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Deconstructing the receptive field: Information coding in macaque area MST

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Abstract

When cells respond well to complex stimuli, it is often difficult to determine which aspects of the stimulus are most relevant. We present a technique to describe the encoding of information on many stimulus features by a single cell. Based on the concept of conditional mutual information, we distinguish cells that are mono-, dual- or synergistic encoders, depending on their amount of specialisation for stimulus features. As an application of the technique, we show that cells in the macaque medial superior temporal area encode information on the direction of heading, but simultaneously on local features such as the direction of motion in small parts of their large spatial receptive field.

Keywords: Information theory; Extrastriate visual cortex; Heading perception

1. Introduction

Moving higher up the hierarchy of the visual processing pathway, stimuli that drive a cell become more and more complex. The complexity of a stimulus and the co-variation of features in a stimulus often lead to an ambiguity about which aspect of a stimulus actually drives the cell; tuning for one feature dimension is often difficult to separate from tuning for another. One could deal with this ambiguity by using an experimental design that varies the features of the stimulus factorially. Two problems arise in this approach. Firstly, the recording time required to quantify a neuron's

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response grows exponentially with the number of stimulus features. Secondly, some of the combinations in the factorial design will be quite unnatural. Unless a neuron's response properties are linear, knowing the response to a stimulus that the neuron never gets confronted with in the real world is of doubtful value. The time spent on trying to measure the whole factorial space could better be spent on trying to determine the response to natural stimuli with higher accuracy. Another approach to the ambiguity problem is to consider only cells that respond invariantly to a particular stimulus dimension. This is not an easy task for a neuron and, depending on the stringency with which "invariance" has been defined, invariant neurons have proven difficult to find.

We describe an information theoretic approach that deconstructs the receptive field along multiple feature dimensions. This characterises the encoding of multiple stimulus features by single cells. No factorial designs are required, hence stimuli can be restricted to natural stimuli, improving the relevance of the data as a description of the real-world operation of the cells. The method does not look for invariant responses, but rather assumes that a cell can, in principle, provide information on all features in the stimulus. The problem of co-variation of features is dealt with by calculating conditional information: the amount of information encoded on a particular feature, given knowledge of a different feature. This concept allows us to determine whether cells encode information on a feature dimension that is not already expected from its encoding of another feature dimension. Section 2 describes the formal details of receptive field deconstruction. In Section 3, we apply the method to the analysis of data recorded in the medial superior temporal (MST) area of the macaque during optic flow stimulation.

2. Receptive field deconstruction

In the typical situation where this method can be applied, a stimulus varies along two or more feature dimensions, but these dimensions are not independent. For instance, consider a set of visual stimuli with varying sizes and velocities, in which small objects tend to have low speeds. Such correlations arise in natural scenes due to the fact that far-away objects appear both small (geometrical perspective) and move slowly (motion parallax). In this example, the features size and velocity are correlated and any tuning for size will be correlated with tuning for velocity.

We start by estimating the information encoding on the stimulus features without regard for stimulus correlations. For this we use standard information theoretic methods [5]. The first decision that has to be made, is what code to use. This decision is guided by assumptions about what is important to the brain, but also limited by the amount of data one can record from a single cell. A simple assumption is that the mean rate r forms the code. We then construct a contingency table that tabulates how often a stimulus feature is followed by a particular codeword r. From such a table, an estimate of information can be calculated. This direct method of information estimation overestimates the amount of information, but we use the methods of [3] to correct for the limited-sampling bias.

Assuming there are two stimulus features a and b, we construct contingency tables for both and estimate the information in the code (r) on either of the features: $I(r; a)$ and $I(r; b)$. If, however, stimulus features a and b are correlated, these information estimates are not independent. For instance, if a particular feature $a = a^*$ always co-occurs with $b = b^*$, then a cell that encodes information on a^*, will inevitably encode information on b^*. There is nothing wrong or invalid about this information on b^*, but because it is due to the stimulus correlations, that same information may not be present in a different stimulus set, or in the real-world where the fortuitous correlation between a^* and b^* may not exist. To claim that a cell encodes information on multiple feature dimensions, we should show that the information on b cannot be obtained from the information on a together with a knowledge of the correlations between a and b.

