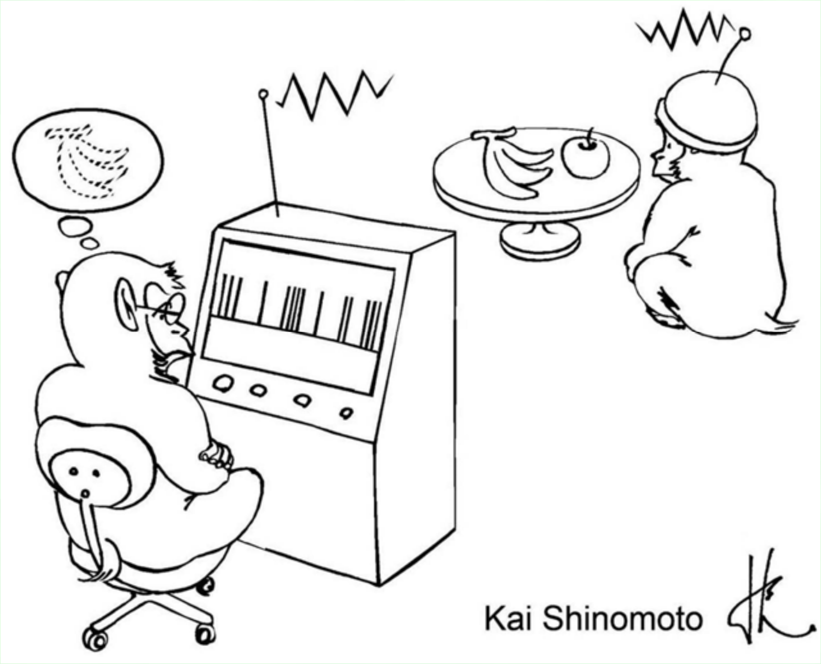
German-Japanese program in computational neuroscience
OIST, March 2-5, 2010

Defining the firing rate for a non-Poissonian spike train

--- a nerdish study ---

Shigeru Shinomoto Kyoto Univ., Japan



A message from a neuron

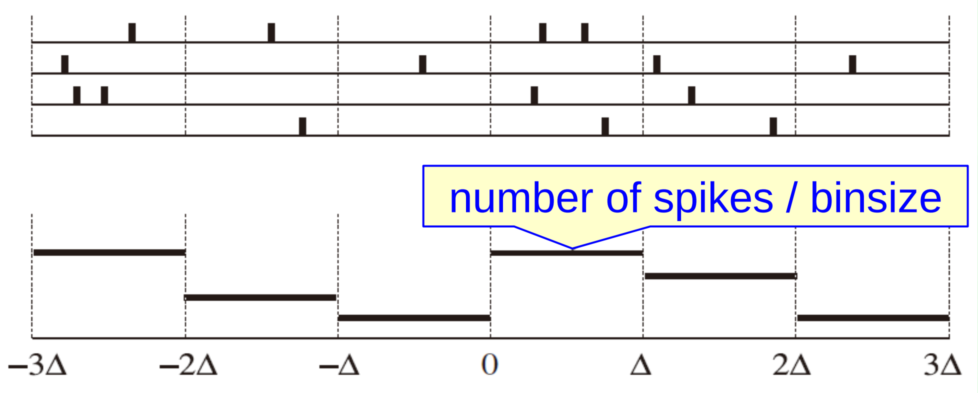
We have established several methods for optimizing rate estimators:

1. **PSTH --- 2007**
2. **Kernel smoother --- 2010**
3. **Bayesian inference --- 2005, 2009**

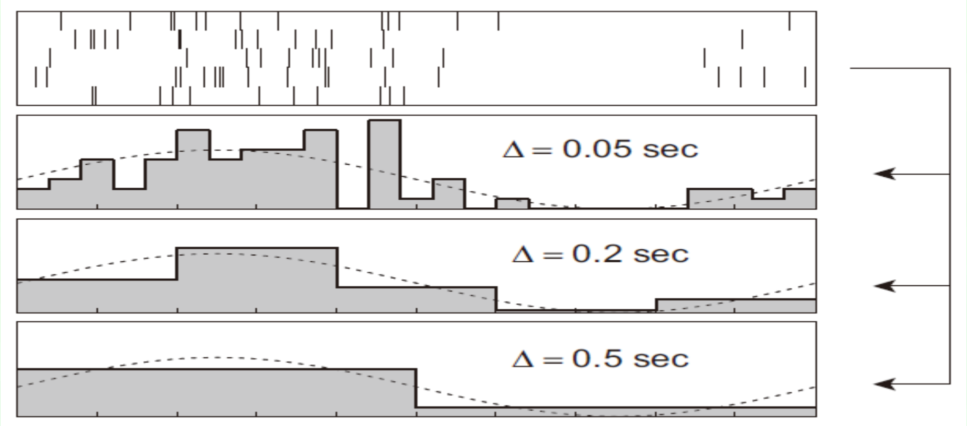
PSTH

Spike Sequences

PSTH
Peri-Stimulus Time Histogram



Time dependence may be depicted.
But…



Multiple interpretations: Which is a likely message ?

