Measuring information spatial densities

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Abstract

A novel definition of the stimulus-specific information is presented, which is particularly useful when the stimuli constitute a continuous and metric set, as for example, position in space. The approach allows one to build the spatial information distribution of a given neural response. The method is applied to the investigation of putative differences in the coding of position in hippocampus and lateral septum.

1 Introduction

It has longly been known that many of the pyramidal cells in the rodent hippocampus selectively fire when the animal is in a particular location of its environment (O’Keefe and Dostrovsky, 1971). This phenomenon gave rise to the concept of place fields and place cells, that is to say, the association between a given cell and the particular region of space where it fires.
Many computational models of hippocampal coding for space (Tsodyks, 1999) are based on the idea that the information provided by each place cell concerns whether the animal is or is not at a particular location—the place field. It is clear, however, that at least in principle, it could be possible that a given cell provided an appreciable amount of information about the position of the animal without having a place field in the rigorous sense. For example, it could happen that a cell indiscriminately fired all over the environment except in one specific location, where it remained silent. Such a coding would be particularly informative in those occasions where the neuron did not fire. More generally, a cell could fire throughout the whole environment but with a stable and reproducible distribution of firing rates strongly selective to the position. Place field coding would mean that such a firing distribution is a very specific one, namely, one where the cell remains silent everywhere, except inside the place field. In this sense, the idea of a place cell is to the coding of position what in other contexts has been referred to as a grandmother-cell. Whether a given place cell behaves strictly as a grandmother-cell or not, depends on the size of the spatial bins. However, broadly speaking, place cells use a sparse code and only respond to a very small fraction of all possible locations.

In Figure 1 we show four examples of the firing rate distribution of four different neurons when a rat is exploring an 8 arm maze. Similar to previous reports (Zhou et al. 1999), all of these neurons provide an appreciable amount of information about the location of the animal (see caption of Figure 1). Table 1 summarizes the data corresponding to the

| case | type of neuron       | \( \langle r \rangle \) spikes / sec. | \( I/t \) bits / sec. |
|------|----------------------|-------------------------------------|----------------------|
| a    | hipp. pyramidal cells| 0.1981                              | 0.7431               |
| b    | hipp. interneuron    | 15.8995                             | 2.1941               |
| c    | lat. septum          | 2.2688                              | 1.2921               |
| d    | med. septum          | 10.4878                             | 0.4411               |

Table 1: Data corresponding to the cells whose firing density is shown in Figure 1. \( \langle r \rangle \) indicates the mean firing rate of the cell, averaged throughout the maze, while \( I/t \) is the (corrected) information rate (see equations (20) and (7)).

figure. Chart (a) shows a typical place field, the cell only fires when the animal reaches the end point of the right arm. In (b) and (c) we show two different distributed codes, the first corresponds to an hippocampal interneuron and the latter to a neuron in the lateral septum that selectively fires when the rat occupies the endpoints of the maze. Finally, (d) shows a cell in the medial septum whose discharge corresponds to all locations.
Figure 1: Firing rate distribution of four different neurons when a rat is exploring an 8-arm maze. In each case, the density of the color is proportional to the number of spikes per unit time, as a function of space. Since cells of different types have very dissimilar mean firing rates, each plot has been normalized. The absolute rates are shown in Table 1. Each cell provides an amount of information which is at least as large as $\langle I \rangle + \sigma_I$, where $\langle I \rangle$ is the mean information provided by the whole set of cells of that particular type, and $\sigma_I$ is its standard deviation (see Table 2 in Section 3 for the quantitative details).

Within the environment, with a somewhat lower rate in the endpoints of the maze, specially in the upper arm. These examples show that there might be different coding schemes for position, other than localized place fields. Here, we explore such coding strategies, both in hippocampal pyramidal neurons and in lateral septal cells of behaving rats. The latter cell type receives a massive projection from the hippocampus (Swanson et al. 1981, Jakab et al. 1995), which presumably provides information about spatial location. Our aim is to see whether different types of neurons use different codes to represent position.

