

## How much information is associated with a particular stimulus?

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### Abstract

Although the Shannon mutual information can be used to reveal general features of the neural code, it cannot directly address which symbols of the code are significant. Further insight can be gained by using information measures that are specific to particular stimuli or responses. The *specific information* is a previously proposed measure of the amount of information associated with a particular response; however, as I show, it does not properly characterize the amount of information associated with particular stimuli. Instead, I propose a new measure: the *stimulus-specific information* (SSI), defined to be the average specific information of responses given the presence of a particular stimulus. Like other information theoretic measures, the SSI does not rely on assumptions about the neural code, and is robust to non-linearities of the system. To demonstrate its applicability, the SSI is applied to data from simulated visual neurons, and identifies stimuli consistent with the neuron's linear kernel. While the SSI reveals the essential linearity of the visual neurons, it also successfully identifies the well-encoded stimuli in a modified example where linear analysis techniques fail. Thus, I demonstrate that the SSI is an appropriate measure of the information associated with particular stimuli, and provides a new unbiased method of analysing the significant stimuli of a neural code.

### 1. Introduction

Information theory provides measures for comparing different coding schemes of neurons and neural ensembles, avoiding both biases caused by preconceptions of the neural code and complications inherent in analysing neuronal systems with non-linearities and under conditions of complex stimuli. As a result, information theory has been used to analyse neural data in a variety of sensory systems (for a review, see Borst and Theunissen 1999). Such studies typically make comparisons between the Shannon mutual information given different classifications of

stimulus and response ensembles, but do not address which stimuli and responses within these ensembles are significant in information transmission.

As a result, DeWeese and Meister (1999) proposed an information theoretic measure of the significance of particular symbols in the neural code: the *specific information*. The specific information of a particular response is defined as the reduction in uncertainty in the stimulus gained by the observation of that response. Since the mutual information represents the *average* reduction in the uncertainty of the stimulus gained by one measurement, specific information is intuitively a good representation of the degree to which a given response contributes to the overall mutual information. Furthermore, DeWeese and Meister (1999) show that specific information has unique properties that are appropriate for a measure of the information of a response.

Specific information can be applied to both particular stimuli and particular responses due to the symmetry between stimulus and response in information measures. However, because of the asymmetry of stimulus and response with respect to causality (i.e., stimuli cause responses and not vice versa), here I show that specific information does not provide a good measure of stimulus significance. I propose a new measure, the ‘stimulus-specific information’ (SSI), which is defined to be the average reduction in uncertainty of one observation given a particular stimulus.

Since the definition of the SSI relies on a measure of the information associated with responses (i.e., specific information), I will first define specific information (proposed by DeWeese and Meister 1999). Using a simple example, I will then show that it does not provide a good measure of the information associated with particular stimuli, and motivate the definition of the SSI.

To demonstrate its effectiveness, the SSI is applied to data from realistic simulations of neurons in the lateral geniculate nucleus (LGN) presented with full-field white-noise stimuli (Keat *et al* 2001), and to a modified version of this model that defies typical linear analyses. In both cases, the SSI identifies the most significant stimuli and offers additional insight into the underlying neural code.

## 2. Decomposing mutual information into response-specific information

Consider a system presented with an ensemble of stimuli  $S$  and whose behaviour can be classified into a set of responses  $R$ . The Shannon mutual information between the stimulus  $S$  and response  $R$  ensembles of this system is given by

$$I[R, S] = \sum_{s \in S} \sum_{r \in R} p(s, r) \log_2 \frac{p(s, r)}{p(s)p(r)} \quad (1)$$

where  $p(s, r)$  is the joint probability distribution, i.e., the probability of simultaneously observing the stimulus  $s \in S$  and the response  $r \in R$ . The joint probability distribution  $p(s, r)$  can be computed by counting the frequency of each stimulus–response pair over a sufficient amount of time, over which the ‘natural’ ensemble of stimuli is sampled with the probability given by the *prior distribution*  $p(s)$ .

