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1 Motivation

1.1 Effect of binning

In their review entitled ‘Measuring and interpreting neural correlations’, Cohen and Kohn studied the effects of response strength and time bin width on neural correlation measurement. Using simulated data, they found that correlation measurements taken between weakly responding neurons (i.e. neurons with firing rates of < 10 spikes per s) will be less than the true pairwise correlation value. They also found that binning the neural spiking data into small time bins can cause the measured correlation to be less than the true value. How small is ‘small’ in this case is related to width of the cross-correlogram of the pair of neurons. But, it was shown in simulation that time bins should be at least 0.1 seconds wide in order for the measured correlation value to be close to the true correlation value [1].

Our aim here is to measure a big enough sample of pairwise correlations from actual neural data across a selection of time bin widths and compare our results to those of Cohen and Kohn. In order to do this we used data collected using ‘Neuropixels’ probes [2]. These data are made available publicly online by Dr. Nick Steinmetz ¹.

One disadvantage of measuring correlations is that only the linear relationship between the quantities is captured. The mutual information is a model free pairwise measurement that can capture information about linear and non-linear dependencies between quantities. Therefore we also measured the mutual information between pairs of neurons across the same selection of time bin widths. In doing this, we investigated the effect of binning on mutual information measurements.

1.2 Regional Spike Correlation & Mutual Information distributions

We aimed to investigate the distributions of spike count correlations and mutual information within the different brain regions from which we have data available. We measured correlations and mutual information from 1000 randomly chosen pairs in each region. We made histograms of the results in order to investigate their distributions visually. We used statistical tests to measure the probability of these samples coming from different distributions.

2 Data

The recent development of Neuropixels probes has allowed extracellular voltage measurements to be collected from multiple brain regions simultaneously routinely, and in much larger numbers than traditional methods.

Using two probes, spiking activity was simultaneously collected from over 800 neurons in an awake mouse brain for a period of 84 minutes. During this period, the mouse was shown various visual stimuli. The 800 neurons were distributed across 5 different brain regions: V1, hippocampus, thalamus, motor cortex, and striatum.

The data consist of spike timings and cell/cluster identifiers associating spikes with a certain cell/cluster and a certain time. Each cell/cluster is classified as ‘good’, ‘multi-unit

¹<http://data.cortexlab.net/dualPhase3/>

activity’, or ‘unsorted’, referring to the quality of spike sorting. This classification was performed by those who analysed the data. Only the cell/clusters classified as ‘good’ are used in this project.

2.1 Stimulus

The stimulus was a full field moving bar grating. There were 17 stimulus conditions corresponding to 16 drift directions (0 degrees to 337.5 degrees in 22.5 degree increments) with 2Hz temporal frequency and 0.08 cycles/degree spatial frequency (conditions 1 – 16) plus a blank condition (17). Each condition was presented 10 times for 2 seconds each time, with 1.5 seconds between trials.

3 Methods

3.1 Binning data

The data were divided into time bins of various widths ranging from 0.01 to 2 seconds. If the bin width was not an integer divisor of the trial period (2 seconds), only the bins that lay totally within the trial period were included. For example, when dividing the trials into bins of 0.3 seconds, the final bin of 0.2 seconds was excluded. We measured the number of spikes in each time bin.

When performing calculations on the binned data, each bin was treated as an individual measurement. For example, when calculating the spike count correlation coefficient for a given pair of neurons, if the time bin used was 2.0 seconds, then we had 10 measurements for each neuron with which to calculate the coefficient. But, if we were using a bin width of 1.0 second, then we would have 20 measurements for each neuron.

3.2 Geometric Mean

The geometric mean of a set of numbers x_1, \dots, x_n is defined by

$$\sqrt[n]{\prod_{i=1}^n x_i} = \sqrt[n]{x_1 \cdot x_2 \cdots x_n} \quad (1)$$

This quantity is an alternative to the algebraic mean. It is often used when finding the mean of quantities whose range of possible values differ. For example, imagine we wish to find the mean firing rate of two neurons, but one neuron responds much more strongly than the other. The algebraic mean of the firing rates will be dominated by the strongly responding neuron. But the geometric mean will be influenced by both responses.

A surface plot showing the geometric mean of two variables as they vary between 0 and 50 can be seen in figure 1.

3.3 Finding a suitable time bin width

In this research, we needed to choose a suitable bin width to use when making our measurements. To do this we took these measurements using different time bin widths. One

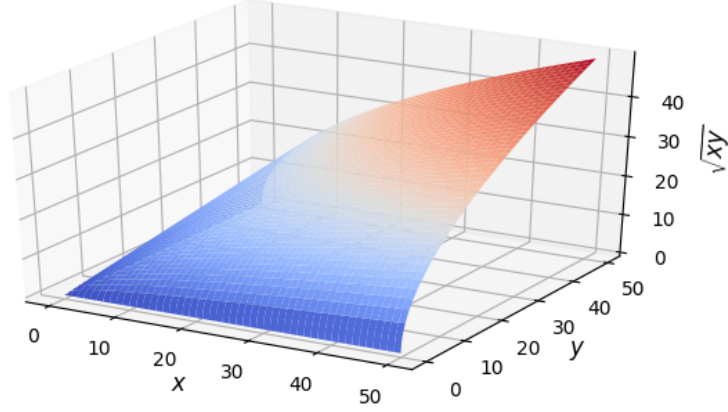


Figure 1: Surface showing the geometric mean of two numbers x and y (i.e. \sqrt{xy}) as they each vary from 0 to 50.

of the measurements we took is spike count correlation. But, a weak response or low firing rate has a diminishing effect on measured spike count correlation [1]. In order to avoid this effect, we filtered out any neurons with a mean firing rate of less than 10 spikes per second measured across the 10 trials of 2 seconds. Neurons that met this requirement were regarded as ‘strongly responding’.

We analysed these strongly responding neurons by themselves as well alongside all other responding neurons during the course of this research.

3.4 Correlation coefficients

We calculated Pearson’s correlation coefficient for pairs of neurons. For jointly distributed random variables X and Y , Pearson’s correlation coefficient is defined as:

$$\rho_{XY} = \frac{\text{cov}(X, Y)}{\sigma_X \sigma_Y} \quad (2)$$

$$= \frac{E[(X - \mu_X)(Y - \mu_Y)]}{\sigma_X \sigma_Y} \quad (3)$$

where E denotes the expected value, μ denotes the mean, and σ denotes the standard deviation. The correlation coefficient is a normalised measure of the covariance. It can take values between 1 (completely correlated) and -1 (completely anti-correlated). Two independent variables will have a correlation coefficient of 0. But, having 0 correlation does not imply independence.

If we do not know the means and standard deviations required for equation 2, but we have samples from X and Y , Pearson’s sample correlation coefficient is defined as:

$$r_{XY} = \frac{\sum_{i=1}^n (x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^n (x_i - \bar{x})^2} \sqrt{\sum_{i=1}^n (y_i - \bar{y})^2}} \quad (4)$$

where $\{(x_i, y_i)\}$ for $i \in \{1, \dots, n\}$ are the paired samples from X and Y , and $\bar{x} = \frac{1}{n} \sum_{i=1}^n x_i$, and $\bar{y} = \frac{1}{n} \sum_{i=1}^n y_i$ are the sample means.

In practice we used the python function `scipy.stats.pearsonr` to calculate the correlation coefficients.

3.4.1 Spike Count Correlation, r_{SC}

The spike count correlation (r_{SC}) of two cells is the correlation between the spike counts of those cells in response to a given stimulus condition.

3.4.2 Signal Correlation, r_{signal}

The signal correlation of two cells (r_{signal}) is the correlation between the mean responses of those cells to each stimulus condition. Note the difference between this and the spike count correlation in section 3.4.1. The spike count correlation is in response to a given stimulus condition. The signal correlation is the correlation in the mean response to each stimulus condition.

3.4.3 Separating Correlations & Anti-correlations

In order to compare the effect of bin width on measures of negative r_{SC} (anti-correlation) and positive r_{SC} separately, we had to separate correlated and anti-correlated pairs. To do this, we simply measured the mean r_{SC} , taking the mean across all the bin widths. If this quantity was positive or zero we regarded the pair as positively correlated. If this quantity was negative we regarded the pair as anti-correlated.

3.5 Mutual Information

3.5.1 Entropy $H(X)$

The entropy of a random variable X , with outcomes x_1, \dots, x_N , and corresponding probabilities p_1, \dots, p_N is defined as

$$H(X) = - \sum_{n=1}^N p_n \log_2 p_n \quad (5)$$

This quantity is also known as the information entropy or the ‘surprise’. It measures the amount of uncertainty in a random variable. For example, a variable with a probability of 1 for one outcome, and 0 for all other outcomes will have 0 bits entropy, because it contains no uncertainty. But a variable with a uniform distribution will have maximal entropy as it is the least predictable. This quantity is analogous to the entropy of a physical system [3]. Note that any base may be used for the logarithm in equation 5, but using base 2 means that the quantity will be measured in ‘bits’.

The joint entropy of two jointly distributed random variables X and Y , where Y has outcomes y_1, \dots, y_M , is defined as

$$H(X, Y) = - \sum_{n=1}^N \sum_{m=1}^M P(X = x_n, Y = y_m) \log_2 P(X = x_n, Y = y_m) \quad (6)$$

If X and Y are independent then $H(X, Y) = H(X) + H(Y)$. Otherwise $H(X, Y) < H(X) + H(Y)$. When X and Y are completely dependent $H(X, Y) = H(X) = H(Y)$.

The conditional entropy of Y conditioned on X is defined as

$$H(Y|X) = - \sum_{n=1}^N \sum_{m=1}^M P(X = x_n, Y = y_m) \log_2 \frac{P(X = x_n, Y = y_m)}{P(X = x_n)} \quad (7)$$

When X and Y are independent $H(Y|X) = H(Y)$. Intuitively, we learn nothing of Y by knowing X , so Y is equally uncertain whether we know X or not. If Y is totally dependent on X , then the fraction in the logarithm is 1, which gives $H(Y|X) = 0$.

These entropy measures are the basis of the mutual information measure.

3.5.2 Maximum entropy limit

When spiking data is binned into spike counts there is an upper limit on the entropy of these data. The maximum entropy discrete distribution is the discrete uniform distribution. A random variable with this distribution will take values from some finite set with equal probabilities. Binned spike count data will take values between 0 and some maximum observed spike count n_{\max} . A neuron with responses that maximises entropy will take these values with equal probability, i.e. if $i \in \{0, \dots, n_{\max}\}$ then $P(X = i) = \frac{1}{n_{\max} + 1}$. The entropy of this neuron will be

$$\begin{aligned} H(X) &= - \sum_{i=0}^{n_{\max}} P(X = i) \log_2 P(X = i) \\ &= - \sum_{i=0}^{n_{\max}} \frac{1}{n_{\max} + 1} \log_2 \left(\frac{1}{n_{\max} + 1} \right) \\ &= - \log_2 \left(\frac{1}{n_{\max} + 1} \right) \\ &= \log_2 (n_{\max} + 1) \end{aligned}$$

Therefore, the maximum entropy of the binned spike counts of a neuron is $\log_2 (n_{\max} + 1)$. Of course, it would be very unusual for a neuron to fire in accordance with the discrete uniform distribution. Most measures of entropy taken on binned spiking data will be much lower than the maximum. See figure 2 to see the maximum entropy as a function of the maximum observed spike count.