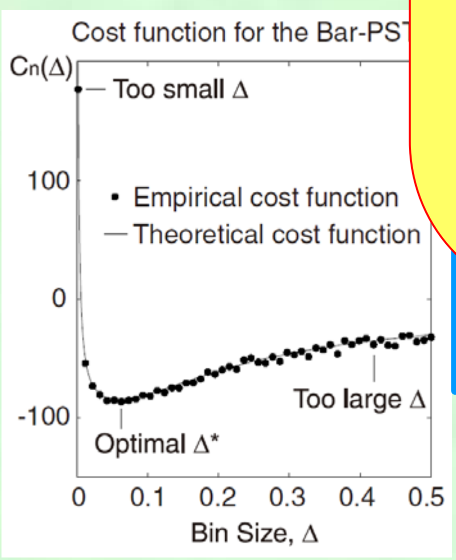
Optimizing time histograms

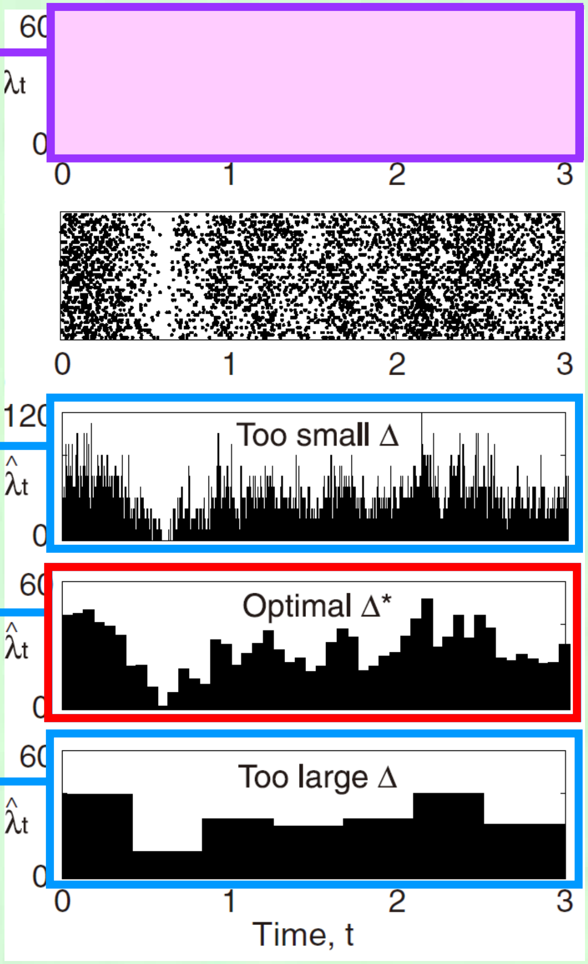
Hideaki Shimazaki

Mean **I**ntegrated **S**quared **E**rror

$$\mathrm{MISE} = \frac{1}{T}\int_0^T \left(\hat{\lambda}_t - \square\right)^2 dt$$

rigorous inference





underlying rate

spike data

PSTH 1

PSTH 2

PSTH 3

Shimazaki and Shinomoto, Neural Comput. (2007) 19: 1503-1527.

RECIPE

Rule is simple:

Algorithm 1: A Method for Bin Size Selection for a Bar-PSTH

i. Divide the observation period T into N bins of width Δ, and count the number of spikes k_i from all n sequences that enter the ith bin.

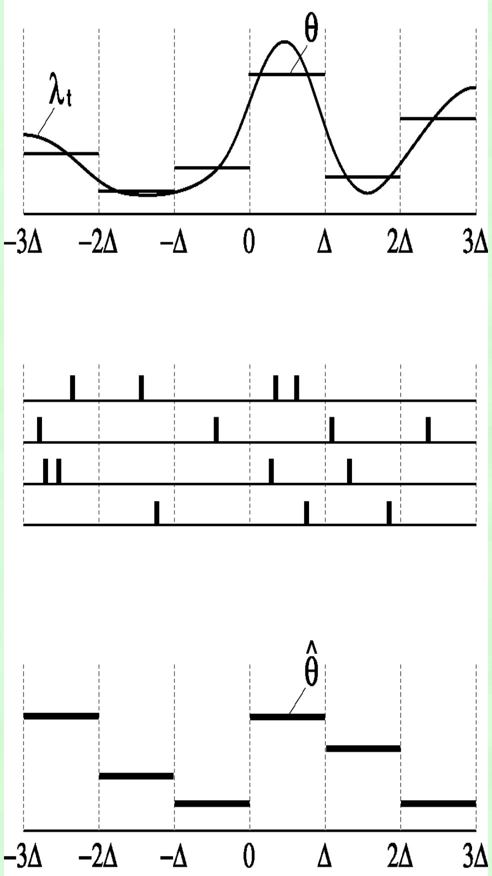
ii. Construct the mean and variance of the number of spikes $\{k_i\}$ as

$$\bar{k} \equiv \frac{1}{N}\sum_{i=1}^{N} k_i, \text{ and } v \equiv \frac{1}{N}\sum_{i=1}^{N}(k_i - \bar{k})^2.$$

iii. Compute the cost function:

$$C_n(\Delta) = \frac{2\bar{k} - v}{(n\Delta)^2}.$$

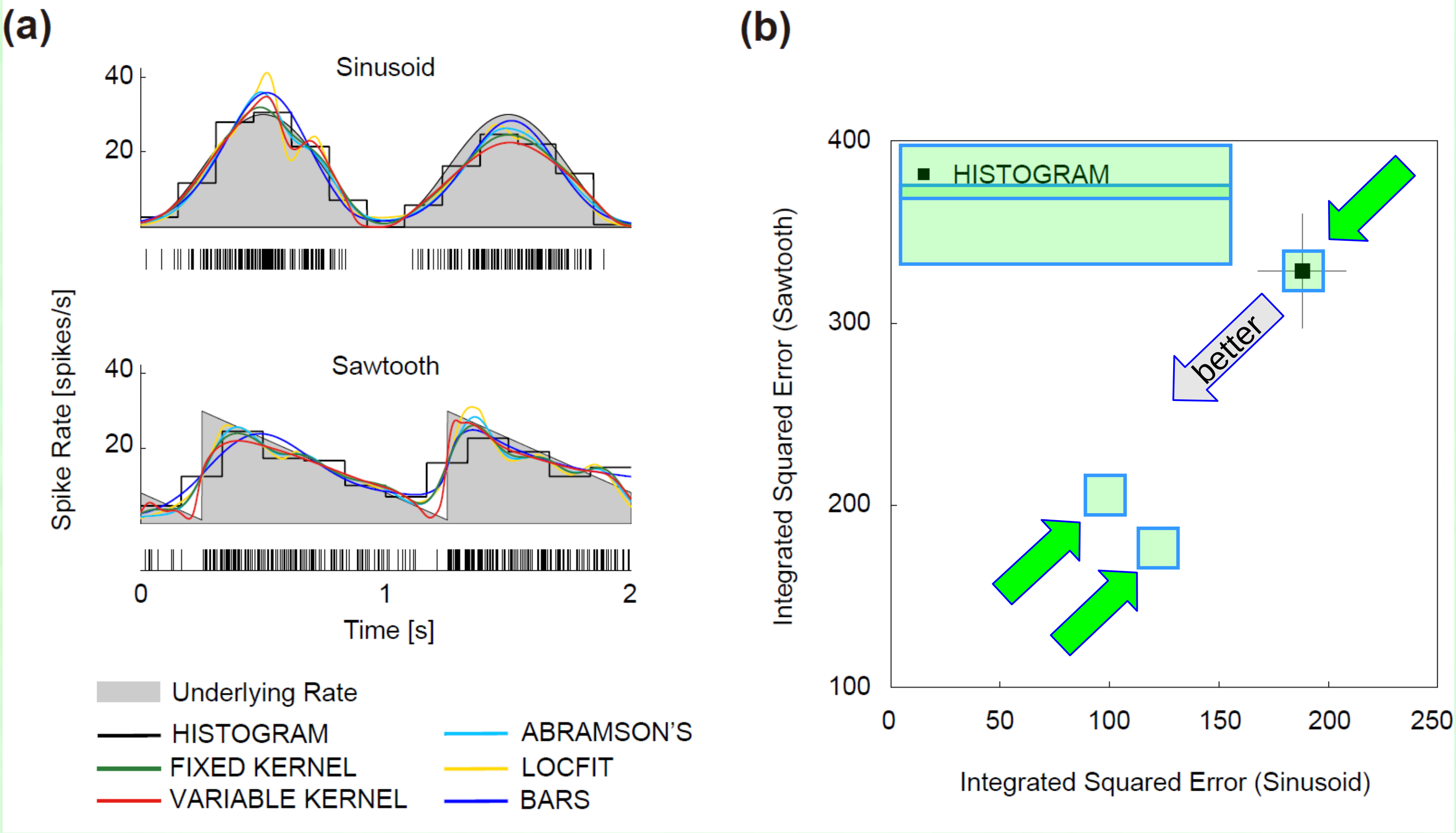
iv. Repeat i through iii while changing the bin size Δ to search for Δ^* that minimizes $C_n(\Delta)$.



Shimazaki and Shinomoto, Neural Comput. (2007) 19: 1503-1527.

Kernel optimization

Hideaki Shimazaki



Shimazaki and Shinomoto, J. Comput Neurosci (2010) 29:171-182.

RECIPE

Rule is fairly simple:

Algorithm 1 A method for selecting a fixed kernel bandwidth

i Superimpose n spike sequences. Obtain a series of spike times $\{t_i\}_{i=1}^{N}$, where N is the total number of spikes.

ii Compute the cost function for the bandwidth w of the kernel function $k_w(t)$:

$$C_n(w) = \frac{1}{n^2}\sum_{i,j}\psi_w\left(t_i, t_j\right) - \frac{2}{n^2}\sum_{i\neq j}k_w\left(t_i - t_j\right),$$

where $\psi_w\left(t_i, t_j\right) = \int_a^b k_w\left(t - t_i\right) k_w\left(t - t_j\right) dt$†. Here $[a, b]$ is an interval of interest.

iii Find w^* that minimizes $C_n(w)$.

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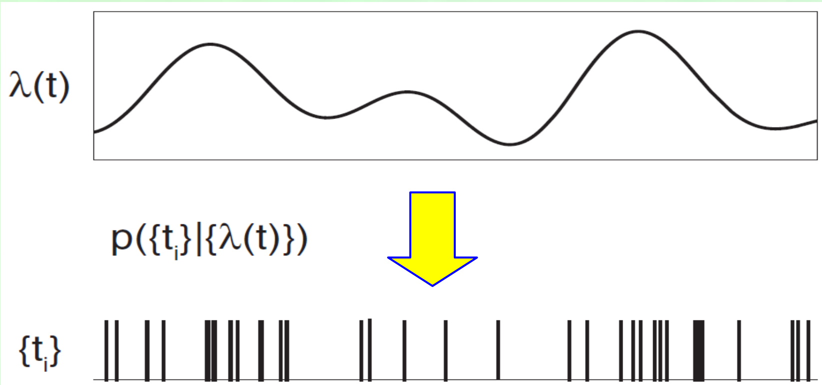
Bayesian inference

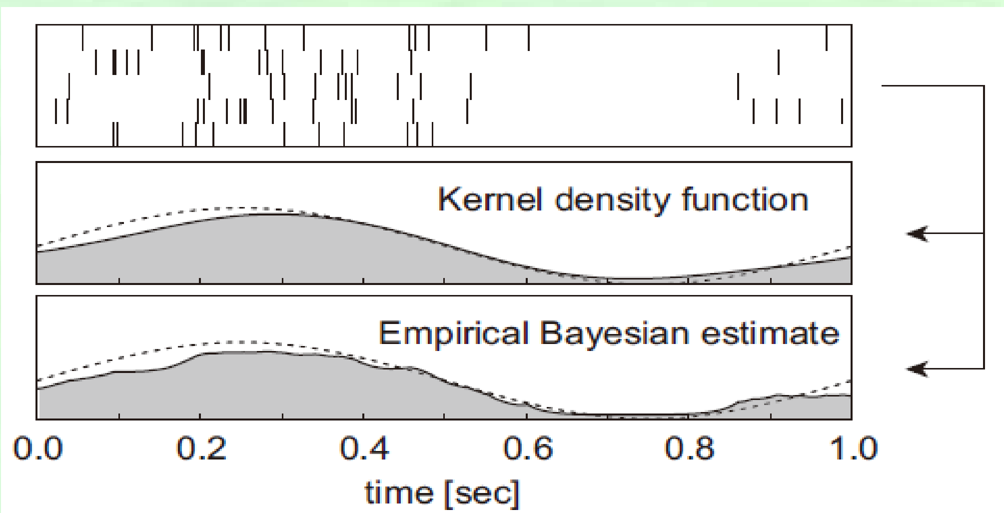
Takeaki Shimokawa



Rate

Spikes

$$p_\gamma(\{\lambda(t)\} \mid \{t_i\}) = \frac{p(\{t_i\} \mid \{\lambda(t)\})\, p_\gamma(\{\lambda(t)\})}{p_\gamma(\{t_i\})}$$



