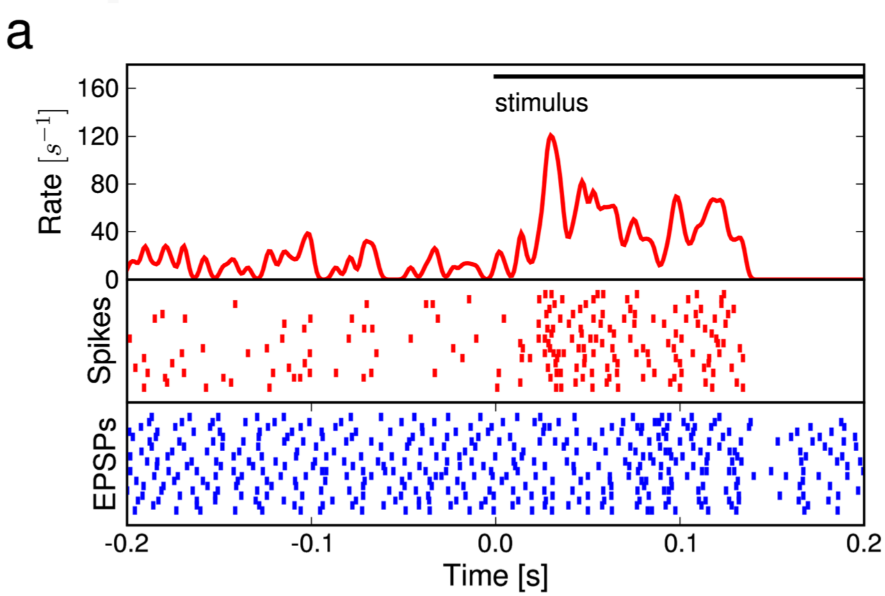
$$M(\phi,\kappa,\mu) = \exp(\kappa\cos(\phi-\mu))/(2\pi I_0(\kappa))$$





Phase dejittering

original



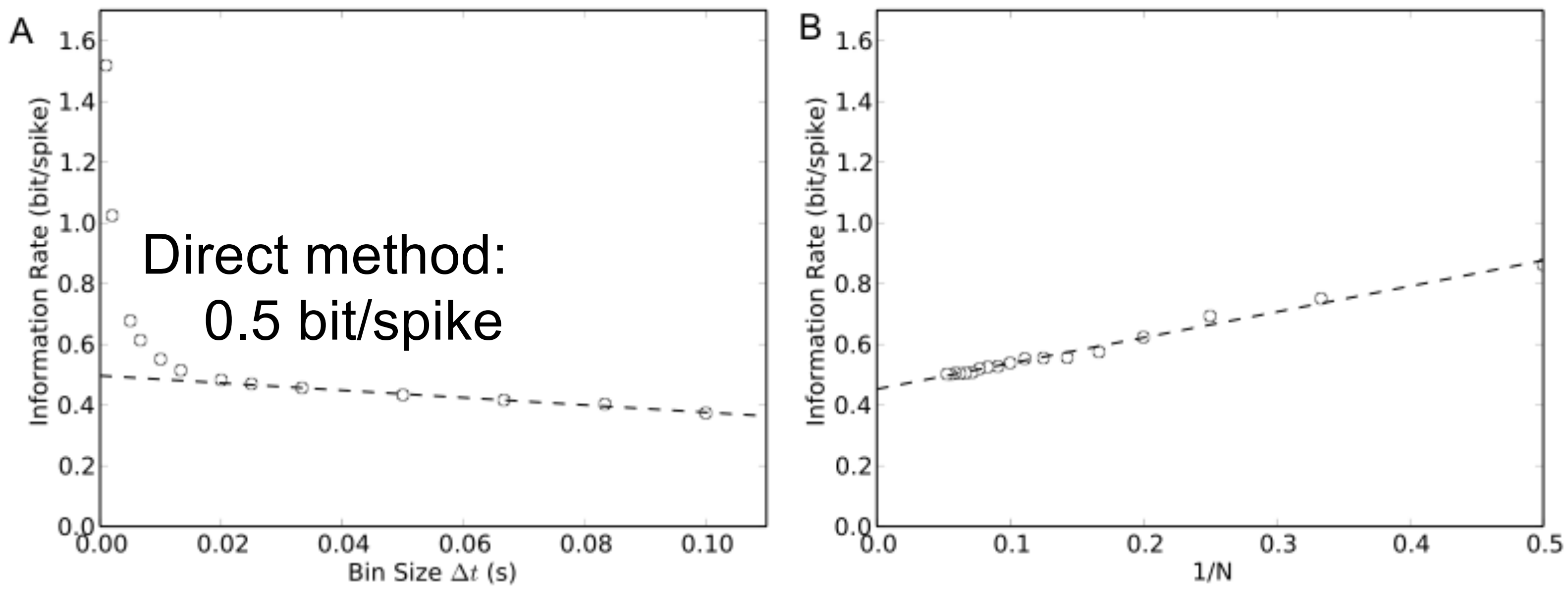
Inter-trial variability of oscillation phase explains variability in stimulus-locked response

Information rate in spikes

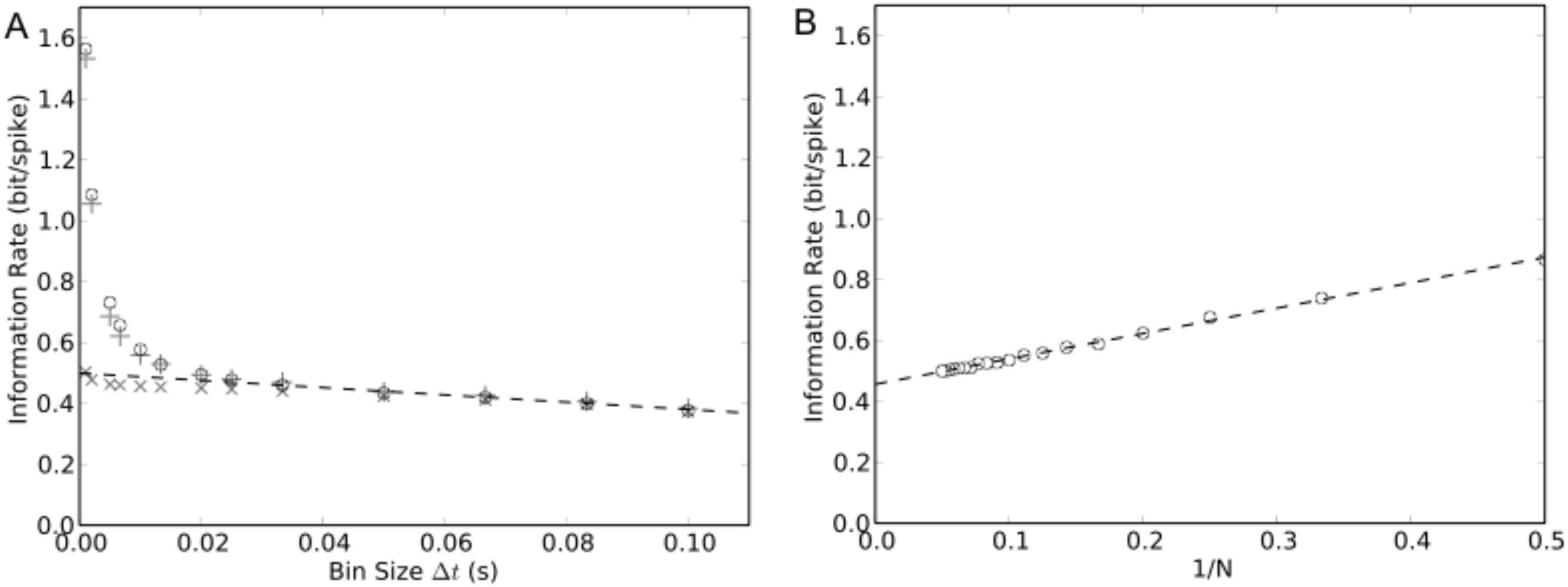
Direct method (Brenner et al., 2000):