While the mutual information can be used to objectively evaluate different coding schemes through different classifications of the stimulus and response ensembles ( $S$  and  $R$ ), it represents an average over the entire set of stimuli  $s \in S$  and responses  $r \in R$ . It is often of interest to know which particular stimuli are effectively encoded by the system, and which particular responses communicate information about the stimuli. Such questions can be addressed by decomposing  $I[R, S]$  into measures that represent the contributions of specific stimuli or responses to the

mutual information, i.e.

$$I[R, S] = \sum_{s \in S} p(s) i(s) = \sum_{r \in R} p(r) i(r). \quad (2)$$

In this sense, the mutual information is explicitly a weighted average over individual contributions from particular stimuli or particular responses.

There are an arbitrary number of ways to perform such decompositions, meaning that there is not one single measure that represents the ‘specific’ information associated with a particular stimulus or response. As a result, an appropriate measure must be chosen that properly signifies the role of particular stimuli and responses in information transmission.

DeWeese and Meister (1999) argue that the information of a response must be *additive*, since intuitively, information should accumulate over consecutive independent measurements such that the total information from multiple measurements is equal to the sum of information gained from each measurement separately. They show that there is only one decomposition of mutual information that is additive, the *specific information*, given by

$$i_{sp}(r) = H[S] - H[S|r] \quad (3)$$

where the *entropy* of the prior distribution is given by  $H[S] = -\sum_s p(s) \log_2 p(s)$  and the *conditional entropy* associated with a particular response  $r$  is given by  $H[S|r] = -\sum_s p(s|r) \log_2 p(s|r)$ .

The specific information has a straightforward intuitive meaning with regards to the process of information transmission. Entropy is a measure of the uncertainty in probability distributions (see Cover and Thomas 1991): broad distributions have large entropy, and narrow distributions (where the variable in question is more localized to particular values) have little entropy. The *specific information* is a difference in entropy of stimulus distributions (equation (3)), and thus represents the amount that the initial uncertainty of the stimulus is reduced by observing the response  $r$ . Furthermore, specific information is calibrated to mutual information: the specific information is a direct measure of the amount learned by a given measurement, the mutual information is the amount learned by a measurement *on average* over all possible responses.

Thus, the specific information serves as an information theoretic measure through which the significance of different responses can be compared. Responses with a high specific information reduce the uncertainty in the stimulus the most and are thus most significant to the system, and responses that do not reduce the amount of uncertainty in the stimulus are less significant.

### 3. The significance of a stimulus is different to that of a response

Shannon’s mutual information is a statistical measure of the interdependence of two random variables, which, in the study of sensory systems, is usually stimulus and response. As a result of this generality, expressions for information theoretic quantities do not distinguish between stimulus and response (for example, see equation (1)), meaning that tools applicable to responses can be applied to stimuli. For example, the specific information of a stimulus can be calculated by interchanging response and stimulus in equation (3):

$$i_{sp}(s) = H[R] - H[R|s]. \quad (4)$$

Is the specific information an appropriate measure of the information associated with a particular stimulus? Below I show that, due to the asymmetry of stimulus and response with respect to causality, a stimulus that is significant to a system does not have the same properties as a significant response.

Consider a simple joint probability distribution  $p(r, s)$  where there are only two stimuli and two responses, with the probabilities of each stimulus–response pair given by

|       |       |       |
|-------|-------|-------|
| $s_2$ | $1/4$ | $0$   |
| $s_1$ | $1/4$ | $1/2$ |
|       | $r_1$ | $r_2$ |

Without a measurement, the probability of stimulus  $s_1$  is  $\frac{3}{4}$  and the probability of  $s_2$  is  $\frac{1}{4}$ , i.e., the prior distribution is  $p(s) = \{\frac{3}{4}, \frac{1}{4}\}$  with an entropy  $H[S] = 2 - \frac{3}{4} \log_2 3 = 0.81$  bits.

