# Probabilistic models for neural data: From single neurons to population dynamics

**NEUROBIO 316QC** 

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Session 3: Generalized linear models #1

# Today

Q&A about previous session

Paper discussion (~1h)

Introducing generalized linear models (remaining time)

### Overview

### Bernoulli distribution, the exponential family & conjugate priors

Bernoulli distribution as spike generation model

Conjugate priors for the Bernoulli distribution

The exponential family of probability distributions

#### **Linear classification models**

Generative vs. discriminative models

Logistic regression: sigmoidal Bernoulli probability

Inhomogeneous Poisson process: sequence of Bernoulli events

Generalized linear models and canonical activation function

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### The Bernoulli distribution

To spike (x = 1) or not to spike (x = 0)?

$$p(x = 1|\mu) = \mu$$

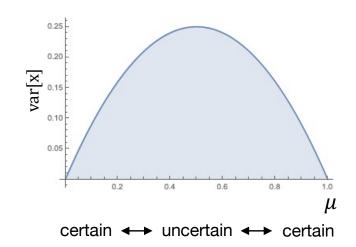
$$p(x = 0|\mu) = 1 - \mu$$

$$p(x|\mu) = \mu^{x} (1 - \mu)^{1-x}$$



#### Moments

$$E[x] = \mu$$
$$var[x] = \mu(1 - \mu)$$



## Conjugate priors

Posterior has same functional form (e.g., Gaussian) as prior

same functional form

$$p(\theta|x) \propto p(x|\theta)p(\theta)$$

depends on likelihood

### **Example: Bernoulli distribution**

$$\log p(\mu|x) = \log p(x|\mu) + \log p(\mu) + \text{const.}$$

$$= x \log \mu + (1-x) \log(1-\mu) + \log p(\mu) + \text{const.}$$

$$= x \log \mu + (1-x) \log(1-\mu) + (\alpha-1) \log \mu + (\beta-1) \log(1-\mu) + \text{const.}$$

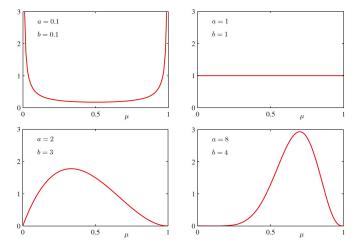
$$= \log \mu + (1-x) \log(1-\mu) + (\alpha-1) \log \mu + (\beta-1) \log(1-\mu) + \text{const.}$$
Beta distribution prior  $B(\mu|\alpha,\beta) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} \mu^{\alpha-1} (1-\mu)^{\beta-1}$ 

$$= (x + \alpha - 1) \log \mu + (1-x+\beta-1) \log(1-\mu) + \text{const.}$$

Beta distribution posterior  $B(\mu | \alpha + x, \beta + 1 - x)$ 

For multiple observations,  $x_1, x_2, ...$ :

$$\tilde{\alpha} = \alpha + \sum_{n} x_{n}$$
 $\tilde{\beta} = \beta + \sum_{n} (1 - x_{n})$ 



## The exponential family of distributions

base measure natural parameters 
$$p(\boldsymbol{x}|\boldsymbol{\eta}) = h(\boldsymbol{x})g(\boldsymbol{\eta}) \exp(\boldsymbol{\eta}^T\boldsymbol{u}(\boldsymbol{x}))$$
 normalizer sufficient statistics

Base measure: density  $p(x|\eta) = h(x)$  for  $\eta = 0$ 

Normalizer: ensures  $\int p(x|\eta) dx = 1$ 

Sufficient statistics: consider i.i.d. data  $x_1, ..., x_N$ 

$$p(\mathbf{x}_{1:N}|\mathbf{\eta}) \propto_{\mathbf{\eta}} g(\mathbf{\eta})^N \exp\left(\mathbf{\eta}^T \sum_{n=1}^N u(\mathbf{x}_n)\right)$$

summarizes what  $x_{1:N}$  tells us about  $\eta$ 

Fisher-Darmois-Koopman-Pitman theorem: (finite) sufficient statistics only exist for exponential family

Conjugate prior: follows directly from form of exponential familty

Instances: Bernoulli, Beta, Gaussian, Poisson, Laplace, ...

Mixture models are not members of the exponential family

## Interim summary: Bernoulli distribution & exponential family

Bernoulli distribution: models binary events (e.g., spike/no spike in small time window)

Conjugate priors: posteriors have same functional form

Including information from likelihood: updating distribution parameters

Beta distribution is conjugate prior for Bernoulli probability

Exponential family: large family of probability distributions

Only family that can efficiently summarize information from data (i.e., finite suff. stats)

Members: Bernoulli Gaussian, Poisson, Exponential, Laplace, ...

