Relating evoked and spontaneous activities in a generative modeling framework

Gergő Orbán
Fiser Lab
Volen Center for Complex Systems
Brandeis University

Statistical structure of neural activities

Evoked activity $\longrightarrow$ samples from $P(y \mid x)$

Statistical structure of neural activities

Evoked activity $\longrightarrow$ samples from $P(y \mid x)$

Spontaneous activity $\longrightarrow$ samples from $P(y)$

Statistical structure of neural activities

Evoked activity ⟶ samples from $P(y\,|\,x)$

Spontaneous activity ⟶ samples from $P(y)$

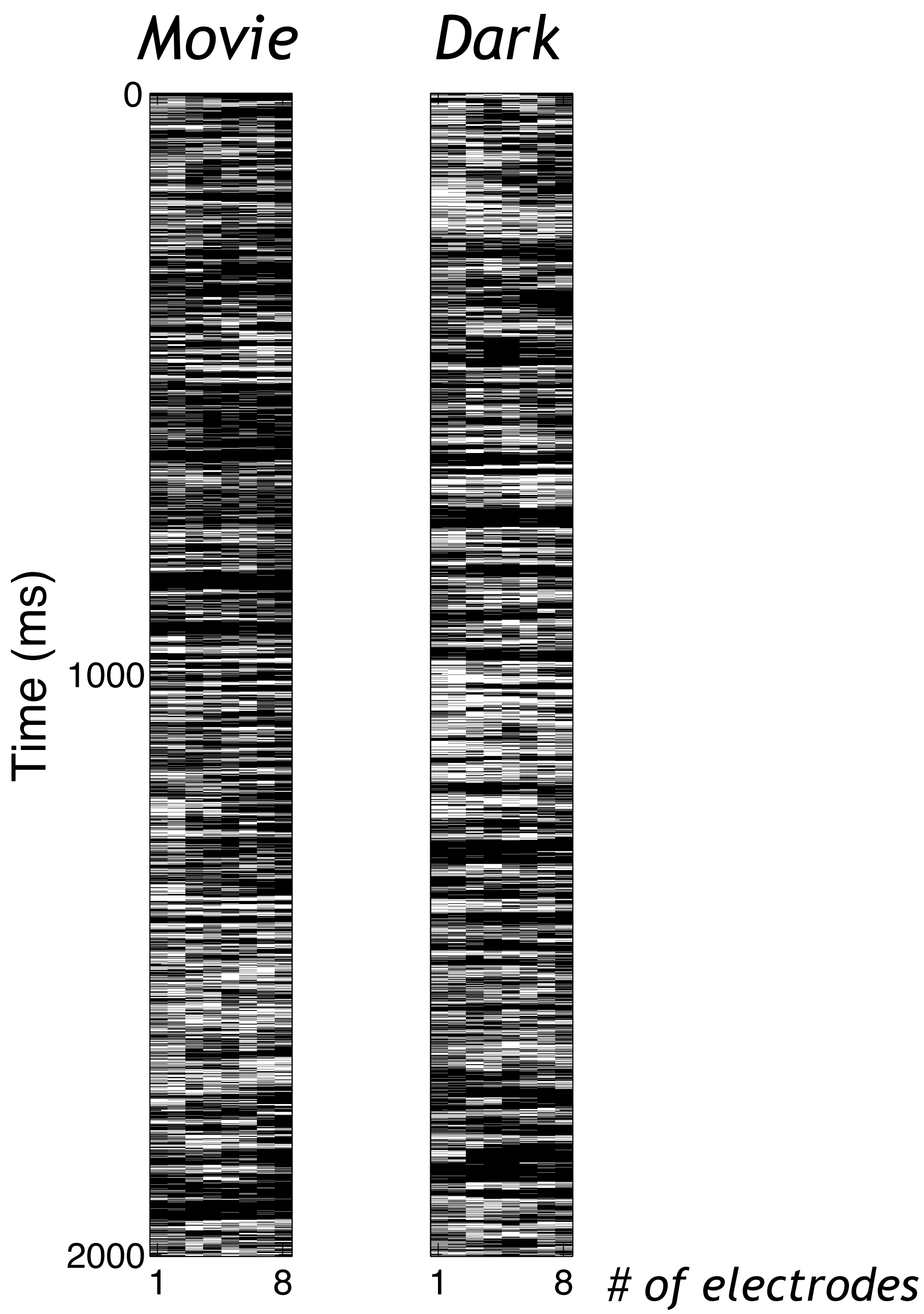
$$\underbrace{\hat{P}(y)}_{\text{spontaneous activity}} = \int \underbrace{\hat{P}(y\,|\,x)}_{\text{evoked activity}}\ \underbrace{P(x)}_{\text{stimulus statistics}}\ dx$$

Statistical structure of neural activities

Evoked activity ⟶ samples from $P(y \mid x)$

Spontaneous activity ⟶ samples from $P(y)$

$$\underbrace{\hat{P}(y)}_{\text{spontaneous activity}} = \int \underbrace{\hat{P}(y \mid x)}_{\text{evoked activity}} \; \underbrace{P(x)}_{\text{stimulus statistics}} \, dx$$