$$I(spike;s) = \frac{1}{T}\int_0^T dt\,\frac{r(t)}{\bar{r}}\log_2\left(\frac{r(t)}{\bar{r}}\right) \quad \text{bit/spike}$$

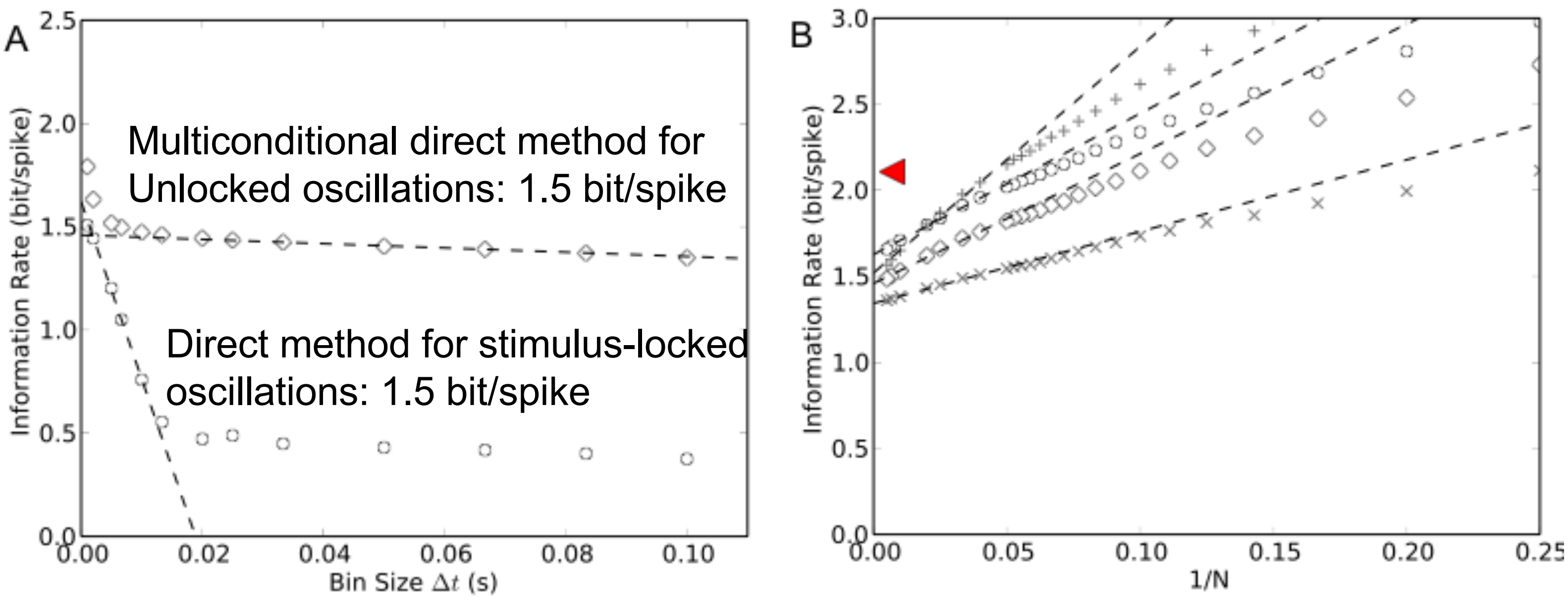
I(spike;s) in LGN spike train (20 repeats)



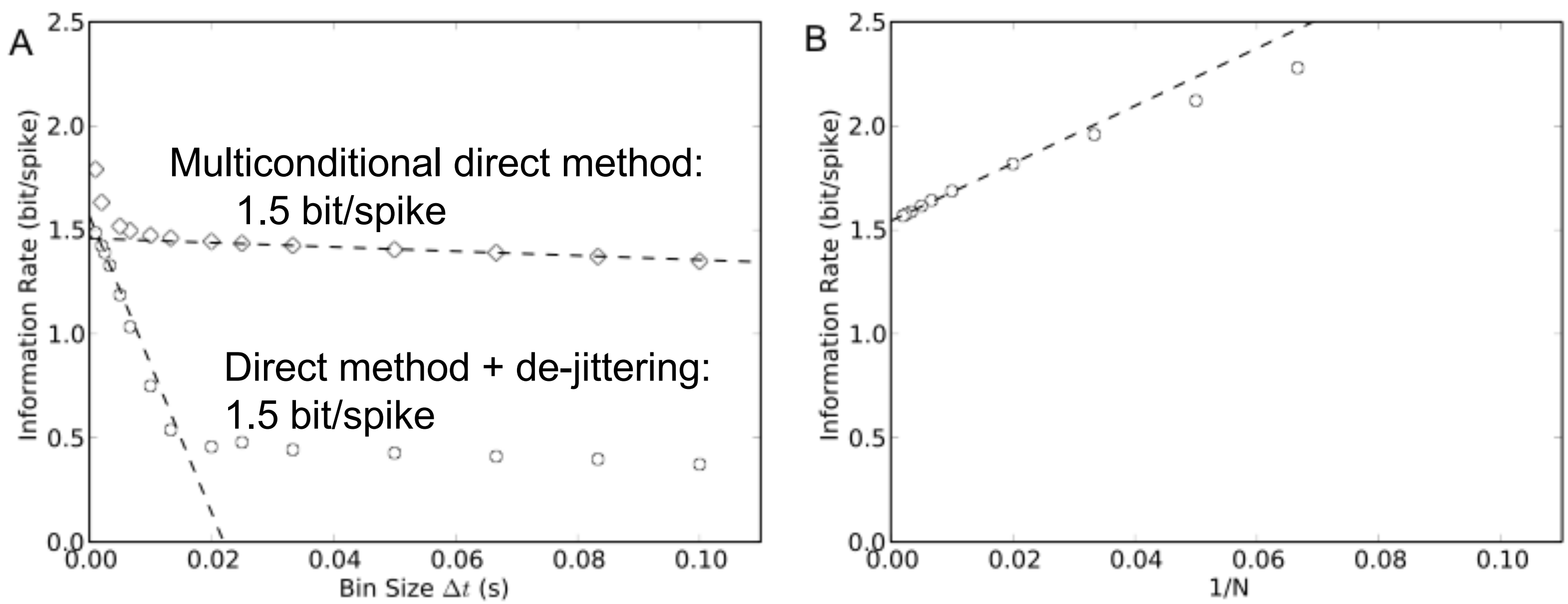
I(spike;s) in simulations with 20/500 repeats