Before addressing the question of stimulus significance, consider the significant responses of this system. Each response is equally likely, but conveys different amounts of information about the stimuli. Observation of the first response  $r_1$  designates an ambiguous situation, with equal probability of either stimulus:  $p(s|r_1) = \{\frac{1}{2}, \frac{1}{2}\}$ :  $H[S|r_1] = 1$  bit. The second response, however, clearly designates  $s_1$ , since  $p(s|r_2) = \{1, 0\}$ :  $H[S|r_2] = 0$  bits. The information content of each response is reflected in its specific information, with  $i_{sp}(r_1) = -0.19$  bits (uninformative), and  $i_{sp}(r_2) = H[S] = 0.81$  bits. The total mutual information (equation (1)) can be calculated from the specific informations as their weighted average over the ensemble of responses (equation (2)):  $I[R, S] = 0.31$  bits.

This example was devised to place an intuitive notion of stimulus significance at odds with the specific information applied to stimuli. With  $s_2$  present, the response is completely predictable ( $r_1$ ), whereas the presence of  $s_1$  could result in either response. As a result, the specific information applied to stimuli is higher for  $s_2$ :  $i_{sp}(s_1) = 0.08$  bits versus  $i_{sp}(s_2) = 1$  bit.

However, recall that *responses* encode information about *stimuli*, and not the reverse. Though  $s_2$  has the maximal specific information, neither response specifies it: observation of  $r_1$  gives an equal probability of  $s_1$  and  $s_2$ , and observation of  $r_2$  unambiguously designates  $s_1$ . As a result, from an information transmission standpoint,  $s_1$  is encoded more effectively than  $s_2$ , in contrast to their specific informations.

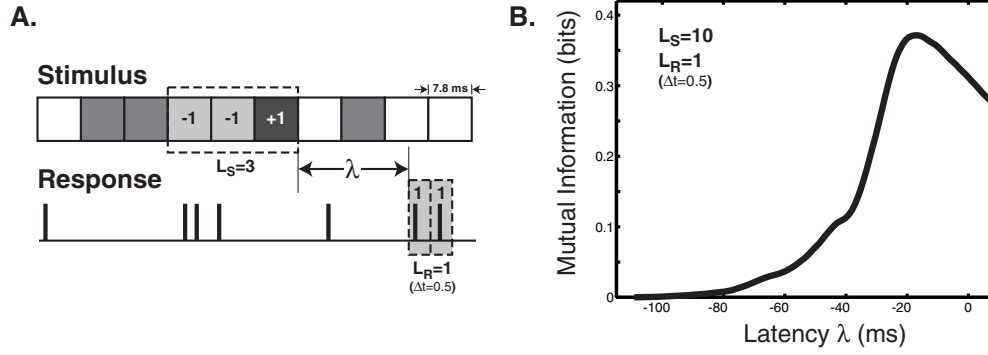
Why does specific information fail to select the more effectively encoded stimulus? Specific information is largest for those stimuli that have few responses associated with them, without regard to whether these responses are informative. For example, consider a neuron (such as the example discussed later in this paper) that is unresponsive (does not fire) to many stimuli. These stimuli would have a large specific information because ‘not firing’ is the only response associated with them. But observing a ‘not firing’ response would be very ambiguous since there are many stimuli that do not cause the neuron to fire. Thus, the specific information of a stimulus that the neuron does not respond to would be relatively high, but one would not say that it was well encoded.

#### 4. Stimulus-specific information

I therefore propose that the most informative stimuli are those that cause the most informative responses, and are thus well encoded by the system. The responses associated with a stimulus  $s$  are given by the conditional distribution  $p(r|s)$ , and the information conveyed by a particular response  $r$  is given by its specific information  $i_{sp}(r)$ . Thus, I propose an information theoretic measure of stimulus significance called the SSI, given by

$$i_{ssi}(s) \equiv \sum_r p(r|s) i_{sp}(r) = \sum_r p(r|s) \{H[S] - H[S|r]\}. \quad (5)$$

Since the specific information  $i_{sp}(r)$  is the reduction in uncertainty of the stimulus gained by the particular observation  $r \in R$ , the SSI  $i_{ssi}(s)$  is the average reduction of uncertainty gained from one measurement given the stimulus  $s \in S$ .



**Figure 1.** Mutual information between full-field flicker stimuli and neuronal spikes. (A) A three-frame stimulus word  $[-1, -1, +1]$  and a one-frame response word  $[1, 1]$  are associated at a given latency  $\lambda$  between the end of the stimulus word and beginning of the response word. (B) Mutual information is calculated between stimulus and response given a choice for  $L_S = 10$ ,  $L_R = 1$ , and  $\Delta t = 1/2$ , and is shown as a function of latency  $\lambda$ .