3.5.3 Mutual Information $I(X; Y)$

The mutual information can be defined mathematically in a number of ways, all of which are equivalent. These definitions illustrate the different ways of interpreting the mutual information.

For two jointly distributed random variables X and Y , the mutual information $I(X; Y)$ is defined as

$$I(X; Y) = H(Y) - H(Y|X) \quad (8)$$

$$= H(X) - H(X|Y) \quad (9)$$

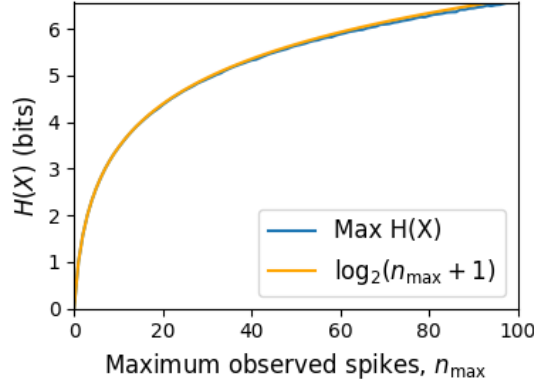


Figure 2: **Entropy Limit:** The upper limit on entropy of binned spike count data as a function of the maximum observed spike count. The orange line is the analytical maximum. The blue line is the entropy of samples with $N = 1000$ data points taken from the discrete uniform distribution.

Equation 8 fits with the following intuition: The mutual information between X and Y is the reduction in uncertainty about X gained by knowing Y , or vice versa. We could also say the mutual information is the amount of information gained about X by knowing Y , or vice versa.

Another useful entropy based definition for the mutual information is

$$I(X; Y) = H(X) + H(Y) - H(X, Y) \quad (10)$$

This definition is useful because it does not require the calculation of conditional probabilities. This was the form we used when performing calculations.

The mutual information can also be defined in terms of marginal, joint, and conditional distributions. For example,

$$I(X; Y) = - \sum_{n=1}^N \sum_{m=1}^M P(X = x_n, Y = y_m) \log_2 \frac{P(X = x_n, Y = y_m)}{P(X = x_n)P(Y = y_m)} \quad (11)$$

Notice that this can be rewritten as a Kullback–Leibler divergence.

$$I(X; Y) = D_{KL}(P(X, Y) || P(X)P(Y)) \quad (12)$$

So, we can also think of the mutual information as a measure of the difference between the joint distribution of X and Y , and the product of their marginal distributions. Since the product of the marginal distributions is the joint distribution for independent variables, we can think of the mutual information as a measure of the variables' dependence on one another.

The minimum value that $I(X; Y)$ can take is 0. This occurs when the random variables X and Y are independent. Then we have $H(X|Y) = H(X)$, and $H(Y|X) = H(Y)$, which according to equation 8, gives $I(X; Y) = 0$. We also have that $H(X, Y) = H(X) + H(Y)$ in this case, which according to equation 10, gives $I(X; Y) = 0$. Finally, we also have $P(X, Y) = P(X)P(Y)$, which leaves us with 1 in the argument for the logarithm in equation 11, which again gives $I(X; Y) = 0$.

The mutual information reaches its maximum value when one of the variables X and Y is completely determined by knowing the value of the other. In that case $I(X; Y) = \min\{H(X), H(Y)\}$.

3.5.4 Symmetric Uncertainty $U(X; Y)$

The symmetric uncertainty is a normalised version of the mutual information. It is defined as

$$U(X; Y) = 2 \frac{I(X; Y)}{H(X) + H(Y)} \quad (13)$$

The symmetric uncertainty attains its minimum value when the mutual information is 0, i.e. independence. $U(X; Y)$ attains its maximum value when one of the variables X and Y is completely determined by knowing the value of the other. In that case $U(X; Y) = 1$.

3.5.5 Measuring entropies the mutual information

In practice, we measured the mutual information using Python and the python package `pyentropy` [4]. This also enabled us to use the ‘quadratic extrapolation’ bias correction technique to measure $I(X; Y)$ more accurately [5, 6].

3.6 Kolmogorov-Smirnov Statistical Test

The Kolmogorov-Smirnov test is a statistical test of the equality of one dimensional probability distributions. It can also be used to measure the probability of a sample coming from a reference distribution. We used it to measure the probability of two samples coming from the same distribution. This is more commonly referred to as the ‘two sample K-S test’.

3.6.1 Empirical distribution function

The empirical distribution function is the empirical analogue of the cumulative distribution function. Given some sample \mathbf{X} with n data points, the empirical distribution function is a step function that increases by $1/n$ at each data point value. Mathematically,

$$\hat{F}_n(t) = \frac{1}{n} \sum_{i=1}^n \mathbf{1}_{X_i \leq t} \quad (14)$$

where $\mathbf{1}_A$ is the indicator function of condition A .

Assuming there is some underlying distribution $P(X)$ for the sample, with cumulative distribution function $F(t)$, in the regime where $n \rightarrow \infty$, $\hat{F}_n(t) \rightarrow F(X)$.

3.6.2 Two sample K-S test

Given two samples \mathbf{X}_1 and \mathbf{X}_2 , with n and m data points respectively, and with two corresponding empirical distribution functions $F_{1,n}(t)$ and $F_{2,m}(t)$, the Kolmogorov-Smirnov statistic is defined as

$$D_{n,m} = \sup_t |F_{1,n}(t) - F_{2,m}(t)| \quad (15)$$

The null hypothesis is that both samples come from the same distribution. This null hypothesis is rejected at confidence level α if

$$D_{n,m} > c(\alpha) \sqrt{\frac{n+m}{nm}} \quad (16)$$

where

$$c(\alpha) = \sqrt{\frac{-\ln \alpha}{2}} \quad (17)$$

Note that the two sample K-S test tests if two samples come from the same distribution, but doesn't make any assumptions about the underlying distribution(s).

In practise, we used the python function `scipy.stats.ks_2samp` to calculate the K-S test statistic and p-value.

4 Results

4.1 Varying bin width

In order to investigate the effect of bin width on the various measures we used, we took these measurements using a number of different values for the bin width. We found that the bin width used had an effect on the spike count correlation, and the mutual information.

4.1.1 Spike count correlations at various bin widths

For each stimulus condition and each region, we randomly chose 30 pairs of strongly responding neurons (or chose as many pairs as we could find), measured their absolute spike count correlations ($|r_{SC}|$) and absolute signal correlation ($|r_{signal}|$) using various values for the time bin width and examined the relationship between the coefficients and the bin width. We found that $|r_{SC}|$ increased approximately log-linearly up to a width of 1s and appeared to level off thereafter, see figure 3, or figure 4 for a linear version. This is in agreement with the findings of the simulated experiment in [1]. For these figures, we chose the stimulus condition that evoked the strongest response from a given region. This guaranteed us 30 strongly responding pairs for each region.

4.1.2 Correlations & Anti-correlations

We separated the 30 randomly chosen pairs into correlated and anti-correlated pairs as per section 3.4.3. We then measured r_{SC} across various bin width values. We found that the positive r_{SC} got more positive as the bin width increased. We also found that the negative r_{SC} got more negative as the bin width increased. Both positive and negative coefficients showed a log-linear increase similar to the absolute spike count correlation coefficients. See figure 5.

4.1.3 Signal Correlations

We found that $|r_{signal}|$ maintained a constant value across different bin widths. This was the case in all regions, with some variations in V1. See figure 6.

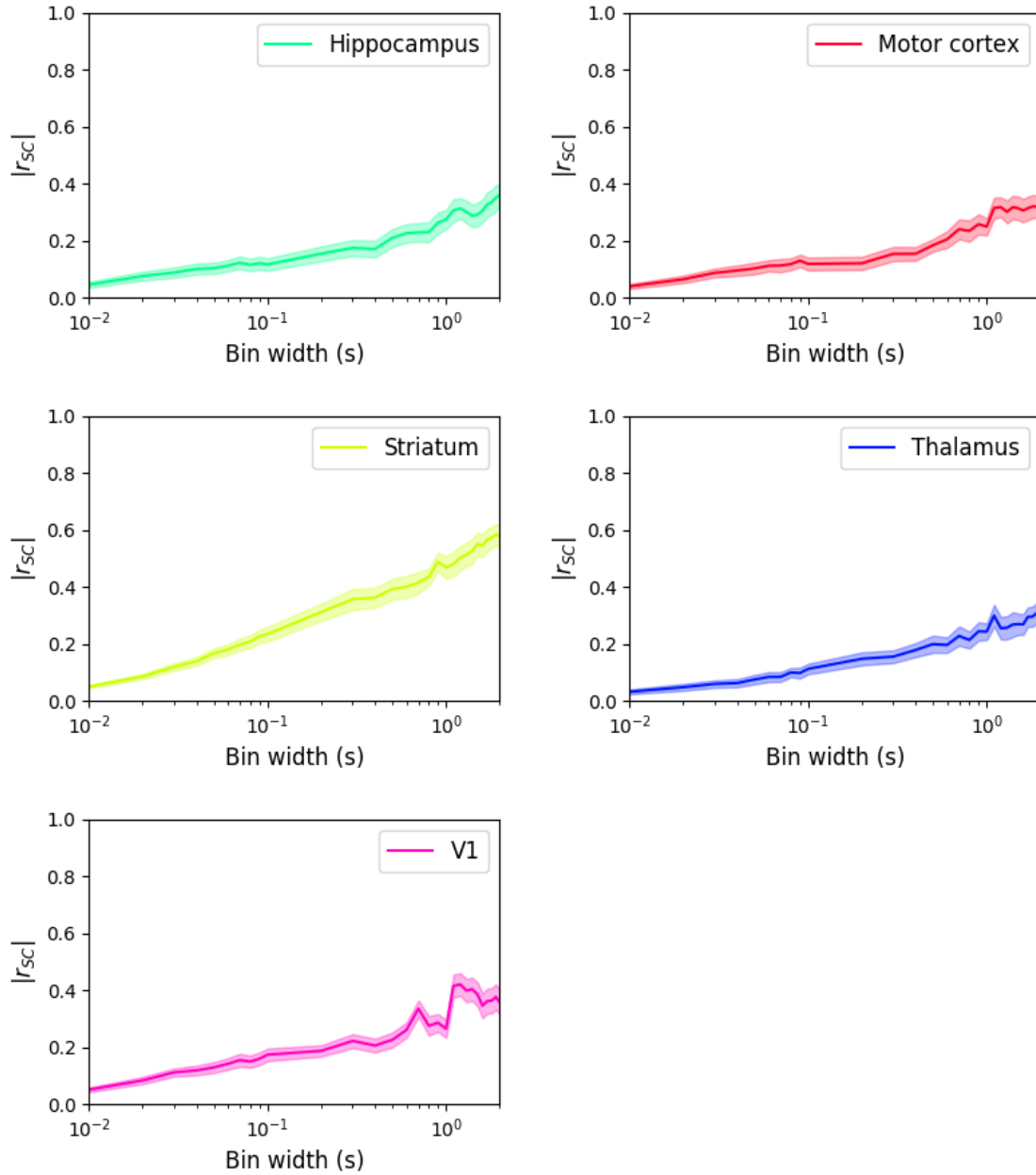


Figure 3: **Spike Count Correlations:** Absolute values of correlation coefficients measured using different time bin widths. Shaded areas indicate standard errors. One figure for each brain region from which data were available. The absolute correlation increases approximately log-linearly with the bin width up to a bin width of 1 second and levels out somewhat thereafter.