I(spike;s,ϕ) for stimulus-locked and unlocked oscillations in a simulated spike train (500 repeats)



I(spike;s,ϕ) for stimulus-unlocked oscillations in a simulated spike train (500 repeats)



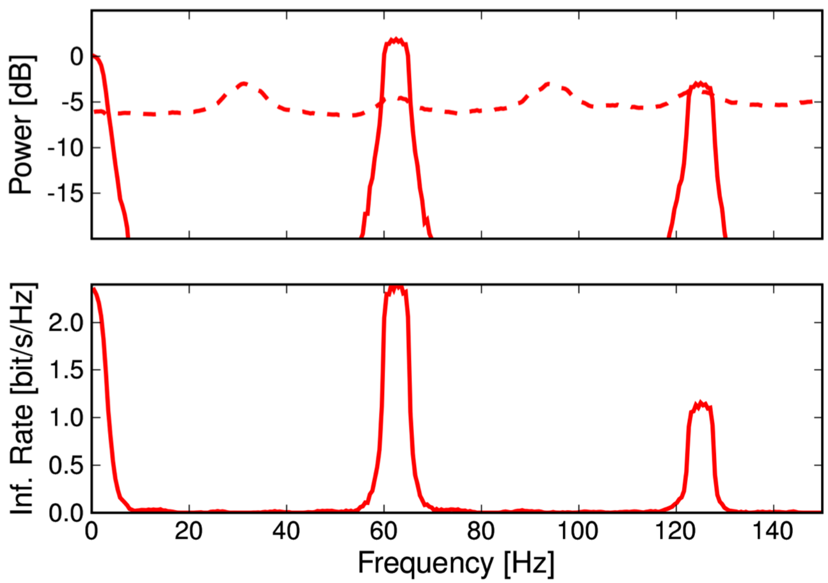
Information rates for de-jittered LGN spike train (Gaussian approximation)

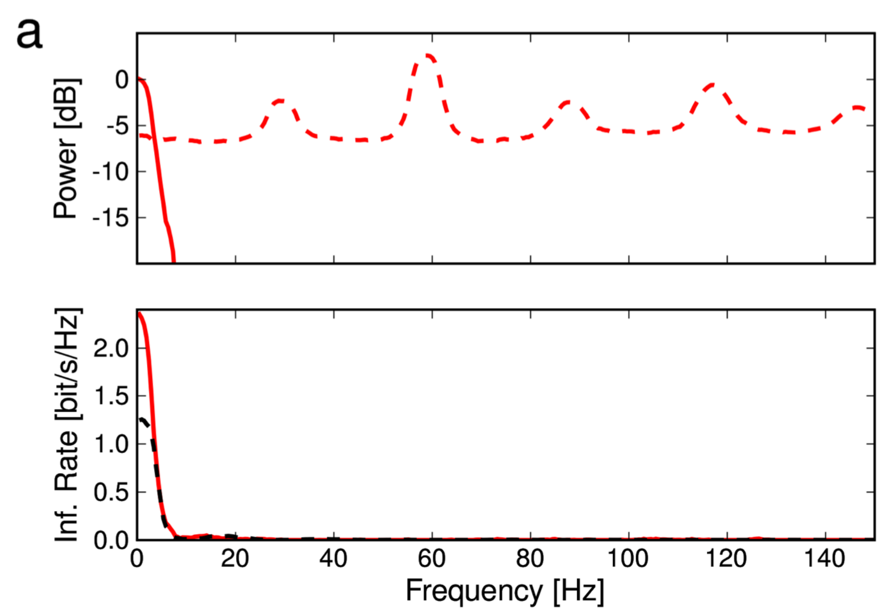
I(spike; s, ϕ)

I(spike; s)

Power spectra
signal (solid)
noise (dashed)

Spectral infor-
mation rate





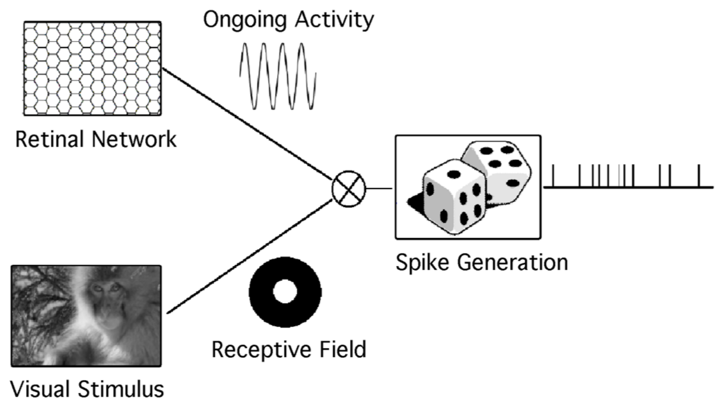
Total information rates: 1.5 bit/spike

0.4 bit/spike

Information gain from phase-coding: 1.1 bit/spike

How can the channel be encoded?

Multiplicative model



Spike generation with inhomogeneous Gamma process:

$$p_t(t_i \mid t_{i-1}) = \frac{k\lambda(t_i)}{\Gamma(k)}\left[k\int_{t_{i-1}}^{t_i} \lambda(u)du\right]^{k-1} \exp\left\{-k\int_{t_{i-1}}^{t_i} \lambda(u)du\right\}$$

with instantaneous rate:

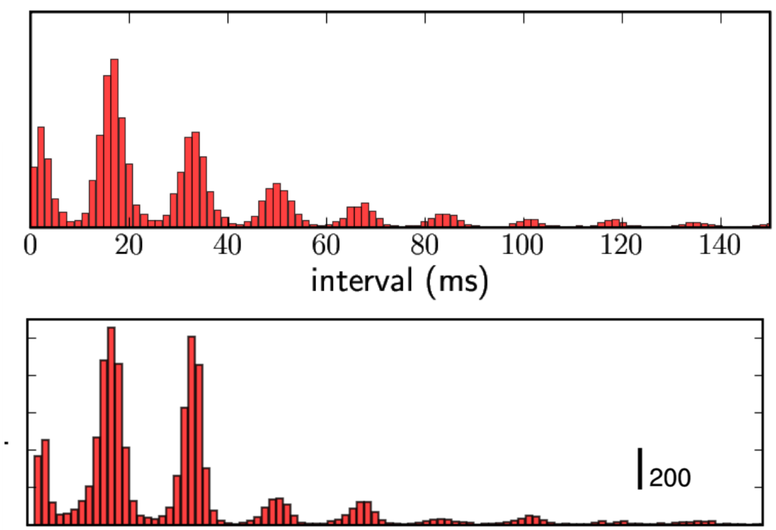
$$\lambda(t) = 2\pi(RF \otimes s(t)) \cdot M(\phi(t), \kappa, \mu)$$