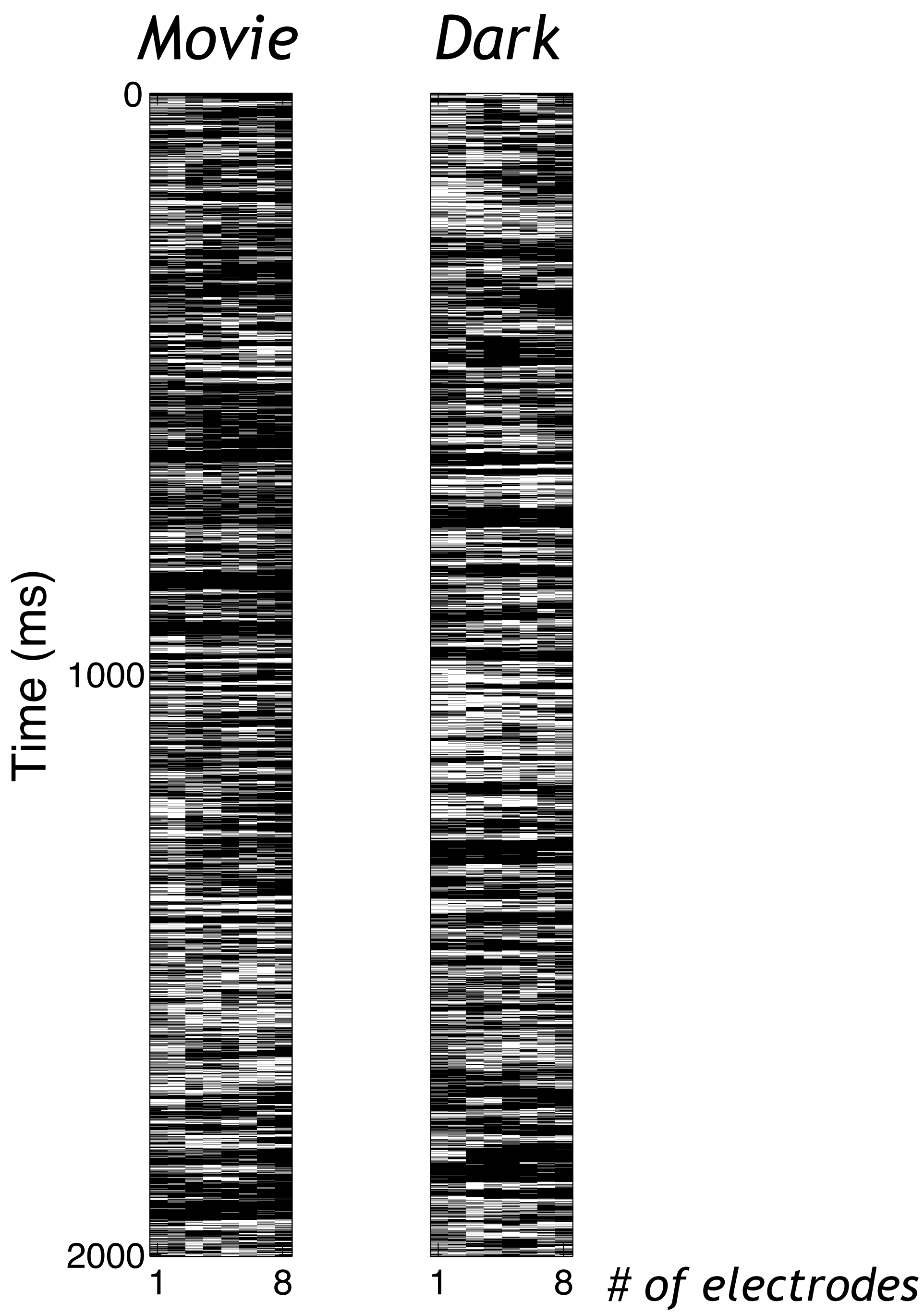


Statistical structure of neural activities

Evoked activity ⟶ samples from $P(y\,|\,x)$

Spontaneous activity ⟶ samples from $P(y)$

$$\underbrace{\hat{P}(y)}_{\text{spontaneous activity}} = \int \underbrace{\hat{P}(y\,|\,x)}_{\text{evoked activity}}\ \underbrace{P(x)}_{\text{stimulus statistics}}\ dx$$



- we need to assess the differences between high-dimensional multivariate distributions

How to evaluate distributions of activities?
Available methods

How to evaluate distributions of activities?
Available methods

- measuring receptive fields
  - mean activities
  - no account of variability
  - no joint covariability

How to evaluate distributions of activities?
Available methods

- measuring receptive fields
  - ☐ mean activities
  - ☐ no account of variability
  - ☐ no joint covariability
- LNP models
  - ☑ variability incorporated
  - ☑ recent models account for joint covariability
  - ☑ considers unrecorded neurons as well
  - ☐ conditional distribution only: neural activity is only interpreted with respect to a stimulus

How to evaluate distributions of activities?
Available methods

- measuring receptive fields
  - ☐ mean activities
  - ☐ no account of variability
  - ☐ no joint covariability
- LNP models
  - ☑ variability incorporated
  - ☑ recent models account for joint covariability
  - ☑ considers unrecorded neurons as well
  - ☐ conditional distribution only: neural activity is only interpreted with respect to a stimulus
- histogram technique
  - ☐ undersampling

How to evaluate distributions of activities?
Available methods

- measuring receptive fields
  - ☐ mean activities
  - ☐ no account of variability
  - ☐ no joint covariability
- LNP models
  - ☑ variability incorporated
  - ☑ recent models account for joint covariability
  - ☑ considers unrecorded neurons as well
  - ☐ conditional distribution only: neural activity is only interpreted with respect to a stimulus
- histogram technique
  - ☐ undersampling
- maximum entropy models
  - ☑ handles the whole distribution of activities
  - ☐ level of correlations needs to be determined a priori
  - ☐ number of parameters grows exponentially

How to compare distributions of activities?

Kullback-Leibler divergence

$$\mathrm{KL}\left[Q\left(y\right), P\left(y\right)\right] = -\int dy\, Q(y) \log P(y) - H\left(Q(y)\right)$$

How to compare distributions of activities?
Kullback-Leibler divergence

$$\mathrm{KL}\left[Q\left(y\right),P\left(y\right)\right]=-\int dy\, Q(y)\log P(y) - H\left(Q(y)\right)$$

cross entropy *entropy*

How to compare distributions of activities?

Kullback-Leibler divergence

$$\mathrm{KL}\left[Q\left(y\right),P\left(y\right)\right] = \boxed{-\int dy\, Q(y) \log P(y)} \boxed{-\, H\left(Q(y)\right)}$$

cross entropy *entropy*

- quantifies differences between two PDFs
- is always >=0
- 0 when the two distributions are the same
- not symmetric
- generally, the integral is intractable

How to compare distributions of activities?

Kullback-Leibler divergence

$$\mathrm{KL}\left[Q\left(y\right), P\left(y\right)\right] = \underbrace{-\int dy\, Q(y) \log P(y)}_{\text{cross entropy}} - \underbrace{H\left(Q(y)\right)}_{\text{entropy}}$$

cross entropy *entropy*

- quantifies differences between two PDFs
- is always >=0
- 0 when the two distributions are the same
- not symmetric
- generally, the integral is intractable

- *LNP models*: P(y) is not available, only P(y | x), therefore the stimulus ensemble has to be marginalized
- *max entropy models*: partition function for P(y) needs to be determined

Latent variable density estimator

- probabilistic model
- latent variables can account for higher-order correlations
- functional interpretation of the density estimator

Latent variable density estimator

- probabilistic model
- latent variables can account for higher-order correlations
- functional interpretation of the density estimator

$$\mathrm{KL}\left[Q\left(y\right), P\left(y\right)\right] = -\int dy\, Q(y) \log P(y) - H\left(Q(y)\right)$$

Latent variable density estimator

- probabilistic model
- latent variables can account for higher-order correlations
- functional interpretation of the density estimator

$$\mathrm{KL}\left[Q\left(y\right), P\left(y\right)\right] = -\int dy\, Q(y) \log \boxed{P(y)} - H\left(Q(y)\right)$$

- with a good choice of density estimators (directed models) it is easy to evaluate P(y)

Latent variable density estimator

- probabilistic model
- latent variables can account for higher-order correlations
- functional interpretation of the density estimator

$$\mathrm{KL}\left[Q\left(y\right),P\left(y\right)\right] = -\int dy\, Q(y) \log P(y) - H\left(Q(y)\right)$$

- with a good choice of density estimators (directed models) it is easy to evaluate P(y)
- samples can be used to evaluate a Monte Carlo integral:

$$\int dy\, Q(y) \log P(y) \approx \frac{1}{N_{\mathrm{samples}}} \sum_{i=1}^{N_{\mathrm{samples}}} \log P(y_i)\,, \qquad y_i \in Q$$

