# Transfer entropy for population data. 

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Edinburgh, June 2022

## Thanks for the invitation



## Populations - Neurons - Behaviours



## What is this talk about

First we'll discuss estimating mutual information and then we'll discuss estimating transfer entropy.

## Shannon's entropy

$$
H(X)=-\sum_{x} p(x) \log _{2} p(x)
$$

## Shannon's entropy

| $1 / 2$ | $1 / 4$ | $1 / 8$ | $1 / 16$ | $1 / 32$ | $1 / 64$ | $1 / 128$ | $1 / 128$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 000 | 001 | 010 | 011 | 100 | 101 | 110 | 111 |
| 0 | 10 | 110 | 1110 | 11110 | 111110 | 1111110 | 111111 |

average code length $=\frac{1}{2}+\frac{1}{4} 2+\frac{1}{8} 3+\frac{1}{16} 4+\ldots=H(X) \approx 1.98<3$

## Mutual information



## Mutual information



## Mutual information



## Mutual information

Mutual information is the true way we measure the relationship between variables; but we ignore it because it is so hard to estimate.

## Classical approach

- Discretize.

- Split into words.

$$
010001000000100 \rightarrow 01000,10000,00100
$$

## Classical approach

- Estimate probability of words. For example, say $w_{8}=01000$ then estimate

$$
p\left(w_{8}\right) \approx \frac{\# \text { occurrences of } w_{8}}{\# \text { words }}
$$

- Calculate

$$
H(W)=-\sum_{i} p\left(w_{i}\right) \log _{2} p\left(w_{i}\right)=-\left\langle\log _{2} p\left(w_{i}\right)\right\rangle
$$

## ms scale information in blow fly spike trains.



Bialek, de Ruyer van Steveninck, Strong and other coworkers, late 1990s.

## Difficulties with the classical approach.

- Undersampling.
- 100 ms words and 2 ms bins gives $2^{50}=1125899906842624$ words.
- Lots of clever approaches to this, for example Nemenman et al. (PRE 2004, BMC Neuroscience 2007) where a cunning prior is used for $p\left(w_{i}\right)$.
- Sampling bias.
- An even distribution will never give equal counts for each word, giving different $p\left(w_{i}\right)$.
- Lots of clever approaches to this too, see Panzeri et al. (J Neurophys. 2007).


## Many fixes but still . . .

- Neuron - neuron mutual information.
- Maze - neuron mutual information.
- Mutual information between populations.
- Mutual information between neurons and field potentials.


Also ignores the proximity structure!


Also ignores the proximity structure!


Also ignores the proximity structure!


Also ignores the proximity structure!


Also ignores the proximity structure!


## Classical approach

- Discretize.

- Discretize.



## van Rossum metric



Spike trains mapped to functions and a metric on the space of functions induces a metric on the spike train space.

## Multi-unit van Rossum metric

- There is a multi-unit easily computed version of the van Rossum metric.
- It relies on a time constant and a population parameter.


## The rules

We want to estimate mutual information for data on a metric space

- There is a KDE version of this, here we use a Kozachenko-Leonenko approach
- It ends up somewhat similar to the Kraskov, Stögbauer and Grassberger (KSG) estimator.


## A dart board



## A dart board



## Probability mass function


$\operatorname{prob}($ dart lands in $B)=\int_{B} p(x) d V$

## Estimating using the number of number of holes


$\langle$ number of holes in $B\rangle=\int_{B} p(\times) d V \times($ total number of holes $)$
where the total volume is normalized.

## Estimating the probability mass function

If the mass function varies slowly:

$$
\int_{B} p(x) d V \approx p\left(x_{0}\right) \times \operatorname{vol} B
$$

so

$$
\text { number of holes in } B \approx p\left(x_{0}\right) \times \operatorname{vol} B \times(\text { total number of holes })
$$

Using this to find the mutual information gives a Kozachenko-Leonenko estimator.

## Estimating using the number of number of holes

$$
p\left(x_{0}\right) \approx \frac{\# B}{n \times \operatorname{vol} B}
$$

where $n$ is the total number of points and $\# B$ is the number of points in $B$.