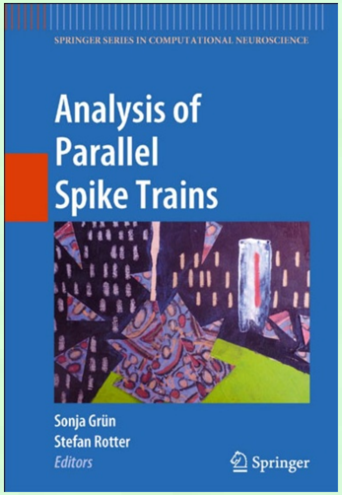
Inverse probability = Bayes

Shimokawa & Shinomoto, Neural Computation (2009) 21:1931-1951.

Poissonian assumption

$$p(\{t_i\} \mid r(t)) = \left[\prod_{i=1}^{N_s} r(t_i)\right] \exp\left(-\int_0^T r(t)dt\right)$$

poisson



Well done! Our rate estimation algorithms are derived rigorously.

However, they are all based on Poissonian assumption.

We should test Poissonian.
But how can we do it?

Capture non-Poissonian

How do we test Poissonian?

Rescale the time axis!

Bermann (1982)
Ogata (1988) ~ seismology
Reich, Victor & Knight (1998)
Oram, Wiener, Lestienne & Richmond (1999)
Barbieri, Quirk, Frank, Wilson & Brown (2001)
Smith & Brown (2003)
Koyama & Shinomoto (2005)
Shimokawa & Shinomoto (2009)
Shimokawa, Koyama & Shinomoto (2010)

How to

Estimate non-Poisson feature

(1) Conjecture a time-dependent rate.

(2) Rescale the time axis with this rate.

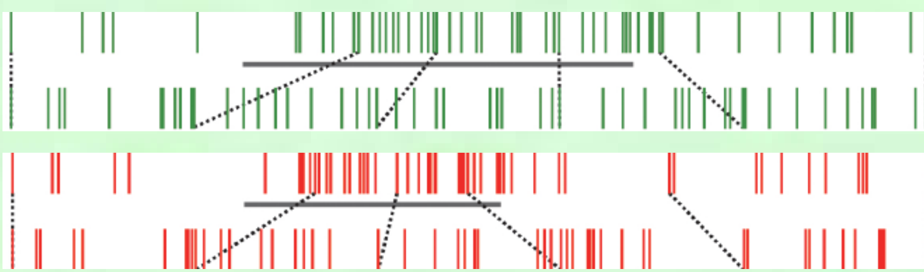
Non-Poisson: regular

(3) Conjecture an inter-spike interval distribution.

(4) Estimate the likelihood.

Repeat (1) - (4) to search for the maximum likelihood.

>>> Obtain (non-Poisson feature & rate revised).



Poisson: random

Non-Poisson: bursty

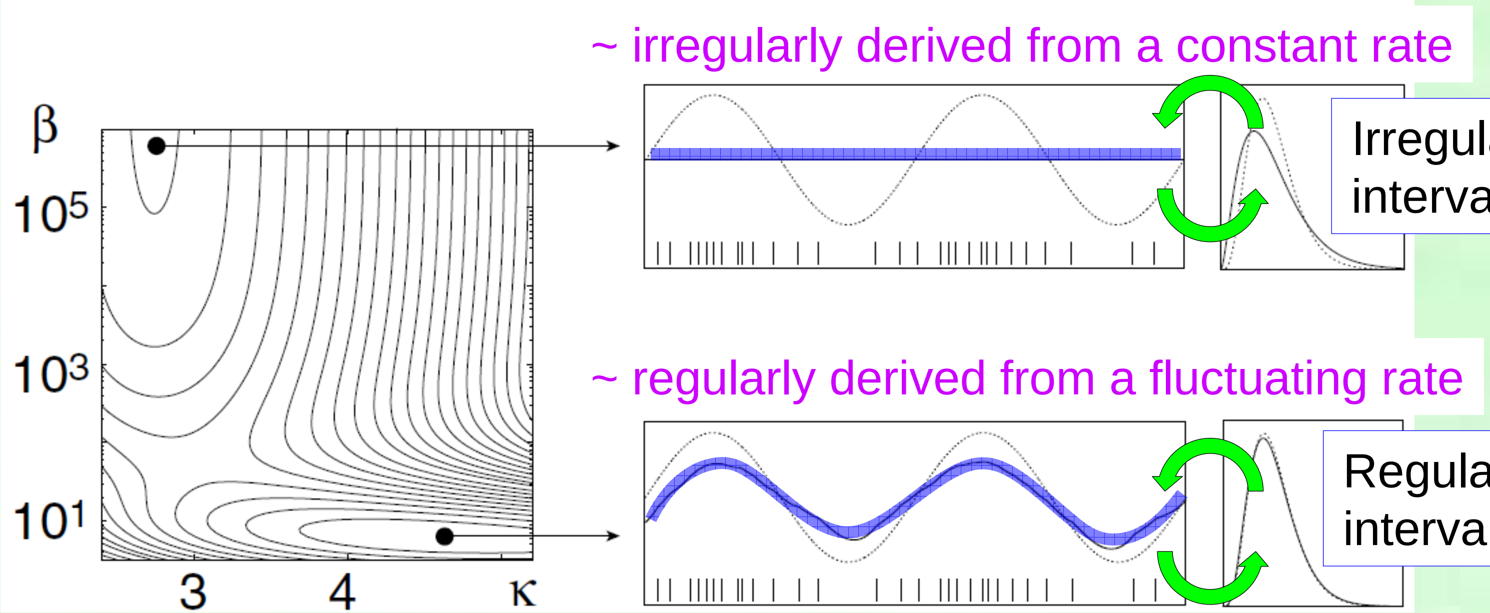
Bayesian interpretations

Shinsuke Koyama

marginal likelihood

$$p_{\kappa,\beta}\left(\{t_i\}_{i=0}^{n}\right) = \int p_{\kappa}\left(\{t_i\}_{i=0}^{n} \middle| \{\lambda(t)\}\right) p_{\beta}(\{\lambda(t)\})\, \mathrm{d}\{\lambda(t)\}$$

For a single spike train, two interpretations arise.