Latent variable density estimator

- probabilistic model
- latent variables can account for higher-order correlations
- functional interpretation of the density estimator

$$\mathrm{KL}\left[Q\left(y\right), P\left(y\right)\right] = -\int dy\, Q(y) \log P(y) - H\left(Q(y)\right)$$

- with a good choice of density estimators (directed models) it is easy to evaluate P(y)
- samples can be used to evaluate a Monte Carlo integral:

$$\int dy\, Q(y) \log P(y) \approx \frac{1}{N_{\mathrm{samples}}} \sum_{i=1}^{N_{\mathrm{samples}}} \log P(y_i)\,, \qquad y_i \in Q$$

- KL divergences are calculated with respect to a reference condition

$$\mathrm{KL}[P_{\mathrm{ref}}(y),\ P_1(y)] - \mathrm{KL}[P_{\mathrm{ref}}(y),\ P_2(y)] = \mathrm{CE}[P_{\mathrm{ref}}(y),\ P_1(y)] - \mathrm{CE}[P_{\mathrm{ref}}(y),\ P_2(y)]$$

Calculation of Küllback-Leibler divergence

$$\mathrm{KL}\left[Q\left(y\right), P\left(y\right)\right] = -\int dy\, Q(y) \log P(y) - H\left(Q(y)\right) =$$

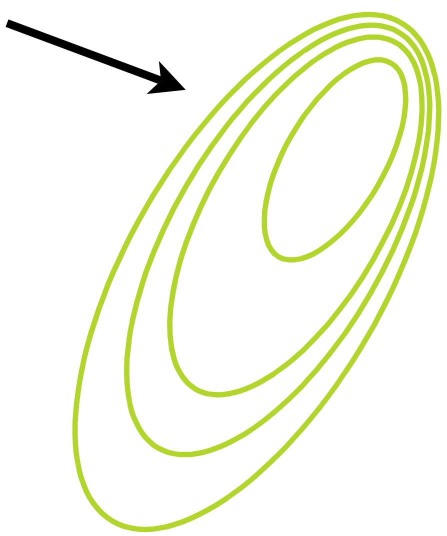
$$\mathrm{CE}\left[Q\left(y\right), P\left(y\right)\right] - H\left(Q(y)\right)$$

Calculation of Küllback-Leibler divergence

$$\mathrm{KL}\left[Q\left(y\right),P\left(y\right)\right] = -\int dy\, Q(y) \log P(y) - H\left(Q(y)\right) =$$