To clarify this, assume that a cell encodes information on a (i.e. $I(r; a) > 0$). Consider the ways in which information on b can also become represented in r. Firstly, changes in b could be correlated with changes in a which in turn cause changes in r. Secondly, b could, independently from a, affect the rate. Thirdly, joint changes in a and b could cause changes in r. These possibilities are in fact a part of continuum of possibilities that can be described by the conditional mutual information. The conditional mutual information between r and b given a, denoted by $I(r; b \mid a)$ is the mutual information between r and b given knowledge of a. If information in r on b is only due to correlations between a and b, then $I(r; b \mid a) = 0$. In other words, if you already know a then knowing r does not give you any *extra* information on feature b. To calculate the conditional mutual information, express it in terms of entropy H [1]

$$I(r; b \mid a) = \left\langle \log \frac{p(r, b \mid a)}{p(r \mid a)p(b \mid a)} \right\rangle_{p(r,a,b)} = H(r \mid a) - H(r \mid b, a),$$

where the $\langle\ \rangle$ denote the expectation value over the joint probabilities. The entropies can easily be calculated from the contingency tables based on the data. By calculating $I(r; b \mid a)$ we can divide cells into three classes:

Mono encoders: $I(r; b \mid a) = 0$. Although there may be information on b in r, this information could have been determined by combining the information in r on a with the stimulus correlations. There is no *extra* information on b in r.

Dual encoders: $0 < I(r; b \mid a) < I(r; b)$. Part of the information on b in r is due to stimulus correlations with a, but there is also some information that cannot be obtained from stimulus correlations.

Synergistic encoders: $I(r; b \mid a) > I(r; b)$. There is extra information on b in r, but moreover, knowing a helps to get more information on b from r. One way this could happen is that particular combinations of a and b-features are encoded by a cell.

To test for significant encoding of multiple features, we must refute that $I(r; b \mid a) = 0$. In other words, we must refute the null hypothesis that r and b are *conditionally independent* given a. Under the assumption of this null hypothesis, the joint probability $p(r, a, b)$, can be expanded as:

$$p^0(r, a, b) = p(r \mid a)p(b \mid a)p(a) = p(r, a)p(a, b)/p(a).$$

The alternative hypothesis is that the joint probability distribution $p(r,a,b)$ cannot be reduced $p^1(r,a,b) = p(r,a,b)$. The joint probabilities in these expressions can be estimated from the contingency tables. For instance, $n(r,a)$ is the contingency table where each entry is the number of times that a particular rate r followed feature a. Defining N as the number of stimuli, the maximum likelihood estimate for a joint probability of a and r is: $p(r,a) = n(r,a)/N$ Similarly, to estimate the joint probability $p(r,a,b)$ from the data, construct the three-way contingency table $n(r,a,b)$. Clearly, large amounts of data are needed to estimate three-way tables. In terms of the contingency tables the null and alternative hypotheses becomes

$$p^0(r,a,b) = n(r,a)n(a,b)/(N * n(a)),$$

$$p^1(r,a,b) = n(r,a,b)/N.$$

The log-likelihood of these hypotheses given the data n can be determined from the binomial distribution

$$ll^i = \log\left[\frac{N!}{\Pi_{r,a,b} n(r,a,b)!}\right] + \sum_{r,a,b} n(r,a,b)\log[p^i(r,a,b)], \quad \text{for } i = 0,1.$$

To test the null hypothesis, calculate twice the difference of log-likelihoods: $2(ll^1 - ll^0)$. This quantity, called the deviance, has an asymptotic χ^2 distribution with the degrees of freedom given by the difference in the number of estimated parameters in p^0 and p^1. The null-hypothesis is tested by comparing the deviance to the χ^2 distribution. If we can reject that $I(r,b\,|\,a) = 0$ at some level of significance, then there is information in r on feature b that cannot be obtained from the information r on feature a together with the stimulus correlations between a and b. The magnitude of the non-zero conditional information $I(r;\, b\,|\,a)$ can be used to classify the cell as a dual or synergistic encoder.

3. Application to information coding in MST

Cells in the MST area of the macaque respond well to whole-field optic flow and are tuned to global properties of these flow fields such as the focus of expansion [2]. While varying the focus of expansion, however, the experimenter also varies the local structure in the flow field, such as the average speed, and direction in small parts of the visual field. Hence, a cell's response to a change in the focus of expansion could in principle also be due to changes in either of these two local features. The confounding of these stimulus dimensions and the near impossibility to control for this confound with naturalistic stimuli make these cells ideal targets for the deconstruction analysis.

