# Characterizing neural dependencies with Poisson copula models

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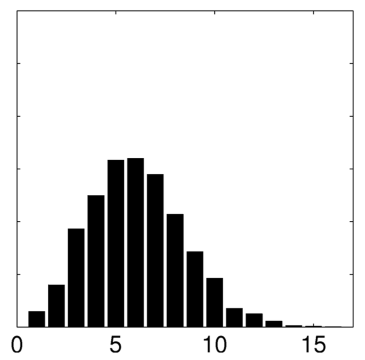
## Introduction

- 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

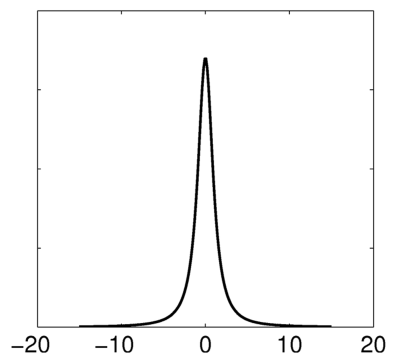
### What is a copula model?

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

**Select marginal distributions**

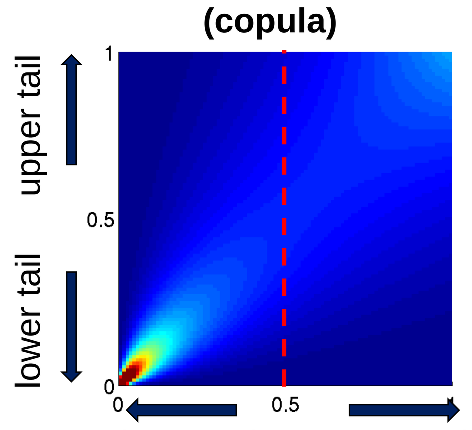


Poisson pdf



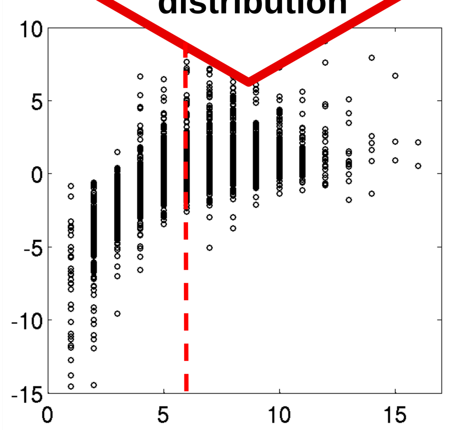
Student-t pdf

**Select dependency structure (copula)**




**Combine to obtain the joint distribution**

Correlation coefficient in the lower part of the distribution = **0.60**



Correlation coefficient in the upper part of the distribution = **0.07**

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

**Sklar's theorem (1959):** *Given* $u_1, \ldots, u_n$ *random variables with* continuous *distribution functions* $F_1,\ldots,F_m$ *and joint distribution* F, *there exists a unique copula* C *such that for all x:*

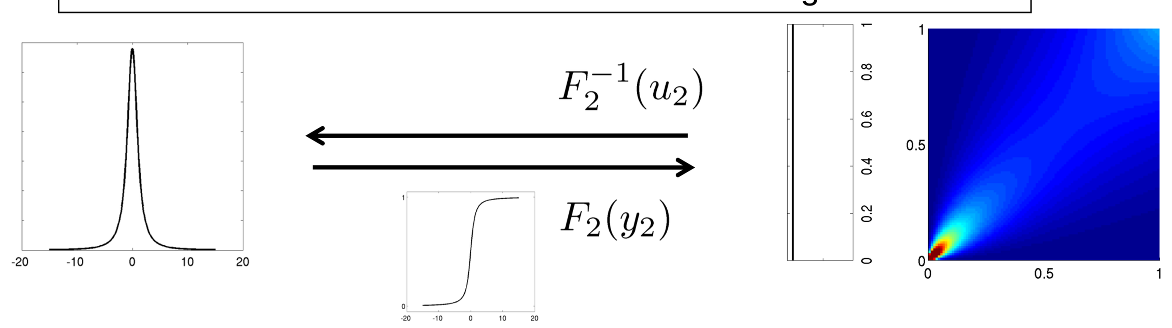
$$C(u_1, \ldots, u_n) = F(F_1^{-1}(u_1), \ldots, F_m^{-1}(u_m))$$

*Conversely, given any distribution functions* $F_1,\ldots,F_m$ *and copula* C,

$$F(y_1, \ldots, y_n) = C(F_1(y_1), \ldots, F_n(y_n))$$

*is a n-variate distribution function with marginal distribution functions* $F_1, \ldots, F_m$.

