Linking spontaneous activity and statistically optimal internal models in the cortex

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Outline

- How visual information is encoded in the cortex
- Challenges of the standard model
- Proposal: the sampling hypothesis
- How sampling can address the challenges
- Supporting empirical evidence

The standard view on vision

- The fundamental method of information processing in the visual system can be described as
  - deterministic computation with added neural noise
  - feed-forward

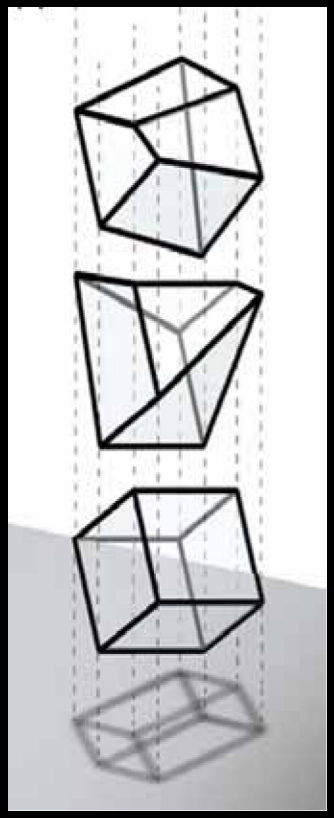
- The function of the primary visual cortex in this framework is
  - restricted to represent only visual information
  - to create a faithful representation of the sensory stimulus with a neural code that is as sparse and independent as possible

Challenges

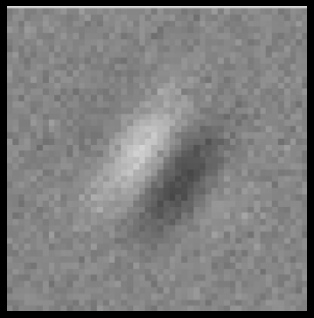
- *Behavioral:* In many cases, animals' and humans' perception, action and learning is best captured by models that assume probabilistic representation and computation in the brain

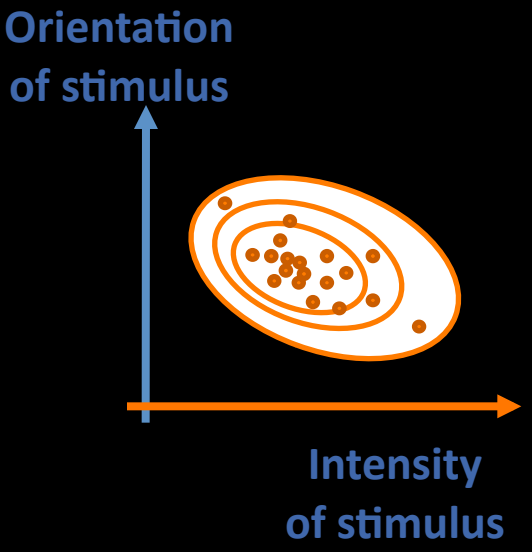
Life is uncertain and ambiguous…

- 2D to 3D



s: stimulus





- Proposal

The brain encodes both the value and the uncertainty of the stimulus during perception.

Probabilistic approaches in …

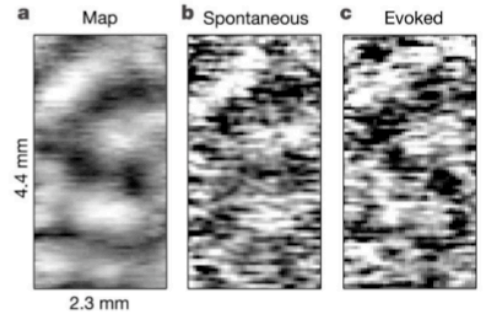
- Classical conditioning *(Courville et al. TICS 2006)*
- Perceptual processes *(Kersten et al. Ann. Rev. Psych. 2006)*
- Visuo-motor coordination *(Kording & Wolper Nature 2004)*
- Cue combination *(Atkins et al. Vis Res 2001; Ernst & Banks Nature 2002)*
- Decision making *(Trommershäuser et al. TICS 2008)*
- High-level cognitive processes *(Griffiths & Tenenbaum TICS 2006)*
- Visual statistical learning *(Orban et al. PNAS 2008)*

Is the neural computation deterministic?

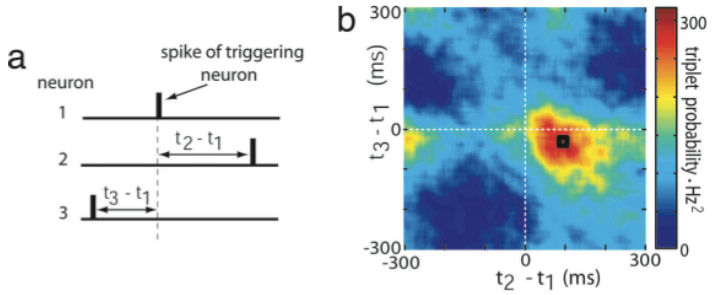
Challenges

- *Behavioral:* In many cases, animals' and humans' perception, action and learning is best captured by models that assume probabilistic representation and computation in the brain
- *Physiological:* High level of structured spontaneous activity in the cortex that questions the feed forward nature of information processing