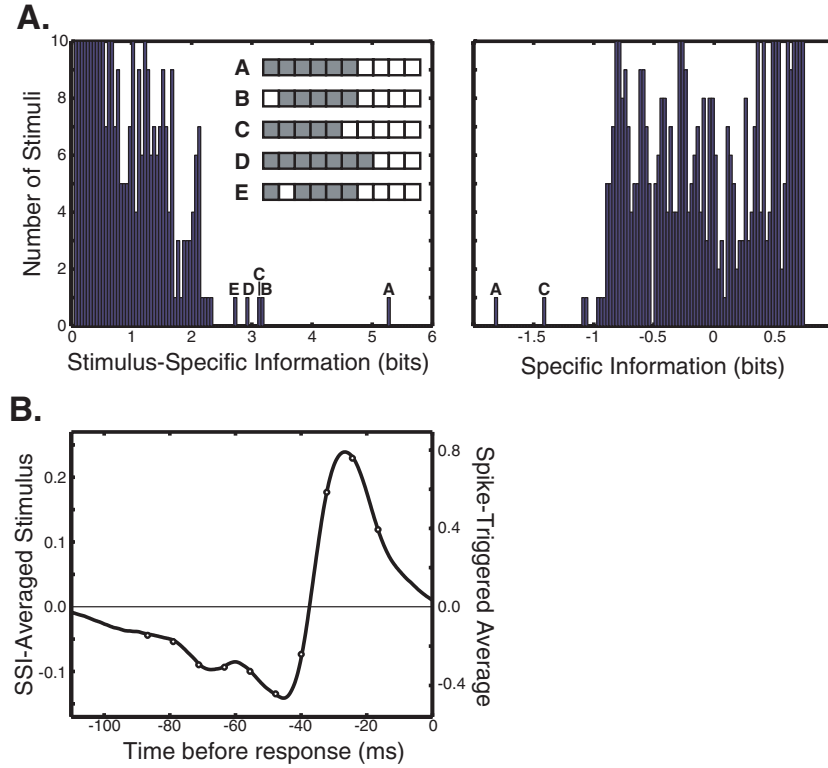
When calculated using the example of the last section, we see that  $i_{ssi}(s_1) = 0.48$  bits, and  $i_{ssi}(s_2) = -0.19$  bits. Like the specific information, the weighted average of  $i_{ssi}(s)$  over the stimulus ensemble  $s \in S$  gives the mutual information, and the value of the SSI is calibrated to the mutual information and specific information. For example, the value of  $i_{ssi}(s_1)$  is consistent with the fact that an observation completely determines the stimulus (giving close to 1 bit of information) half of the time, and otherwise is not informative. The SSI of  $s_2$  demonstrates that the only possible measurement that can result when  $s_2$  is presented is uninformative.

## 5. Simulated visual neurons

To demonstrate the use of SSI, I perform an information theoretic calculation on simulated visual neurons. Data were generated using a model proposed by Keat *et al* (2001), which accurately reproduces the timing of single action potentials as well as their statistical distribution over multiple trials. Using model parameters that simulate the behaviour of cat LGN neurons, spike trains were generated in response to random full-field flicker stimuli presented at 128 Hz (see methods).

Information quantities between the full-field flicker stimulus  $S$  and resulting spike trains  $R$  can be calculated as a function of several parameters: the length of the stimulus word  $L_S$ , the length and time resolution of the response word ( $L_R$  and  $\Delta t$ ), and the latency  $\lambda$  between them (see figure 1(A)). This method of calculating information is similar to those of Liu *et al* (2001). For this paper, I will use  $L_S = 10$  frames,  $L_R = 1$  frame, and  $\Delta t = 0.5$  frames, where  $L_S$  is chosen to be as large as possible given the limited number of data (see methods), and  $L_R$  and  $\Delta t$  are sufficiently representative of results found with longer response words (data not shown). General questions about the dependence of mutual information on stimulus and response word length and resolution are addressed elsewhere (Liu *et al* 2001).