In the following section, the local information is defined, and its relation to previous similar quantities is established. By taking the limit of a very
fine binning, such a local information gives rise to a spatial information density, that can be used to explore the coding strategy of a cell. In Section 3 the spatial information distribution is calculated for actual recordings in rat hippocampal and lateral septal cells. We end in Section 4, with some concluding remarks.

2 Stimulus-specific informations

Our analysis is based on the calculation of the mutual information between the neural response of each single cell and the location of the animal

$$I = \sum_j \sum_n P(n, x_j) \log_2 \left[ \frac{P(n, x_j)}{P(n)P(x_j)} \right],$$

(1)

where $x_j$ is a small region of space, and $n$ is the number of spikes fired in a given time window. $P(r, x_j)$ is the joint probability of finding the rat at $x_j$ while measuring response $n$, and can always be written as $P(n, x_j) = P(n|x_j)P(x_j)$. The a priori probability $P(x_j)$ is estimated from the ratio between the time spent at position $x_j$ and the total time. The probability of response $n$ reads

$$P(n) = \sum_j P(n, x_j).$$

(2)

The mutual information $I$ measures the selectivity of the firing of the cell to the location of the animal. It quantifies how much can be learned about the position of the rat by looking at the response of the neuron. In contrast to other correlation measures, its numerical value does not depend on whether the cell only fires in a particular location, or whether it only remains silent there. It may happen, however, that the neural responses are highly selective to some very specific locations, and not to others. It is clear that the quantity defined in (1) provides the total amount of information, averaged over all positions. The scope of the present section is to characterize the detailed structure of the spatial locations where the cell is most informative. To do so, we would like to build a spatial information map; that is a way to quantify the amount of information provided by the cell about every single location $x_j$. This issue has been discussed in De Weese and Meister (1999), although in the context of more general stimuli, not specifically position in space. Two definitions (among infinitely many) have been pointed out, namely, “the stimulus specific surprise” (which in the present case will be addressed as the position specific surprise)

$$I_1(x_j) = \sum_n P(n|x_j) \log_2 \left[ \frac{P(n|x_j)}{P(n)} \right],$$

(3)
and the “stimulus specific information” (*position* specific information)

\[ I_2(x_j) = -\sum_n P(n) \log_2 [P(n)] + \sum_n P(n|x_j) \log_2 [P(n|x_j)]. \]  

(4)

Both of these quantities, when averaged in \(x_j\), give the total information

\[ \sum_j P(x_j) I_{1,2}(x_j) = I. \]  

(5)

However, none of the two is, by itself, a proper information. The stimulus specific surprise (3) is guaranteed to be positive, but may not be additive, while the stimulus specific information (4) is additive, but not always positive. Moreover, any weighted sum of \(I_1\) and \(I_2\) is also a valid estimator of the information to be associated to each location (De Weese and Meister, 1999). However, in specific situations these two local information estimators can be very different, which means that their weighted sum can, in practice, lead to any possible result.

Let us examine the behavior of \(I\) and \(I_{1,2}\) in the short time limit. We consider a time interval \(t\), and a cell whose mean firing rate at position \(x_j\) is \(r(x_j)\). Therefore, if \(t \ll 1/r(x_j)\) the cell will most probably remain silent at \(x_j\), only seldom firing a spike. The short time approximation involves discarding any response consisting of two or more spikes. Rigorously speaking, it does not mean that such events will not occur, but rather, that the set of symbols that are considered as informative responses are the firing of a single spike, with probability \(P(1|x_j) \approx r(x_j)t\), and whatever other event—which we call response 0—with probability \(P(0|x_j) = 1 - P(1|x_j)\). Therefore, as derived in Skaggs et al. (1993) and Panzeri et al. (1996),

\[ I = t \sum_j P(x_j) \left\{ r(x_j) \log_2 \left[ \frac{r(x_j)}{\langle r \rangle} \right] + \frac{\langle r \rangle - r(x_j)}{\ln 2} \right\} + O(t^2), \]  

(6)

where

\[ \langle r \rangle = \sum_j P(x_j)r(x_j). \]  

(7)

The short time limit of \(I\) is much more easily evaluated from recorded data than the full equation (1), since it does not need the estimation of the conditional probabilities. Only the firing rates at each location are needed. The first term in the curled brackets comes from the firing of a spike in \(x_j\), while the second describes the silent response.