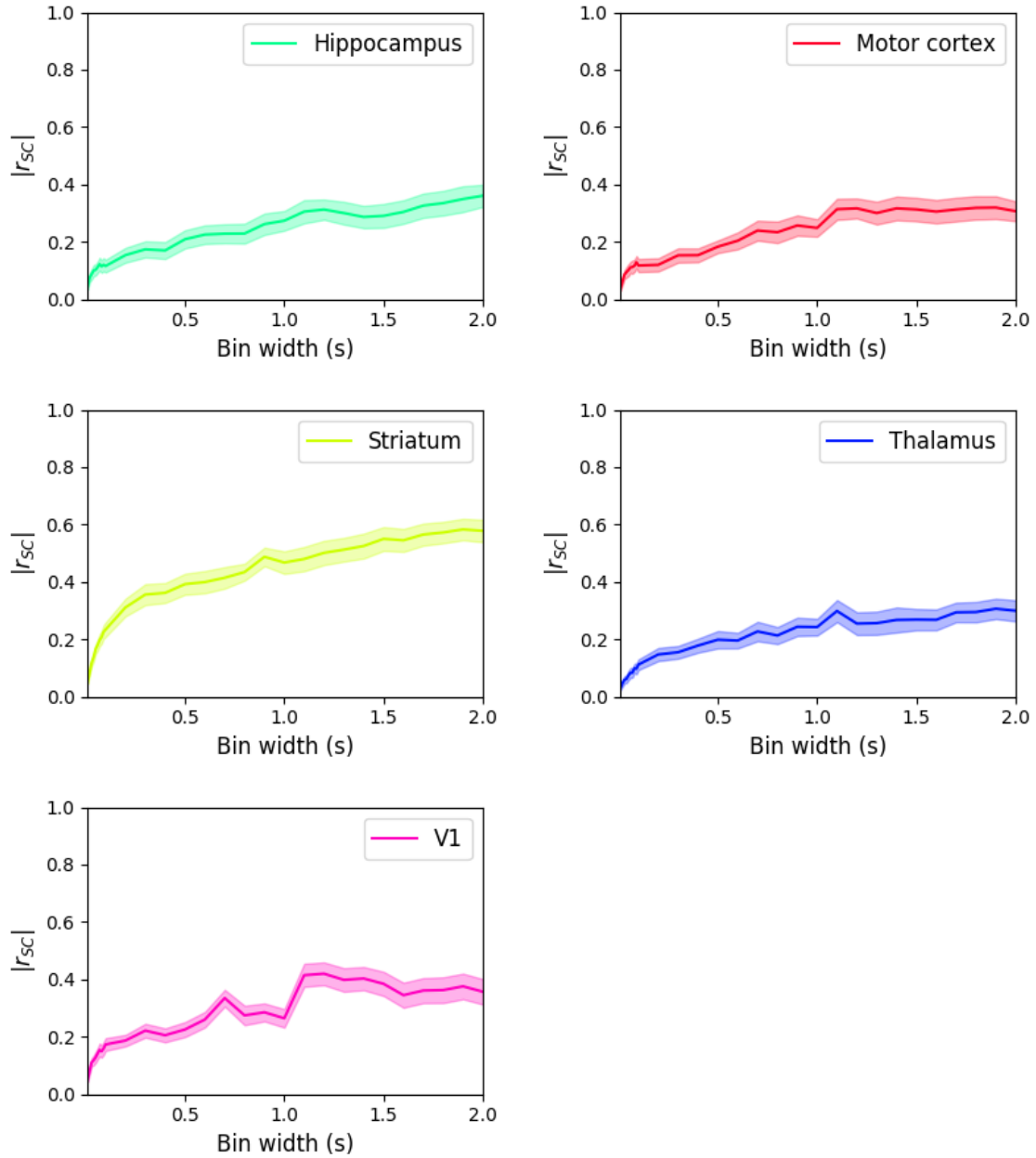


Figure 4: **Spike Count Correlations:** Absolute values of correlation coefficients measured using different time bin widths. Shaded areas indicate standard errors. One figure for each brain region from which data were available. The absolute correlation increases approximately log-linearly with the bin width up to a bin width of 1 second and levels out somewhat thereafter.

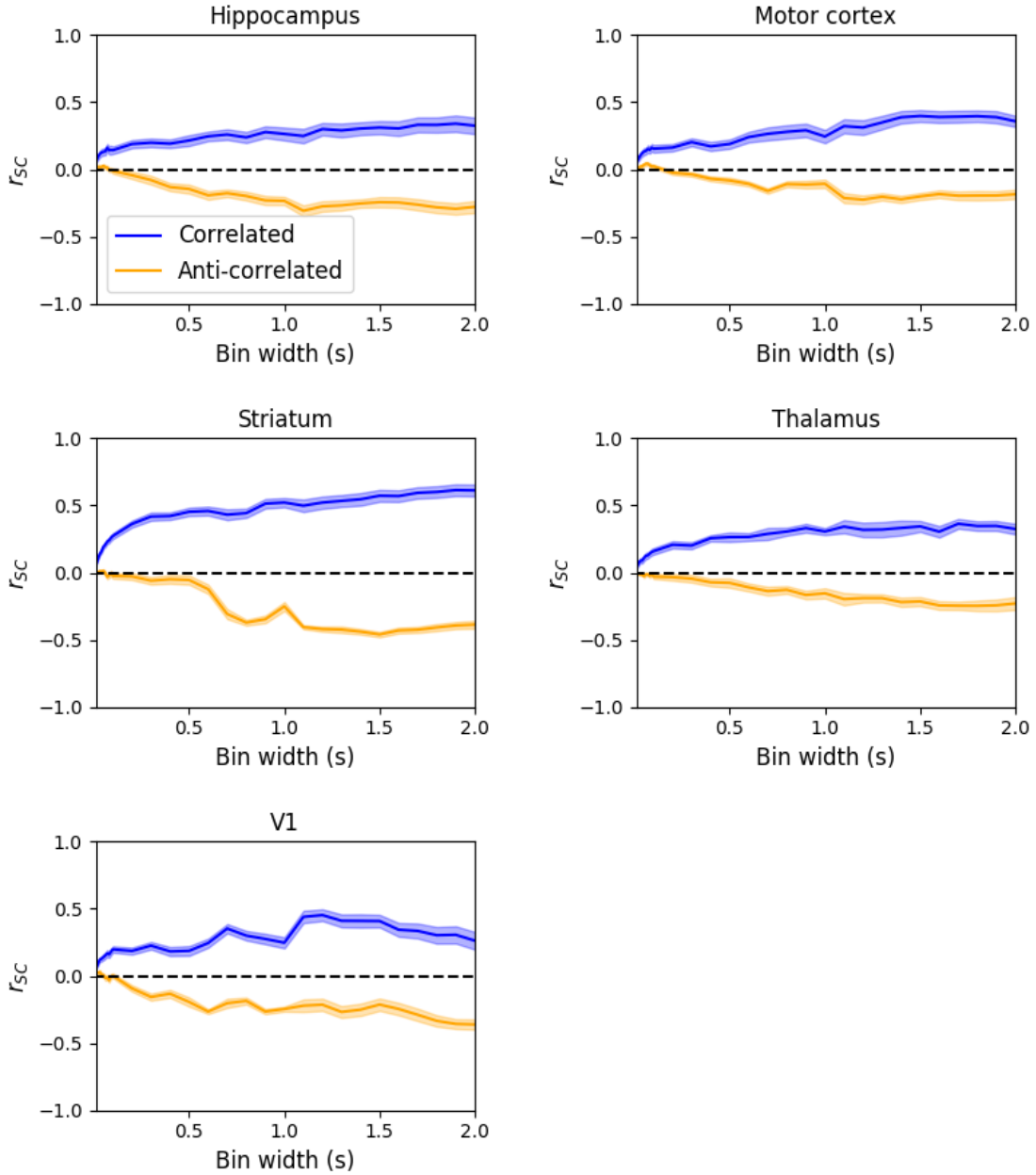


Figure 5: **Spike Count Correlations and Anti-correlations:** Correlation coefficients measured using different time bin widths and separated into positive and negative sets. Shaded areas indicate standard errors. One figure for each brain region from which data were available. The correlations or anti-correlations get stronger as the bin width increases. We see the log linear increase similar to figures 3 and 4.