The mutual information  $I[R, S]$  is shown in figure 1(B) as a function of latency  $\lambda$ . It peaks at a latency of  $-16.5$  ms, when the average response carries 0.37 bits about the stimulus. Since  $I[R, S]$  can be decomposed into SSI (see equation (2)), the total mutual information can be thought of as an average that includes both stimuli that are well encoded and those that are not. To determine the contribution of each stimulus to the total mutual information, the SSI is calculated for each of the  $2^{10} = 1024$  stimuli.



**Figure 2.** Information measures of particular stimuli. (A) SSI  $i_{ssi}(s)$  and specific information  $i_{sp}(s)$  are calculated for the  $2^{10}$  stimuli at a latency  $\lambda$  of  $-16.5$  ms and their distributions are displayed as histograms in the left and right frames respectively. Bins with greater than 10 elements are cut off to focus on the few outlying stimuli. The five stimuli with the largest SSI are labelled **A–E** and shown in the inset of the left frame. Two of them, **A** and **C**, have the lowest specific information (right frame). (B) To identify the features of the stimulus ensemble that are well encoded, an average stimulus is calculated by weighting each stimulus by its SSI (circles). This SSI-weighted average stimulus is approximately proportional to the spike-triggered average stimulus of the neuron up to a scale factor (solid curve). Note that the spike-triggered average stimulus is scaled so it is directly comparable to the units of average SSI.

The left panel of figure 2(A) shows a histogram of the SSI distribution of the stimulus ensemble. The minimum SSI was 0.085 bits (leaving the lowest bin between 0 and 0.05 bits empty). However, over half the stimuli (599 out of 1024) have SSIs in the next lowest bin (between 0.05 and 0.1 bits). On the other extreme, the top five stimuli are well separated from the rest of the distribution, and are shown in the inset. Note that the ‘best’ stimulus (**A**) is a simple off-to-on transition which occurs at  $-47.8$  ms. Other stimuli with lower SSI have a slightly different off-to-on latency (**C** and **D**), or an ‘on’ frame instead of an ‘off’ frame at large latencies (**B** and **E**).

For comparison, the right panel of figure 2(A) shows the distribution of specific informations for the same stimuli ( $i_{sp}(s)$ , given by equation (4)). Specific information gives nearly the opposite classification of stimuli as SSI: 486 out of 1024 stimuli are clustered in the largest occupied bin (0.74 bits). At the same time, stimuli with some of the highest SSIs have some of the lowest specific informations; stimuli **A** and **C** have the two lowest specific informations (figure 2(A), right), and stimuli **B**, **D**, and **E** are lost in the broader distribution.

As explained above, this is due to the fact that many stimuli rarely elicit a spike, meaning that they are associated with only one response ('no spike'), and have high specific information. At the same time, stimuli that often result in a spike cause an uncertain response since they may or may not elicit a spike.

Of course, the five stimuli with the largest SSIs are only presented 0.5% of the time, and almost 90% of the stimuli have an SSI less than 1 bit but account for almost half of the information conveyed. To determine the important features in the stimulus ensemble that lead to informative responses, I calculate an average stimulus based on each stimulus's fractional contribution to the mutual information  $p(s)i_{ssi}(s)/I[R, S]$ . This 'SSI-weighted average stimulus' is shown as *circles* in figure 2(B), and is compared to a more common measure of significant stimuli: the spike-triggered average stimulus (STA), shown as a *solid curve*. Note that these results apply for a given latency  $\lambda = -16.5$  ms, meaning that since the SSI-weighted average has a resolution of one frame (7.8 ms), there are ten discrete points in this average ( $L_S = 10$ ). The SSI-weighted average calculated for other latencies is in similar agreement to the STA (data not shown).

The close agreement between the spike-triggered and SSI-weighted average stimulus results from a combination of two factors:

- (1) the ability particular stimuli to evoke spikes in the Keat model is proportional to a linear convolution with the stimulus (see the methods for more details); and
- (2) the majority of information in the responses of this neuron is carried by spikes (found by calculating the specific information of responses  $i_{sp}(r)$  of equation (3)—data not shown).