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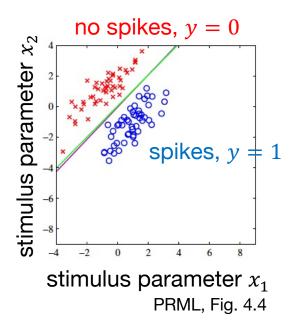
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### Linear models for classification



Standard linear model?

$$y = \mathbf{w}^T \mathbf{x} + \eta$$

Better: non-linear linear model, s.t.  $y \in \{0,1\}$ 

$$y = 1$$
 if  $\mathbf{w}^T \mathbf{x} + \eta > \theta$ ,  $y = 0$  otherwise

leads to

$$p(y=1|\mathbf{x},\mathbf{w})=f(\mathbf{w}^T\mathbf{x})$$

**Generative model**: specify p(x|y, w), i.e., distribution over stimuli to generate spike  $p(y|x, w) \propto p(x|y, w)p(y)$ 

provides full model of stimulus distribution (many parameters, might be hard to learn)

**Discriminative model**: specify p(y|x, w), i.e., spike probabilities given stimulus Does not a-priori model stimulus distribution (fewer parameters, might be easier to learn)

They are related by Bayes' rule! (one implicitly determines part of the other)

### Discriminative linear models

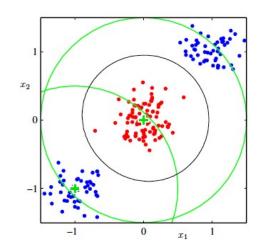
Monotonically increasing activation/link function  $f(\cdot)$ : y=1 if  $w^Tx+\eta>\tilde{\theta}$  (noisy) **linear threshold in** x

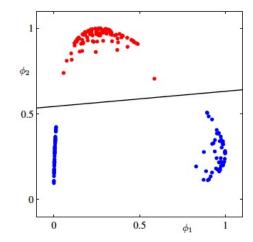
(Non-linear) linear in parameters, not 'inputs'

as for linear models, can use non-linear functions  $\Phi(x)$  of input

$$p(y = 1 | x, w) = f(w^T \Phi(x))$$

Non-linear functions can make (linear) non-discriminable data discriminable





# Logistic regression

Assumes log-odds linear in x (or  $\Phi(x)$ )

log-posterior ratio

log-likelihood ratio (LLR)

$$\log \frac{p(y=1|x,w)}{p(y=0|x,w)} = \log \frac{p(x|y=1,w)}{p(x|y=0,w)} + \log \frac{p(y=1)}{p(y=0)} \equiv a(x,w)$$

leads to

$$p(y = 1 | \mathbf{x}, \mathbf{w}) = \frac{1}{1 + e^{-a(\mathbf{x}, \mathbf{w})}} \equiv \sigma(a(\mathbf{x}, \mathbf{w}))$$
logistic sigmoid

 $\sigma(a)$ 

Assuming Gaussian likelihoods, 
$$p(x|y) = N(x|\mu_y, \Sigma)$$
  $a(x, w) = -\frac{1}{2}(\mu_0 - \mu_1)^T \Sigma^{-1} x + \text{const.}$  
$$p(y = 1|x, w) = \frac{1}{1 + e^{-w^T x}}$$

In general: compatible with any generative model for which LLR  $\sim w^T x + \text{const.}$ 

## Moving to spike trains

Logistic regression: for individual spikes in small time bins (spike or no spike?)

Assume spike train  $y_{1:N}$  with i.i.d. Bernoulli probabilities,  $p(y_n|\mathbf{x}_n,\mathbf{w}) = \lambda(\mathbf{x}_n,\mathbf{w})\delta t$  (very)small time bin

$$\begin{split} \log p(y_{1:N}|\boldsymbol{x}_{1:N}) &= \sum_{n} y_n \log \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t + \sum_{n} (1 - y_n) \log (1 - \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t) \\ &\approx \sum_{n} y_n \log \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t - \sum_{n} (1 - y_n) \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t \\ &= \sum_{n} y_n (\log \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t + \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t) - \sum_{n} \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t \\ &\approx \sum_{n} y_n \log \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t - \sum_{n} \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t - \sum_{n} \log y_n! \end{split} \quad \begin{cases} |\log \lambda \delta t| \gg |\lambda \delta t| \\ |\log y_n! = 0 \end{cases}$$

$$= \log \prod_{n} \operatorname{Pois}(y_n | \lambda(\boldsymbol{x}_n, \boldsymbol{w}) \delta t)$$

time-discretized inhomogeneous Poisson process

## Properties of the (in)homogeneous Poisson process

Derivable from i.i.d. Bernoulli probabilities: spiking only depends on instantaneous rate  $\lambda$ , otherwise independent across time