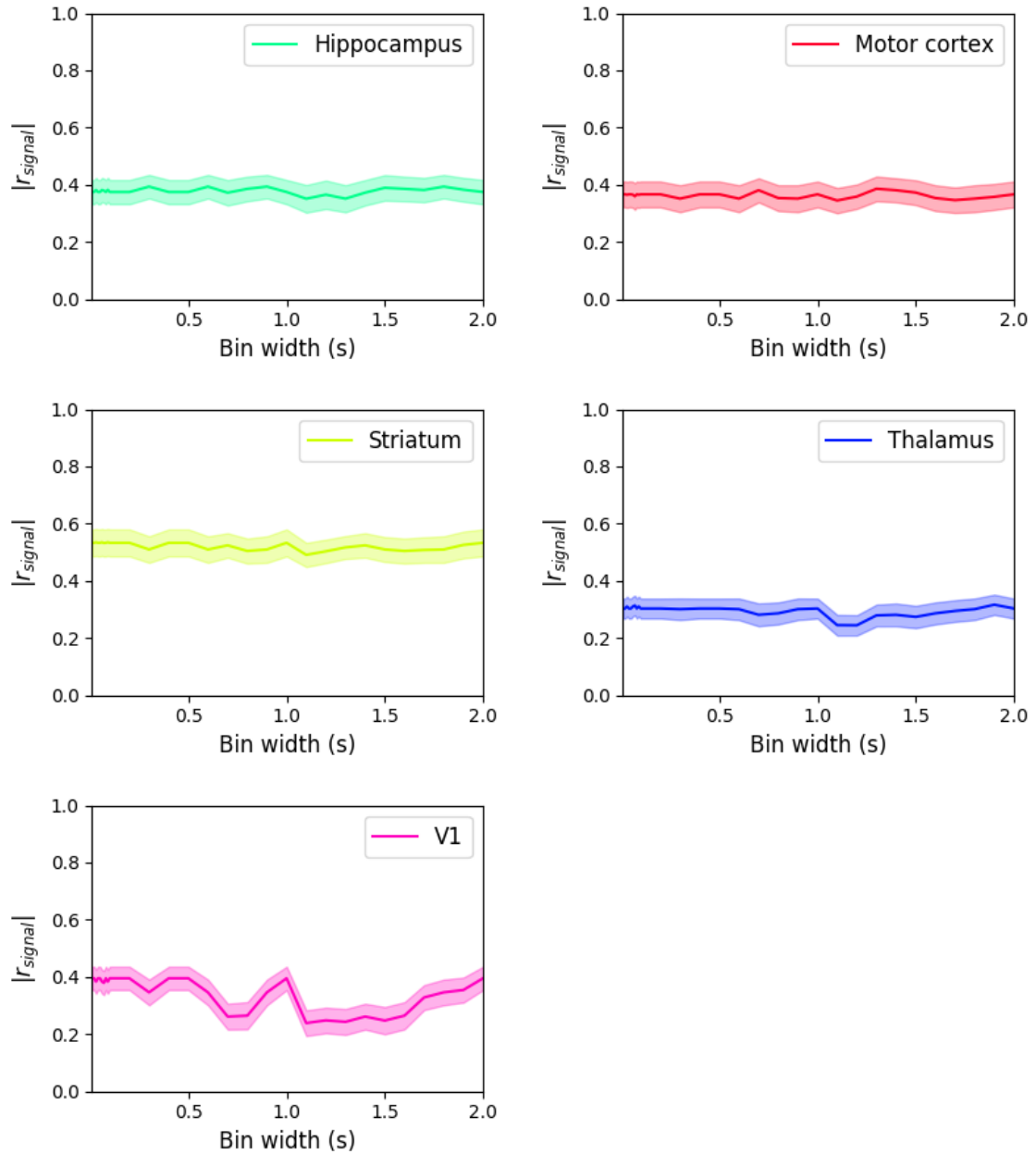


Figure 6: **Signal Correlations:** Absolute values of signal correlation coefficients measured using different time bin widths. Shaded areas indicate standard errors. One figure for each brain region from which data were available. The signal correlation maintains a fairly constant value across bin widths for most brain regions, with some variations in V1.

4.1.4 Mutual Information

As in section 4.1.1, we randomly chose 30 pairs of strongly responding cells in each region for each stimulus condition and measured the mutual information ($I(X; Y)$) between these pairs using different values for the bin width. As with the spike count correlations, we found that the mutual information increased as the bin width increased up to a bin width of 1 second, and levelled off thereafter, see figure 7.

4.1.5 Firing rate

We also measured the affect of bin width on firing rate measurement. As expected, the affect was minimal.

4.2 Firing rate distributions

In order to examine the distribution of firing rates in a given region,

1. We chose a stimulus condition that evoked the most strong responses in that region
2. We measured the average firing rate for each neuron responding to that stimulus condition, averaging across trials.
3. We created a histogram of these average firing rates.

We followed this procedure for each region and presented the results in figure 8.

4.3 Spike count correlation & Mutual Information distributions

4.3.1 Histograms

For each region, we found all of the cells that responded to the stimulus. We randomly selected 1000 pairs from all possible pairs of these cells, and we measured their pairwise spike count correlations, mutual information, and symmetric uncertainty using a bin width of 1.0s. We created histograms using these data in order to examine the distributions of r_{SC} , $I(X; Y)$ and $U(X; Y)$ in each region, see figures 9, 10 and 11.

4.3.2 Statistical tests

We tested if the spike count correlations and mutual information measurements taken from each region could have the same underlying distributions. We used the two sample Kolmogorov-Smirnov test to do this (see section 3.6). Given a pair of regions, we tested the samples of 1000 spike count correlations and mutual information measurements from each region. We did this for all 10 possible pairs of regions. Results can be seen in tables 1 and 2.

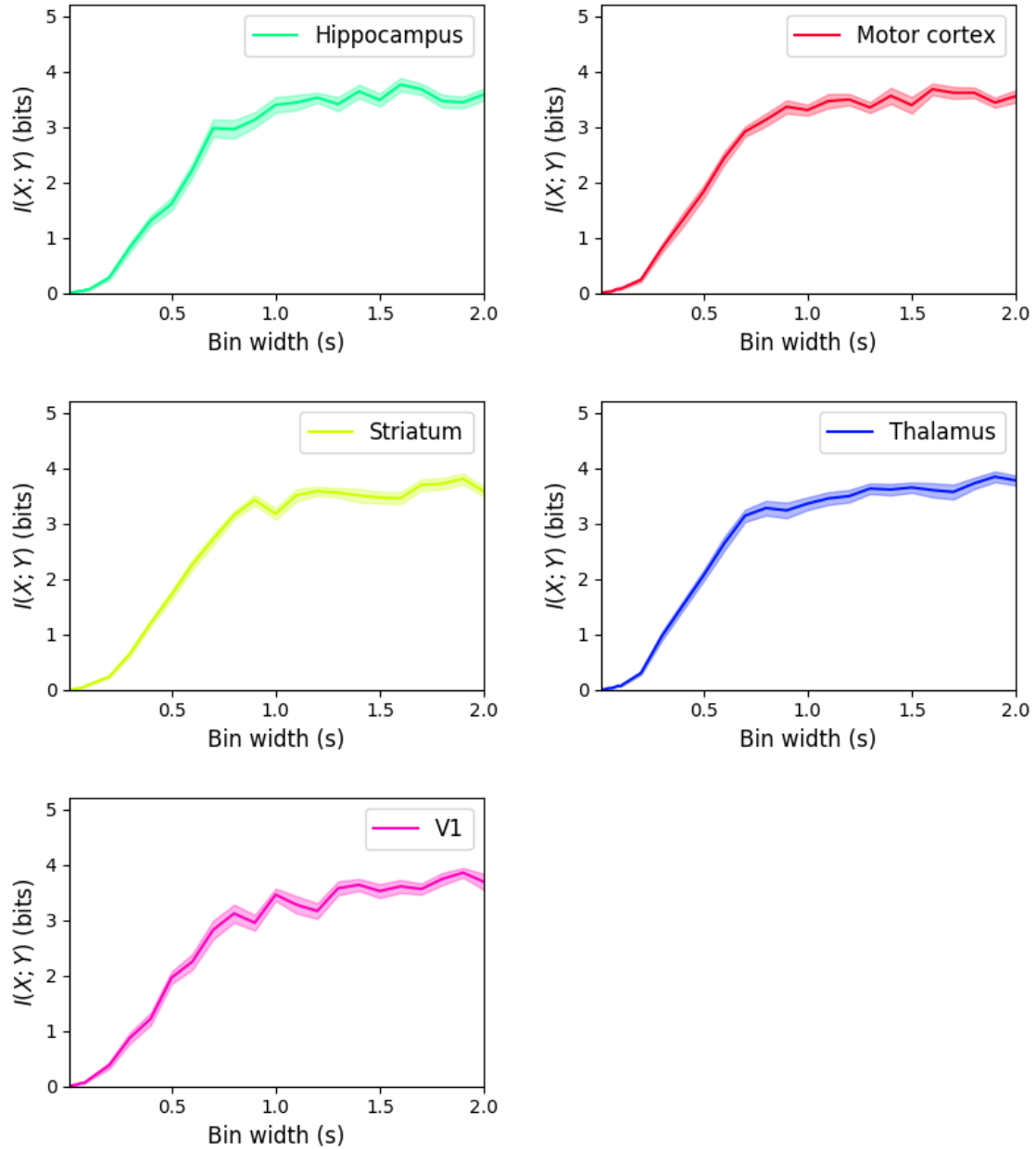


Figure 7: **Mutual Information:** Mutual information measured using different time bin widths. Shaded areas indicate standard errors. One figure for each brain region from which data were available. The mutual information increases as the the bin width increases, reaching a limit of about 3 bits for bin widths ≥ 1 s.

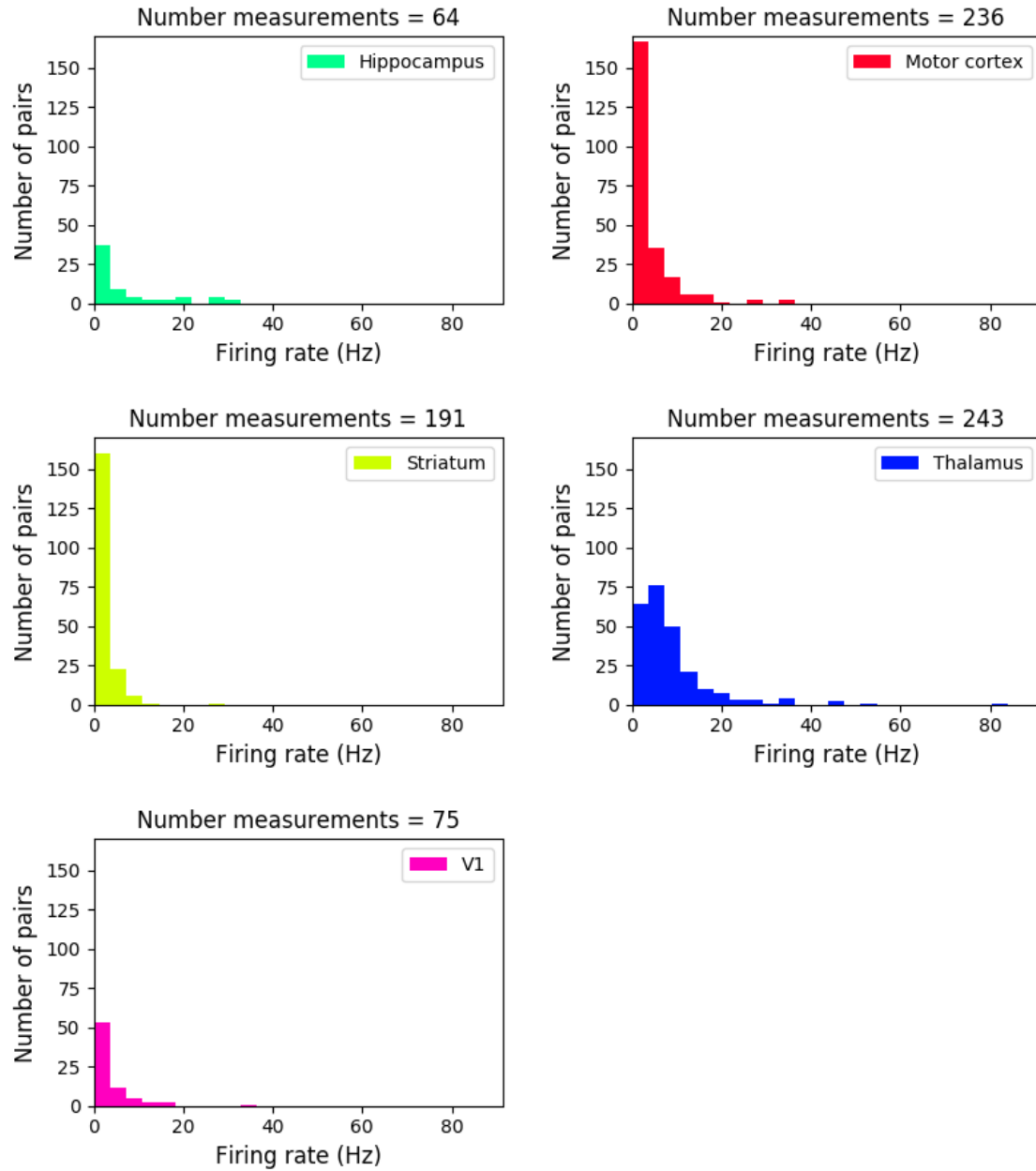


Figure 8: **Firing Rate Histograms:** Histograms of the average firing rates within each region. Most neurons have an average firing rate of < 10 Hz.