$$\mathrm{CE}\left[Q\left(y\right),P\left(y\right)\right] - H\left(Q(y)\right)$$

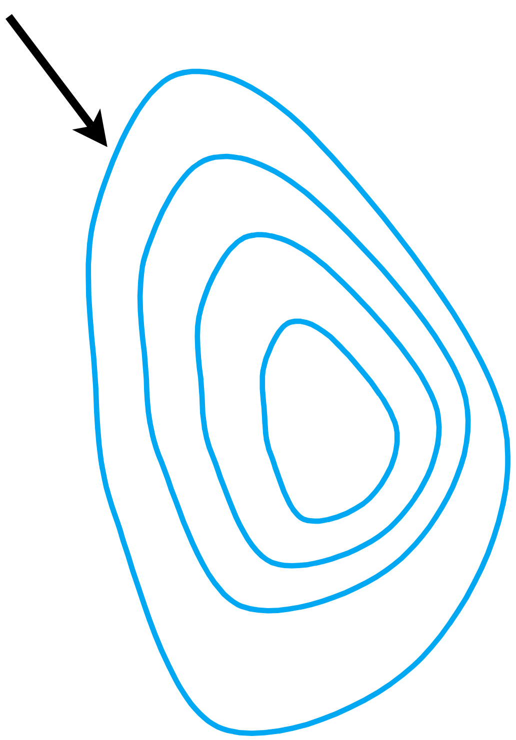
$Q(y)$



$Q(y)$ 

$P(y)$ 

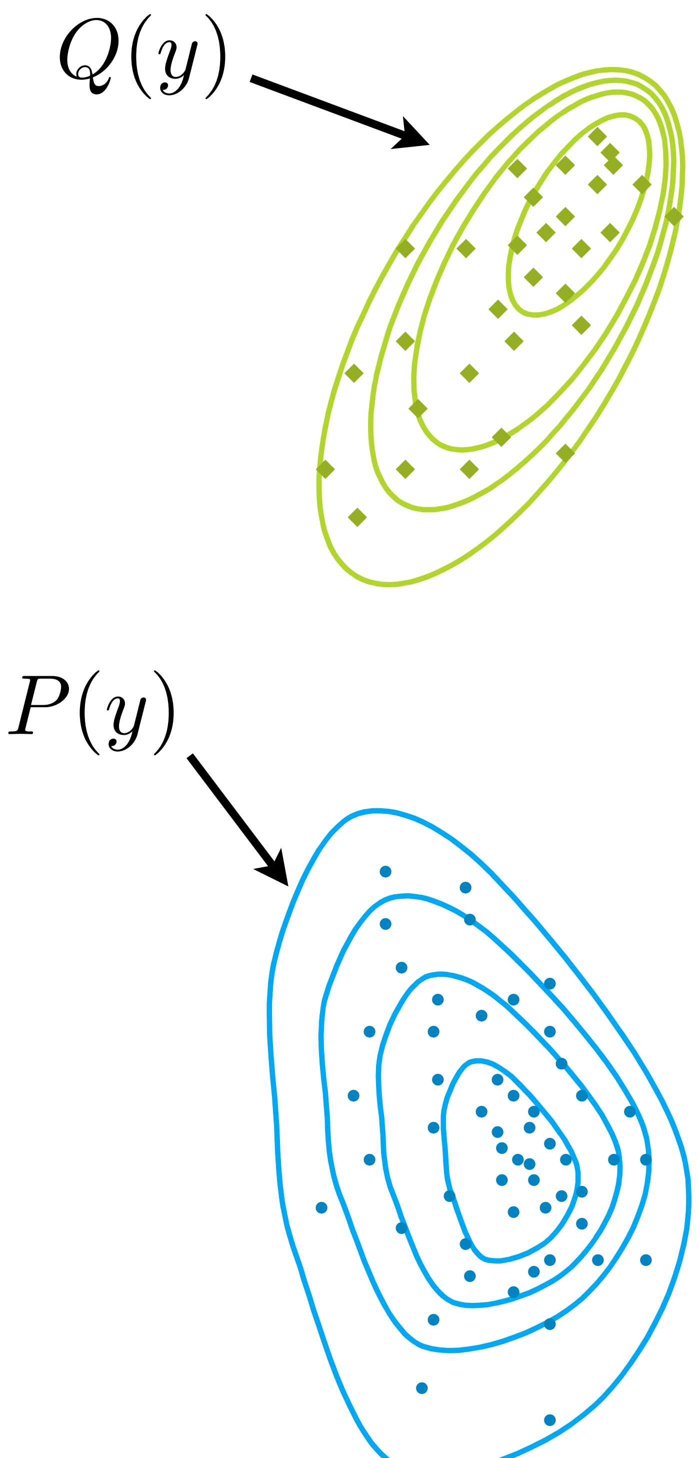
$P(y)$

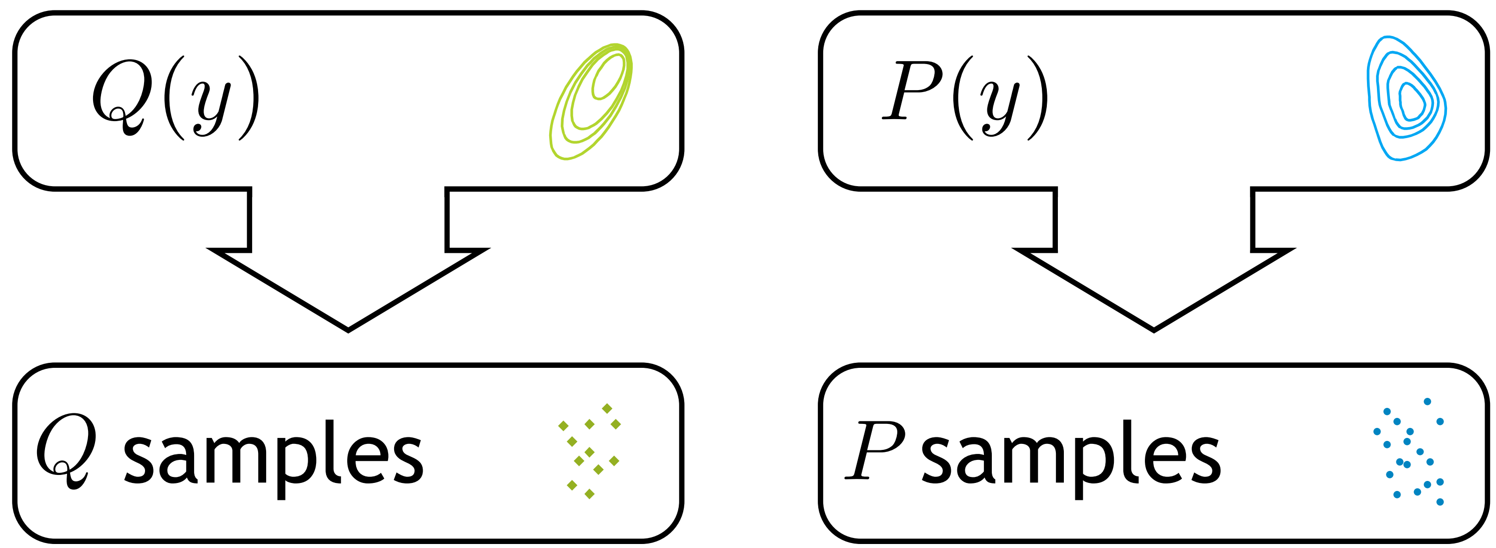


Calculation of Küllback-Leibler divergence

$$\mathrm{KL}\left[Q\left(y\right), P\left(y\right)\right] = -\int dy\, Q(y) \log P(y) - H\left(Q(y)\right) =$$

$$\mathrm{CE}\left[Q\left(y\right), P\left(y\right)\right] - H\left(Q(y)\right)$$