More generally: spike counts of any two non-overlapping time periods are independent

Spike count within any time interval is distributed by a Poisson distribution

Within any small time-interval  $\delta t$  with instantaneous rate  $\lambda_t$ : Spike count N satisfies  $\mathrm{E}[N] = \lambda_t \delta t$  and  $\mathrm{var}[N] = \lambda_t \delta t$ ; Fano factor  $= \frac{\mathrm{var}[N]}{\mathrm{E}[N]} = 1$ 

### Special case: homogeneous Poisson process ( $\lambda_t = \text{const.}$ )

Within any time interval  $\Delta$ : spike count N has distribution  $N \sim \text{Pois}(\lambda \Delta)$  Expected number of spikes in that interval are  $E[N] = \lambda \Delta$ 

Inter-spike interval have exponential distribution

## The exponential family and canonical activation functions

**Linear regression**: Gaussian noise + identity activation function, f(x) = x

$$\log p(y_{1:N}|\mathbf{x}_{1:N},\mathbf{w}) \propto -\sum_{n} (\mathbf{w}^{T} \mathbf{\Phi}(\mathbf{x}_{n}) - y_{n})^{2}$$

gradient for single n:

$$\nabla_{w} \log p(y_{n}|\mathbf{x}_{n}, \mathbf{w}) \propto -(\mathbf{w}^{T} \mathbf{\Phi}(\mathbf{x}_{n}) - y_{n}) \mathbf{\Phi}(\mathbf{x}_{n})$$
estimate target

**Logistic regression**: Bernoulli noise + sigmoidal activation function,  $f(x) = \sigma(x)$ 

$$\log p(y_{1:N}|\boldsymbol{x}_{1:N}, \boldsymbol{w}) = \sum_{n} y_n \log \sigma(\boldsymbol{w}^T \boldsymbol{\Phi}(\boldsymbol{x}_n)) + (1 - y_n) \log \left(1 - \sigma(\boldsymbol{w}^T \boldsymbol{\Phi}(\boldsymbol{x}_n))\right)$$
ant for single  $n$ :

gradient for single n:

$$\nabla_{w} \log p(y_{n}|x_{n}, w) = -(\sigma(\mathbf{w}^{T} \mathbf{\Phi}(\mathbf{x}_{n})) - y_{n}) \mathbf{\Phi}(\mathbf{x}_{n})$$
estimate target

**Poisson regression**: Poisson noise + exponential activation function,  $f(x) = e^x$ 

Same gradient form: supports the same Iterated Recursive Least Squares (IRLS) algorithm **Generally**: likelihood  $p(y_n|x_n, w)$  determines *canonical* activation function (RPML 4.3.6)

## Interim summary

Generative and discriminative linear models are related by Bayes' rule

Discriminative logistic regression assumes generative log-likelihood ratio (LLR) linear in w

Inhomogeneous Poisson processes = Bernoulli spikes with probability rate  $\times \delta t$ Assume spikes independent across time (conditional on rate)

Exponential family distributions have canonical activation function that support IRLS Poisson regression has exponential activation function

# Summary

Bernoulli distribution: simple model for instantaneous spiking

Assuming i.i.d. Bernoulli spikes in small time windows  $\delta t$ : Inhomogeneous Poisson process, instantaneous rate = spike probability /  $\delta t$ 

Exponential family: large family of probability distributions with convenient properties

- conjugate prior: easily parameter updates
- ability to summarize data in finite sufficient statistics for parameter inference

Linear models for classification Generative vs. discriminative models Logistic regression: discriminative model assuming LLR linear in  $\Phi(x)$ 

Generalized linear models Likelihood function & canonical activation function Includes linear regression, logistic regression, Poisson regression, etc.

### Until next week

Read paper and prepare presentation (see notes for Session 4)

Read statistical methods sections (see notes for Session 4)

#### **Next session**

Q&A for previous session (~15min)

Paper discussions (~1h)

Generalized linear models, graphical models & state space models (~30min)