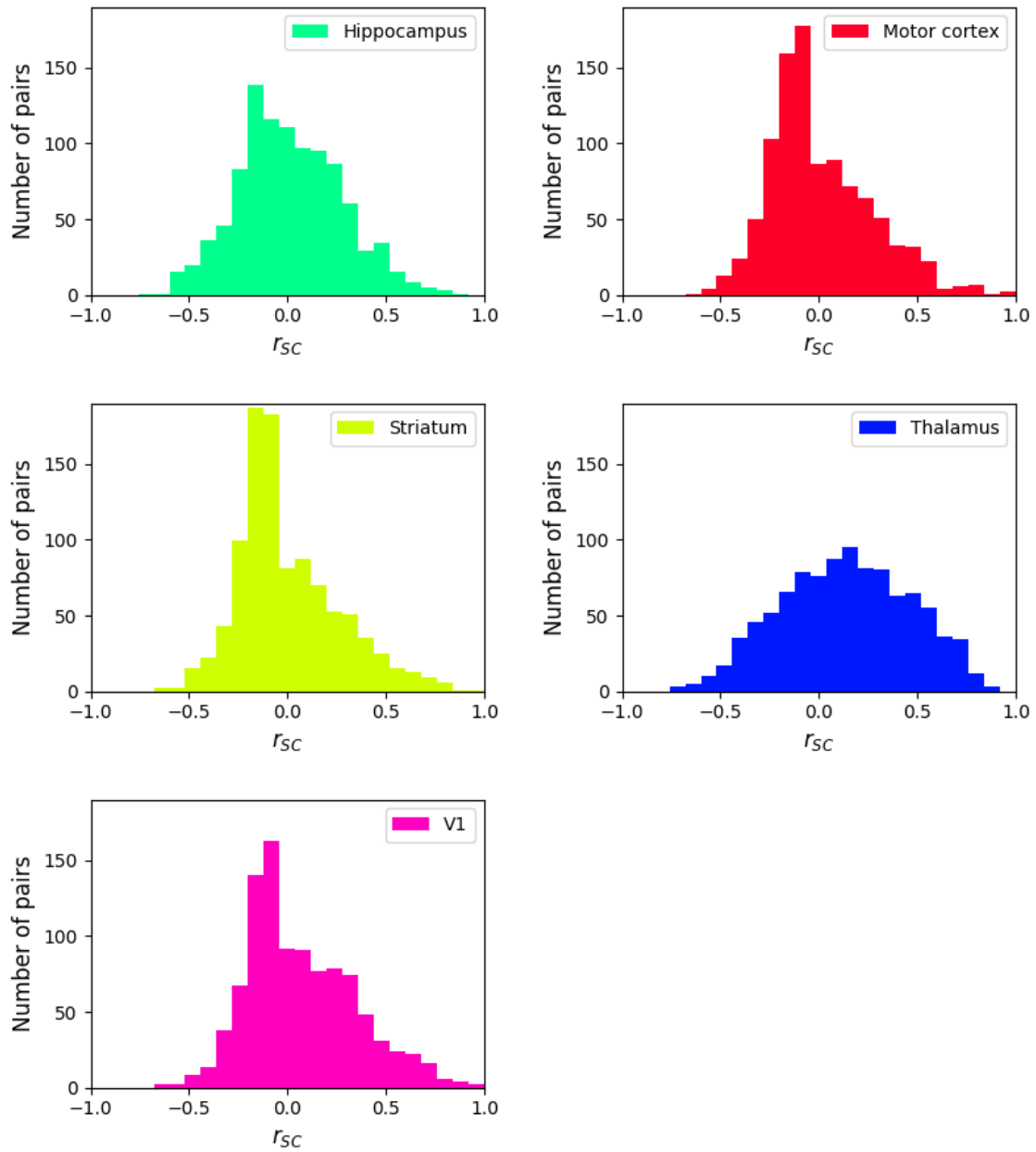


Figure 9: **Spike Count Correlation Histograms:** Histograms of the spike count correlations of 1000 randomly chosen pairs of neurons from within each region. The time bin width used was 1.0s. The motor cortex, V1, and striatum all have similar distributions. For these regions the mean r_{SC} is positive, but the median r_{SC} is negative, so their distributions are skewed. The hippocampus is slightly different in that both the median and the mean are positive but close to 0. The thalamus is different to all the other regions. Both its mean and median are positive and are approximately equal to 0.14.

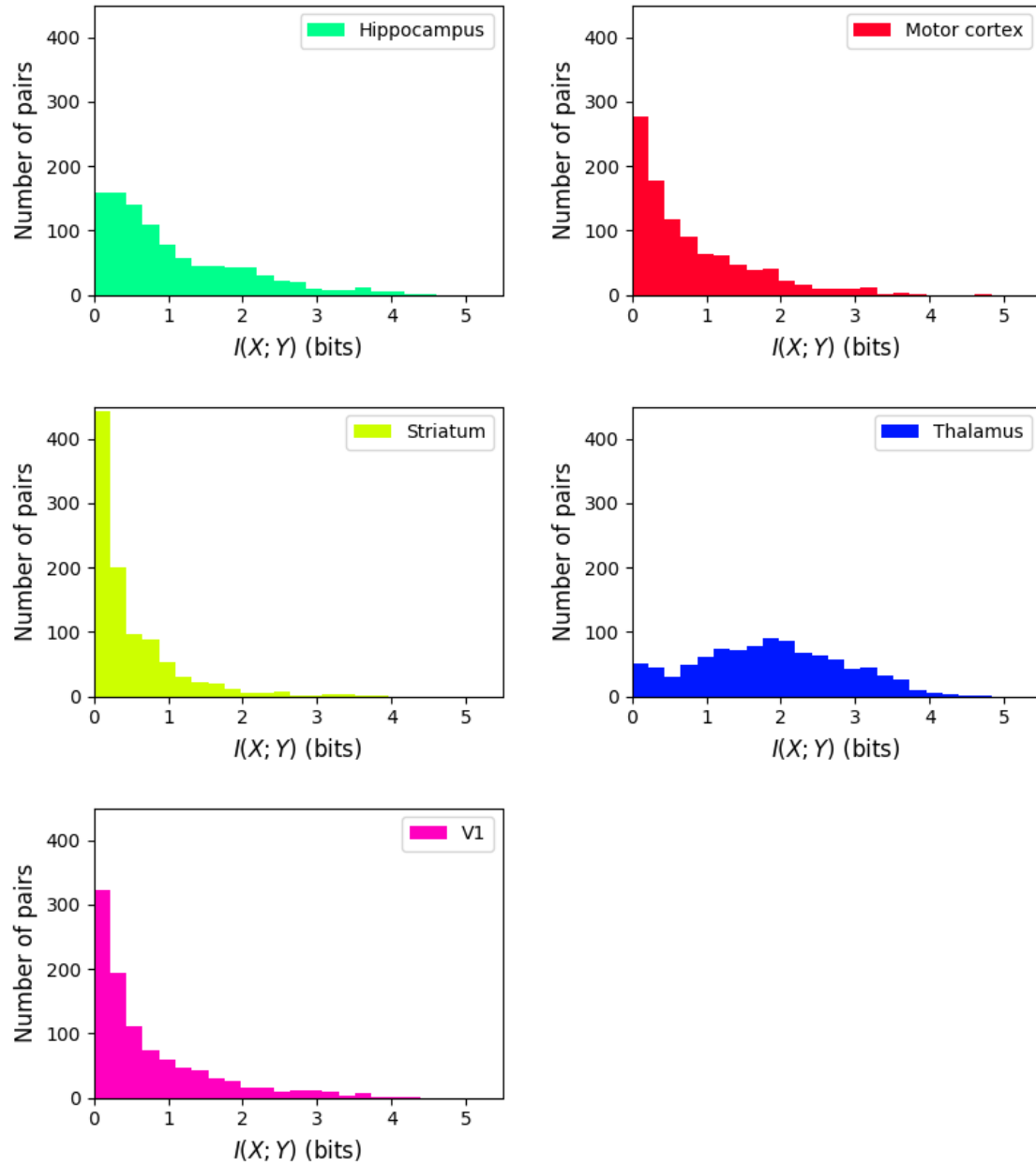


Figure 10: **Mutual Information Histograms:** Histograms of the mutual information of 1000 randomly chosen pairs of neurons from within each region. The time bin width used was 1.0s. In motor cortex, V1, and striatum most pairs have mutual information of ≤ 1 bit. The hippocampus is slightly different more spread out into greater values. In the thalamus, the pairs appear to be more dependent than in the other regions.