Similarly, \(I_{1,2}\) tend to

\[ I_1(x_j) = t \left\{ r(x_j) \log_2 \left[ \frac{r(x_j)}{\langle r \rangle} \right] + \frac{\langle r \rangle - r(x_j)}{\ln 2} \right\} + O(t^2), \]  

(8)

\[ I_2(x_j) = t \left\{ \frac{\langle r \rangle - r(x_j)}{\ln 2} + r(x_j) \log_2 [r(x_j)t - \langle r \rangle \log_2 (\langle r \rangle t)] \right\} + O(t^2). \]  

(9)
Equation (8) states that the stimulus specific surprise also rises linearly as a function of \( t \). Its first term comes from those cases when the cell fires a spike, while the second corresponds to the silent response. The stimulus specific information, on the other hand, diverges. However, since for some stimuli \( I_2(x) \) is negative and for some others it is positive, the average of them all is finite, as stated in Eq. (6). The infinitely large discrepancy between Eqs. (8) and (9) shows that for small \( t \), the choice of any one of these estimators is particularly meaningless.

As pointed out above, although this procedure is usually referred to as a short time limit, the crucial step in deriving equations (6 - 9) is to partition the set of all possible responses into two subsets: one containing a single response, namely the case \( n = 1 \), and the complementary one. The conditional probabilities for the occurrence of the distinguished response \( (n = 1) \) is taken proportional to a parameter \( t \) which is supposed to be small. Such a procedure with the response variable inspires the exploration of an analogous partition in the set of locations.

### 2.1 A spatial information density

To find a well behaved measure of a location specific information we now introduce the local information \( I^\ell(x_j) \), which quantifies how much can be learned from the responses about whether the animal is or is not in \( x_j \). In other words, we partition the set of possible locations into two subsets, one containing position \( x_j \) and the complementary set \( \bar{x}_j = \{x / x \text{ does not belong to region } j \} \). Mathematically,

\[
I^\ell(x_j) = \sum_{n=0}^{+\infty} P(n) \left\{ P(x_j | n) \log_2 \left[ \frac{P(x_j | n)}{P(x_j)} \right] + P(\bar{x}_j | n) \log_2 \left[ \frac{P(\bar{x}_j | n)}{P(\bar{x}_j)} \right] \right\},
\]

(10)

where \( P(n) \) is the probability of the cell firing \( n \) spikes no matter where, \( P(x_j) \) is the probability of visiting location \( x_j \), \( P(\bar{x}_j) = 1 - P(x_j) \) is the probability of not being in \( x_j \), \( P(x_j | n) \) is the conditional probability of being in \( x_j \) when the cell fired \( n \) spikes, \( P(\bar{x}_j | n) \) is the conditional probability of not being in \( x_j \) while the cell fires \( n \) spikes, and can be obtained from

\[
P(x_j | n) + P(\bar{x}_j | n) = 1.
\]

(11)

Equation (11) defines a proper information, in the sense that it is positive and additive. It should be noticed that in contrast to the short time limit, in the case of the local information, there is no preferred location to be separated out. That is why we calculate as many \( I^\ell(x_j) \) as there are positions \( x_j \). As \( j \) changes, however, \( I^\ell(x_j) \) refers to a different partition of the environment. This means that one should not average the various \( I^\ell(x_j) \).
In parallel to the short time limit, we now make the area $\Delta$ of region $x_j$ tend to zero. To do so, we assume that both $P(x_j)$ and $P(x_j|n)$ arise from a continuous spatial density $\rho$,

$$P(x_j) = \int_{\text{region } j} \rho(x) dx,$$

$$P(x_j|n) = \int_{\text{region } j} \rho(x|n) dx,$$

where

$$\rho(x) = \sum_{n=0}^{+\infty} P(n) \rho(x|n). \quad (14)$$

For $\Delta$ sufficiently small,

$$P(x_j|n) \approx \Delta \rho(x|n)$$

$$P(x_j) \approx \Delta \rho(x). \quad (15)$$

The continuity of $\rho$ allows us to drop the sub-index $j$. Expanding $I^\ell(x)$ in powers of $\Delta$ it may be seen that the first term is

$$I^\ell(x) = \Delta \sum_{n=0}^{+\infty} P(n) \left\{ \rho(x|n) \log_2 \left( \frac{\rho(x|n)}{\rho(x)} \right) + \frac{\rho(x) - \rho(x|n)}{\ln 2} \right\} + O(\Delta^2). \quad (16)$$