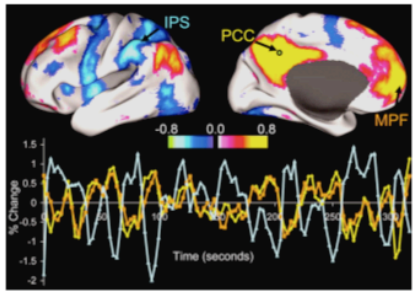
Spontaneous activity in the awake brain



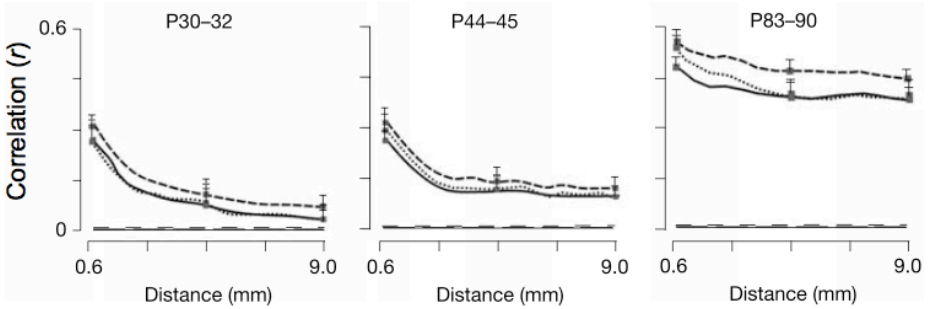
Kenet et al., 2003



Luczak et al., 2007



Fox et al., 2005



Fiser et al., 2004

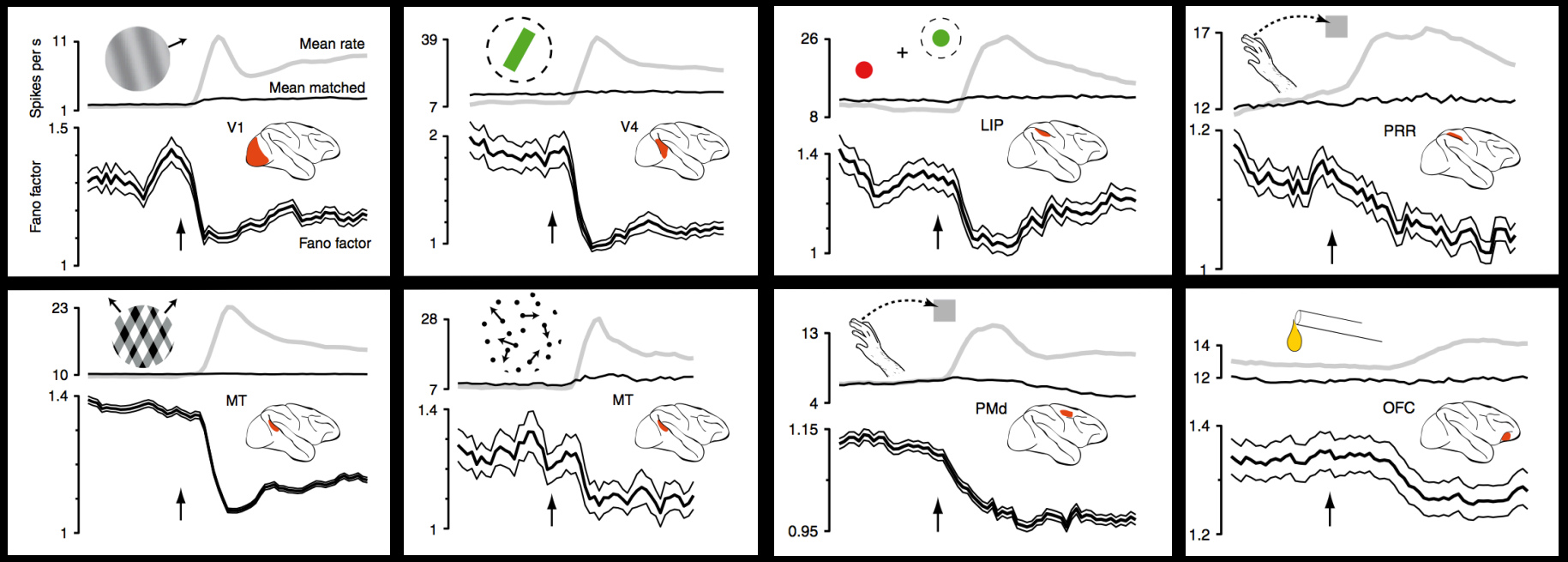
Is it really noise?

Challenges

- *Behavioral:* In many cases, animals' and humans' perception, action and learning is best captured by models that assume probabilistic representation and computation in the brain
- *Physiological:* High level of structured spontaneous activity in the cortex that questions the feed forward nature of information processing
- *Coding:* High trial-to-trial variability of cell responses even in primary sensory cortices that strongly interferes with reliable neural computation

Example: Stimulus onset quenches trial-to-trial variability

Churchland & >25; Nat Neuro 2010



Why?

Challenges

- *Behavioral:* In many cases, animals' and humans' perception, action and learning is best captured by models that assume probabilistic representation and computation in the brain
- *Physiological:* High level of structured spontaneous activity in the cortex that questions the feed forward nature of information processing
- *Coding:* High trial-to-trial variability of cell responses even in primary sensory cortices that strongly interferes with reliable neural computation

Approach

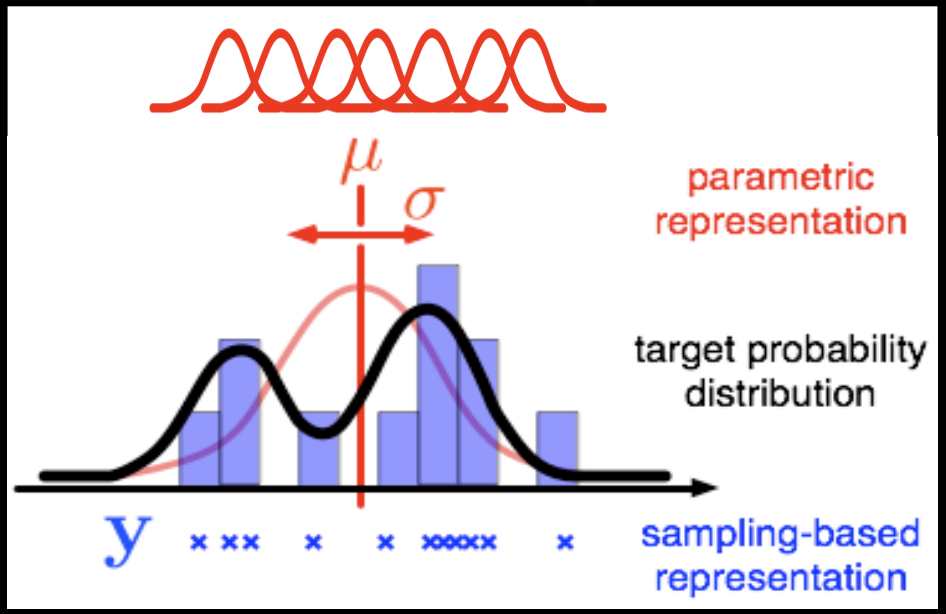
- Give a biologically plausible functional framework
- Address the above challenges
- Provide experimental support

Probabilistic representation in the cortex

Parametric

- Probabilistic Population Codes (PPCs)
- Predecessors: Kernel Dens. Estimation

Distr. Population Codes

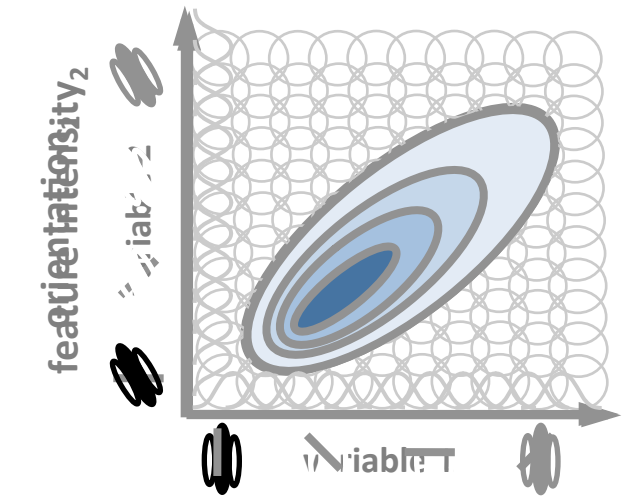


Sampling-based

- Earlier proposals:
  - Lee & Mumford 2003
  - Hoyer & Hyvarinen 2003
- Implicit examples:
  - Boltzmann machine
  - Helmholtz machine
- Special cases:
  - Olshausen & Field 1996
  - Karklin & Lewicki 2009