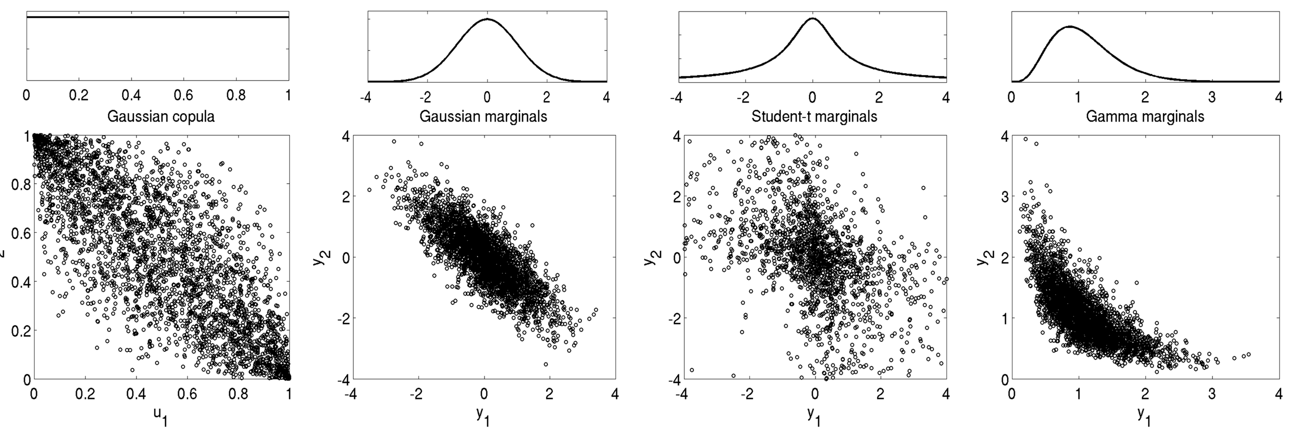
**Key idea:** Every distribution can be transformed into a uniform distribution between 0 and 1 using its cdf



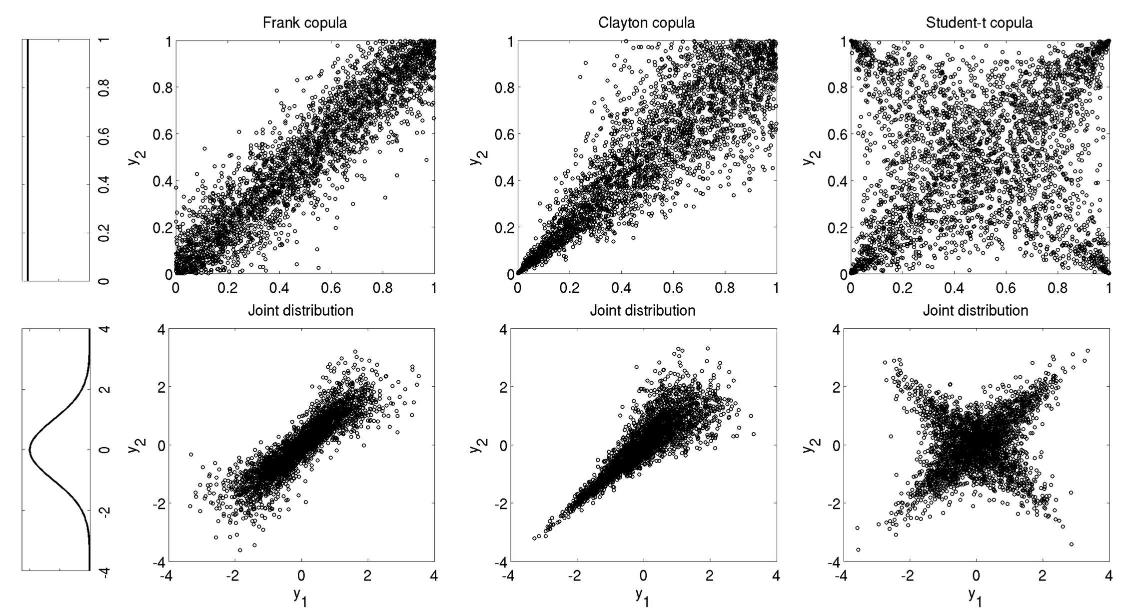

Copulas also provide a principled way to quantify dependencies that go beyond correlation coefficients (which are only appropriate for elliptical distributions), in a manner that is independent of rescaling of individual variables (Nelsen, 1999) and are applicable to the problem of estimating the mutual information between stimulus and response, as discussed in (Jenison & Reale, 2004).