One interpretation is selected according to statistical plausibility.

Koyama & Shinomoto, J. Phys. A (2005) 38: L531-L537.

Bayesian inference

Takeaki Shimokawa

Estimating the rate and irregularity instantaneously.

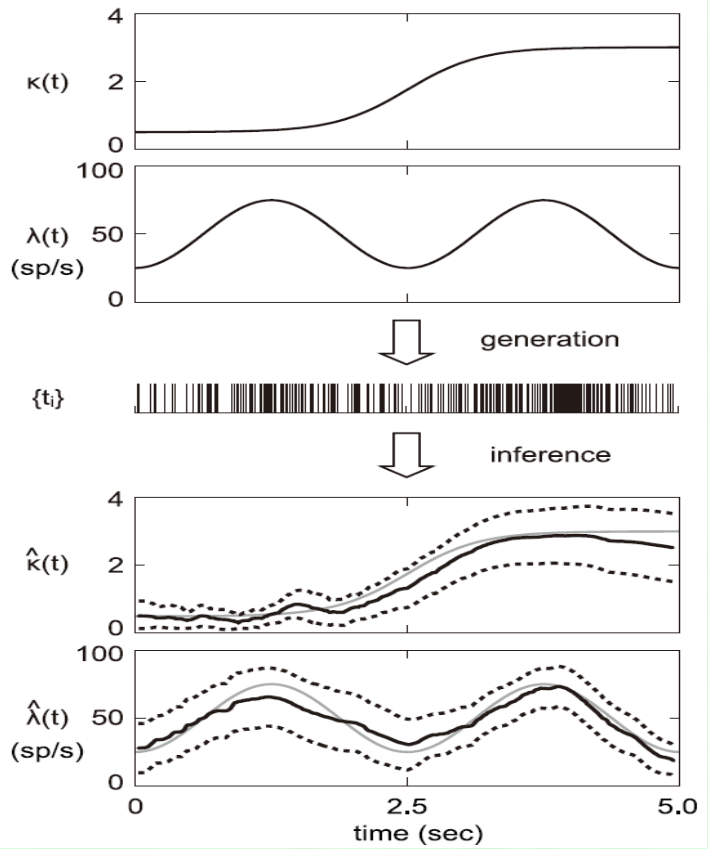
regularity

rate

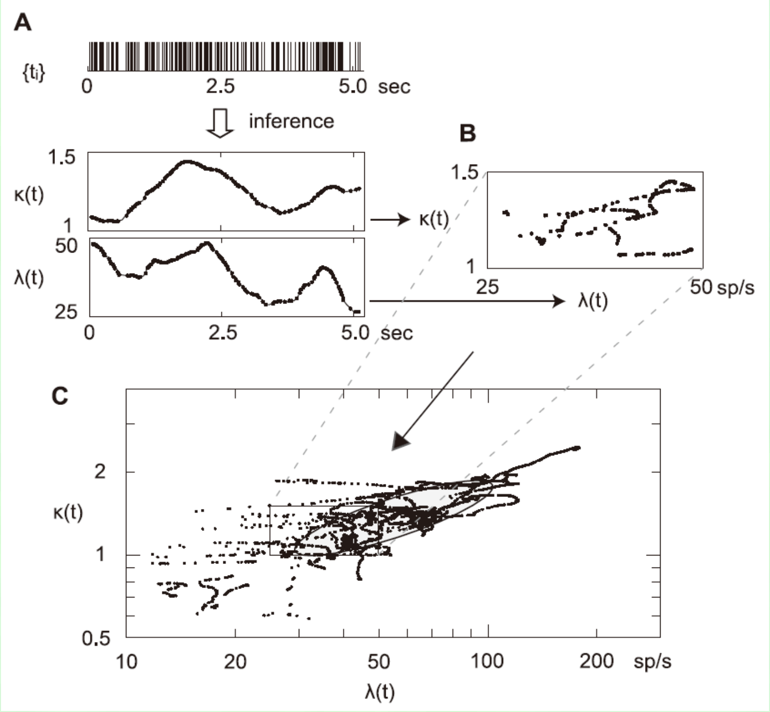
spike train

estimated regularity

estimated rate



$$p(\{\lambda(t)\},\{\kappa(t)\}\mid\{t_i\}_{i=0}^{n};\gamma_\lambda,\gamma_\kappa)=\frac{p(\{t_i\}_{i=0}^{n}\mid\{\lambda(t)\},\{\kappa(t)\})\,p(\{\lambda(t)\};\gamma_\lambda)\,p(\{\kappa(t)\};\gamma_\kappa)}{p(\{t_i\}_{i=0}^{n};\gamma_\lambda,\gamma_\kappa)}$$



Shimokawa & Shinomoto, Neural Computation (2009) 21:1931-1951.