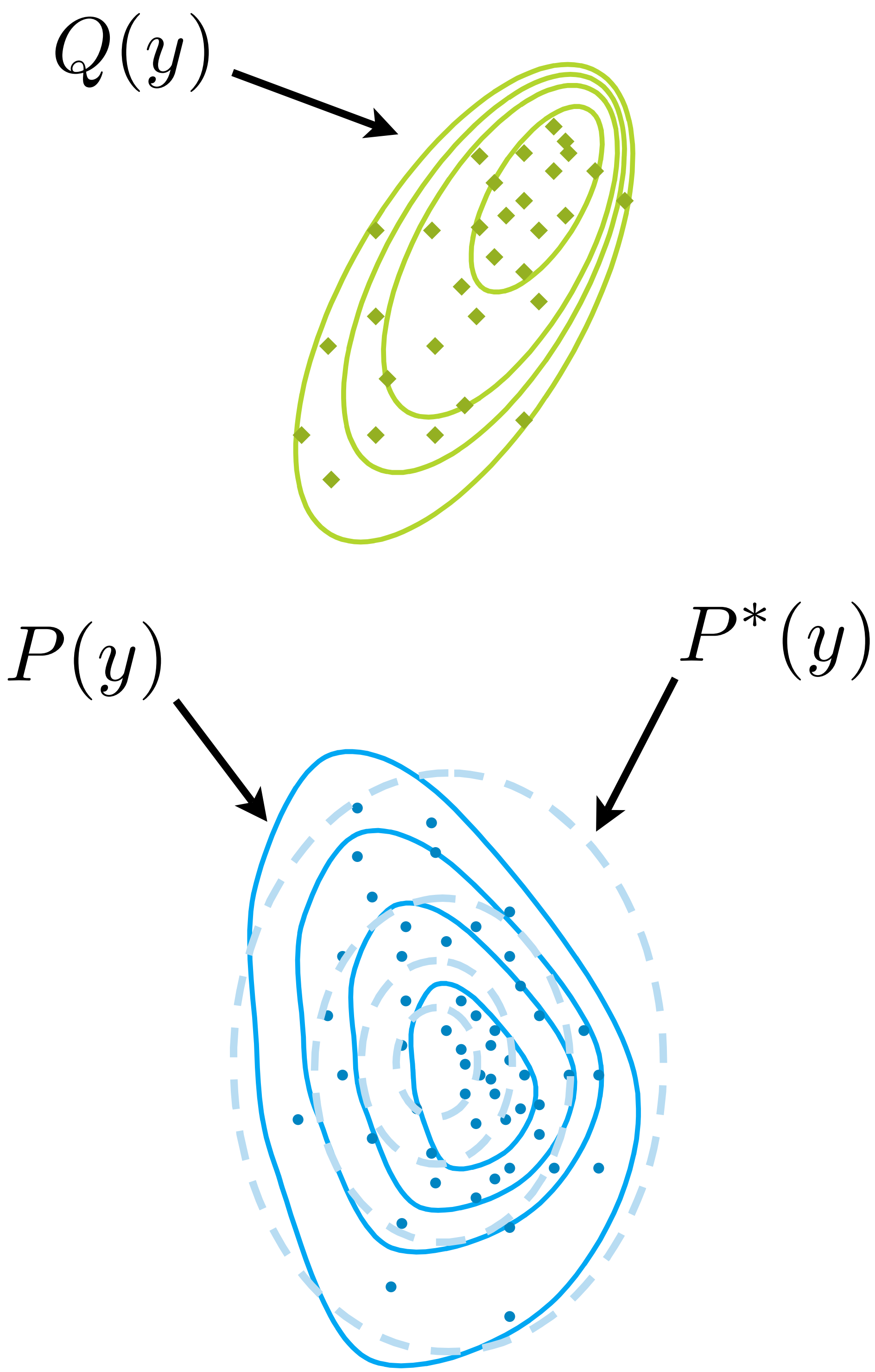


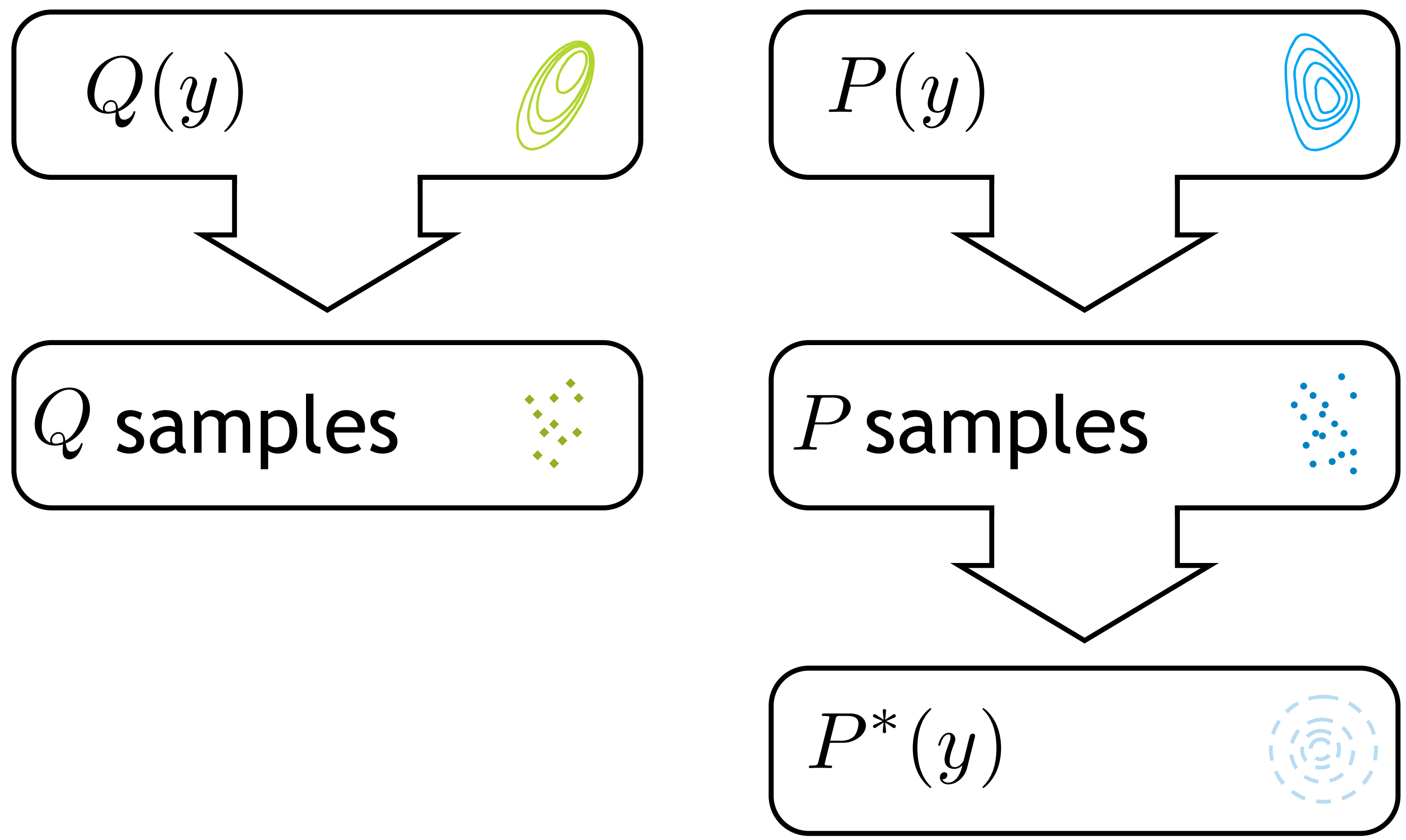


Calculation of Küllback-Leibler divergence

$$\mathrm{KL}\left[Q\left(y\right),P\left(y\right)\right]=-\int dy\,Q(y)\log P(y)-H\left(Q(y)\right)=$$