## Copulas zoo

**Gaussian dependency structure, different marginals**



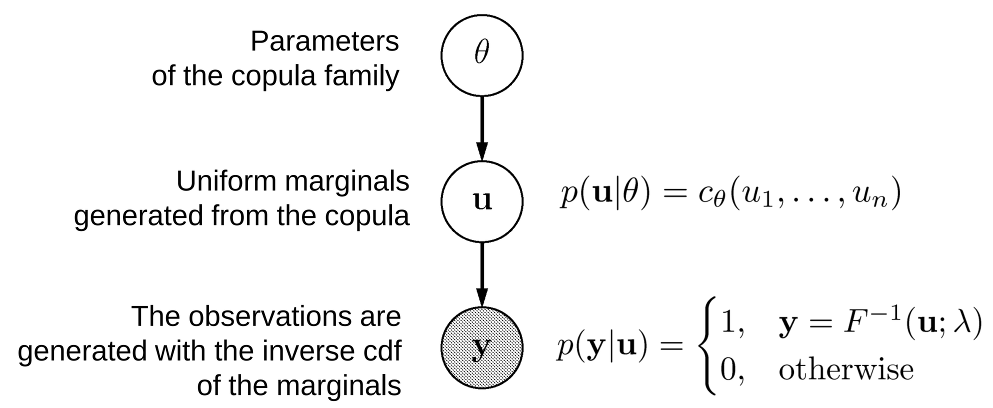

**Gaussian marginals, different dependency structures**




## 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 data to a finite set of points in the copula space (Genest & Naslehova, 2007). Our strategy is to derive a generative model on the data and **integrate** over the uniform marginals:




Likelihood function:

$$p(\mathbf{y}|\theta) = \int p(\mathbf{y}|\mathbf{u},\theta)p(\mathbf{u}|\theta)\,\mathrm{d}\mathbf{u} = \int_{F_1(y_1-1)}^{F_1(y_1)} \cdots \int_{F_n(y_n-1)}^{F_n(y_n)} c_\theta(u_1, \ldots, u_n)\,\mathrm{d}\mathbf{u}$$

For example, in the bivariate case:

$$p(\mathbf{y}|\theta) = C_\theta(F_1(y_1), F_2(y_2)) + C_\theta(F_1(y_1-1), F_2(y_2-1)) - C_\theta(F_1(y_1-1), F_2(y_2)) - C_\theta(F_1(y_1), F_2(y_2-1))$$

Estimation is unbiased for a wide range of parameters.

## Kinds of neural dependency

**Description of neural data**

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

We modeled the marginal distributions of neuronal firing rate using Poisson distributions and fitted copula dependency models using our Maximum Likelihood method.