Here $\phi(t)$ is the phase of a band-passed random signal $f \pm \sigma_f$

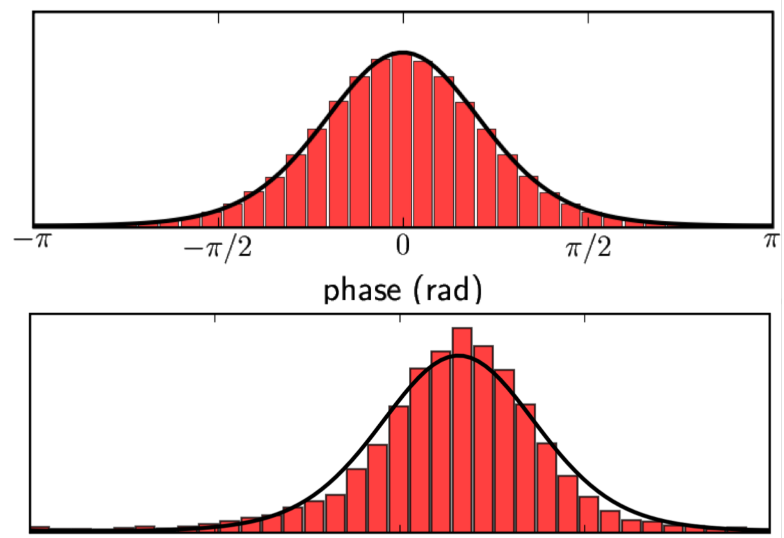
Free parameters of the model: k, κ, f, σ_f