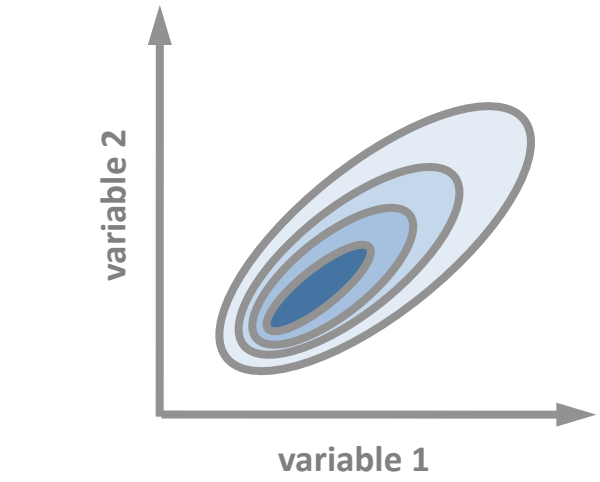
Logic of the two types of representation

PPC



firing rate

Sampling-based



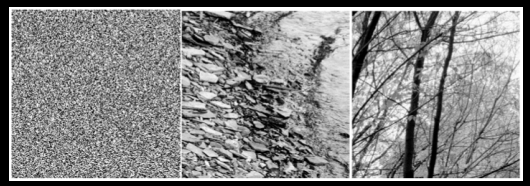
Comparing the two schemes

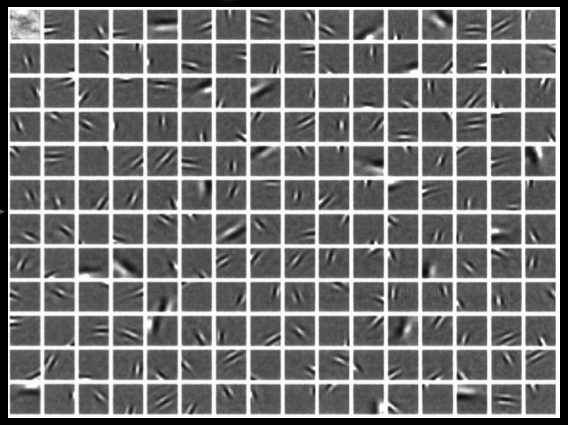
	PPC	Sampling-based
neurons correspond to	parameters	variables
network dynamics required (beyond the first layer)	deterministic	stochastic (self consistent)
representable distributions	must correspond to a particular parametric form	can be arbitrary
critical factor in accuracy of encoding a distribution	number of neurons	time allowed for sampling
instantaneous representation of uncertainty	complete, the whole distribution is represented at any time	partial, a sequence of samples is required
number of neurons needed for representing multimodal distributions	scales exponentially with the number of dimensions	scales linearly with the number of dimensions
implementation of learning	unknown	well-suited

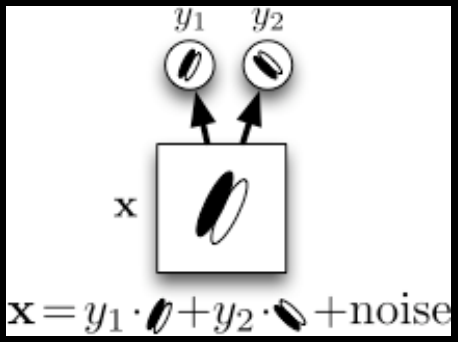
A simple model of the early visual system

- e.g. Olshausen & Field 1996

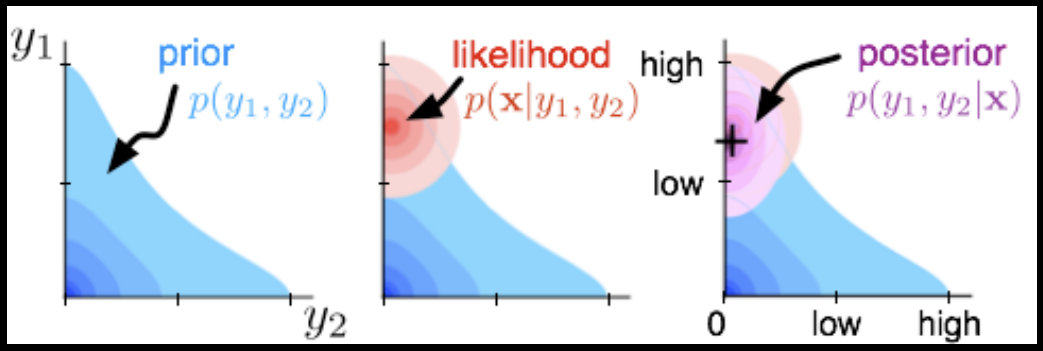
Sparseness and independence







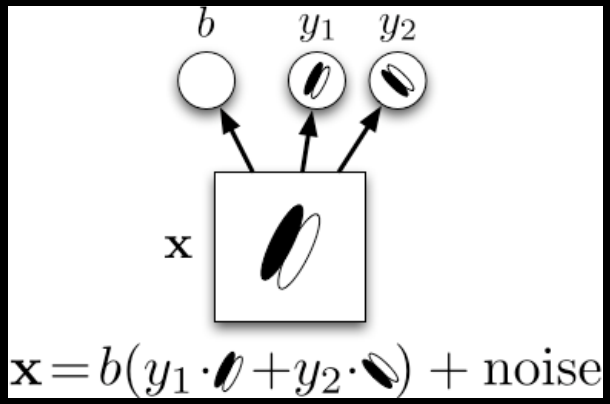
- probabilistic formulation

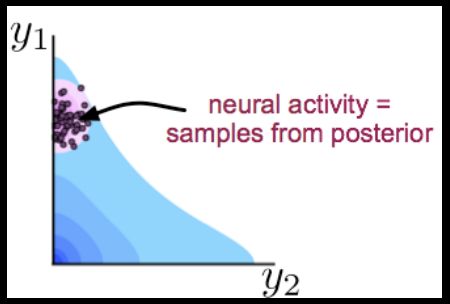


Perception is an inference process which is always based on internally available prior information