$$\mathrm{CE}\left[Q\left(y\right),P\left(y\right)\right]-H\left(Q(y)\right)$$

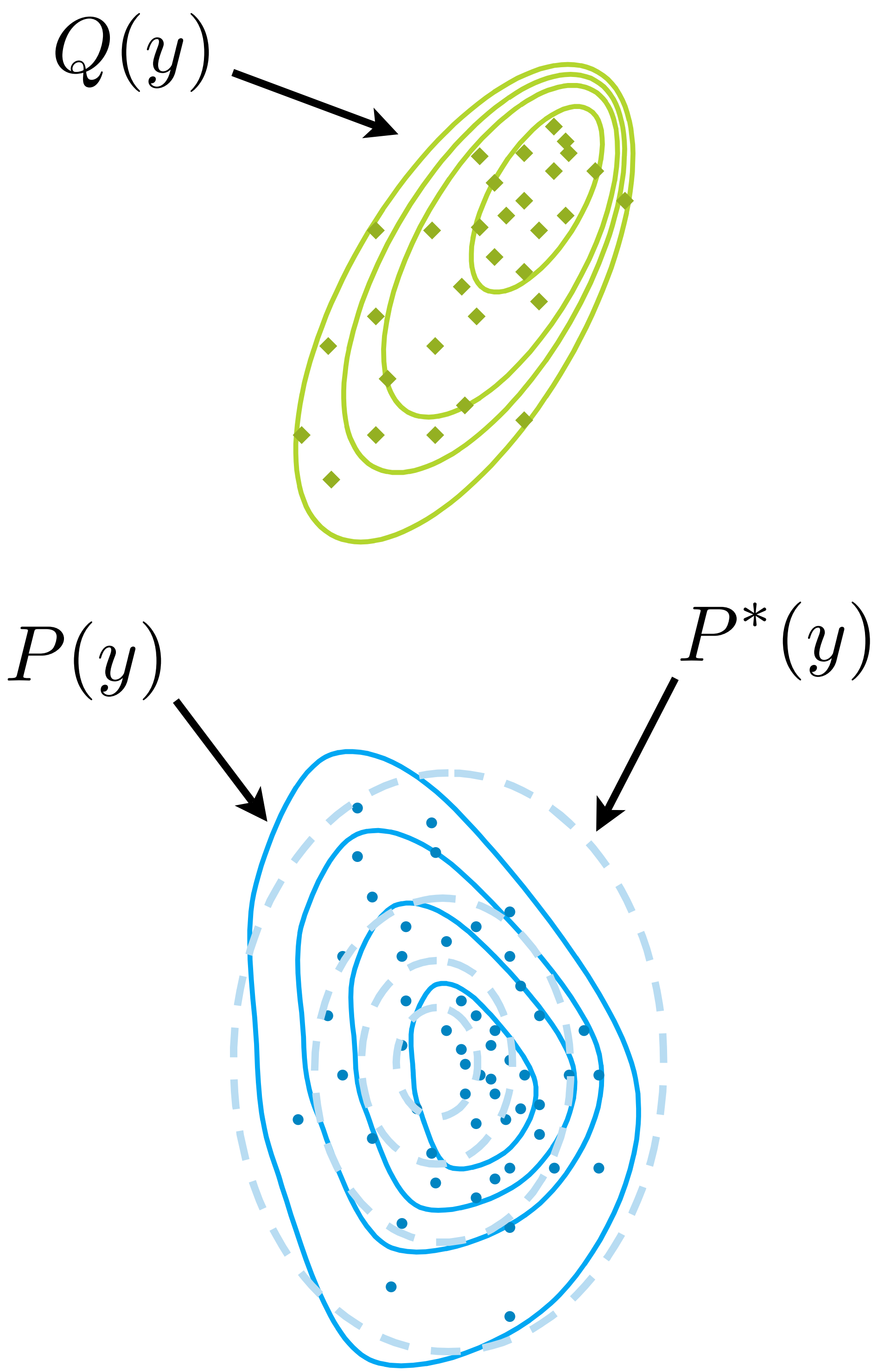


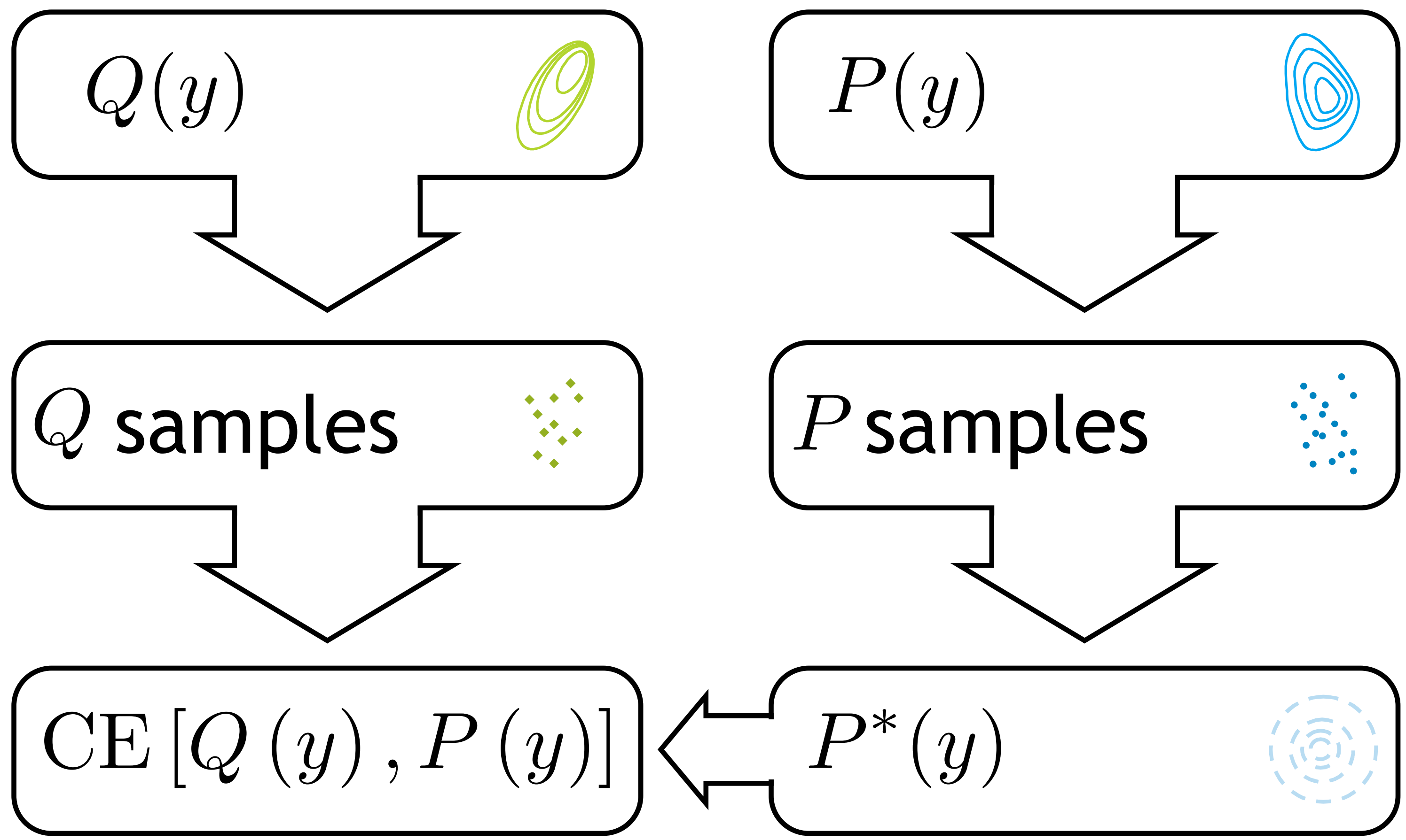


Calculation of Küllback-Leibler divergence

$$\mathrm{KL}\left[Q\left(y\right), P\left(y\right)\right] = -\int dy\, Q(y) \log P(y) - H\left(Q(y)\right) =$$

$$\mathrm{CE}\left[Q\left(y\right), P\left(y\right)\right] - H\left(Q(y)\right)$$





Demonstration on synthetic data

Evaluating SA and EA distributions

$$\underbrace{\hat{P}(y)}_{\text{spontaneous activity}} = \int \underbrace{\hat{P}(y\,|\,x)}_{\text{evoked activity}} \; \underbrace{P(x)}_{\text{stimulus statistics}} \; dx$$

Demonstration on synthetic data

Evaluating SA and EA distributions

$$\underbrace{\hat{P}(y)}_{\text{spontaneous activity}} = \int \underbrace{\hat{P}(y\,|\,x)}_{\text{evoked activity}} \; \underbrace{P(x)}_{\text{stimulus statistics}} \, dx$$

- **Prediction:** Activity evoked by *natural images* is required to be more similar to spontaneous activity than that evoked by *noise*
- CE between natural image EA and SA
noise pattern EA and SA