Modeling results

ISI distributions



Phase distributions

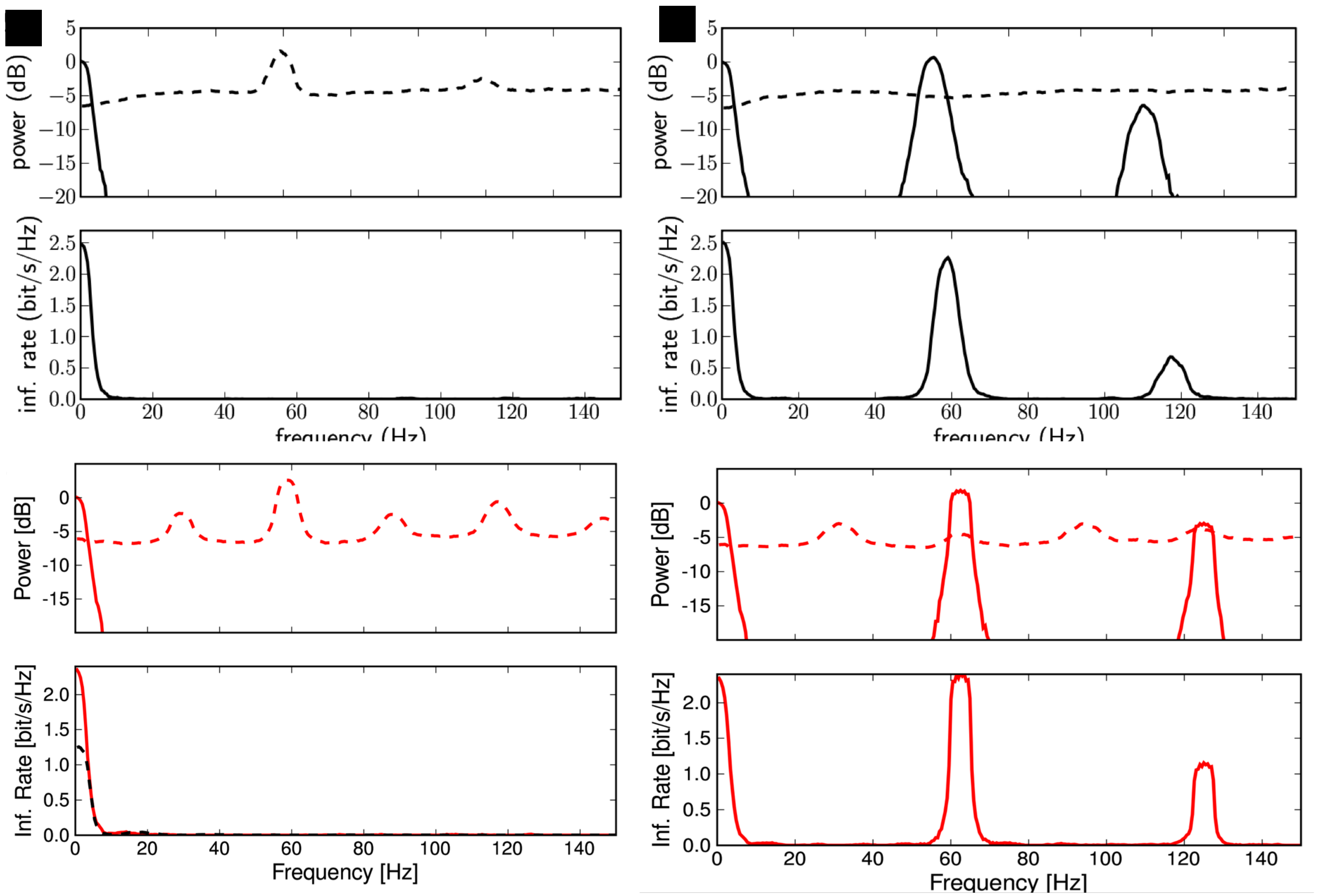


Modeling results

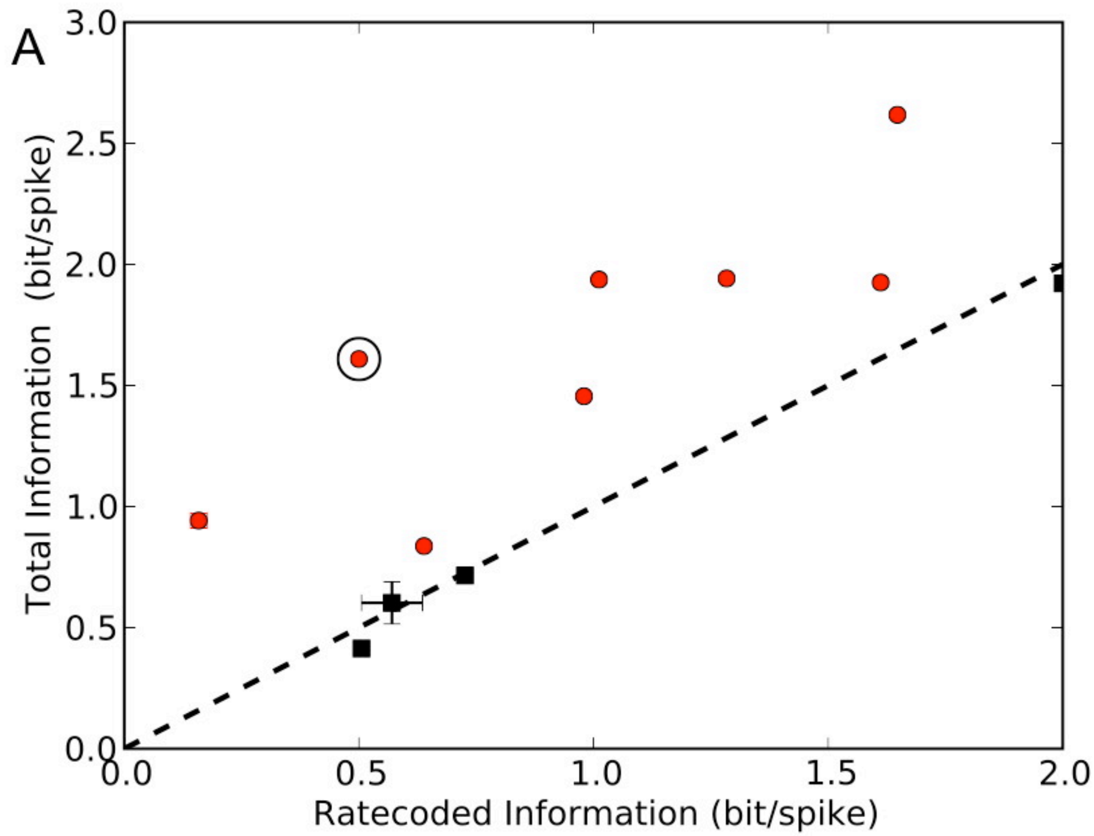
Stimulus locked | Dejittered

Model

Data



Information carried in oscillation based channel



8/14 relay cells convey significant amount of information about retinal gamma oscillations

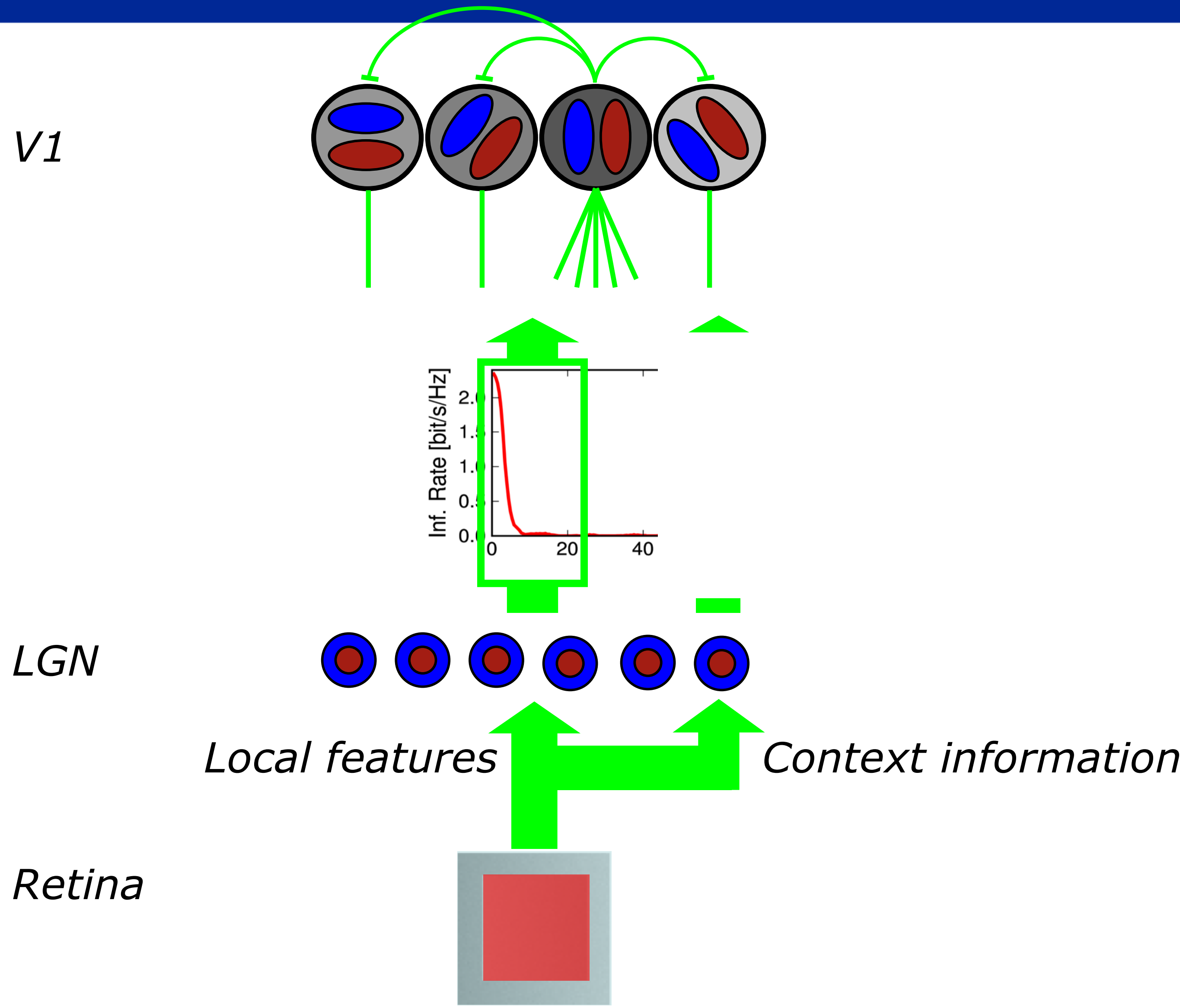
Summary 2)

Many thalamic relay cells receive periodic retinal inputs and the spikes sent to cortex are tightly time-locked with these inputs

In 8/14 cells the high-frequency channel provided significant additional information

What information is encoded? Maybe nonlocal contextual features extracted in retinal network. Retinal gamma oscillations have been causally linked to behavior based on nonlocal image features (Ishikane et al., 2005)