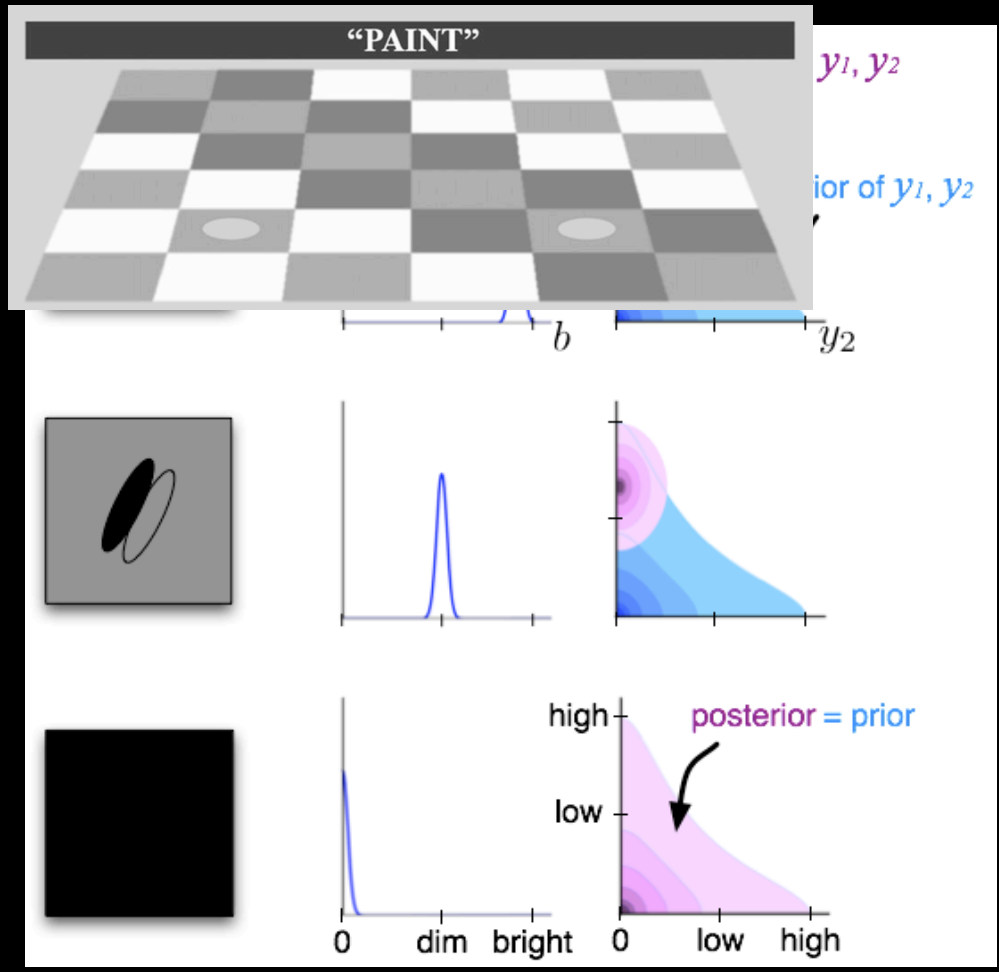
Functional role of spontaneous activity

- Brightness coding in the primary visual cortex is factorized
  (Rossi et al. Science 1996)

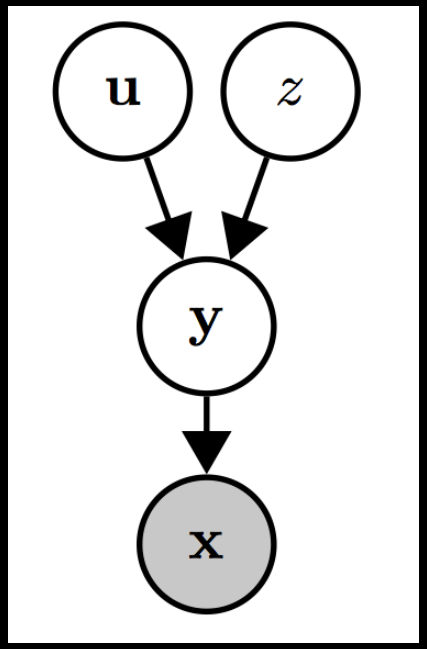




- Spontaneous activity = samples from the prior



Simulations



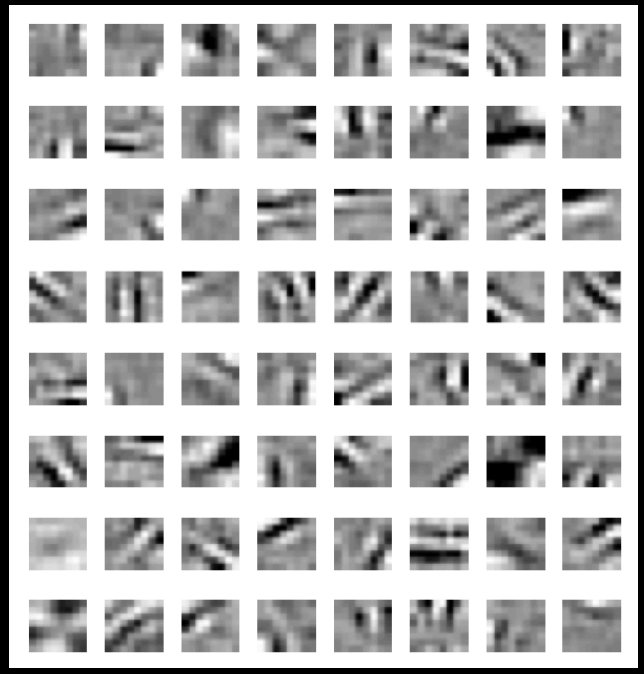
$$\mathrm{P}(\mathbf{x}|\mathbf{y}) = \mathcal{N}(\mathbf{x}; \mathbf{A}\mathbf{y}, \sigma_x^2 \mathbf{I})$$

$$\begin{aligned} \mathbf{y} &= z\,\mathbf{u} \\ \mathrm{P}(\mathbf{u}) &= \mathcal{N}(\mathbf{u}; \mathbf{0}, \mathbf{C}) \\ \mathrm{P}(z) &= \mathrm{Gamma}(z; k, \theta) \end{aligned}$$

- u – membrane potential

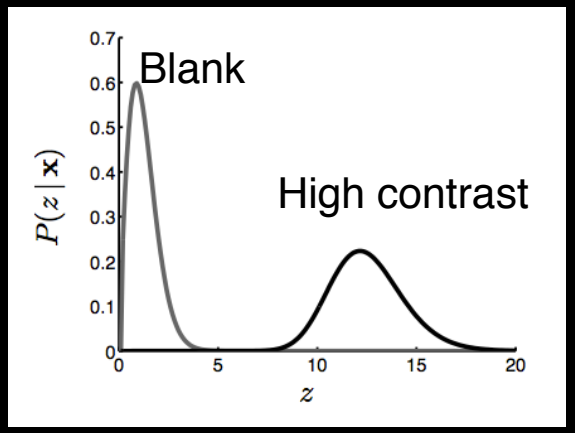
$$\begin{aligned} r_i &= 12.7\,[u - 0.1]_+^{2.1} \\ n_i &\sim \mathrm{Poisson}(\tau\, r_i) \end{aligned}$$

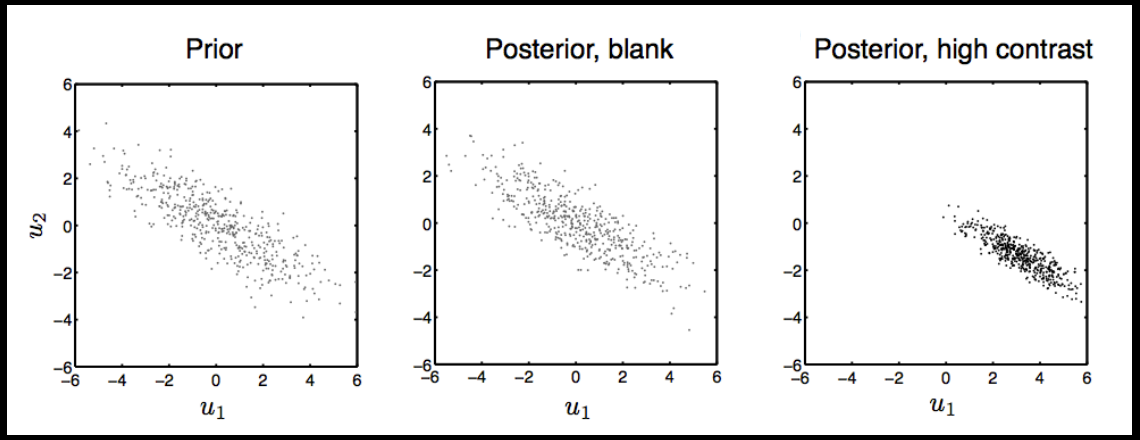
- r_i - Poisson rate
- n_i - spike count