SO

$$
p(\circ)=\frac{4}{n \mathrm{vol} B}
$$

## Problem

How do we work out the volume in the space of functions? We have no coordinates $x y z$ to do

$$
\operatorname{vol} B=\int_{B} d x d y d z
$$

We must respect the rules and use only the metric, well the metric and the existence of the probability density.

Use the mass function as a measure!


$$
\operatorname{vol} B=\int_{B} p(x) d V
$$

## Volume by counting holes

vol $B \approx \frac{\text { number of holes in } B}{\text { total number of holes }}$

## Volume by counting holes



A ball with volume $h / n$ around the circled point, where $n$ is the total number of holes and $h=4$.

## Metric

To make a ball you need a metric; not to measure the radius since the size is being defined by the volume, but to define 'the nearest $h$ points'.

## Oh no

$$
p\left(x_{0}\right) \approx \frac{\# B}{n \times \operatorname{vol} B}=\frac{h}{n h / n}=1
$$

and using this meaure gives $H(X)=0$; in fact the differential entropy is not well-defined. However the mutual information is!

## Mutual infomation

$$
I(X, Y)=H(Y)-H(Y \mid X)
$$

has two probability distributions: $p_{Y}(y)$ and $p_{Y \mid X}(y \mid x)$ !

IDEA: use one to estimate volume, the other can then be estimated by counting!

## Formula - discrete case

This is for the case where $X$ is a discrete random variable and everything exciting is happening in $Y$ space.

$$
I(X, Y)=\frac{1}{n} \sum_{y_{i}} \log _{2} \frac{n \# y_{i} B}{h}
$$

where $\#_{y} B$ are the number of points in $B$ that correspond to the $X$ value as $y$ and $n_{s}$ is the number of stimuli.

## Formula - discrete case

$$
I(X, Y)=\frac{1}{n} \sum_{y_{i}} \log _{2} \frac{n_{s} \#_{y_{i}} B}{h}
$$



## h

There are two approximations:

$$
\int_{B} p(x) d V \approx \# B \times \operatorname{vol} B
$$

and

$$
\int_{B} p(x) d V \approx V \times p\left(x_{0}\right)
$$

The first approximation gets better if the volume is bigger, the second gets worse; the correct choice of $h$ is a compromize between these two. There is actually a successful approach to picking $h$ that seems to work, based on the bias, which can be calculated analytically.

## Two continuous variable

This also works for the case where $X$ and $Y$ are both continuous; as for example, when comparing neuronal populations!

## Two continuous variable

In this case we use exploit the fact that there are two probability distributions on the joint space $(X, Y)$.

The joint distribution:

$$
p_{X, Y}(x, y)
$$

and the marginalized distribution

$$
p_{X}(x) p_{Y}(y)
$$

## Two continuous variables

$$
I(X, Y)=\frac{1}{n} \sum_{i=1}^{n} \log _{2} \frac{n \#\left[C\left(x_{i}, y_{i}\right)\right]}{h^{2}}
$$

with $C\left(x_{i}, y_{i}\right)=C_{X}\left(x_{i}, y_{i}\right) \cup C_{Y}\left(x_{i}, y_{i}\right)$

Two continuous variables


## Two continuous variables



## Transfer entropy

Work with Jake Witter . . . with a paper in preparation.

## What about transfer entropy?

The transfer entropy is a measure of causality!

## What about transfer entropy?

Isn't that Granger causality? Transfer entropy reduces to Granger causality for vector auto-regressive processes!

## Transfer entropy

$$
T(X \rightarrow Y)=I[X(\text { past }), Y(\text { now }) \mid Y(\text { past })]
$$

## Transfer entropy

Transfer entropy is a sort of conditional mutual information.

$$
I(X, Y \mid Z)
$$

and this suffers even more acutely from sampling problems.

## Conditional mutual information

The metric Kozachenko-Leonenko estimator can be extended to this case; it involves three-way intersections of the nearest-neighbour sets.


## Ising model



## Transfer Entropy



## Transfer Entropy



## Transfer Entropy



## The End

THANK YOU!