Benefit

1. **Characterize non-Poissonian feature.**

2. **Improve the firing rate estimation by taking account of the non-Poissonian feature.**

Lv is doing time-rescaling

Local Variation, Lv

$$Lv = \frac{3}{n-1}\sum_{i=1}^{n-1}\left(\frac{I_i - I_{i+1}}{I_i + I_{i+1}}\right)^2$$

$$\left(\frac{I_i - I_{i+1}}{I_i + I_{i+1}}\right)^2 = 1 - \frac{4 I_i I_{i+1}}{(I_i + I_{i+1})^2}$$

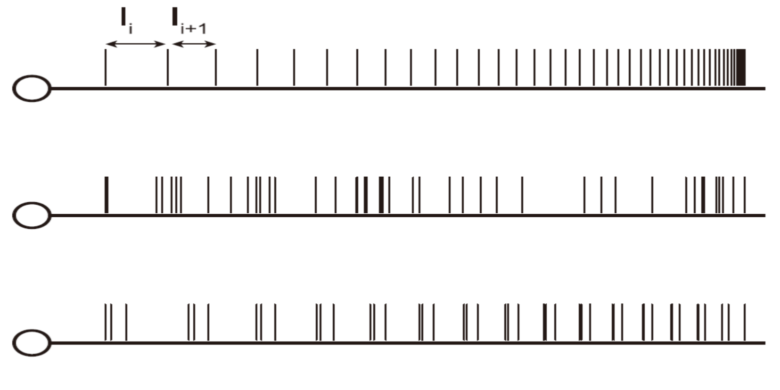
⇨ cross correlation

⇨ instantaneous rate^2

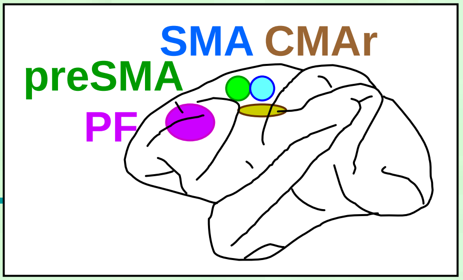
Coefficient of Variation, Cv

$$Cv = \Delta I / \bar{I}$$

Lv=0.1	regular	Cv=1.0
Lv=1.0	random	Cv=1.0
Lv=1.4	bursty	Cv=1.0

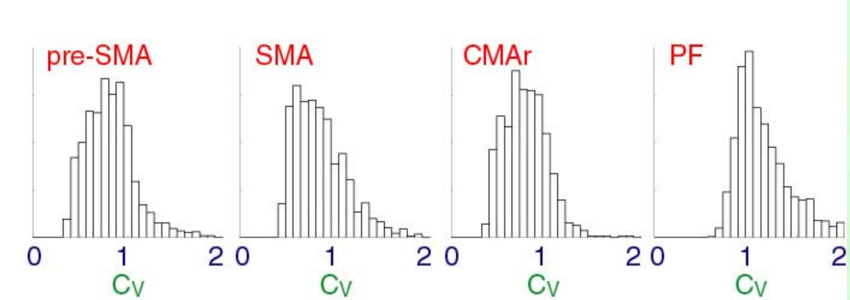


Neuronal firing patterns



Coefficient of Variation

$$Cv = \Delta I / \bar{I}$$



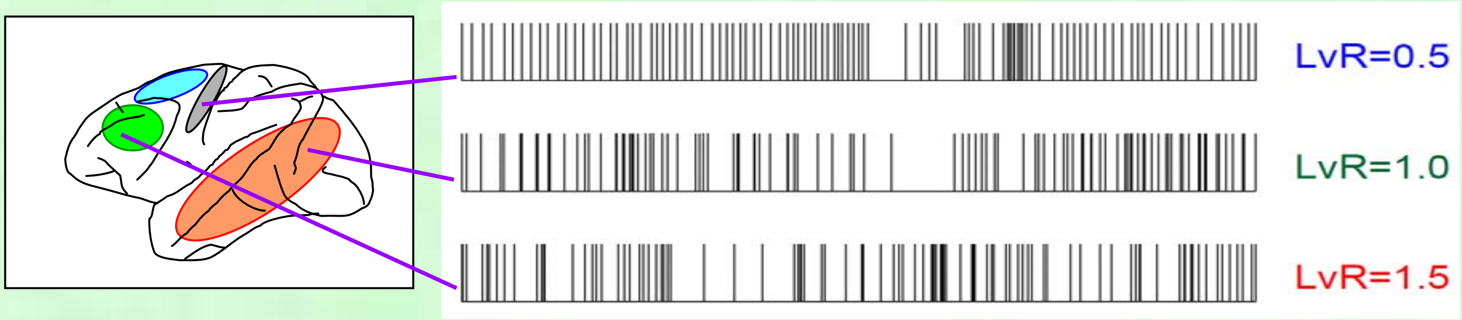
unimodal

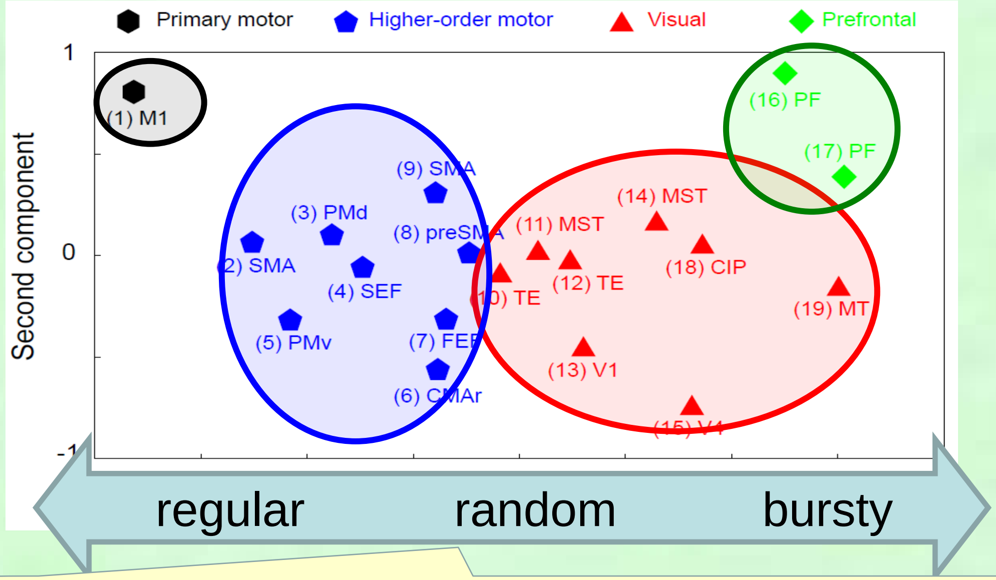
Neurons are not necessarily the Poisson spike generators.