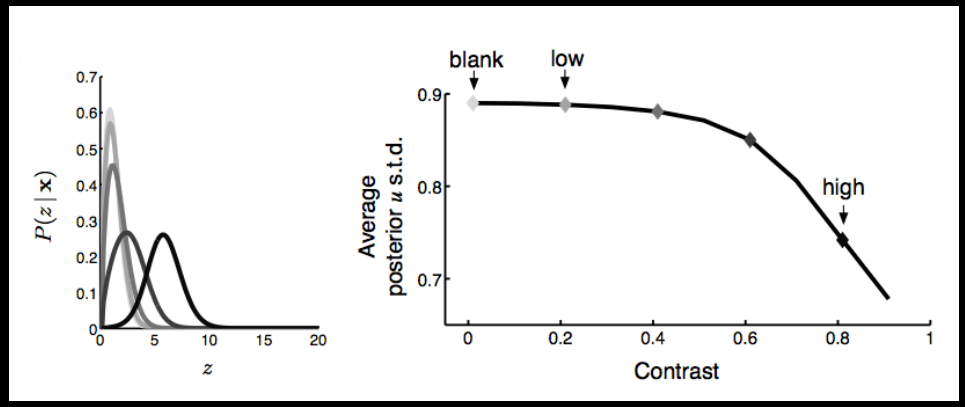


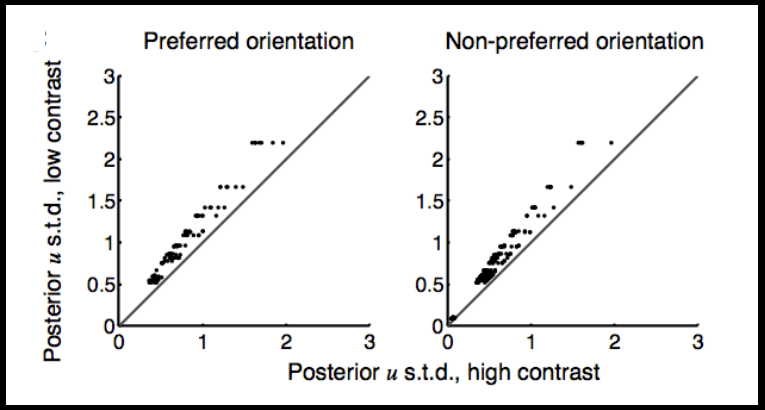
- Trained on 80 000 patches of size 8x8 from the van Hateren image database
- Maximum likelihood learning using Expectation Maximization

Contrast dependent variability of u





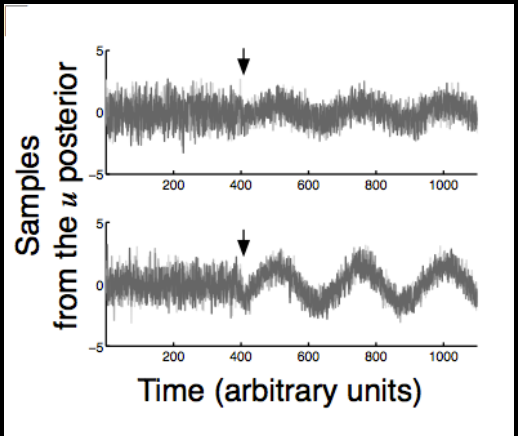


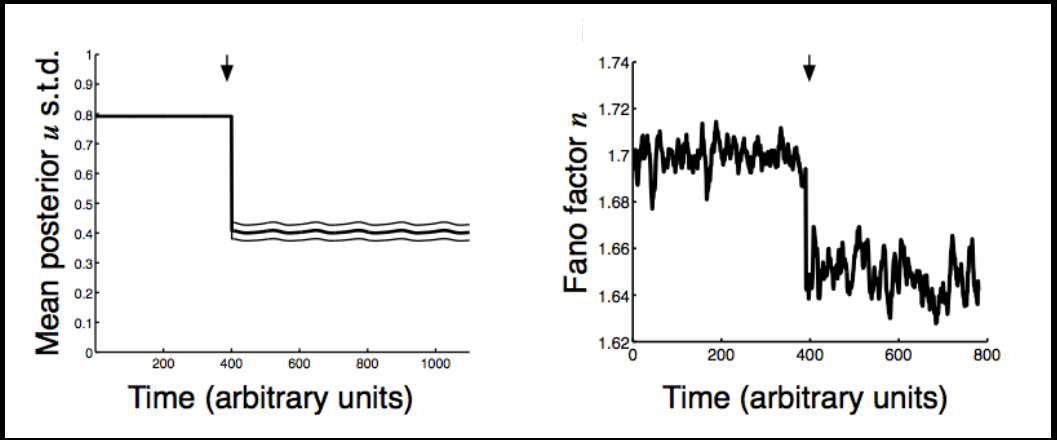


- Sampling gives a natural explanation *(Finn et al. Neuron 2007)*

Effect of stimulus onset

Non-preferred





Preferred

- Sampling can reproduce the quenching effect of stimulus onset reported by Churchland et al.

Formalizing the relationship between SA and EA

- Activity *p(y | x)* in absence of input stimuli (x) represent samples from the prior *p(y)* - and *this is* the spontaneous activity.

$$P_\theta(y) \xrightarrow[P_{data}(x)]{learning\ from} \int P_\theta(y \mid x) \cdot P_{data}(x)\, dx$$

$$P_{SA}(y) \longrightarrow \langle P_{EA}(y \mid x) \rangle_{P_{data}(x)}$$

Spontaneous activity

Evoked activity

Natural scenes

Predictions

With accumulating visual experience, the distribution of spontaneous activity should become increasingly similar to the distribution of evoked activity averaged over natural stimuli .

