Characterizing neural dependencies with Poisson copula models

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Introduction

- The activities of individual neurons in cortex and many other areas of the brain are often well described by Poisson distributions
- Neurons display strong dependencies due to common input and network connectivity
- We introduce copula models as a principled, parametric method to combine Poisson marginals into a joint distribution with desired dependencies.

What is a copula model?

Copulas provide a way to model a joint distribution by specifying the marginal distribution and the dependency structure separately.

Definition: A copula C is a multivariate distribution over the unit cube with uniform marginals.

Sklar’s theorem (1959): Given u₁,..., uₙ random variables with continuous distribution functions F₁,...,Fₙ and joint distribution F, there exists a unique copula C such that for all x:

\[ C(u₁,...,uₙ) = F(F₁⁻¹(u₁),...,Fₙ⁻¹(uₙ)) \]

Conversely, given any distribution functions F₁,...,Fₙ and copula C:

\[ F(u₁,...,uₙ) = C(F₁(u₁),...,Fₙ(uₙ)) \]

is a n-variate distribution function with marginal distribution functions F₁,...,Fₙ.

Select marginal distributions (copula)

Select dependency structure (copula)

Key idea: Every distribution can be transformed into a uniform distribution between 0 and 1 using its cdf.

Copulas also provide a principled way to quantify dependencies that go beyond correlation coefficients (which are only appropriate for elliptical distributions), and are applicable to the problem of estimating the mutual information between stimulus and response, as discussed in (Jenison & Reale, 2004).

Copulas zoo

Gaussian dependency structure, different marginals

Gaussian marginals, different dependency structures

Modeling neural dependencies

- We propose to fit parametric families of copula models to joint neural activity by Maximum Likelihood estimation
- Different copula families are able to capture dependencies of different kinds. The selection of an appropriate parametric family for the copula distribution can be addressed by cross-validation

Dealing with discrete marginals: Learning a copula model with discrete marginals requires care, because the cdf maps a city to a finite set of points in the copula space (Genest & Næs, 2007). Our strategy is to derive a generative model on the data and integrate over the uniform marginals.

Kinds of neural dependency

Description of neural data

We analyzed pairwise dependencies in 36 neurons simultaneously recorded using a 100-electrode silicon array from the arm area of area M1 of a monkey. Neural activity and hand kinematics were recorded for several minutes during a tracking task (Samora et al., 2002), and collected in 70 ms bins.

We modeled the marginal distributions of neuronal firing rates using Poisson distributions and fitted copula dependency models using our Maximum Likelihood method. Two thirds of the data (3531 bins, approx. 247 sec) was used for training, and the remaining third was kept for cross-validation.

We considered a total of ten copula families (Gauss, Student-t, Clayton and associated copulas, Gumbel, Frank, and the two-parameter family BB1). Based on cross-validation and redundancies between the copulas, we selected four families that consistently fit the data better.

Clayton copula

Negative Clayton copula

Clayton survival (UI) copula

Frank copula

Future work - LNP-copula models: Preliminary results show that after fitting a Linear-Nonlinear-Poisson (LNP) model to the data, there are residual dependencies that can be captured by copula models.

References