## Mutual information between successive reorientations

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#### Abstract

We show how mutual information can be used to describe the independence of successive reorientations

### 1 Reorientation sequences

sec:reoseq

As a worm navigates, it performs a sequence of turns. When turns occur sufficiently close to each other, they are grouped into a reorientation event. These reorientations have several characteristics, e.g. the types of turn of which it is composed, the difference in heading direction before and after, the duration of the run leading into it. We wish to know if the characteristics of one reorientation are independent of the characteristics of previous reorientations.

Consider a sequence of r successive reorientations. The values of a particular characteristic of these reorientations is an r-tuple of random variables:  $(X_1, \ldots, X_r)$ . We are asking whether or not  $P(X_1, \ldots, X_r) = P(X_1) \ldots P(X_r)$ . We will discuss some measures of independence in §2.

These probability distributions can be estimated from the frequencies in a sample sequence (described schematically in fig.1). However, as a consequence of finite sample size, this process has both systematic and random errors. We will look at several methods for removing systematic errors in §3 and one method for estimating random errors in appendix A.

In principle we should look at all the characteristics together. However, increasing the dimensionality of the data at each reorientation increases the number of bins used, which in turn increases the number of samples needed. Therefore, we will have to be satisfied with looking at each characteristic separately.

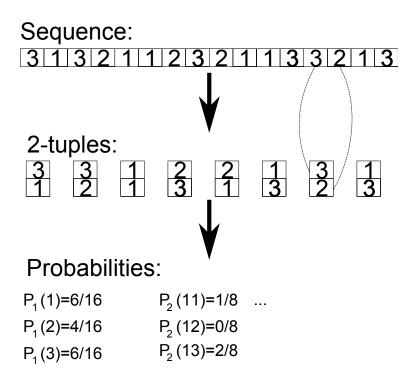


Figure 1: Schematic calculation of probabilities. (a) Sample sequence of reorientations. (b) Grouping sequence into r-tuples (r = 2). (c) Estimating probabilities for individual members and for r-tuples from relative frequencies in sample.

fig:schemati

### 2 Entropy and mutual information

ec:entropy

The **entropy** of a probability distribution is a measure of the lack of information we have about a random variable:

$$H(X) = \langle -\log P(X) \rangle$$
. (1) eq:ent

It takes its minimum value of 0 when X can only take one value. It takes its maximum value of  $\log n$  when X has a uniform distribution over n possibilities.

With several random variables, we can define a joint entropy from their joint probability distribution:

$$H(X_1, \dots, X_r) = \langle -\log P(X_1, \dots, X_r) \rangle$$
. (2) eq:jointent

It satisfies the bounds

$$\max_{i} H(X_i) \le H(X_1, \dots, X_r) \le \sum_{i=1}^{r} H(X_i). \tag{3}$$
 [eq:entbounds]

The lower bound is saturated when one of the variables is enough to determine the others. The upper bound is saturated when the  $X_i$  are independent:

$$P(X1, \dots, X_r) = \prod_{i=1}^r P(X_i) \quad \Longrightarrow \quad H(X_1, \dots, X_r) = \sum_{i=1}^r H(X_i). \tag{4}$$

We can define the following measure of (lack of) independence:

$$I(X_1, \dots, X_r) = \sum_{i=1}^r H(X_i) - H(X_1, \dots, X_r).$$
 (5) eq:mutinf

In the case r = 2, this is the **mutual information** between  $X_1$  and  $X_2$ . For r > 2, there are many different generalisations of mutual information. This one is called the **total** correlation [1], or multiinformation. It has the properties:

- it vanishes if and only if the random variables are independent
- otherwise, it is positive.
- it is bounded from above by  $\sum_{i=1}^r H(X_i) \max_i H(X_i)$ .

In our cases, the random variables,  $X_i$ , all have the same distribution, so the total correlation satisfies the bounds

$$0 \le I_r(X_1, \dots, X_r) \le (r-1)H(X). \tag{6}$$

We can define a normalised total correlation:

$$C_r = \frac{I_r}{(r-1)H_1}, \qquad 0 \le C_r \le 1. \tag{7} \quad \text{eq:normmutin}$$

The lower bound corresponds to complete independence. The upper bound corresponds to complete redundancy.

### 3 Correcting systematic errors

ec:syscorr

We will compute the quantities defined in the previous section by estimating the probability distributions,  $P_1(X_i)$  and  $P_r(X_1, \ldots, X_r)$  from the relative frequencies in sample sequences of reorientations. As all the  $X_i$  have the same distribution, we will estimate  $P_1(X)$  from the pooled data, rather that estimating the  $P_1(X_i)$  separately. When looking at reorientation types, we will restrict attention to the 5 most common types. When looking at angles and run durations, the data has to be binned. We will follow the approach of [2] and place the bins on quantiles of the data, preserving the coordinate invariance of the mutual information.

The lower bounds on mutual information, (6) and (7), lead to systematic errors which tend to bias these estimates upwards. There are several methods for estimating this bias.