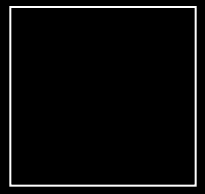
- Probability of exhibiting a given neural activity pattern should be identical
- Probability of transitioning between particular patterns should also match
- Similarity should be specific to natural scenes but not to other stimulus ensembles

Evidence of sampling based probabilistic representation in the awake cortex

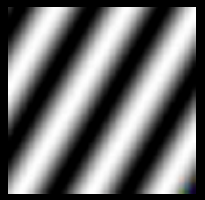
Visual

Data collection

- Awake, head-restrained ferrets
- 4 age groups (P30, P45, P90, P120)
- Multi-electrode recording with 200 μ spacing from layer 2-3 of V1

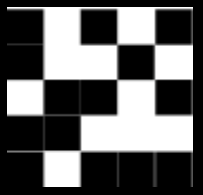


- Complete dark (spont. activity)



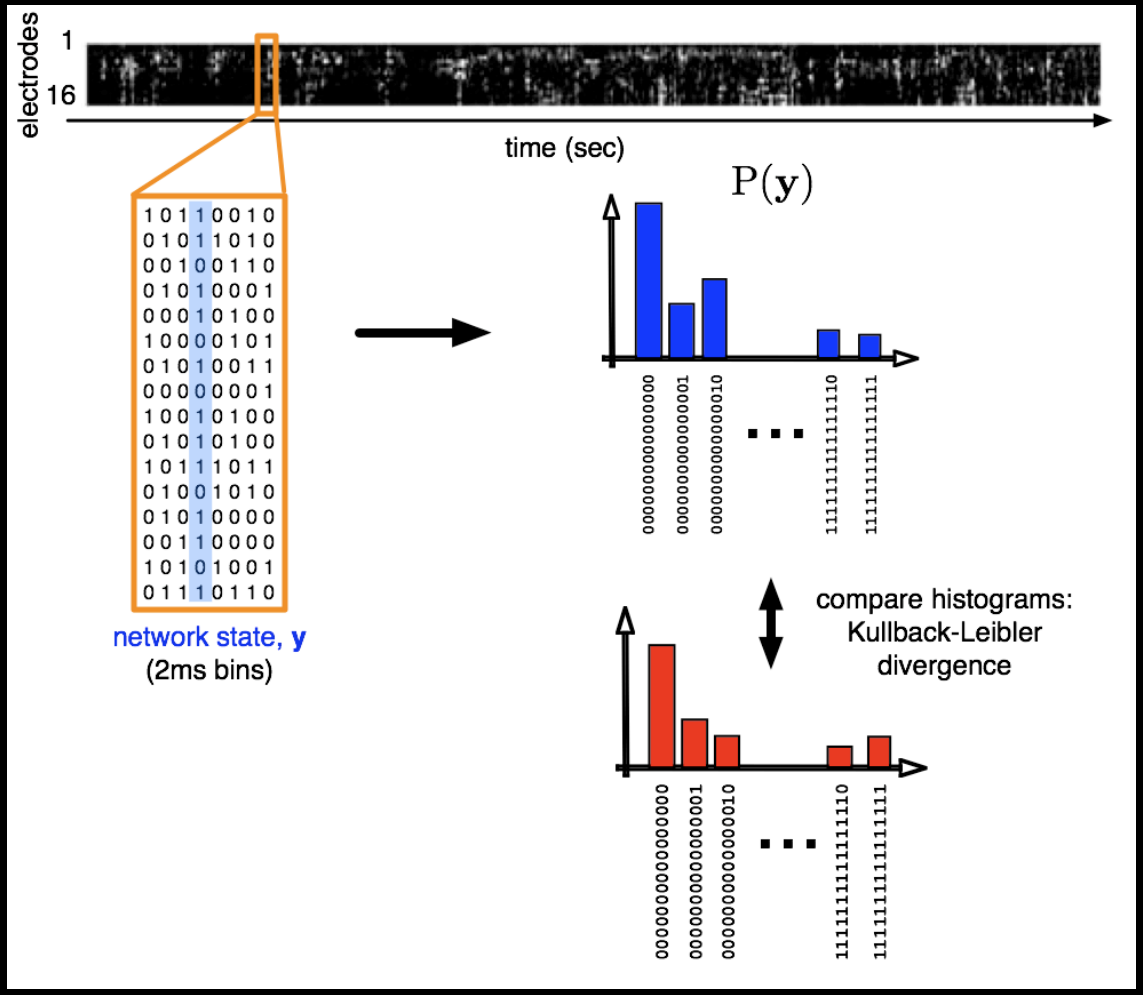
- Drifting grating

- Natural scene movie



- Random noise

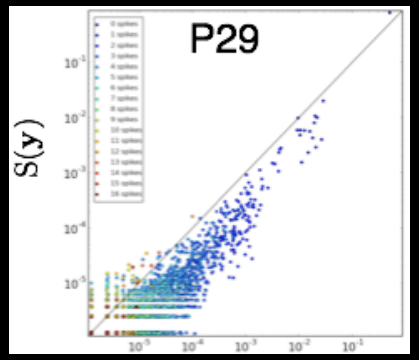
Data analysis

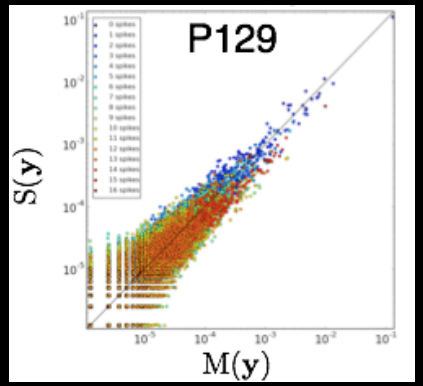


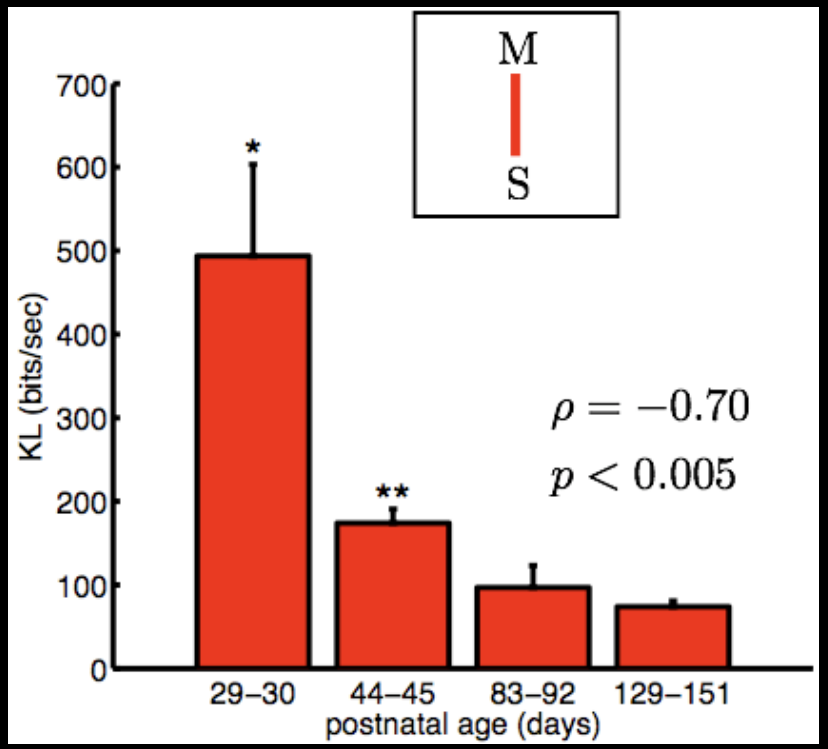
$$KL\left(p_{Movie} \,||\, p_{Spont}\right) = \sum_{X} p_{Movie}(x) * \log \frac{p_{Movie}(x)}{p_{Spont}(x)}$$