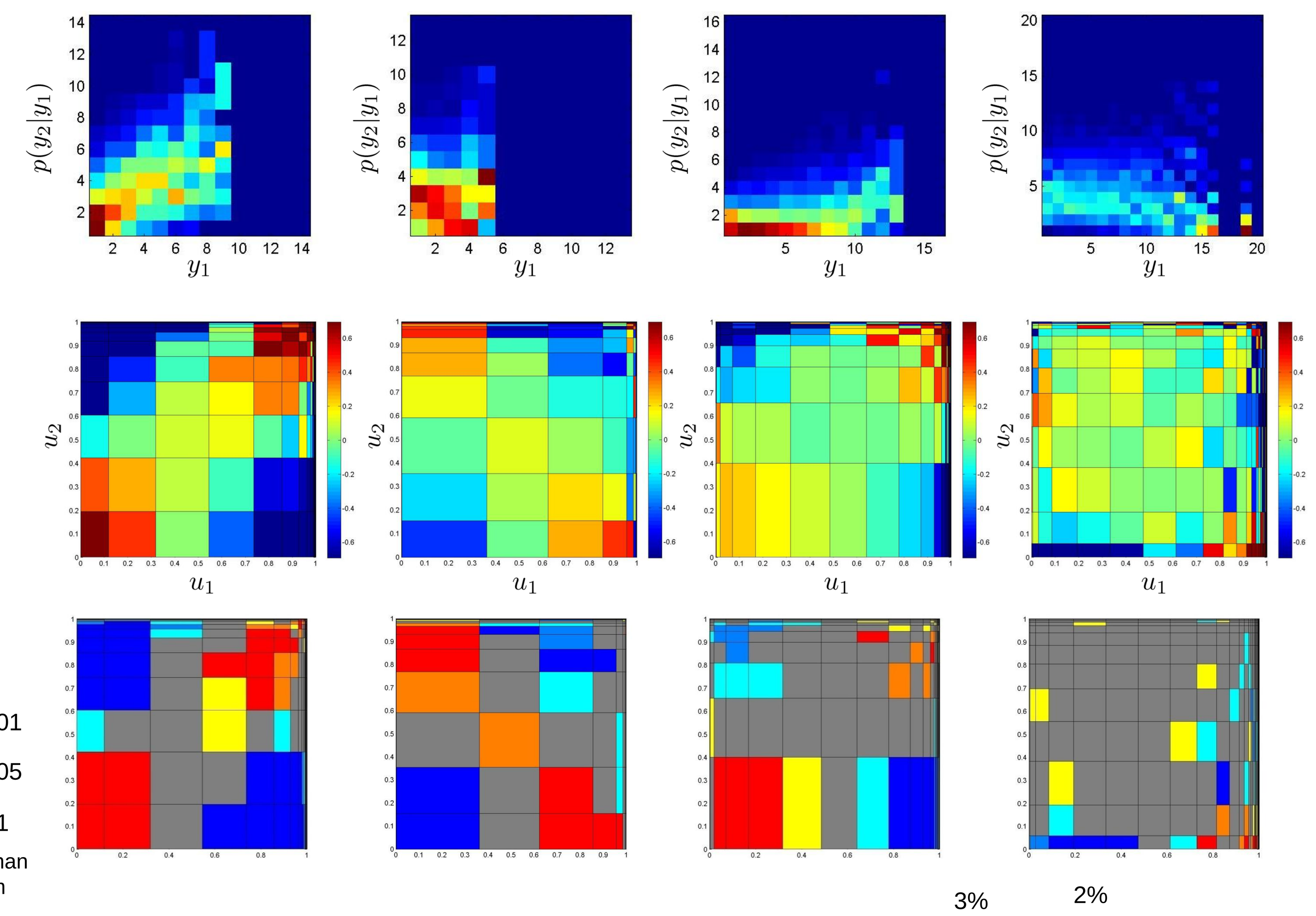
Two third of the data (3531 bins, approx. 247 sec) was used for training, and the remaining third was kept for cross validation.

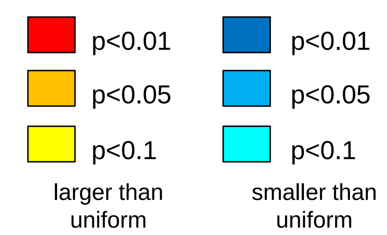
| | Positive dependency | Negative dependency | Upper tails dependency | Upper –lower tails dependency |
|---|---|---|---|---|

**Conditional histograms** of neural activity

**Empirical copulas** (colors represent deviations from uniformity and thus independency)

**Empirical copulas** (colors represent significance levels)

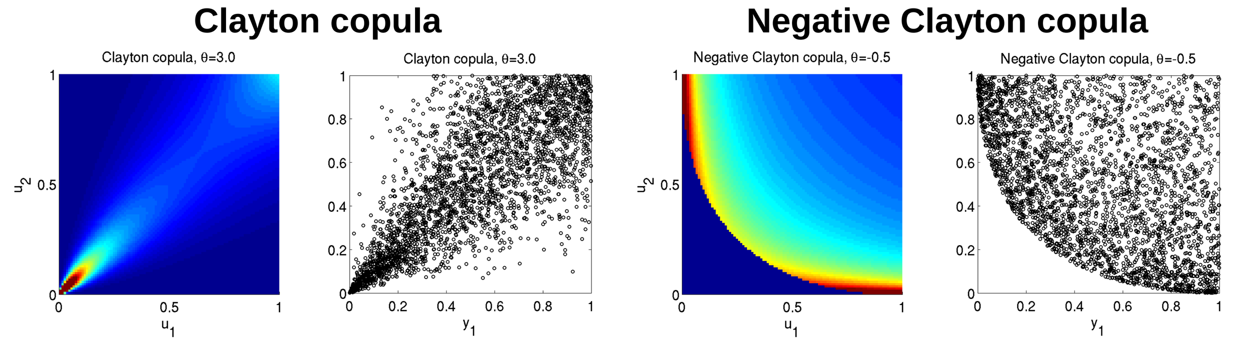





We considered a total of ten copula families (Gauss, Student-t, Clayton and associated copulas, Gumbel, Frank, and the two-parameter family BB1). Based on cross-validation and redundancies between the copulas, we selected four families that consistently fit the data better.