Shinomoto, Shima & Tanji, Neural Computation (2003) 15: 2823-2842.

Relation to function

Kim, Shimokawa, Matsuno, Toyama





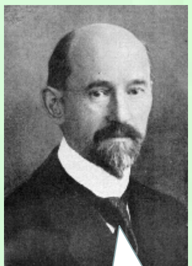
non-Poissonian characteristics

This is in essence due to the time rescaling operation in Lv, or LvR.

PLoS Comput Biol (2009) 5:e1000433.

Structure, function & signal

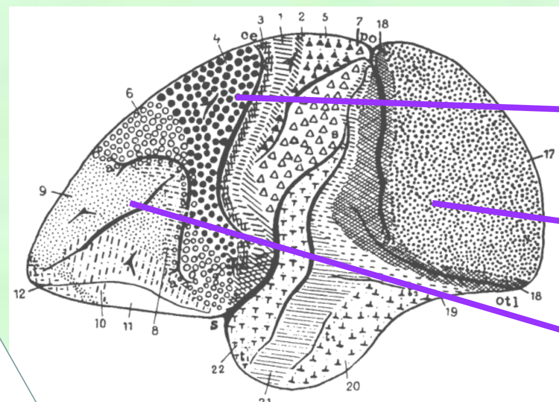
Korbinian Brodmann
(1868 - 1918)



1909 vir e !

cytoarchitectonics and cortical functions

structure ⟷ function



Monkey cortex

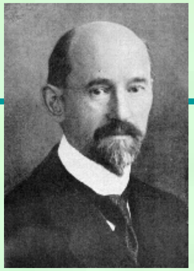
signal

firing patterns

I am a German neurologist. I was born in Liggersdorf, and studied medicine in Munich, Würzburg, Berlin and Freiburg.

Shinomoto, Kim, Shimokawa,et al., PLoS Comput Biol (2009) 5:e1000433.

Cytoarchitecture



MM

PF

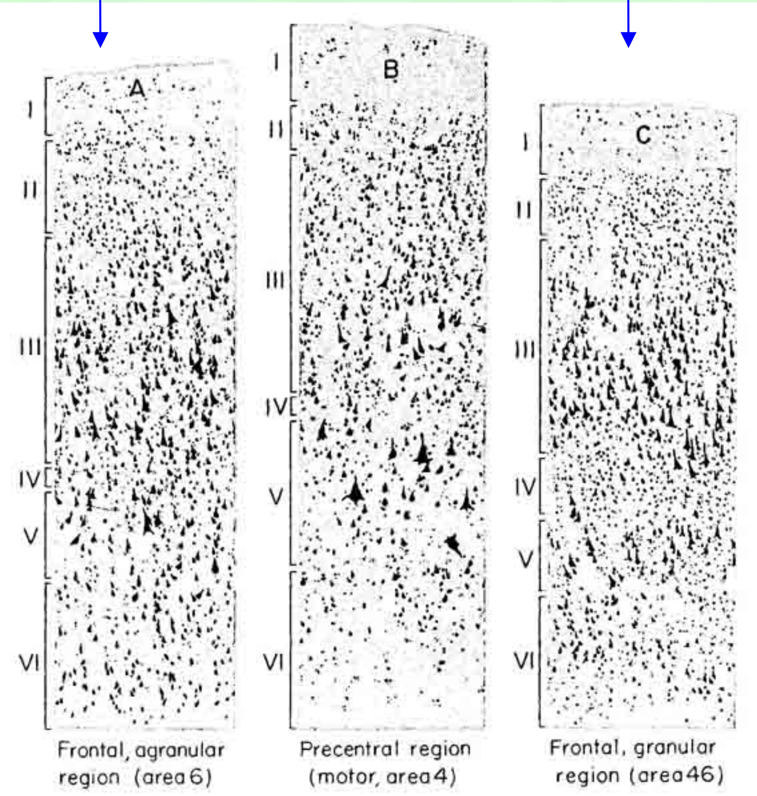


Figure 20.14. Cytoarchitectural pictures of several representative cortical areas.