Results I

- SA and EA in the Movie condition converge with age
- In the adult animal, they do not differ significantly



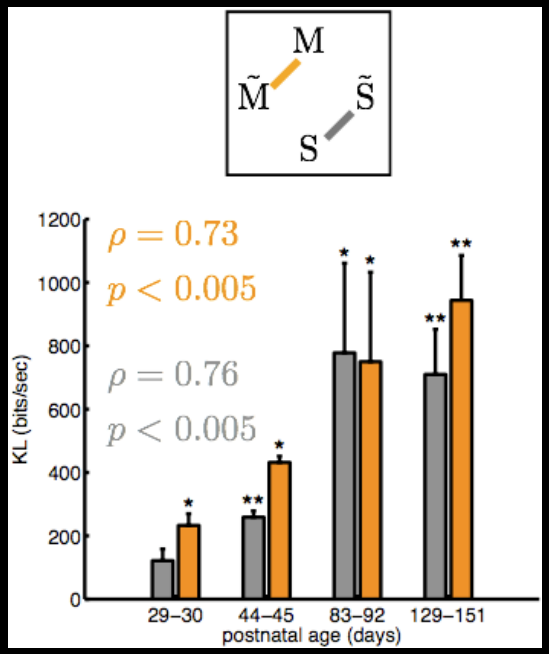


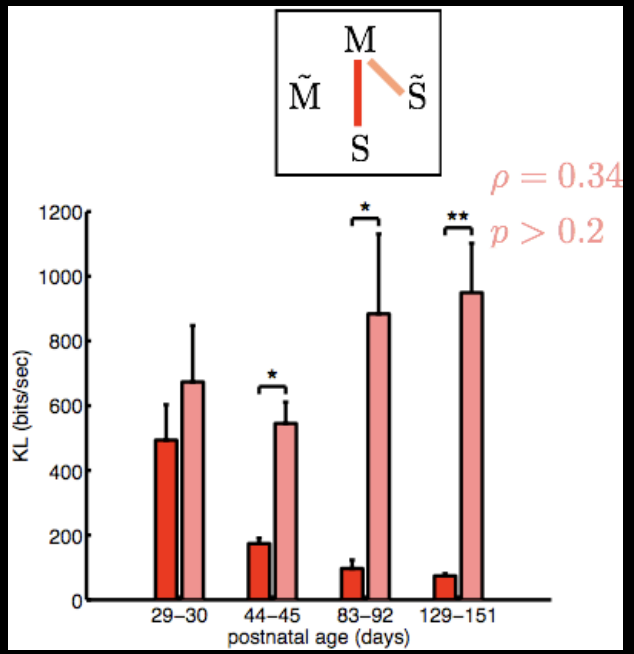


Results II

- Both SA and EA_{Movie} become increasingly correlated
- Spatial correlations are similar between SA and EA_{Movie}

$$\tilde{P}(y) = \prod_{i=1}^{16} P(y_i)$$

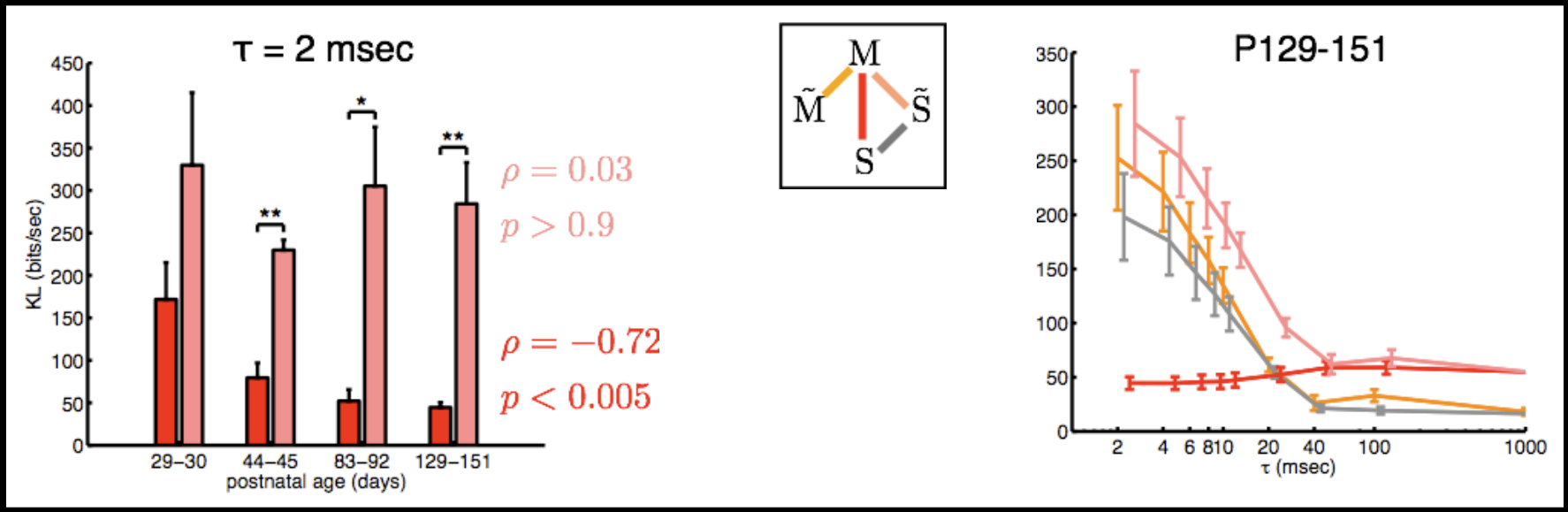




Results III

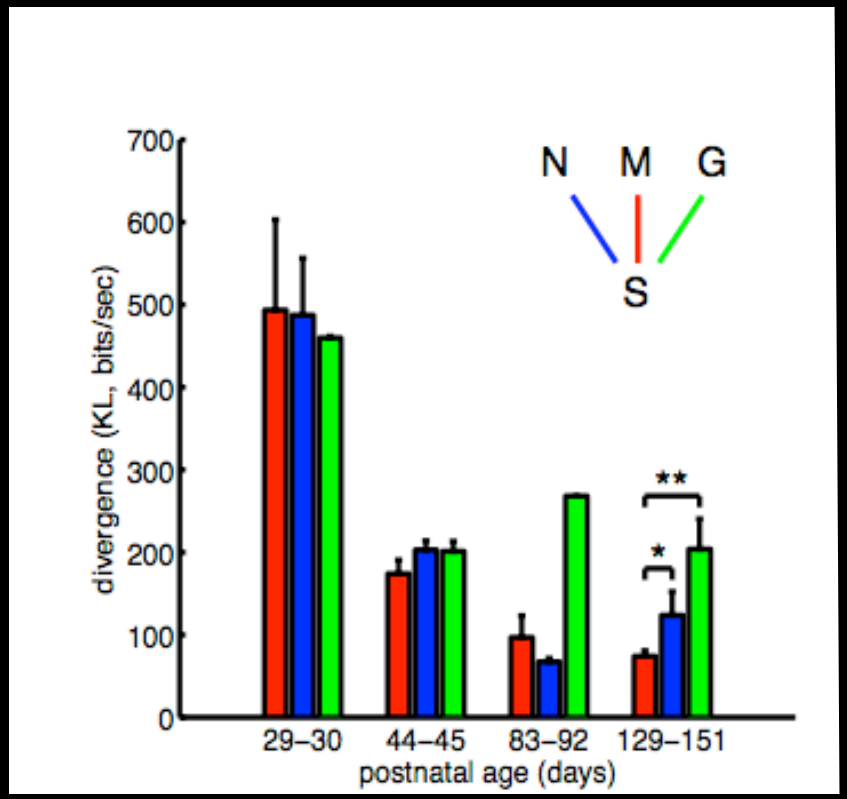
- Temporal correlations are similar between SA and EA_{Movie}