As a result of these two conditions, the SSI of a given stimulus is roughly proportional to the number of spikes that were associated with it, i.e.,  $i_{ssi}(s) \approx p(\text{spike}|s)i_{sp}(\text{spike}) \propto p(\text{spike}|s)$ . Thus, each stimulus contributes to the spike-triggered and SSI-weighted averages in proportion to the number of spikes that each stimulus evokes, resulting in the same shape shown in figure 2(B).

## 6. Specific surprise identifies a different aspect of stimulus significance

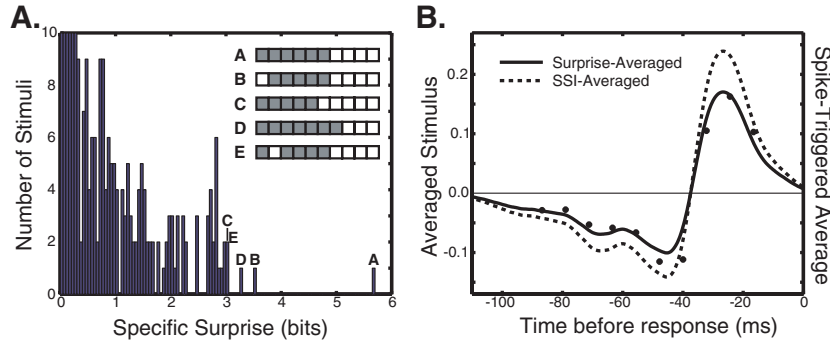
Thus, the SSI gives an appropriate characterization of the 'best encoded' stimuli, in stark contrast to the specific information. However, as mentioned earlier, there are many possible stimulus-specific decompositions of mutual information (equation (2)), some of which might provide alternative but reasonable classifications. For example, in their discussion of a measure of the information associated with individual symbols (i.e., stimuli and responses), DeWeese and Meister (1999) consider the 'specific surprise', given by (when applied to stimuli)

$$i_{sur}(s) = \sum_r p(r|s) \log_2 \frac{p(r|s)}{p(r)}. \quad (6)$$

Note that this is the Kullback–Leibler distance between the conditional probability  $p(r|s)$  and the marginal distribution  $p(r)$ . Below, I demonstrate that the specific surprise provides an alternative measure of stimulus significance, but it highlights other properties of the stimulus in a way that lacks the intuitive meaning of the SSI as a measure of the information associated with a stimulus.

Specific surprise, in the form of equation (6), compares the marginal distribution  $p(r)$  to the conditional distribution  $p(r|s)$ . As discussed above in relation to specific information, such





**Figure 3.** The specific surprise. (A) The distribution of specific surprises over the stimulus ensemble is calculated for same visual neuron as in figure 2. Though the distribution is very similar to the SSI distribution (figure 2(A), left)—with the same top five stimuli, there are subtle differences, such as their order (A–B–D–E–C). (B) The specific-surprise-weighted average stimulus (filled circles) is compared to the spike-triggered average stimulus (solid curve, scaled for the best fit) and the best fit of the SSI-weighted average from figure 2(B) (dotted curve).

a comparison is not intuitively meaningful with respect to causality. However, using Bayes’ law, specific surprise can be re-expressed as

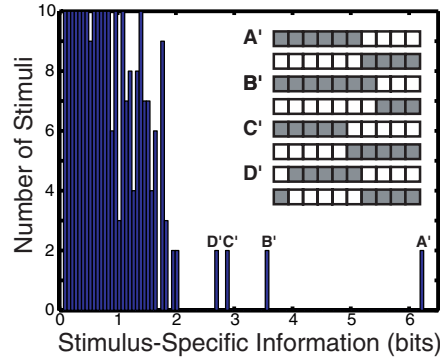
$$i_{sur}(s) = \sum_r p(r|s) \left[ \log_2 \frac{1}{p(s)} - \log_2 \frac{1}{p(s|r)} \right]. \quad (7)$$