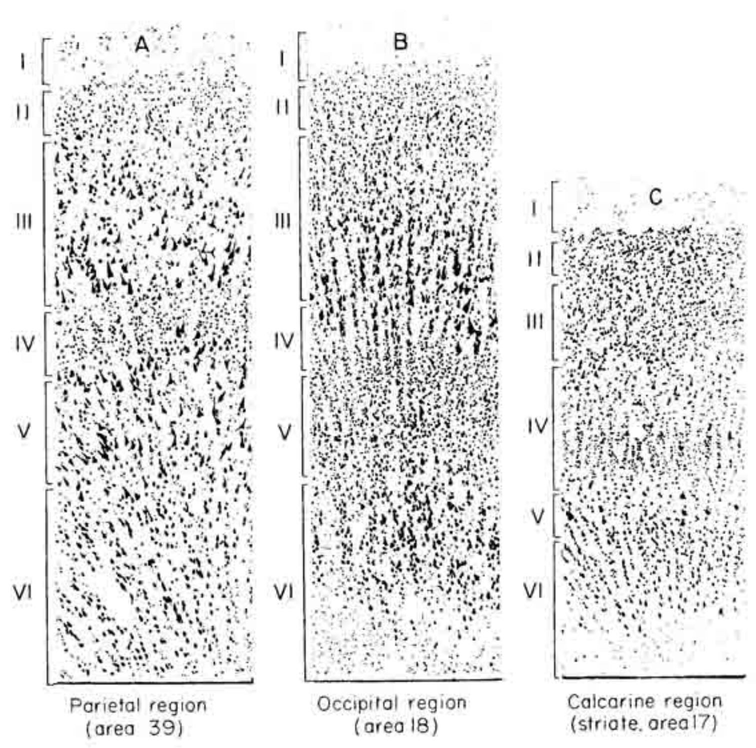
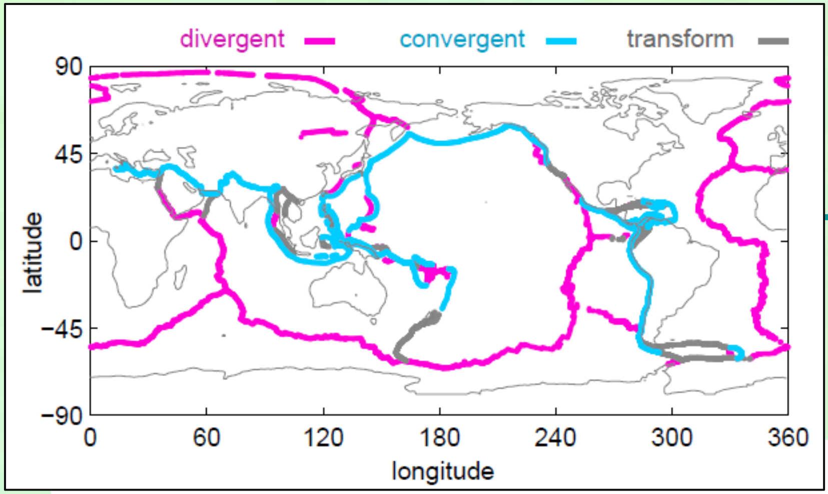
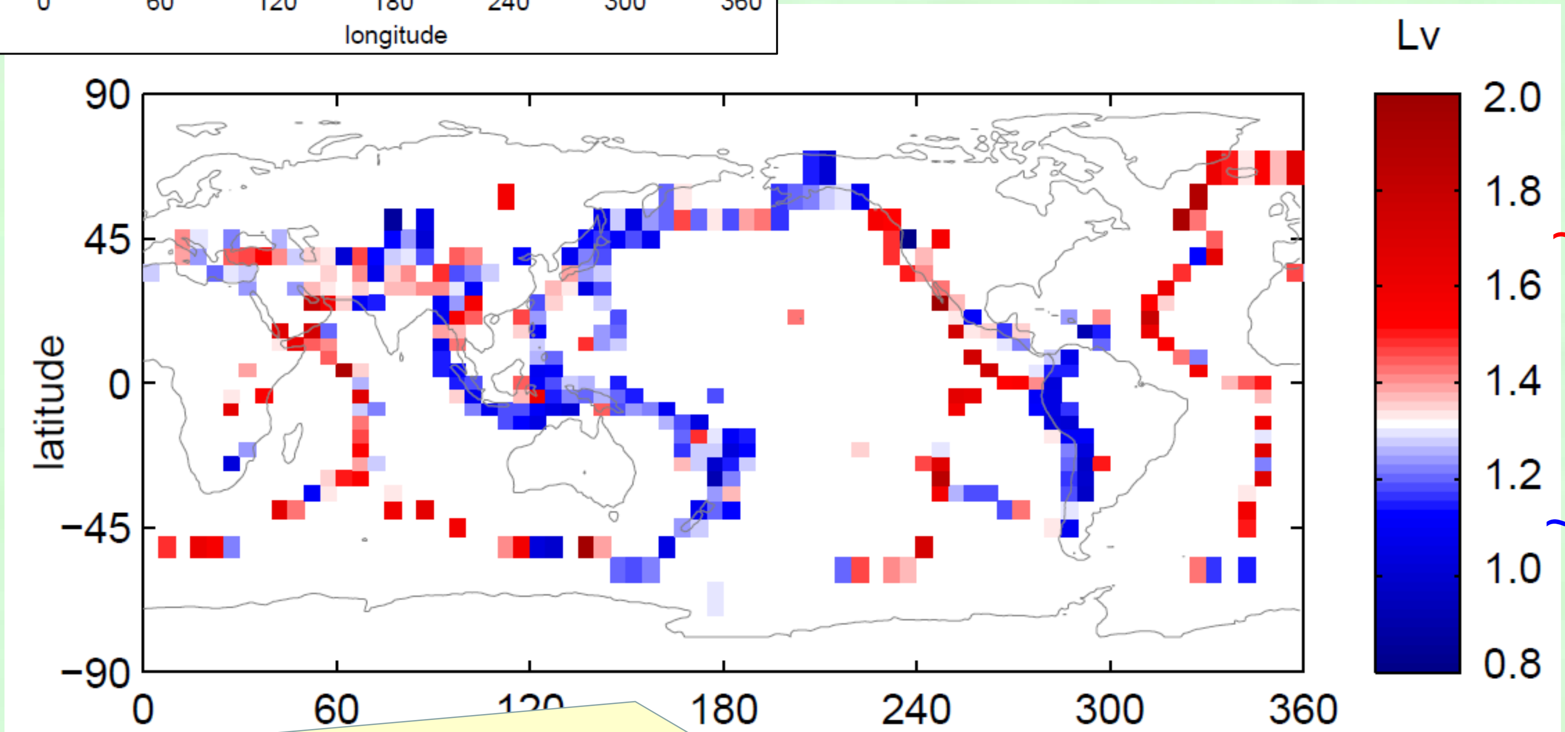


Figure 20.15. Cytoarchitectural pictures of several representative cortical areas.



Zhao, Omi, Matsuno

Lv map of seismology



~bursty

~random

Again, this is in essence due to the time rescaling operation in Lv.

Zhao, Omi, Matsuno, and Shinomoto, New J Phys 12 (2010) 063010.

Benefit

1. Characterize non-Poissonian feature.

2. **Improve the firing rate estimation by taking account of the non-Poissonian feature.**

Another benefit

Rate & irregularity

Shimokawa, Koyama

- In estimating the affection from love letters, we take account of the punctuality of the sender.
- A spike train should be interpreted in terms of a set of (rate & regularity) ~ (affection & punctuality).
- No more and no less !

Shimokawa, Koyama & Shinomoto, J. Comput Neurosci (2010) 29:183-191.