

How do stimulus-dependent correlations between V1 neurons affect neural coding?

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Available online 11 November 2006

Abstract

Nearby neurons in the visual cortex often partially synchronize their spiking activity. Despite the widespread observation of this phenomenon, its importance for visual coding and perception remains to be uncovered. We used information theory to study the coding of the contrast and direction of motion of visual stimuli by pairs of simultaneously recorded neurons in the macaque primary visual cortex. Direction coding showed weak synergistic effects at short timescales, trailing off to informational independence at long timescales. In comparison, contrast coding was dominated by redundancy due to the similarity in contrast tuning curves.

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Keywords: Information theory; Synchronization; Cerebral cortex

1. Introduction

It has been known for many years that neuronal spike trains fired by adjacent cortical neurons exhibit correlations—the probability of one cell firing an action potential depends upon whether another cell fires [10,3,21,8,2,9]. Whether such correlations affect the coding of sensory information is still highly debated. Correlations might act as an extra channel for information, carrying messages about the outside world not carried by other aspects of spike trains, such as their overall firing rates [4,1,14]. However, it has also been noted that for pairs of neurons with overlapping tuning, and without *stimulus dependence* of their correlation, the covariance of neuronal firing would limit the information carried by the neuronal population overall, due to the introduction of redundancy [21].

Several pieces of evidence point to correlations between V1 neurons being direction and contrast dependent [7,18]. The question we are focusing on here is whether the stimulus dependence of this correlation affects the limits correlation imposes upon information transmission [21,14].

We used information theory to address this question: we computed mutual information using the NSB estimator [12], and compared the information available from pairs of cells with the sum of the single cell information values. This allowed us to assess the degree of synergy (or conversely redundancy) in the coding. We have used information theory to examine whether stimulus-dependent correlation could contribute to the neural coding of orientation and contrast by pairs of V1 cells.

2. Methods

To evaluate the effect of correlation on the population coding of sensory information, we recorded responses of pairs of single neurons in primary visual cortex (V1) of the anaesthetized macaque monkey [7]. Stimuli were luminance-modulated, drifting sine-wave gratings presented at a frame rate of 100 Hz. We measured, in order, the direction, spatial and temporal frequency, and size tuning for drifting sine-wave gratings. After characterizing the stimulus preference for each cell independently, we measured correlation for responses evoked by stimuli of different directions and contrasts. The spatial and temporal frequency of these test stimuli were set between the

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preferred values of the two cells or at the value of the cell that responded less vigorously. Stimuli were presented between the receptive field (RF) centres of the cells and covered both RFs.

Spike count covariance and fine-timescale synchrony were previously found to depend on both stimulus orientation and contrast [7]. To examine whether this stimulus-dependent correlation could contribute to the neural coding of stimulus parameters by pairs of V1 cells, we computed Shannon mutual information using the NSB estimator [12], and compared the ensemble information available from the pair of cells (I_{ensemble}) with the sum of the single cell information values (I_{sum}). This allowed us to assess the degree of synergy (or conversely redundancy) in the coding. Responses were quantified by the number of spikes fired by each cell in the pair within a time window T ; for a pair of cells, this thus provides a multinomial response code with cardinality $K = (n_{\text{max},1} + 1)(n_{\text{max},2} + 1)$ where $n_{\text{max},i}$ is the maximum number of spikes fired by cell i of the pair for any trial or stimulus.

In order to test the effectiveness (for our purposes) of the “NSB” entropy estimator developed by Nemenman [12], we performed calculations of the total mutual information conveyed by a single pair of cells in V1 [7] using entropy estimation without any bias correction at all (naive entropy estimations), Panzeri–Treves bias correction [15], and the NSB method. Fig. 1 shows the performance of the information estimation approach we used for a pair of cells with $K = 133$ at $T = 40$ ms. The NSB approach was the only one we found to be adequate across the entire data set, despite the relatively large number of trials available (480–3200) compared to many other information-theoretic analyses in the literature.