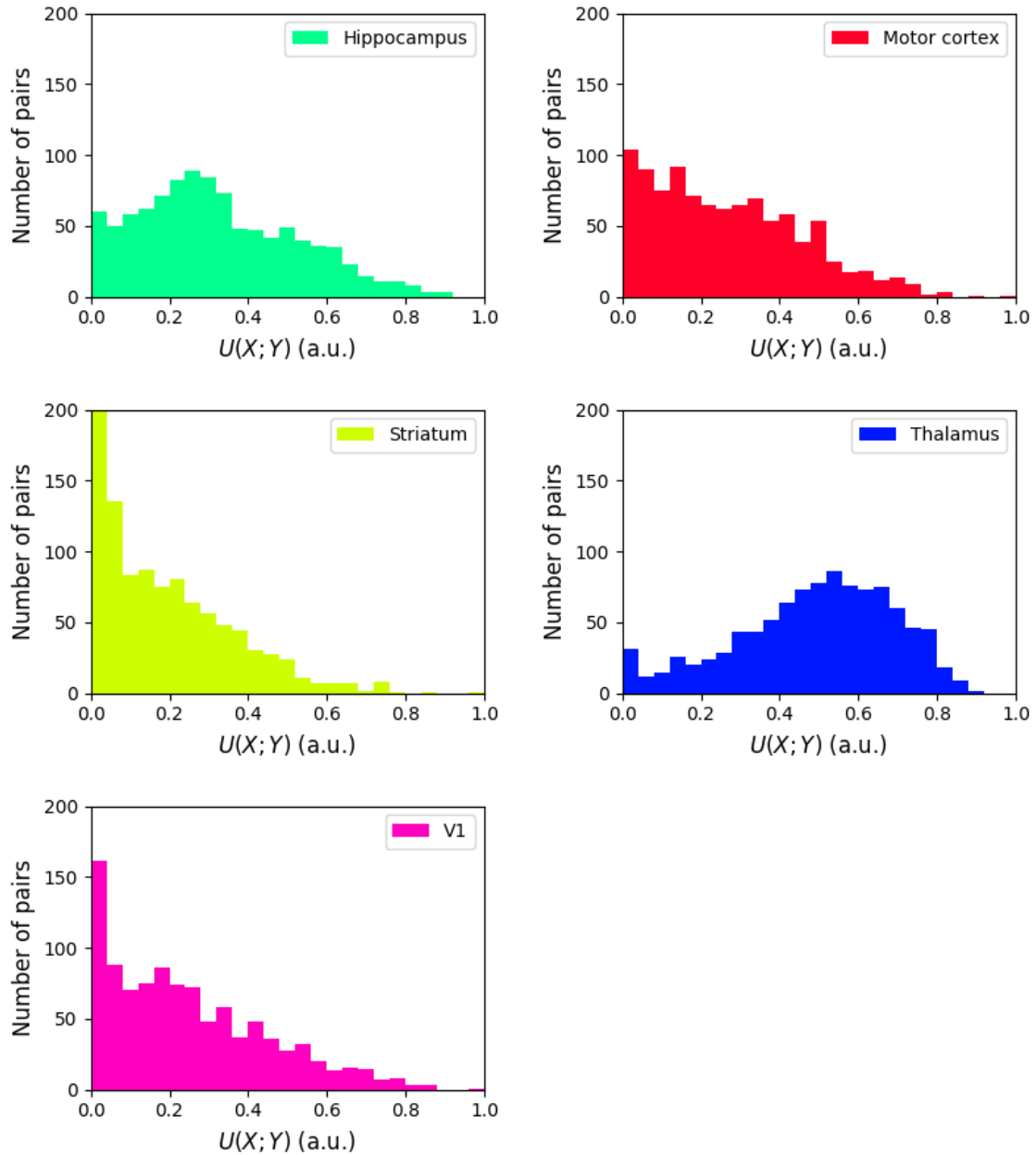


Figure 11: **Symmetric Uncertainty Histograms:** Histograms of the symmetric uncertainty of 1000 randomly chosen pairs of neurons from within each region. The time bin width used was 1.0s. The distribution in each region largely reflects the distribution of the mutual information in the same region shown in figure 10.

Table 1: Spike Count Correlations statistical tests. $P(H_0)$ refers to the probability of the null hypothesis, i.e. the p-value.

Regions		K-S Stat	$P(H_0)$	Statistically Significant
Striatum	Thalamus	0.21	7.0×10^{-19}	Yes
V1	Thalamus	0.2	1.6×10^{-18}	Yes
Motor Cortex	Thalamus	0.2	5.9×10^{-17}	Yes
Hippocampus	Thalamus	0.14	2.1×10^{-9}	Yes
Striatum	Hippocampus	0.12	2.5×10^{-6}	Yes
Motor cortex	Hippocampus	0.09	6.6×10^{-4}	Yes
V1	Hippocampus	0.09	6.6×10^{-4}	Yes
Striatum	V1	0.041	0.363	No
Motor cortex	V1	0.033	0.64	No
Motor cortex	Striatum	0.027	0.85	No

Table 2: Mutual Information statistical tests. $P(H_0)$ refers to the probability of the null hypothesis, i.e. the p-value.

Regions		K-S Stat	$P(H_0)$	Statistically Significant
Striatum	Thalamus	0.69	2.7×10^{-228}	Yes
V1	Thalamus	0.59	2.2×10^{-176}	Yes
Motor cortex	Thalamus	0.57	4.1×10^{-161}	Yes
Hippocampus	Thalamus	0.45	3.8×10^{-106}	Yes
Striatum	Hippocampus	0.3	6.0×10^{-45}	Yes
V1	Hippocampus	0.22	2.7×10^{-16}	Yes
Motor cortex	Hippocampus	0.17	5.7×10^{-12}	Yes
Motor cortex	Striatum	0.14	2.8×10^{-12}	Yes
Striatum	V1	0.11	4.9×10^{-10}	Yes
Motor cortex	V1	0.08	2.6×10^{-3}	Yes

4.3.3 Histograms for strongly responding neurons

We made histograms similar to those described in section 4.3.1 for strongly responding cells only. See figures 12, 13, and 14 for the correlation coefficient, mutual information, and symmetric uncertainty histograms respectively. Note that the number of pairs that were available was significantly less than that for figures 9, 10, and 11 for most regions. Despite that, the mutual information histograms appear to show that the strongly responding neurons are more dependent than their weakly responding counterparts.

We also performed statistical tests comparing the distribution of correlation coefficients and mutual information measurements in pairs of strongly responding neurons with the distributions of those measurements using the 1000 randomly selected pairs as mentioned in section 4.3.1. We found that some regions have the same distribution of correlation coefficients for both strongly and weakly repsonding neurons. But for mutual information, the strongly repsonding neurons always had a different distribution, see tables 3 and 4.

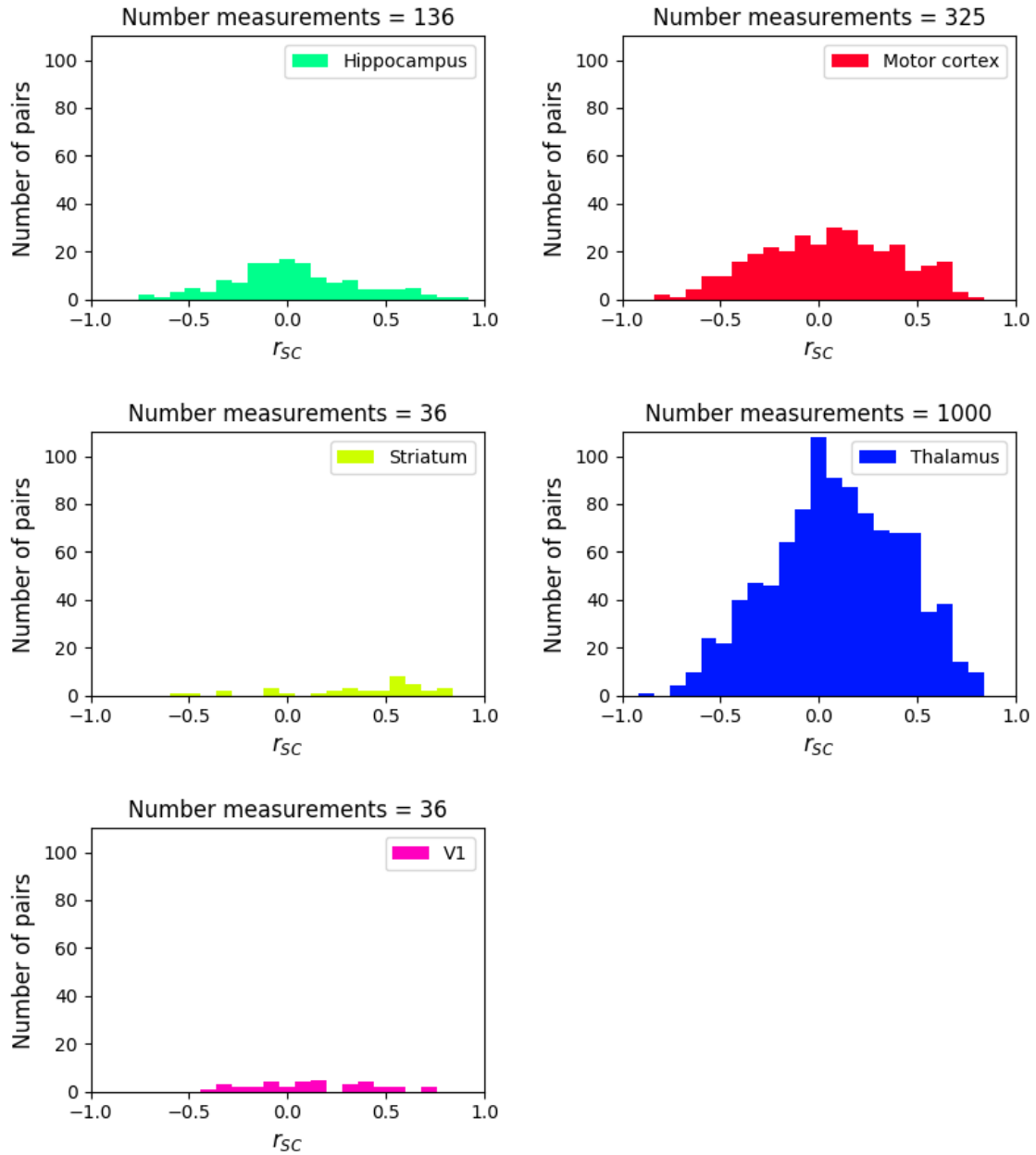


Figure 12: **Spike Count Correlation Histograms, strongly responding cells:** Histograms of the spike count correlations for pairs of strongly responding cells in each region. The time bin width used was 1.0s. For each region, the stimulus that elicited strong responses from the largest number of neurons was used. We can see that the thalamus has by far the most neurons that meet our criteria for 'strongly responding', i.e. a firing rate of at least 10 spikes per second.