The logarithm of the reciprocal probability of a stimulus is often referred to as its ‘surprise’, since rarer stimuli are more ‘surprising’. In this form, specific surprise has a causal meaning: the reduction in surprise of a particular stimulus gained from each response, averaged over all responses associated with that stimulus. Thus, **whereas the SSI weighs each response  $r$  by its effect over the stimulus ensemble (through the change of  $H[S]$  to  $H[S|r]$ ), the specific surprise measures of the effect of the response on just the stimulus in question (through the change of  $p(s)$  to  $p(s|r)$ ).**

How does using a different response weight change the evaluation of stimulus significance? In figure 3(A), the specific surprise is calculated for the simulated visual neuron. It provides classifications of the stimuli similar to the SSI, and identifies the same top five stimuli, though with a different order (A–B–D–E–C). The subtle differences between the two measures in this example are reflected in a comparison between the SSI-weighted average of figure 2(B) and the specific-surprise-weighted average, calculated in the same way, shown in figure 3(B). The specific-surprise-weighted average is shown as solid circles, and the best scaling of the spike-triggered average is shown as a solid curve. In the meantime, since the SSI-weighted average fit the STA almost exactly (figure 2(B)), the STA scaled to the SSI-weighted average is shown as a dotted curve. Note that the shape of the surprise-weighted average stimulus is a different shape to the STA, and it has a smaller magnitude compared to the SSI-weighted average, meaning that larger specific surprise does not as closely correspond to particular features of the stimulus.

The specific surprise and the SSI behave more distinctly in the simple example of the  $2 \times 2$  joint probability distribution described earlier in this paper. In this case, the specific surprise is higher for the second stimulus  $s_2$  (which only had one ambiguous response  $r_1$  associated with it):  $i_{sur}(s_1) = 0.08$  bits and  $i_{sur}(s_2) = 1$  bit. This contrasts with the intuitive notion that  $s_1$  is better encoded than  $s_2$ , since  $s_2$  is never clearly designated by a response. Does this mean that specific surprise is a bad measure of a well-encoded stimulus?





**Figure 4.** A non-linear neuron. The distribution of the SSI for the  $2^{10}$  stimuli is calculated for a non-linear neuron whose spike-triggered average is zero. This neuron is designed such that opposite stimuli evoke the same response, resulting in pairs of stimuli that have the same SSI (inset).

In fact, it is simply a different measure with a different interpretation: while  $s_1$  is unambiguously denoted by an observation of  $r_2$  (changing its probability:  $\frac{3}{4} \rightarrow 1$ ), the measurement of  $r_1$  decreases its likelihood ( $\frac{3}{4} \rightarrow \frac{1}{2}$ ), nearly cancelling the change in surprise:  $i_{sur}(s_1) = 0.08 = \frac{1}{3}(-0.59) + \frac{2}{3}(0.42)$  bits. In the meantime, the specific surprise of  $s_2$  is relatively large ( $i_{sur}(s_2) = 1$  bit) because the only response associated with  $s_2$  is  $r_1$ , and it leads to an increase in the probability of observing  $s_2$ :  $\frac{1}{4} \rightarrow \frac{1}{2}$ . Thus, each possible response contributes to the specific surprise of a particular stimulus  $s$  in relation to how much its observation increases the likelihood of  $s$ .

Why do the specific surprise and the SSI give similar results with the visual neuron? For a response to be informative (i.e., have a large specific information  $i_{sp}(r)$ ), the entropy of its conditional distribution  $p(s|r)$  must be less than that of the prior  $p(s)$ , meaning that the probability of some stimuli must be increased. As a result, in many cases, an informative response will result in the largest changes in probability of the stimuli that are best encoded, and the specific surprise and the SSI will be qualitative agreement. However, as the simple  $2 \times 2$  example made clear, this is not always the case.

So, the specific surprise and the SSI are measuring fundamentally different aspects of stimulus significance. Since the SSI is explicitly measuring an average difference in entropies, it has intuitive meaning with regard to information transmission. As a result, the SSI in both the simple  $2 \times 2$  example and the visual neuron fulfil this intuition of what a well-encoded stimulus is, in contrast to the specific surprise.