**Clayton copula**

**Negative Clayton copula**

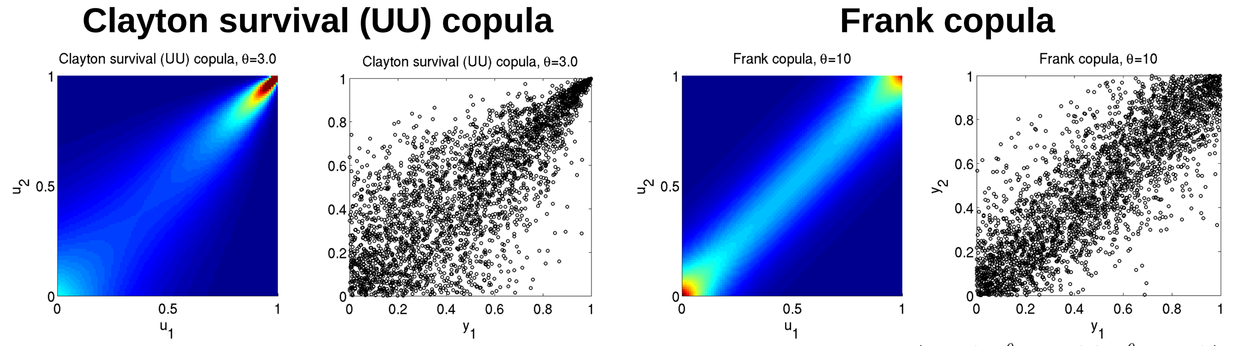



$$C_\theta^{Cl}(u_1, u_2) = (u_1^{-\theta} + u_2^{-\theta} - 1)^{-1/\theta}$$

$$C_\theta^{Neg}(u_1, u_2) = max\{(u_1^{-\theta} + u_2^{-\theta} - 1), 0\}^{-1/\theta}, \theta < 0$$

**Clayton survival (UU) copula**

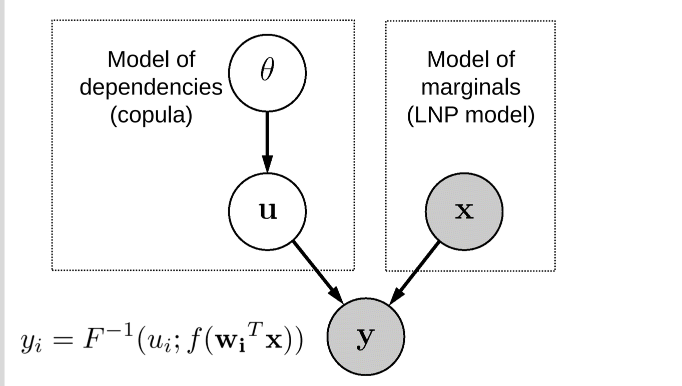
**Frank copula**

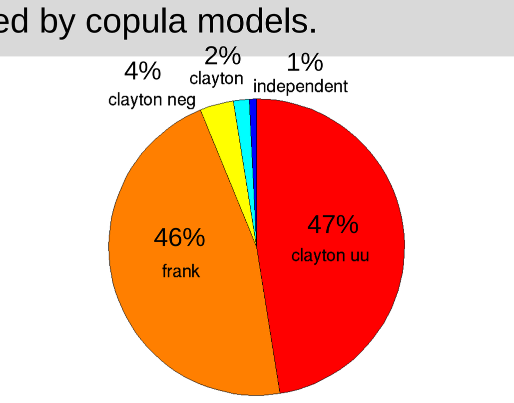



$$C_\theta^{UU}(u_1, u_2) = u_1 + u_2 - 1 + C_\theta^{Cl}(1-u_1, 1-u_2)$$

$$C_\theta^{Fr}(u_1, u_2) = -\frac{1}{\theta}\ln\left(1 + \frac{(e^{-\theta u_1} - 1)(e^{-\theta u_2} - 1)}{e^{-\theta} - 1}\right)$$