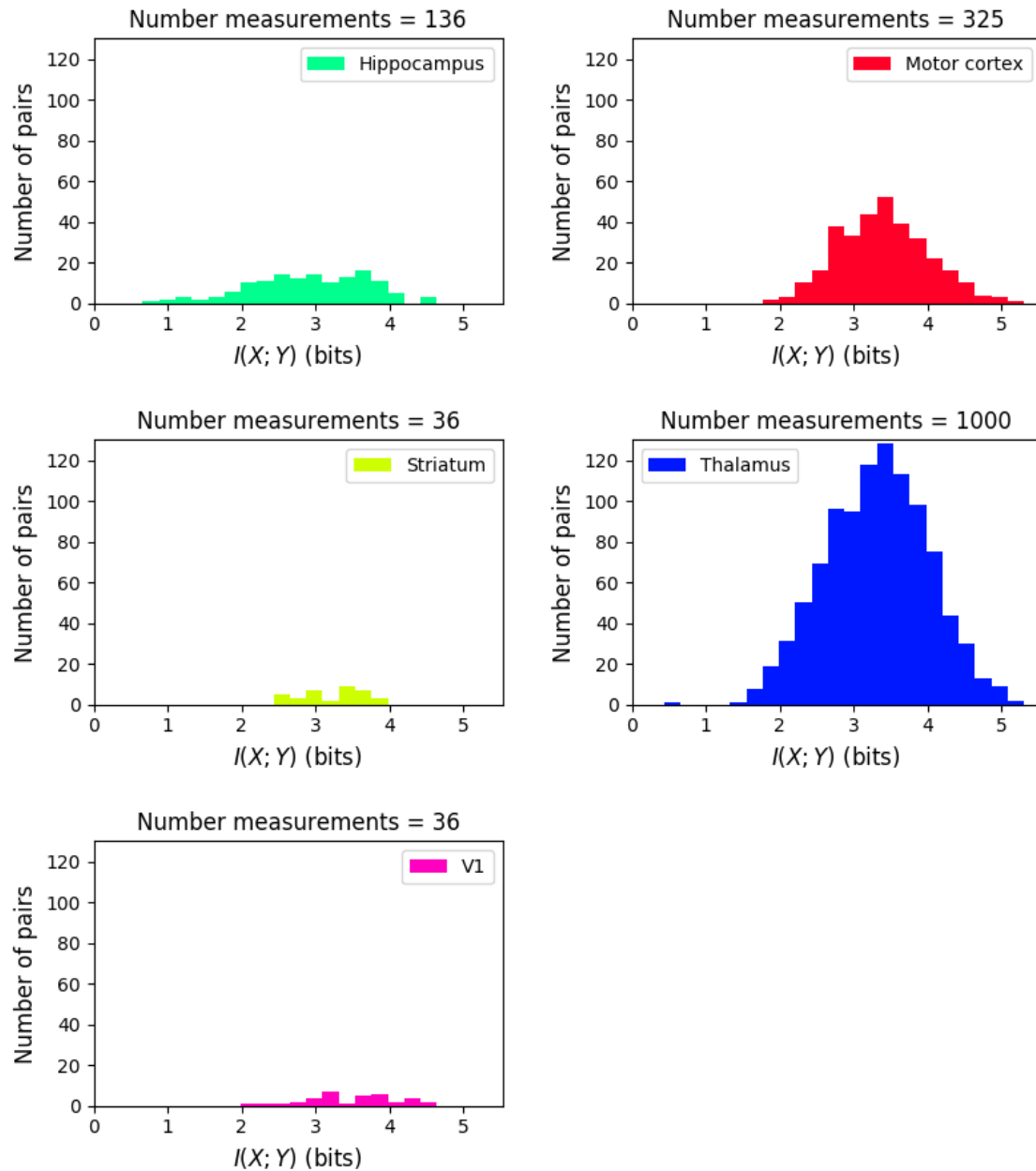


Figure 13: **Mutual Information Histograms, strongly responding cells:** Histograms of the mutual information for pairs of strongly responding cells in each region. The time bin width used was 1.0s. For each region, the stimulus that elicited strong responses from the largest number of neurons was used. In each region, cells that respond more strongly appear to be more dependent on each other than their weakly responding counterparts.

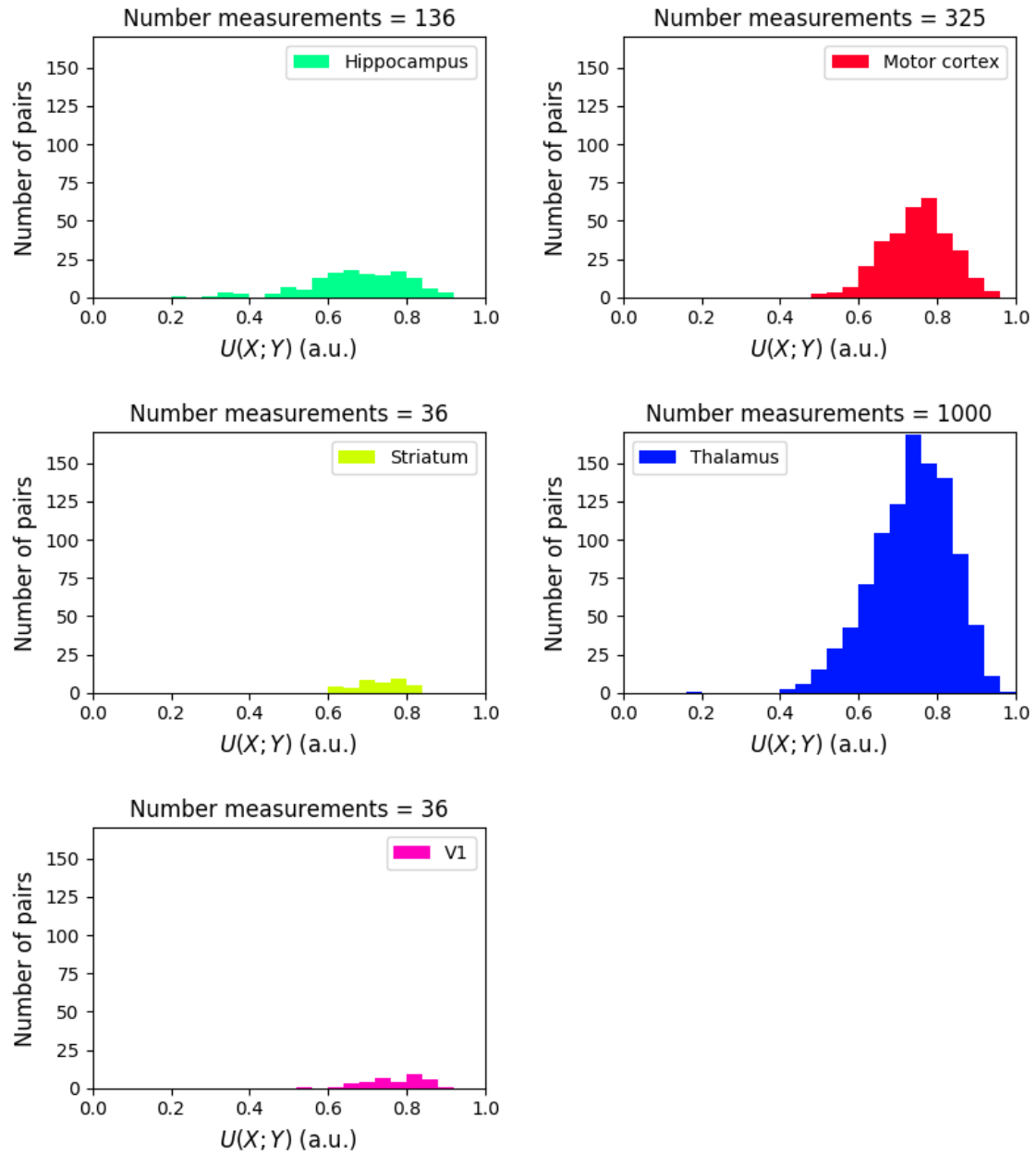


Figure 14: **Symmetric Uncertainty Histograms, strongly responding cells:** Histograms of the symmetric uncertainty for pairs of strongly responding cells in each region. The time bin width used was 1.0s.

Table 3: Statistical tests comparing the distribution of spike count correlations between pairs of strongly responding neurons to the distribution of spike count correlations using all responding neurons. $P(H_0)$ refers to the probability of the null hypothesis, i.e. the p-value.

Region	K-S Stat	$P(H_0)$	Statistically Significant
Striatum	0.57	5.7×10^{-11}	Yes
Motor cortex	0.15	2.1×10^{-5}	Yes
Thalamus	0.062	0.04	Yes
V1	0.18	0.18	No
Hippocampus	0.07	0.45	No

Table 4: Statistical tests comparing the distribution of mutual information measures in strongly responding neurons to the distribution of mutual information in all responding neurons. $P(H_0)$ refers to the probability of the null hypothesis, i.e. the p-value.

Region	K-S Stat	$P(H_0)$	Statistically Significant
Motor Cortex	0.93	5.4×10^{-186}	Yes
Thalamus	0.61	2.7×10^{-163}	Yes
Hippocampus	0.72	1.1×10^{-55}	Yes
Striatum	0.98	9.9×10^{-31}	Yes
V1	0.92	2.3×10^{-27}	Yes

4.4 Firing rate geometric mean, spike count correlation, mutual information

Having measured the firing rates of each neuron, and the spike count correlations and mutual information for many pairs of neurons, we investigated the relationships between these quantities.

4.4.1 Regional spike count correlations & firing rate geometric means

We compared the spike count correlations for pairs of neurons to the geometric means of their firing rates. We did this for each region. There appeared to be little or not correlation between the two quantities, see figure 15.

De la rocha paper in here.

4.4.2 Regional mutual information & firing rate geometric means

We compared the mutual information for pairs of neurons to the geometric means of their firing rates. We did this for each region. There was an obvious positive correlation between the two quantities, see figure 16.

This is to be expected from a numerical point of view. Keeping the bin width constant, as the firing rate of a neuron increases the maximum number of spikes observed in any time bin will increase. This increases the upper limit on the entropy of the neurons'