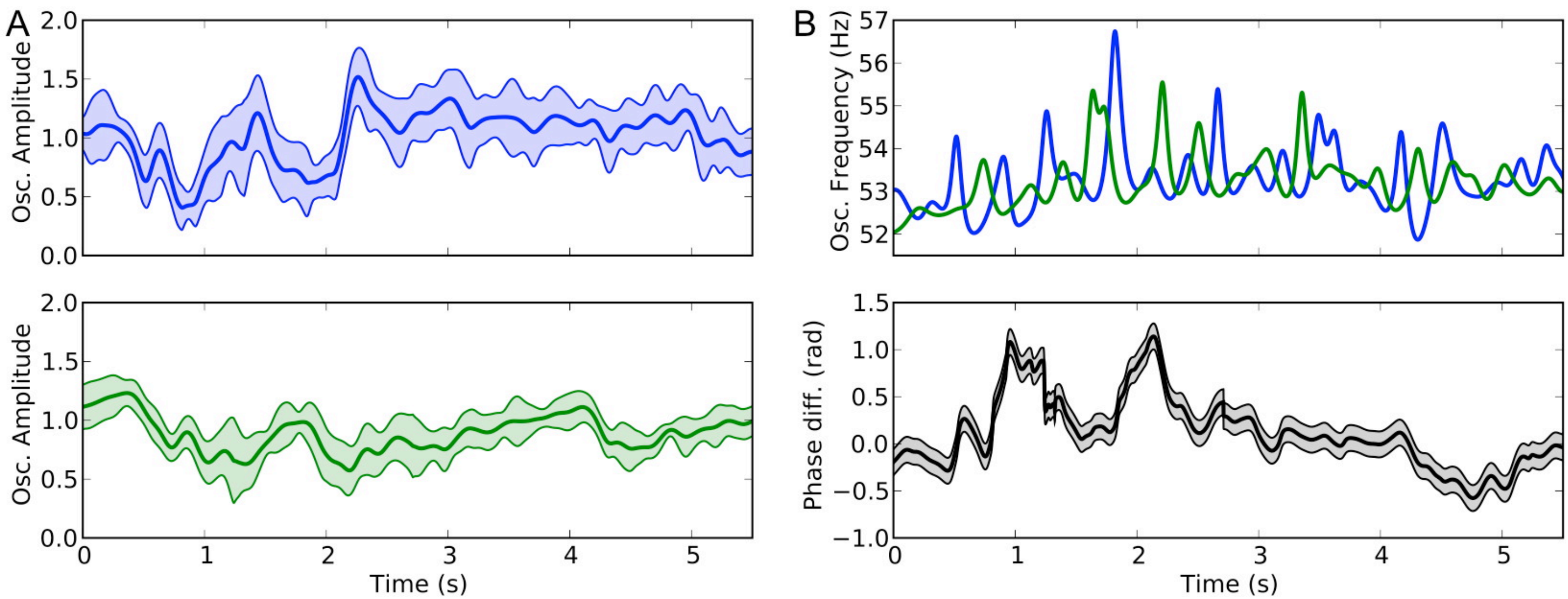
Summary 2)



Koepsell & Sommer, J. Biol. Cybern. 2008
Koepsell et al., 2009, 2010

Visual information carried in phase synchrony?

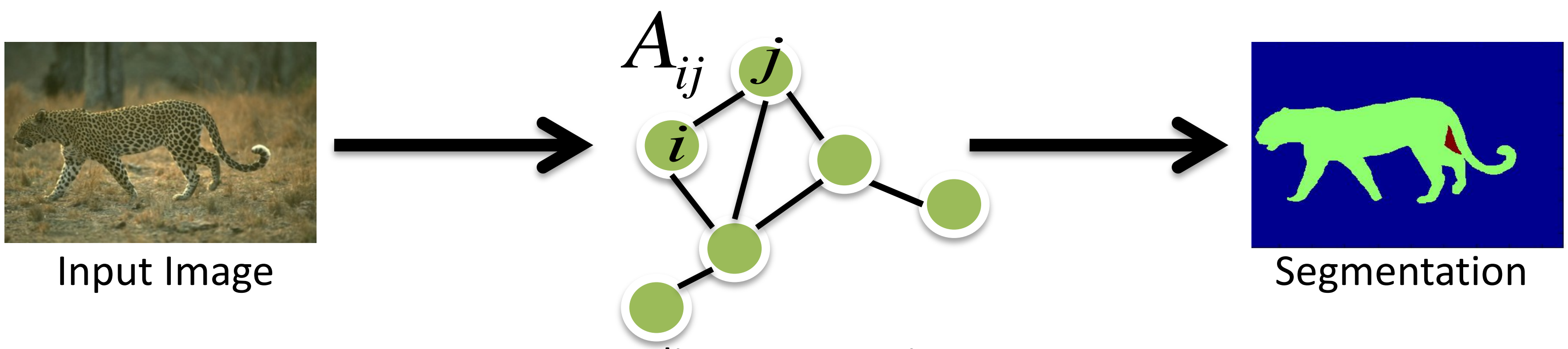
Dan, Usrey, Alonso, Reid (1998): Spike correlations in pairs of relay cells add 20% to information transfer in individual spike rates



Natural stimulus sets relative phase (Hirsch lab, unpublished)

Image segmentation with retinal oscillations

Build adjacency graph for image (Shi & Malik): $A_{ij} = e^{-\frac{(x_i - x_j)^2}{2\sigma_p}} \times e^{-\frac{(i-j)^2}{2\sigma_s}}$
(Topographic pixel similarity)



Input Image

Adjacency matrix

Segmentation

1) Graph Laplacian (Kirchhoff matrix) $L_{ij} = d_i \delta_{ij} - A_{ij}$

Application to image segmentation: Shi & Malik 1999

2) Modularity (Newman & Girvan 2004) $M_{ij} = A_{ij} - \frac{d_i d_j}{2m}$

Topographic extension of modularity

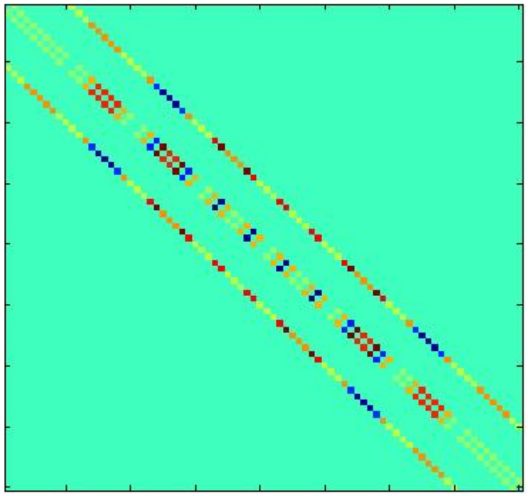
3) Topographic modularity

$$T_{ij} = A_{ij} - d_i d_j b(i-j)$$

$$b(l) = \frac{1}{m-l} \sum_{k=1}^{m-l} A_{k,k+l}$$

Advantages:

- obeys topographic structure
- resulting matrix is sparse

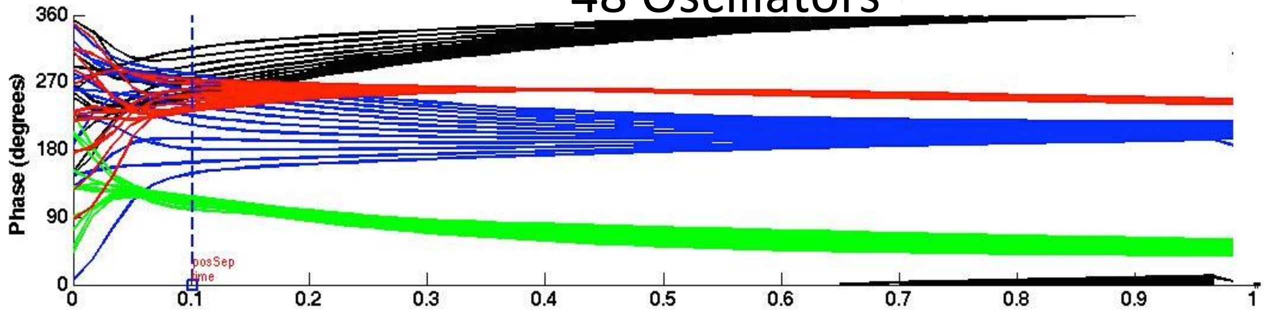


Graph clustering with phase-coupled oscillators

1) Kuramoto model of phase-coupled oscillators (Arenas 2009)

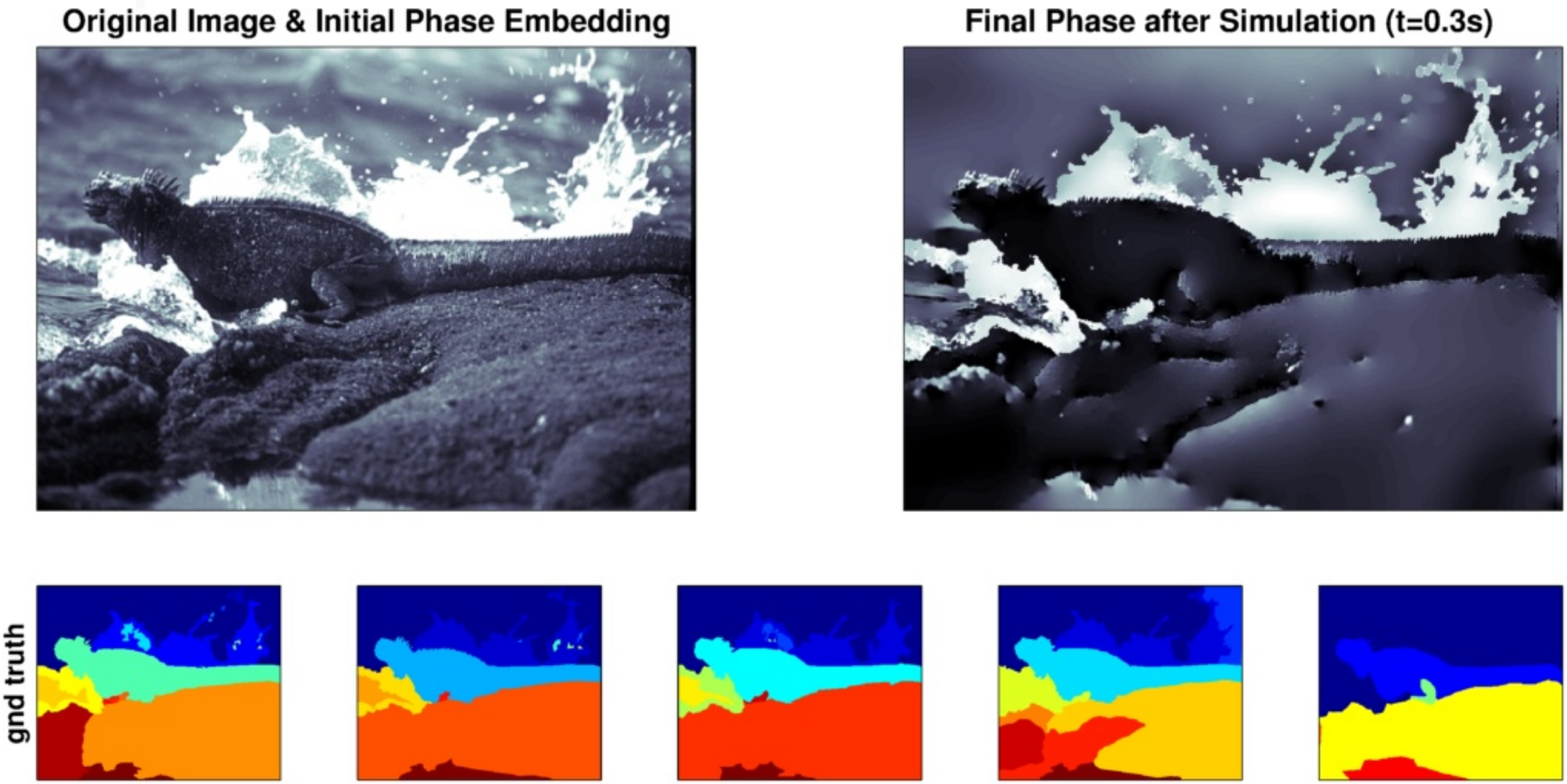
$$E(\varphi) = \sum_{ij} M_{ij} \cos(\varphi_i - \varphi_j)$$

48 Oscillators



Compare M, L and T matrices

Results on individual image



ΔF

blur --> SK

Comparison of Performance (Example Individual Image Patches)