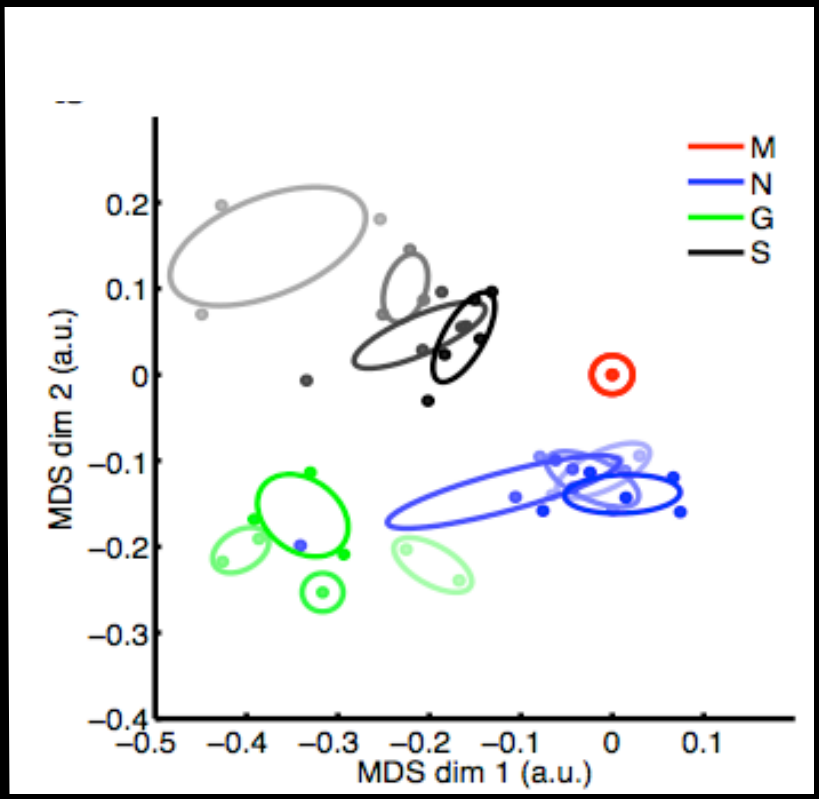
$$State-transition\ distributions:\ P(y_{t+\tau}\mid y_t)$$
$$Control:\ \tilde{P}(y_{t+\tau}\mid y_t)=P(y)$$



Results IV

- The match between SA and EA is specific to natural scenes



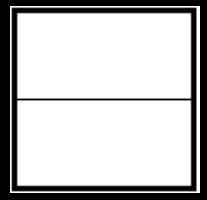


Evidence of sampling based probabilistic representation in the awake cortex

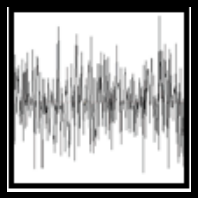
Auditory

Data collection

- Awake, head-restrained ferrets
- One age group (adults)
- Single-electrode single-unit recording in A1



- Complete silence (spont. activity)



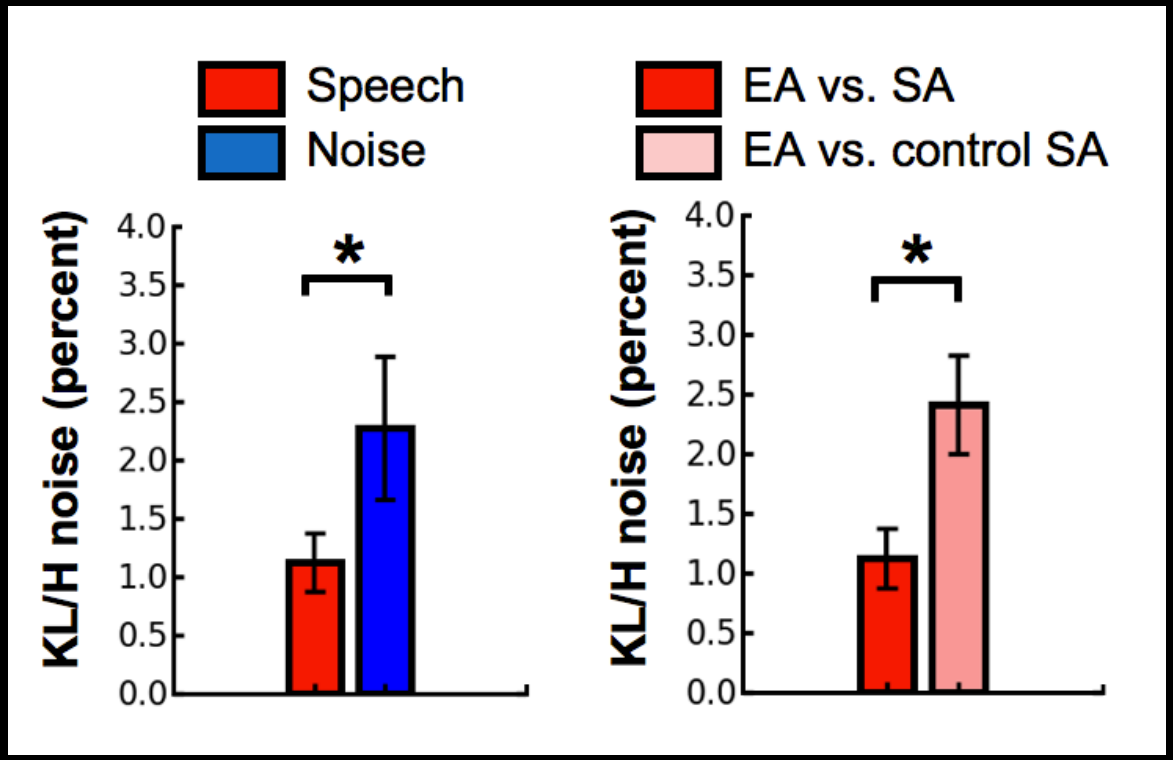
- White noise (0-20 KHz)

- Natural speech

Shamma-lab University of Maryland

Results V

- The match between SA and EA is not specific to the visual modality



Conclusions

- Sampling based probabilistic schemes are viable alternatives for neural representation in the cortex providing a unified framework to investigate learning and instantaneous perception

- Measures based on comparing SA and EA support the idea that the cortex uses sampling based representation and SA has the functional role of providing prior information for probabilistic perceptual inferences

Thank you !