The local information is therefore proportional to $\Delta$, which means that in the limit $\Delta \to 0$ it becomes a differential. Equation (16) is completely analogous to (6). This behavior indicates that the density

$$i(x) = \frac{I^\ell(x)}{\Delta} \quad (17)$$

approaches a well defined limit when $\Delta \to 0$. As pointed out earlier, $I^\ell(x)$ is conceptually different from the full information $I$ defined in equation (4), and for finite $\Delta$, there is no meaning in summing together the $I^\ell(x_j)$ corresponding to different $j$. However, it is easy to verify that when $\Delta \to 0$, the integral of $i(x)$ throughout the whole space coincides with the full information $I$, when the latter is calculated in the limit of very fine binning. Therefore, $i(x)$ behaves as an information spatial density. Moreover, in contrast to $I_1(x)$ and $I_2(x)$, it derives from a properly defined information.

Equation (16) is the continuous version of (10). It should be noticed, however, that in practice one cannot calculate $\rho(x|n)$ from experimental data, for finite time bins. If $\Delta$ is sufficiently small, and the animal moves around with a given velocity, it just never remains within $x_j$ during the chosen time window. Nevertheless, there is no inconvenient in giving a theoretical definition of $\rho(x|n) = \lim_{\Delta \to 0} P(x_j|n)/\Delta$, imagining one could perform the experiment placing the animal in $x_j$ and confining it there throughout the whole time interval. In order to bridge the gap between
the theoretical definition of $\rho(x|n)$ and the actual possibility of measuring an information spatial density with freely moving animals, we now take equation (16) and calculate its short time limit. The result is

$$I^\ell(x) = t\Delta \rho(x) \left\{ r(x) \log_2 \left[ \frac{r(x)}{\langle r \rangle} \right] + \frac{\langle r \rangle - r(x)}{\ln 2} \right\} + \mathcal{O}(\Delta^2) + \mathcal{O}(t^2).$$

(18)

This same expression is obtain if one starts with the full definition (10) and first calculates the limit of $t \to 0$ and subsequently makes $\Delta \to 0$. Comparing equation (18) with (8) it is clear that

$$I^\ell(x) = tP(x)I_1(x) + \mathcal{O}(\Delta^2) + \mathcal{O}(t^2).$$

(19)

We therefore conclude that in the short time limit, the position specific surprise coincides with the local information (multiplied by the probability of occupancy). This gives the position specific surprise $I_1$ a different status than $I_2$ or any combination of the two: even though in a general situation $I_1$ is not additive, when the number of stimuli is very large (or the binning very fine, if the stimuli are continuous) it coincides with a well defined quantity, namely, the local information. It should be kept in mind, however, that such a correspondence between $I^\ell(x)$ and $I_1(x)$ is only valid in the short time limit—or, more precisely, when computing the information provided by one spike.

### 3 Data analysis

In the present section we evaluate $I^\ell(x_j)$ as a function of $x_j$ using electrophysiological data recorded from rodents performing a spatial task. In Subsection 3.1 the experimental procedure is explained, and later, in 3.2 we show that different brain regions use different coding strategies in the representation of space.