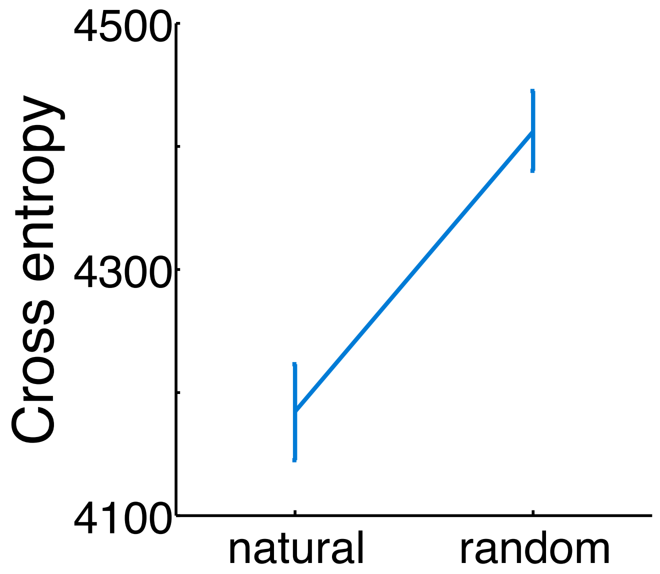
Demonstration on synthetic data

Evaluating SA and EA distributions

$$\underbrace{\hat{P}(y)}_{\text{spontaneous activity}} = \int \underbrace{\hat{P}(y\,|\,x)}_{\text{evoked activity}} \; \underbrace{P(x)}_{\text{stimulus statistics}} \; dx$$

- **Prediction:** Activity evoked by *natural images* is required to be more similar to spontaneous activity than that evoked by *noise*
- CE between natural image EA and SA
  noise pattern EA and SA

Trained model



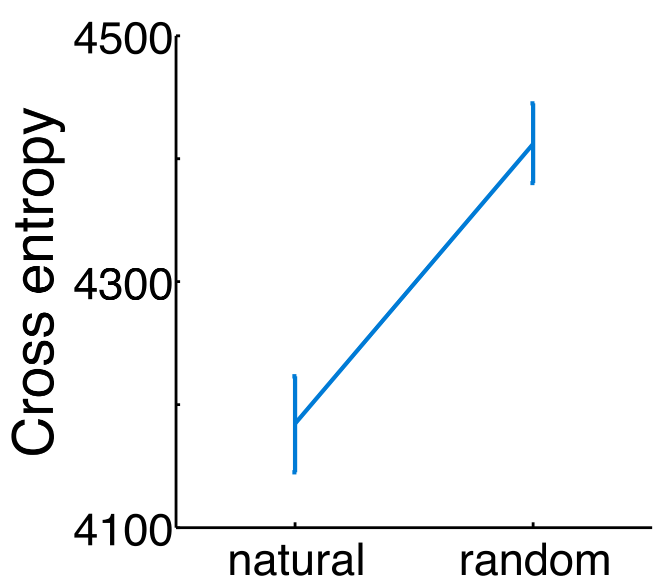
Demonstration on synthetic data

Evaluating SA and EA distributions

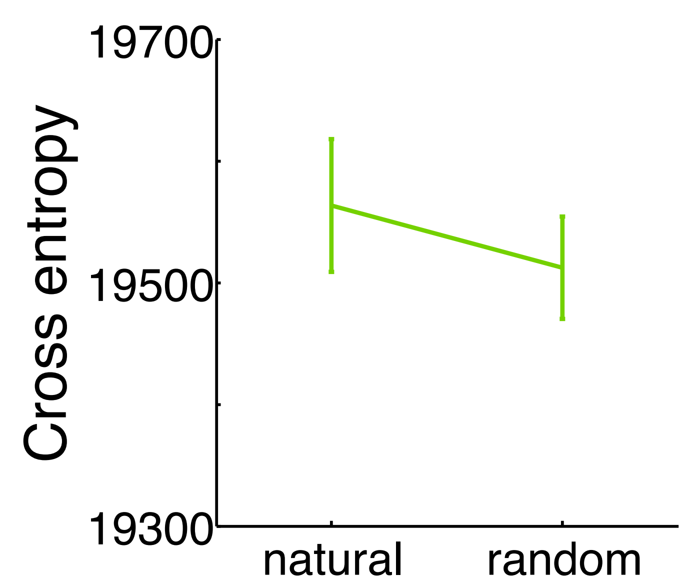
$$\underbrace{\hat{P}(y)}_{\text{spontaneous activity}} = \int \underbrace{\hat{P}(y\,|\,x)}_{\text{evoked activity}} \underbrace{P(x)}_{\text{stimulus statistics}} \, dx$$

- **Prediction:** Activity evoked by *natural images* is required to be more similar to spontaneous activity than that evoked by *noise*
- CE between natural image EA and SA
  noise pattern EA and SA

Trained model



Naive model

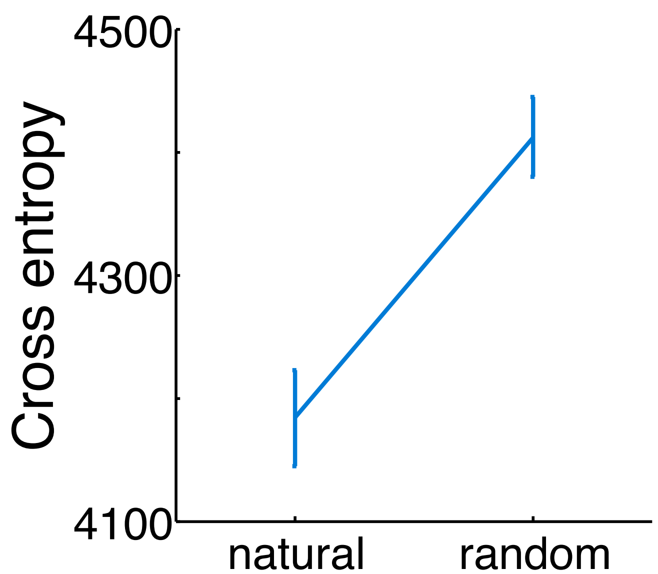


Demonstration on synthetic data
Evaluating SA and EA distributions

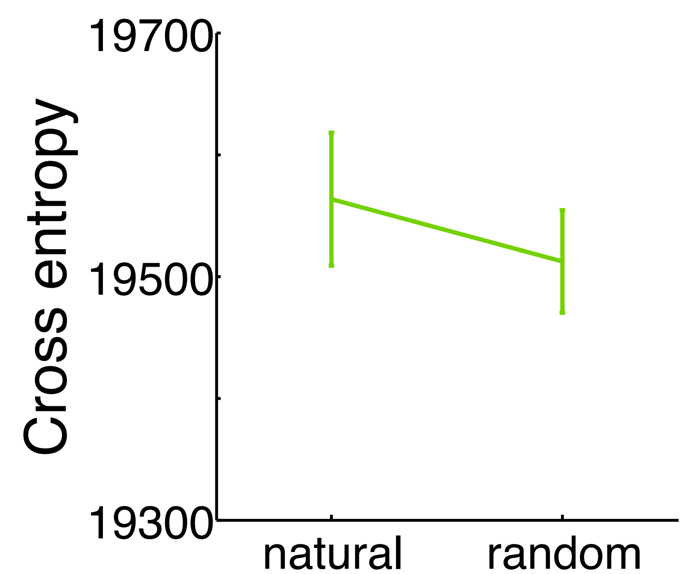
$$\underbrace{\hat{P}(y)}_{\text{spontaneous activity}} = \int \underbrace{\hat{P}(y\,|\,x)}_{\text{evoked activity}} \; \underbrace{P(x)}_{\text{stimulus statistics}} \; dx$$