Paolini et al. [4] recorded extracellularly from single cells in macaque MST during long, continuous optic flow stimulation. The flow patterns represented trajectories through three-dimensional random dot clouds. For details of the stimuli, the electro-physiological and histological methods, see [4]. As an application of the

Table 1
Information coding in MST. The first row shows the average amount of information encoded on the three features ($\pm$ standard error). The second and third row show the percentage of subfields which are dual, or synergistic with respect to heading

	Heading	Direction	Speed
Mean info (bits/s)	0.6 ± 0.07	0.7 ± 0.07	0.4 ± 0.05
Dual	—	16%	1%
Synergistic	—	52%	8%

deconstruction method, we determined the encoding of three stimulus features: heading, local direction and local speed. Heading was defined as the instantaneous translation vector in eye-centred coordinates, and determined every 100 ms. To define local direction and speed we divided the field of view into 25 spatial subfields and determined the average motion vectors in each subfield every 100 ms. The whole flow field was $90^\circ \times 90^\circ$, hence the subfields were $18^\circ \times 18^\circ$. The response of the neurons was characterised by their mean firing rate in 100 ms time bins. To correct for the latency of MST cells, the time bins used to determine the responses were shifted by 25 ms. This implies that we assume that a cell encodes stimulus information by the firing rate in a window between 25 and 125 ms after stimulus onset. Clearly, such a choice is somewhat arbitrary and could be adapted to the neurons that are being studied. With appropriate amounts of data available, a temporal code could also be investigated.

Table 1 shows the results of applying the deconstruction analysis to a set of 81 cells from area MST. The analysis first of all quantifies how much information on the direction of heading MST cells extract from optic flow. This global aspect of the optic flow stimulus is represented with low fidelity per cell, but a small population of cells can easily be seen to encode enough information for the animal to base its behaviour upon. Moreover, because this calculation is based on heading directions calculated every 100 ms in a long trajectory, this shows that the representation of heading in MST follows changes in the environment on this short time scale. The deconstruction analysis additionally shows that, even though these cells have large spatial receptive fields ($\sim 6000\ \mathrm{deg}^2$), they nevertheless encode significant information on the stimulus direction in much smaller subfields ($\sim 650\ \mathrm{deg}^2$). Seventy four percent of cells have at least one subfield for which significant information is encoded on the local velocity.

The simultaneous encoding of local and global information in MST cells suggests that these cells are involved in computations for which both local and global features are important. Global features provide information on where the animal is heading, whereas local features provide information on the depth structure of the environment and possibly the motion of independent objects. A combination of these features is highly suitable for navigation and obstacle avoidance tasks, which we speculate these cells could be involved in.

4. Conclusion

We presented a technique to deconstruct the receptive field along many stimulus feature dimensions. It quantifies how much information cells encode on the many features of a complex stimulus, even when these features are correlated. With the concept of conditional mutual information, the deconstruction technique quantifies whether a cell specialises in encoding a particular feature or whether it provides information on many features at once. We believe this to be a helpful tool that allows one to move away from assigning single tasks to neurons and instead acknowledge that neurons can be a source of information for many different features. This wide range of information is present in the spikes, and is waiting to be read out by any downstream area that needs it.

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References

[1] T.M. Cover, J.A. Thomas, Elements of Information Theory, John Wiley, New York, 1991.
[2] C.J. Duffy, R.H. Wurtz, Response of monkey MST neurons to optic flow stimuli with shifted centers of motion, J. Neurosci 15 (1995) 5192–5208.
[3] S. Panzeri, A. Treves, Analytical estimates of limited sampling biases in different information measures, Network 7 (1996) 87–107.
[4] M. Paolini, C. Distler, F. Bremmer, M. Lappe, K.-P. Hoffmann, Responses to continuously changing optic flow in area mst, J. Neurophysiol. 84 (2000) 730–743.
[5] F. Rieke, D. Warland, R.R. de Ruyter van Steveninck, W. Bialek, Spikes: Exploring the Neural Code, MIT Press, Cambridge, MA, 1997.