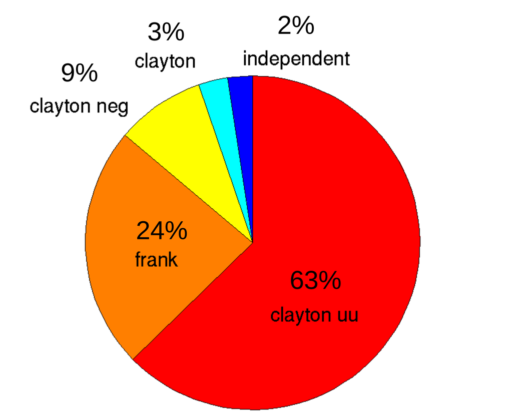
**Future work - LNP-copula models**: Preliminary results show that after fitting a Linear-Nonlinear-Poisson (LNP) model to the data, there are residual dependencies that can be captured by copula models.



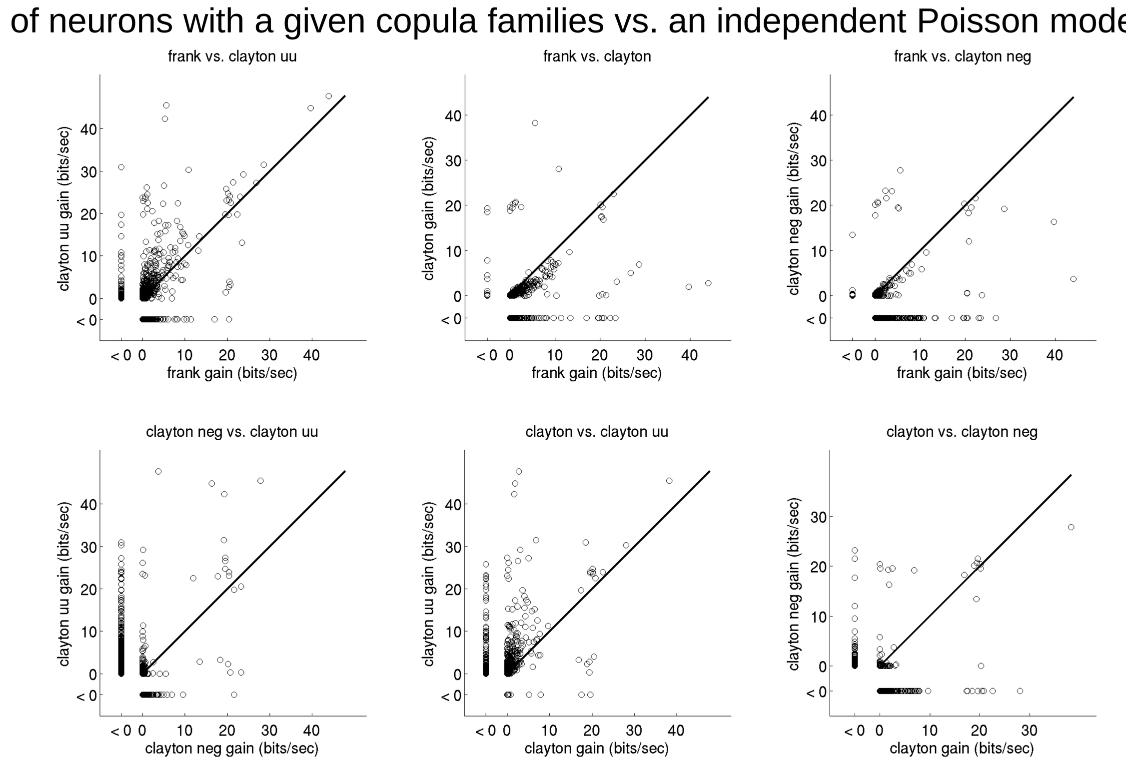

Percentage of pairs best fitted by the different copula families (630 total pairs)

What dependencies can be found between pairs of neurons in M1? **Most neurons show dependencies in the upper tails of their distributions**, and only limited dependency when the firing rate is low.




Percentage of pairs best fitted by the different copula families (630 total pairs)

Number of bits per second gained by considering the dependencies between pair of neurons with a given copula families vs. an independent Poisson model:

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