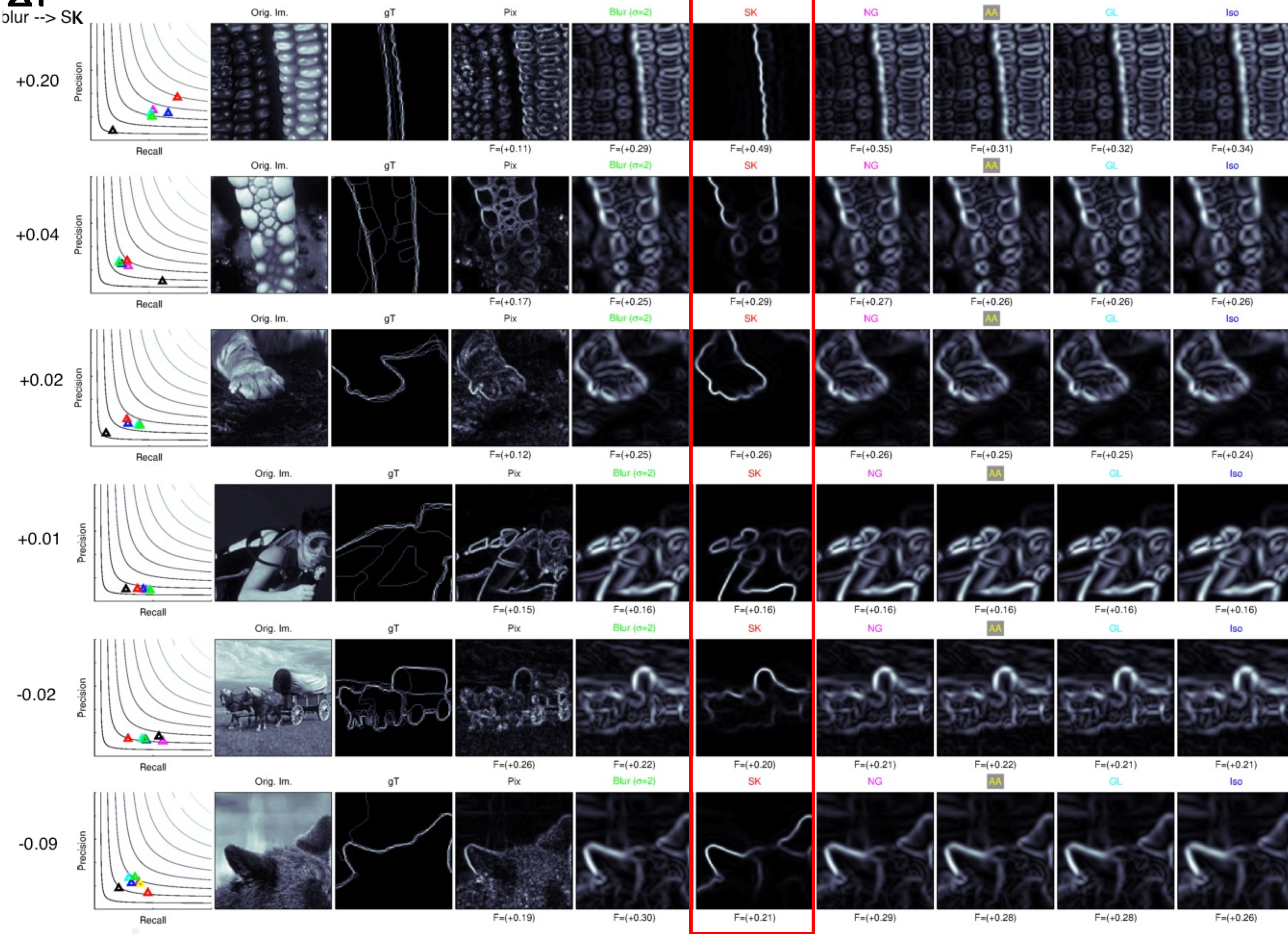
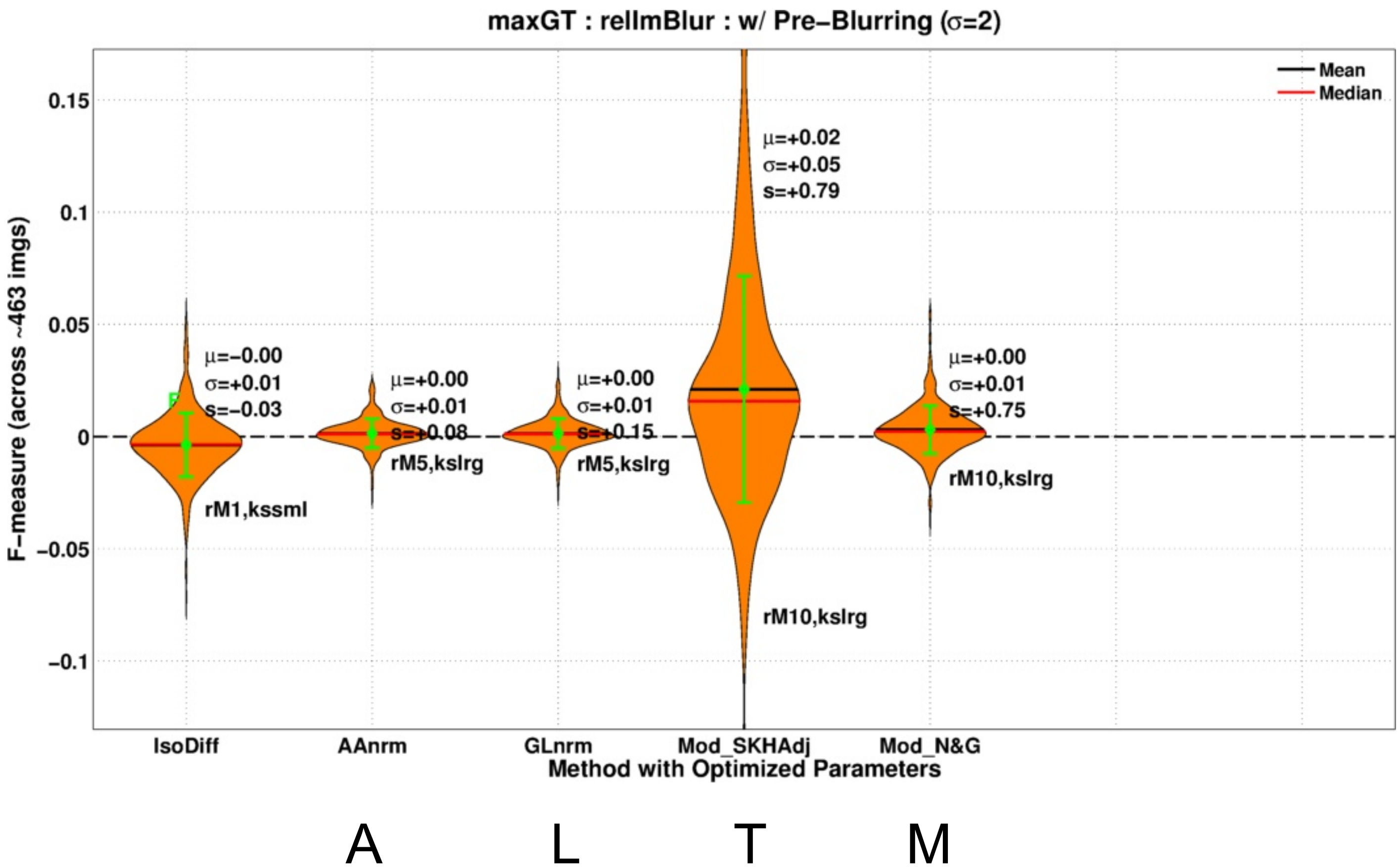


Image Segmentation Performance

Performance on Berkeley Image Segmentation Database:



Warner & Sommer, 2020 https://arxiv.org/abs/2005.02567

Summary

The retinal code is synergistic, it uses single spikes and short ISI spike pairs as words (It is still open why)

LGN transforms retinal code to single spike code

LGN preserves fine timing structure of retinal code. For gamma oscillations in input, information rate about phase can be multiples of the rate code information alone

Oscillations in retina could encode in fine timing structure to multiplex nontemporal stimulus features: Coupled oscillator model for contextual coding in retina:

Model predictions for experiments

Gist channel for contextual features as suggested by Computer Vision)

Causal influence of retinal oscillations on escape behaviour (Ishikane et al., 2005).