One approach involves expending the errors in one over the sample size, see [3] and estimating the leading order correction. One can also estimate the random errors using this approach. Our estimators are slightly different to those used there, the appropriate versions of the estimates are calculated in Appendix A.

As the bias estimates are independent of the actual probability distribution, depending only on sample size and number of bins, we can estimate the bias by computing the mutual information for a completely random sequence in the same way. As the true value is zero, the result of this computation is an estimate of the bias. Furthermore, if the probabilities of the individual elements of the sequence are the same as in the data, this can be regarded as a Monte-Carlo simulation of the null hypothesis – that the individual elements of the sequence are independent of each other. Thus, we can compute a p-value by seeing where the original result ranks amongst the results of the simulation.

We will do this using the non-parametric bootstrap. This is conceptually similar to the common alternative procedure of shuffling the sequence. Shuffling can be thought of as resampling without replacement, whereas the non-parametric bootstrap is resampling with replacement. They both involve removing any information in the sequence without changing the probabilities of the individual elements.

The direct method of [4] consists of varying the sample size and extrapolating to infinity. This can also be used to check that the number of samples is large enough compare to the number of bins.

### **Appendices**

#### A Bias and standard error

sec:stderr

We will follow the approach of [3]. Our situation is slightly different from that one. As all the  $X_i$  have the same distribution, we will estimate P(X) from the pooled data, rather that estimating the  $P(X_i)$  separately. This means that our estimates may not satisfy the bounds, such as (6).

Let  $p_{i_1...i_r}$  denote the probability  $P_r(X_1 = x_{i_1}, ..., X_r = x_{i_r})$  and  $n_{i_1...i_r}$  denote the number of corresponding r-tuples in the sample. We can estimate  $p_{i_1...i_r}$  with

$$q_{i_1\dots i_r} = \frac{n_{i_1\dots i_r}}{N}, \qquad N = \sum_{j_1\dots j_r} n_{j_1\dots j_r}. \tag{8}$$

We can then estimate  $p_j = P_1(X = x_j)$  with

$$q_j = \sum_{i=1}^r \left( \frac{q_{i_1 \dots i_r}}{r} \sum_{r=1}^r \delta_{j,i_a} \right). \tag{9}$$

From now on, we will use A to denote the estimate of A(p) with p replaced by q and  $\widehat{A} = A - \text{Bias}(A)$ , where A is one of  $(H_1, H_r, I_r, C_r)$ .

Our bias estimates are essentially the same as those of [3], except that the number of samples for  $H_1$  is rN rather than N:

$$B_1 = \text{Bias}(H_1) = -\frac{\#b_1}{2rN}, \qquad B_r = \text{Bias}(H_r) = -\frac{\#b_r}{2N},$$
 (10) eq:biasH

where  $\#b_r$  is the number of non-empty bins. The bias estimate for I and C follow in the usual way.

We can estimate the standard errors with

$$\operatorname{Var}(A) \approx \sum_{i_1 \dots i_r} \left( \frac{\partial A}{\partial n_{i_1 \dots i_r}} \right)^2 \operatorname{Var}(n_{i_1 \dots i_r}), \qquad \operatorname{Var}(n_{i_1 \dots i_r}) \approx N q_{i_1 \dots i_r} (1 - q_{i_1 \dots i_r}). \tag{11} \quad \text{eq:stderr}$$

where the first formula is valid provided each term is small(we'll see later that they are proportional to 1/N) and the corrections to the last formula are lower order in N.

We find that

$$\begin{split} \frac{\partial q_{i_1...i_r}}{\partial n_{j_1...j_r}} &= \frac{\left(\prod_a \delta_{i_a,j_a}\right) - q_{i_1...i_r}}{N}, & \frac{\partial B_r}{\partial n_{j_1...j_r}} &= -\frac{B_r}{N}, \\ \frac{\partial q_i}{\partial n_{j_1...j_r}} &= \frac{\frac{1}{r}\left(\sum_a \delta_{i,j_a}\right) - q_i}{N}, & \frac{\partial B_1}{\partial n_{j_1...j_r}} &= -\frac{B_1}{N}, \end{split} \tag{12} \label{eq:dqbydn}$$

which leads to

$$\begin{split} \frac{\partial H_r}{\partial n_{j_1\dots j_r}} &= -\frac{\log q_{i_1\dots i_r} + H_r}{N}, & \frac{\partial I_r}{\partial n_{j_1\dots j_r}} &= -\frac{\left(\sum_a \log q_{j_a}\right) - \log q_{i_1\dots i_r} + I_r}{N}, \\ \frac{\partial H_1}{\partial n_{j_1\dots j_r}} &= -\frac{\frac{1}{r}\left(\sum_a \log q_{j_a}\right) + H_1}{N}, & \frac{\partial C_r}{\partial n_{j_1\dots j_r}} &= \frac{\log q_{i_1\dots i_r} H_1 - \frac{1}{r}\left(\sum_a \log q_{j_a}\right) H_r}{(r-1)N(H_1)^2}. \end{split} \tag{13}$$

All of these formulae are equally true if you put hats on every capital letter (except N).

# References

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