#### 3.1 Experiment design

Nine young adult Long-Evans rats were tested during a forced-choice and a spatial working memory task. Both tasks were performed in an 8 arm radial maze, each arm containing a small amount of chocolate milk in its distal part. In addition, the proximal part of each arm could be selectively lowered, thereby forbidding the entrance to that particular arm (for details see Leutgeb et al., 2000). In the forced choice task, the animal was placed in the center of the maze, while the entrance to a single arm was available.
The other seven arms were kept at a lower level. After the animal had entered into the available arm and taken its food reward, a second arm was raised, and the previous one was lowered. The procedure was continued by allowing the animal to enter just one arm at a time with no repetitions. The session ended when the rat had taken the milk of all eight arms. A pseudo-random sequence of arms was chosen for each trial. The beginning of the working memory task was identical to the forced choice one, until the animal had entered the fourth arm in the sequence. At this point, all arms of the maze were raised, and the rat could move freely. However, only the four new arms still contained food reward. The session continued until the animal had taken all the available chocolate milk or for a maximum of 16 choices. Re-entries into previously visited arms of the maze were counted as working memory errors, since in principle, the animal should have kept in mind that in that arm, the food had already been eaten.

Septal and hippocampal cells were simultaneously recorded during both of the tasks (for recording details see Leutgeb 2000). A head-stage held the FET amplifiers for the recording electrodes as well as a diode system for keeping track of animals position. Single units were separated using an online and off-line separation software. Units are then identified according to their anatomical location and the characteristics of the spikes. Hippocampal pyramidal cells and interneurons as well as lateral and medial septal cells were identified. Animals were tested either in standard illumination condition or in darkness.

### 3.2 Results and discussion

In order to compute $I^f(x_j)$ from the experimental data, both $r(x_j)$ and $P(x_j)$ are needed for each position. In order to compute $r(x)$ the total number of spikes fired in location $x_j$ is divided by the total time spent there. The a priori probability $P(x_j)$ of visiting the spatial bin $j$ was obtained by the ratio of the time spent in $x_j$ and the total duration of the trial. The computation of mutual information typically introduces an upward bias due to limited sampling. Therefore, a correction has been applied, in order to reduce this overestimation, as suggested in Panzeri and Treves (1996). In our case, the first order correction for equations (6) and (10) can be derived analytically

$$I_{corr} = I - \frac{t(N - 1)}{2T \ln 2},$$

(20)

where $N$ is the number of positions $x_j$ in which the environment has been binned and $T$ is the total duration of the recording. Throughout the paper,
when specifying experimental data, we always give the corrected value of $I$—although, for simplicity of notation, we drop the sub-index “corr”. Table 2 summarizes the overall statistics of our experimental data. The

| neuron | number of units | $\langle r \rangle$ | $\sigma_{\langle r \rangle}$ | $\langle I \rangle/t$ | $\sigma_{\langle I \rangle}/t$ |
|--------|-----------------|--------------------|-----------------------------|------------------|------------------|
| HP     | 114             | 0.99665            | 1.2353                      | 0.43851          | 0.39535          |
| HI     | 21              | 15.228             | 6.9618                      | 0.81994          | 0.85995          |
| LS     | 327             | 5.0732             | 7.7119                      | 0.25274          | 0.33575          |
| MS     | 34              | 10.971             | 12.177                      | 0.27802          | 0.46498          |

Table 2: Statistic corresponding to the whole population of recorded neurons, where $\langle r \rangle$ is the mean firing rate averaged throughout the maze, and over all cells, $\sigma_{\langle r \rangle}$ is the average quadratic deviation from the mean, $\langle I \rangle/t$ is the mean information rate, averaged over cells, and $\sigma_{\langle I \rangle}/t$ its mean quadratic deviation. HP stands for pyramidal cells in the hippocampus, HI for interneurons in the hippocampus, while LS for units in the lateral, and MS for units in the medial septum.

values of $I/t$ have been calculated in the short time limit (3) and further subtracting the correction (20).

The proportionality between $I^\ell(x)$ and $\Delta$ (see Eq. 18) was based on the assumption that the conditional probabilities $P(x_j|n)$ emerged from a continuous density $\rho(x|n)$. In order to verify whether such a supposition actually holds, we evaluated $I^\ell(x_j)$ from our experimental data, for different values of the area $\Delta$. In Figure 2 we show a spatial average of our results, namely

$$\langle I^\ell(x) \rangle = \frac{1}{N} \sum_j I^\ell(x_j),$$

(21)

where $N$ is the total number of positions $j$ in which the maze has been binned. Clearly, $N = \text{total area} / \Delta$. The local information $I^\ell(x_j)$ has been evaluated in the short time limit. It is clearly seen that in all cases, the local information grows linearly with $\Delta$, as predicted by Eq. (16).