- **Prediction:** Activity evoked by *natural images* is required to be more similar to spontaneous activity than that evoked by *noise*
- CE between natural image EA and SA
  noise pattern EA and SA

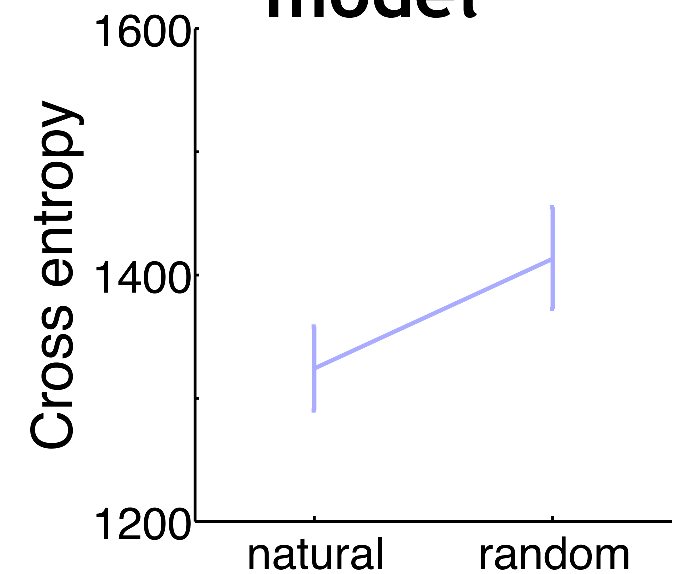
Trained model



Naive model



Partially observed model



Recorded data
EA and SA in the V1 of ferrets

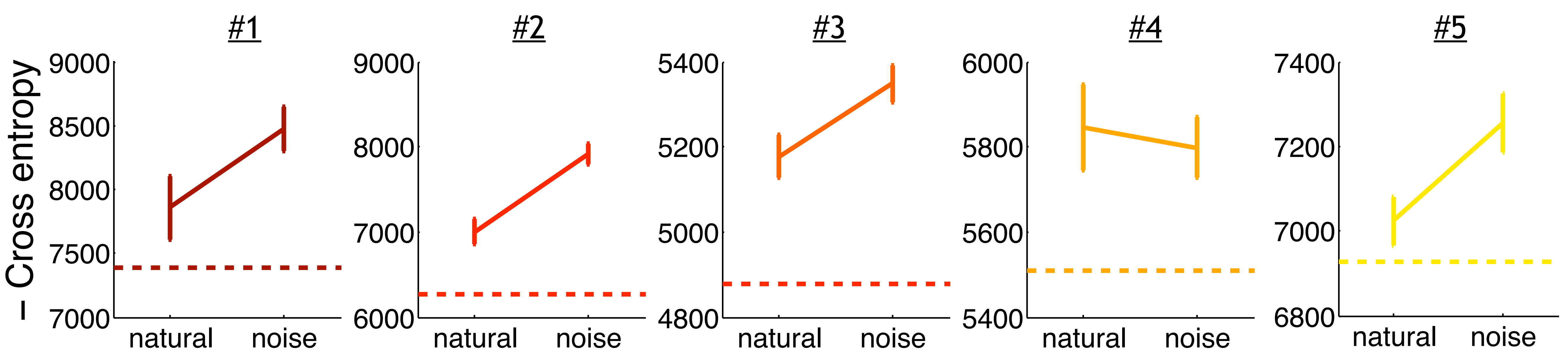
- recordings from adult behaving ferrets
- calculating CE between:
  - natural movie and dark
  - random noise and dark

Recorded data

EA and SA in the V1 of ferrets

- recordings from adult behaving ferrets
- calculating CE between:
  - natural movie and dark
  - random noise and dark

Animals (n=5)



Conclusions

- KL with latent variable density estimators provide a general framework for quantifying the similarity between neural activities
- the method works even on limited number of neurons
- analysis of data from behaving animal is consistent with model predictions
- further analysis is needed to assess whether dark condition or sleep is a better model for spontaneous activity

Acknowledgements

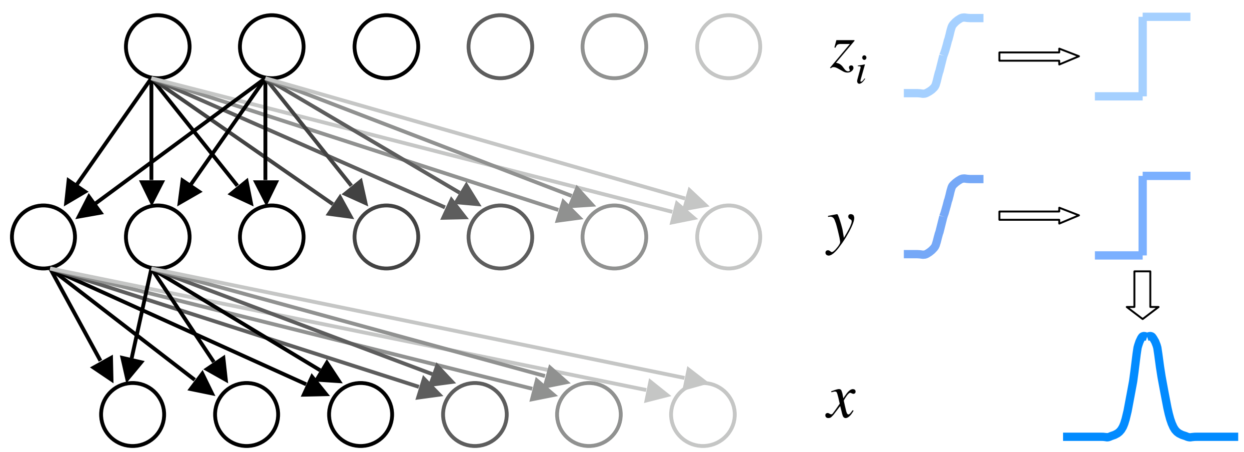
József Fiser (Brandeis University)

Pietro Berkes (Gatsby Unit, UCL)

Máté Lengyel (University of Cambridge)

Swartz Foundation

Validation on a model trained with natural images



$$P(z) = \prod_i P(z_i)$$

$$P(y|z) = \prod_j P(y_j|z)$$

$$P(x|y) = \prod_k P(x_k|y)$$

Evoked activity (EA)	$P_{\mathrm{EA}}(y\|x)$	$\int P(y\|x,z)\,P(z)\,dz \propto \int P(x\|y)\,P(y\|z)\,P(z)\,dz$
Marginalized EA	$P_{\mathrm{mEA}}(y)$	$\int P_{\mathrm{EA}}(y\|x)\,P(x)\,dx$
Spontaneous activity (SA)	$P_{\mathrm{SA}}(y)$	$\int P(y\|z)\,P(z)\,dz$