## 7. Non-linear neurons

In the example of the visual neuron, the SSI correctly identified the significant stimuli to a neuron, in a way that was validated by linear analysis of the neuron, i.e., the spike-triggered average. In this way, the agreement between the spike-triggered and SSI-weighted average stimulus demonstrated that the neuron is essentially linear. Thus, while this example validates the performance of the SSI, it makes clear that linear analysis would have been sufficient in identifying the significant stimuli in this case.

Information theory is most useful in studying neurons with non-linear properties, or those that do not encode the bulk of their information in single spikes. To demonstrate the potential utility of the SSI, the visual neuron model discussed above is modified to exhibit non-linear

behaviour. This modified model retains the same spiking properties, but is designed such that it has, on average, the same response to a stimulus as it does to the opposite stimulus (see the methods for more details). For example, an on-to-off transition will now evoke the same number of spikes as an off-to-on transition with the same latency. As a result, the spike-triggered average stimulus of this neuron is zero, since a spike is just as likely to be evoked by a particular stimulus as its opposite. In this case, important stimuli can only be identified through higher-order statistics, such as the spike-triggered covariance used by Arcas *et al* (2000).

Of course, differences in higher-order statistics are detected by information theoretic measures, and the SSI distribution for the modified non-linear neuron is shown in figure 4 (calculated in the same way as the distribution of figure 2(A)). The six stimuli with the largest SSI are shown in the inset, demonstrating the pairing of each stimulus with its opposite.

## 8. Conclusions

I have shown that the SSI is an appropriate and reliable measure of the information associated with a particular stimulus. As with other information measures, the SSI is calculated without particular assumptions about the coding scheme, and is robust to non-linearities in the system being studied. As a result, the SSI is particularly useful in identifying the stimuli that are significant to a neuron where linear analyses break down. The SSI is also useful in cases where neural responses other than individual spikes carry information, though such examples were not considered in this paper.

Unfortunately, unlike the specific information of a response proposed by DeWeese and Meister (1999), the SSI does not have a mathematical quality that shows it to be the only possible measure of information associated with a stimulus. As previously discussed, there are many possible stimulus-specific decompositions of mutual information; as a result, I have chosen a decomposition that has an intuitive meaning with respect to information transmission, and furthermore have shown it gives expected results in both simple constructed examples and realistic examples using neuronal data.

The SSI has the same drawbacks as other information measures: a significant number of data are required in order to properly estimate the underlying probability distributions needed by such calculations. However, since the same data as are used to calculate Shannon's mutual information can also be used for the specific information of responses and the SSI of stimuli, these specific measures can extend the applicability and use of information studies in neuroscience.

## Methods

### *Simulated visual neurons*

Data for the information calculations performed on the example visual neuron in this paper was generated using a model of visual neurons proposed by Keat *et al* (2001). This phenomenological model is able to reproduce both the precise spike timing and variability of observed cat LGN neurons, and thus generated 'realistic' neuronal data for the purpose of evaluating information quantities.

The simulated neuron is presented as either black or white frames (with equal probability) at 128 Hz, and generates a neural spike train. The basis of the neural response is a linear convolution between the stimulus  $s(t)$  and a linear kernel  $K(\tau)$ :

$$g(t) = \int_{-\infty}^0 d\tau K(\tau) s(t - \tau).$$

This function of time  $g(t)$  is modified by adding correlated Gaussian noise and a term that represents spike-dependent effects, which accounts for a neuronal refractory period. Spikes occur when the total of  $g(t)$ , noise, and spike-dependent effects exceeds a threshold.

For the information calculations, a large data set consisting of 32 million stimulus frames (representing roughly 70 h in real time) was used. This copious data set allowed for an information analysis of long stimulus and response words simultaneously, though information theoretic analysis is possible with far fewer data (see Liu *et al* 2001).

### Non-linear neurons

To generate a neuron with a spike-triggered average of zero, the same model as above was used, with one modification: the linear convolution  $g(t)$  was squared before plugging it into the rest of the model. As a result, opposite stimuli, which result in  $g_0$  and  $-g_0$  in the linear model, now have the same effect on the response:  $(g_0)^2$ . Other parameters of the model were scaled so that this model had the same overall spike rate.

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