We therefore build the local information maps, for all the cells recorded. In other words, we calculate $i(x_j)$ for all the positions $x_j$. We have restrained ourselves from going into a too fine binning, however, in order to avoid limited sampling problems. In Figure 3 we show the information maps corresponding to the firing distributions of Figure 4. The hippocampal pyramidal cell in (a) is only informative at the same location where the cell fires. In this particular case, the intuition seems to be justified: the cell codes for a single position, and does so by increasing its firing rate at
Figure 2: Mean local information rate—defined in equation (21)—as a function of the area $\Delta$ of each bin. Three pyramidal cells in the hippocampus are shown in (a) and three cells in lateral septum cells appear in (b). All cells carry an appreciable amount of information when compared to other cells of the same type. Both (a) and (b) contain one unit with a high firing rate, an intermediate one and a low frequency cell.

that location. However, the other three cases show that the neuron may well provide information not only where it fires most, but also where it fires least. In particular, the hippocampal interneuron in (b), which tends to fire all over the maze, is particularly informative in the upper-left and upper-right end points, where it remains almost silent. In cases (c) and (d) the cells provide information both where there is a high and a low firing rate. As a consequence, we conclude that if a cell has a distributed coding scheme (as opposed to a very local one, more typical of hippocampal place cells), the information map may well not coincide with the firing rate one. In this sense, one should beware not to judge cells with a distributed firing pattern as non-informative. If such a pattern is stable and reproducible, covering a wide range of firing rates, the neuron may well be providing spatial information.

Could a quantitative analysis of the coding strategies of hippocampal pyramidal cells, and neurons in the lateral septum be given? We have not considered hippocampal interneurons nor medial septum cells since in these two cases, we do not have enough statistics to draw conclusions. In addition, on average, they are less informative (see table 2).

One possible measure of the degree of localization of the coding scheme is given by the correlation between the information maps and the firing rates distributions (that is, between the graphs of figures 1 and 3). We
Figure 3: Local information distributions corresponding to the firing densities of Figure 1. In each case, the density of the color is proportional to the number of bits per unit time, as a function of space.


evaluate the Pearson correlation coefficient between the two maps, i.e.

\begin{equation}
C = \frac{\sum_j \left[ I^\ell(x_j) - \langle I^\ell(x_j) \rangle_j \right] \left[ r(x_j) - \langle r \rangle \right]}{N \left[ \sum_j I^\ell(x_j) \right] \left[ \sum_j r(x_j) \right]},
\end{equation}

where \( \langle I^\ell(x_j) \rangle_j \) is the spatial average of the local information. Thus, \( C \) is equal to 1 if \( I^\ell(x_j) - \langle I^\ell(x_j) \rangle_j \) is proportional to \( r(x_j) - \langle r \rangle \), and takes the value -1, if the proportionality factor is negative. Notice that there is one such \( C \) for every single cell. In Figure 4 we show the frequency distribution of the correlation \( C \) for (a) the 114 pyramidal cells recorded in the hippocampus and (b) the 297 units recorded in the lateral septum. It may be seen that pyramidal cells tend to have larger values of the correlation \( C \), indicating that they tend to provide information in the same locations where they fire most. In other words, the code in the hippocampus can be characterized as localized, as is well known, giving rise to place cells and place fields. In contrast, septal cells have a somewhat more symmetrical distribution around zero. If \( C \approx 0 \), then the cell gives as much information in those locations where it fires most, as where it remains silent (or, more
Figure 4: Frequency distribution of the correlation $C$ between the information and firing rate spatial distributions, for (a) 114 pyramidal cells in the hippocampus, and (b) 327 neurons in the lateral septum.

precisely, where it fires less than its average spontaneous rate). A negative value of $C$ indicates that the cell is most informative in the locations where it does not fire (Figures 1 (b) and 3 (b) provide an example from an hippocampal interneuron). As stated in Table 2, hippocampal pyramidal cells are more informative than lateral septal cells. The point we want to stress is that the lateral septum follows a different coding strategy: cells do not specialize in a particular region of space, but rather, respond with a complex, distributed firing pattern all over the place.