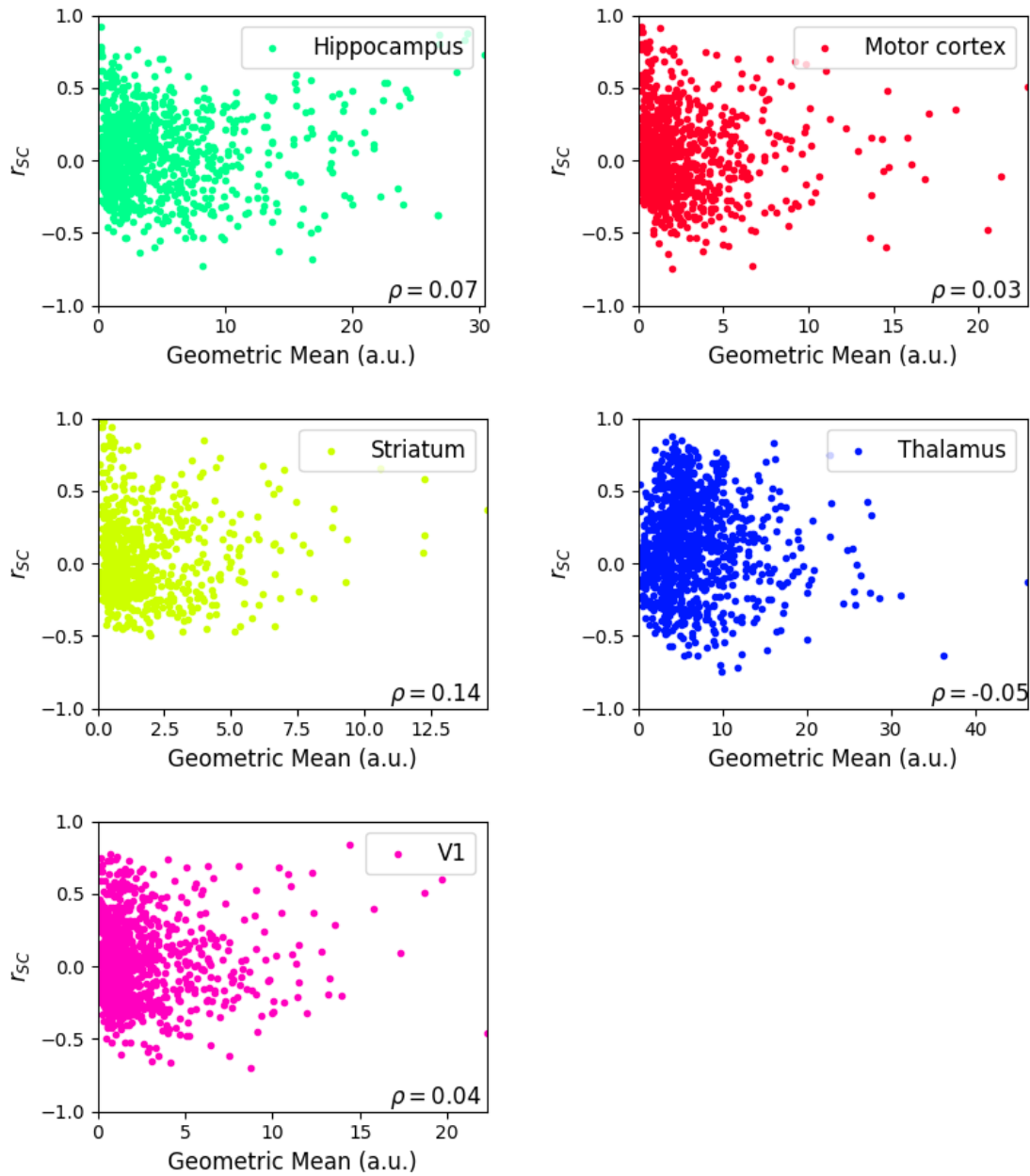


Figure 15: r_{SC} vs firing rate geometric mean: Spike count correlations of pairs of neurons plotted against geometric means of the firing rate of those pairs for each region. Inset, ρ denotes the correlation between these two quantities.

responses (see section 3.5.2). Since the $I(X; Y) \leq \min\{H(X), H(Y)\}$, increasing the firing rate of either neuron in a pair will increase both the geometric mean of the firing rate and the upper limit on the mutual information.

Although an increased firing rate will increase the upper limit on $I(X; Y)$, the lower limit is still 0 bits. It is worth noting that according to figure 16 a high geometric mean rarely corresponds with a low $I(X; Y)$.

4.4.3 Correlation coefficient & Mutual Information

To investigate the relationship between correlation and mutual information, we plotted these two quantities against each other for 1000 randomly chosen responding pairs. We might expect the relationship to be quadratic, with a turning point at $r_{SC} = 0$ as correlated (or anti-correlated) responses should be informative about each other. It is hard to say if this is case, from our results (see figure 17).

Things to discuss with Cian

1. Is all of the above clear?
2. Are my methods sound?
3. Could any of my methods be improved?
4. How can this document be improved? (The figures with the linear x-axis might be better.)

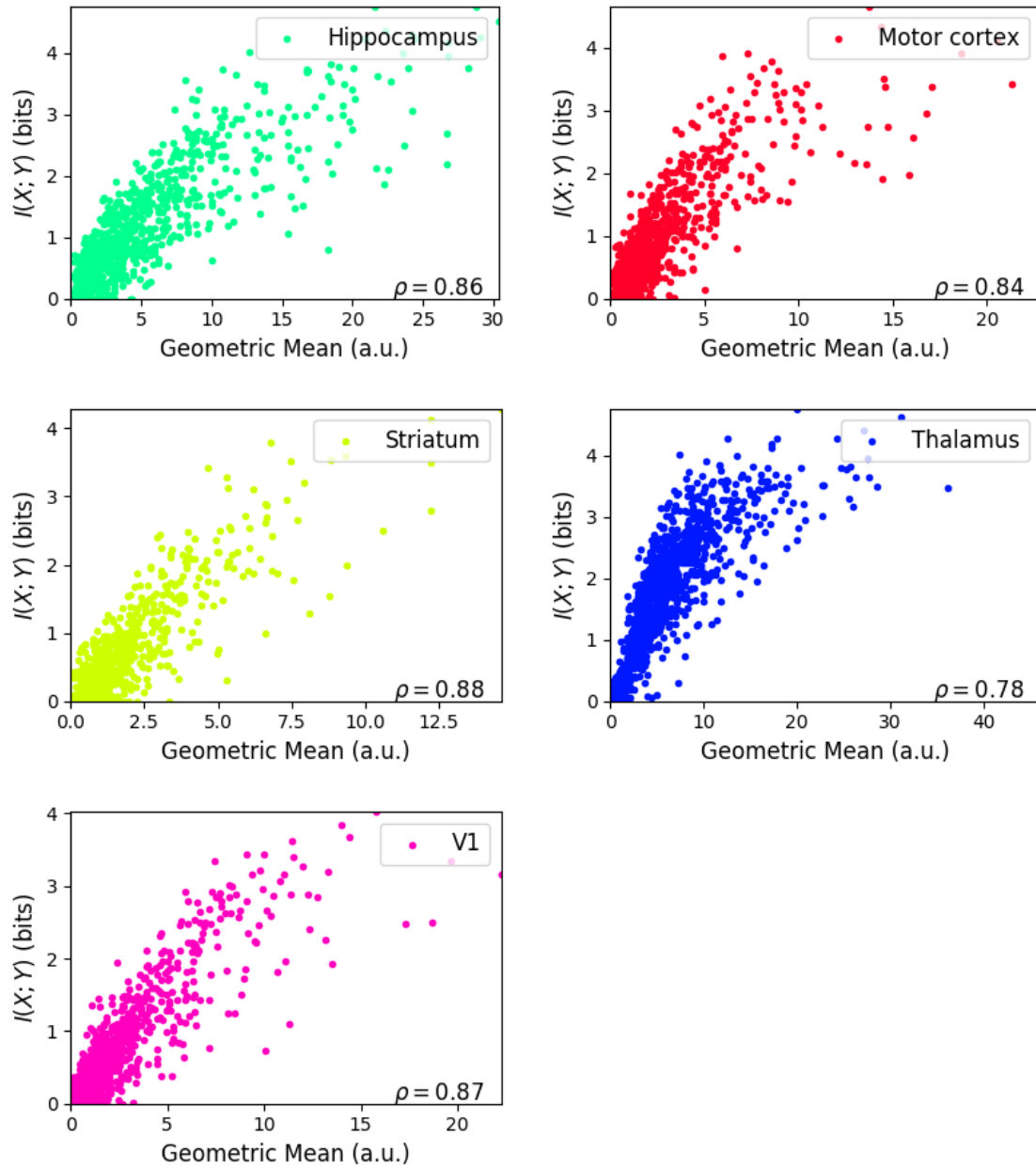


Figure 16: $I(X; Y)$ vs firing rate geometric mean: Mutual information of pairs of neurons plotted against geometric means of the firing rate of those pairs for each region. Inset, ρ denotes the correlation between these two quantities.

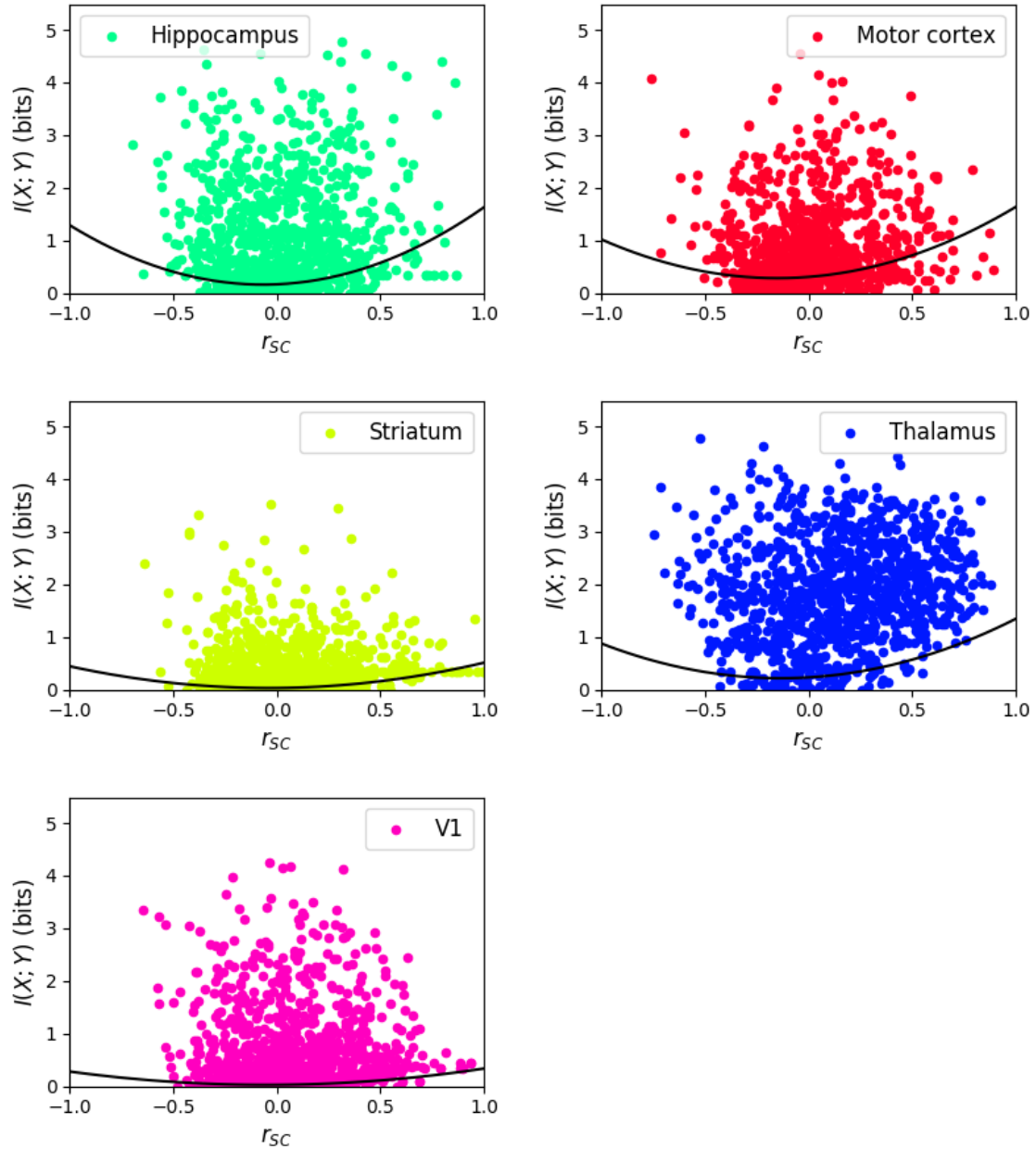


Figure 17: r_{SC} vs $I(X; Y)$: Correlation coefficients of pairs of neurons plotted against the mutual information of those pairs for each region. Each coloured dot represents a pair. The black lines show the fit of a quadratic polynomial, fitted by minimising the squared error. [Question for Cian: Should I remove the quadratic lines?]

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