4 Conclusions

The aim of the present work was to present a characterization of the way the information provided by neural activity distributes among the elements of a given set of stimuli. In our case, the stimuli were the different positions an animal can be located, within its environment. We defined the local information $I^\ell(s)$, namely the information provided by the responses of whether the stimulus is or is not $s$. In other words, it is the mutual information between the responses and a reduced set of stimuli, consisting of only two elements: stimulus $s$, and its complement. In contrast to other quantities introduced previously, this is a well defined mutual information which can be employed in the short time limit. In fact, other possible definitions have some drawbacks; for example, the position specific surprise has the disadvantage of not being additive. From the theoretical point of view it is therefore not a very sound candidate for quantifying the information
to be associated to each stimulus. The position specific information, on the other hand, may not be positive and diverges for \( t \to 0 \), thus making its application to actual data quite cumbersome.

In this paper we have studied the properties of \( I^\ell \) in the particular situation were the stimuli arise from a continuous variable (as position in space) which has an underlying metric. In this case, the binning that transforms the continuous variable (in our case \( x \)) into a discrete set \( \{x_j\} \) may be chosen, in principle, at will. When working with real data, however, the size of the bins is determined by the amount of data, since the mean error in the calculation of the mutual information is linear in the number of bins (see equation (20)).

We have shown analytically that when the size of the bin goes to zero, the local information is proportional to the bin size. This means that \( I^\ell(x)/\Delta \) behaves as an information spatial density, in that it tends to a constant value when \( \Delta \to 0 \), and its integral all over space coincides with the full information \( I \). We point out that these two properties hold only in the limit of \( \Delta \to 0 \), whereas the position specific surprise and the position specific information fulfill equation (5) for any size of the bins.

We have also shown that in the short time limit and for \( \Delta \to 0 \), the local information coincides with the position specific surprise, multiplied by the probability of occupancy. This result may seem puzzling, since \( I_1 \) is known not to be additive, while additivity is guaranteed in \( I^\ell \). However, it should be noticed that the additivity of \( I^\ell \) is more restricted than the one desired for \( I_1 \). If the position specific surprise were to be additive, \( I_1 \) would obey the relation

\[
I_1(x_{j_1}, x_{j_2}) = I_1(x_{j_1}) + I_1(x_{j_2}|x_{j_1}),
\]

where \( I_1(x_{j_1}, x_{j_2}) \) is the information provided by the responses about two particular results of the measurement of the stimulus. As shown by De Weese and Meister (1999), \( I_1 \) does not follow equation (23). The local information, on the other hand, does fulfill the condition

\[
I^\ell(x_a, x_b) = I_1(x_a) + I_1(x_b|x_a),
\]

where \( x_a \) and \( x_b \) may only be \( x_j \) or \( x_j^* \), and \( I^\ell(x_a, x_b) \) represents a true mutual information, between the set of responses and the two sets \( \{x_j, x_j^*\} \) (one set for each measurement). Additivity for \( I_1 \) requires additivity for any choice of \( x_{j_1} \) and \( x_{j_2} \) in (23), while the possible values of \( x_a \) and \( x_b \) are much more restricted in (24). One should therefore not mistrust the fact that \( I_1 \) does not obey a very demanding additivity condition, while \( I^\ell \) fulfills a quite relaxed one.
The local information, as defined here, allows the characterization of the spatial properties of the information conveyed by a given cell. Just by measuring the mutual information between a given neuronal response and the set of possible locations, one sees that there are cells (both in the hippocampus and in the lateral septum) that provide an appreciable amount of information without actually having a place field. By means of the local information, it is possible to draw a spatial information density which may, in these non-typical cases, differ significantly from the rate distribution. In the last section we have shown that the local information can be easily calculated from experimental data, and that it can actually be used to characterize the coding strategy of different cell types. In particular, we saw that hippocampal place cells tend to provide spatial information in the same places where they fire, whereas lateral septal neurons use a more distributed coding scheme. This result is in agreement with the different goals in the encoding of movement related quantities in both regions, as described recently in Bezzi et al. (2000).

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