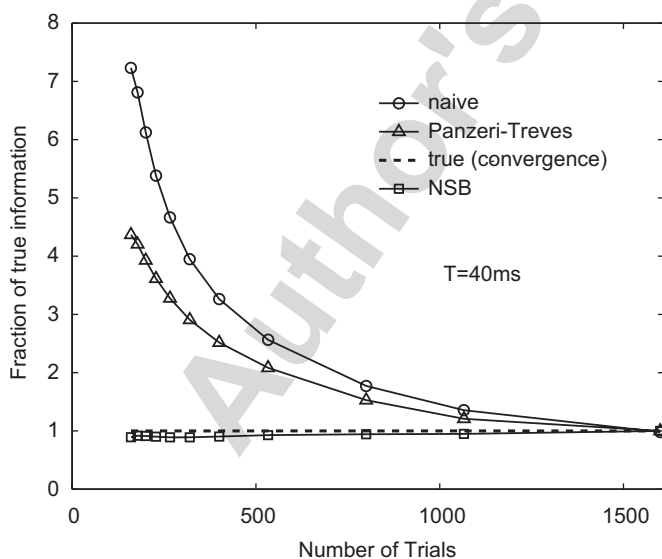


Fig. 1. Comparison of different information estimators, for a typical pair of cells from our data set. A sufficient number of trials was available for *this* pair for all estimators to converge, and thus the true value of the information to be apparent.

3. Direction coding

We present here an analysis of 102 pairs from the original data set of [7]. Fig. 2 shows a typical pair of V1 cells (the same pair used in Fig. 1) with substantial modulation in the height of the central peak of the cross-correlogram of the neurons spike trains: synchronization is maximized at a particular direction that drives the firing of both neurons, and falls off around this stimulus. What is the effect of this stimulus-dependent correlation on the information transmitted by the pair of neurons? This is shown in Fig. 3: the resulting interaction is very mildly

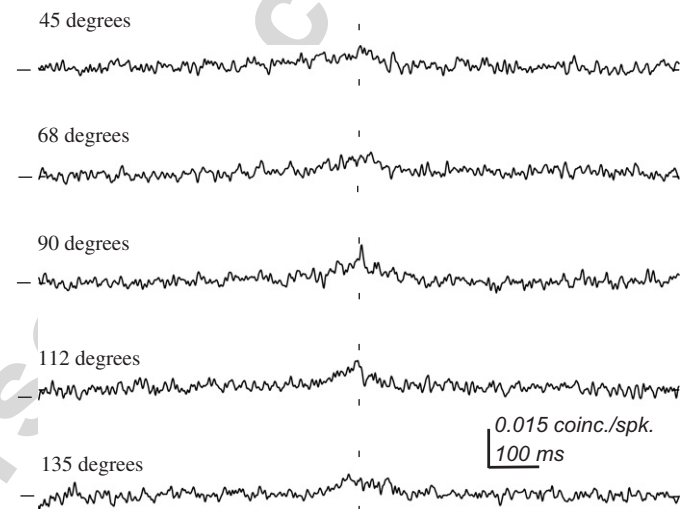


Fig. 2. Cross-correlograms for each of five different stimulus directions, for the same pair as shown in the previous figures.

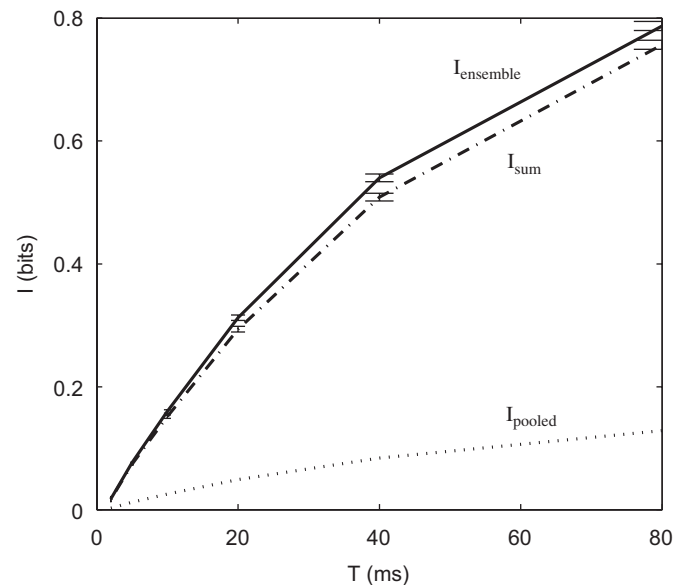


Fig. 3. Comparison of the information available from the pair of neurons (I_{ensemble}) in a time window T , with the sum of the informations obtained from each constituent neuron (I_{sum}) and the information from a pooled code in which the identity of the cell firing each action potential is ignored (I_{pooled}).

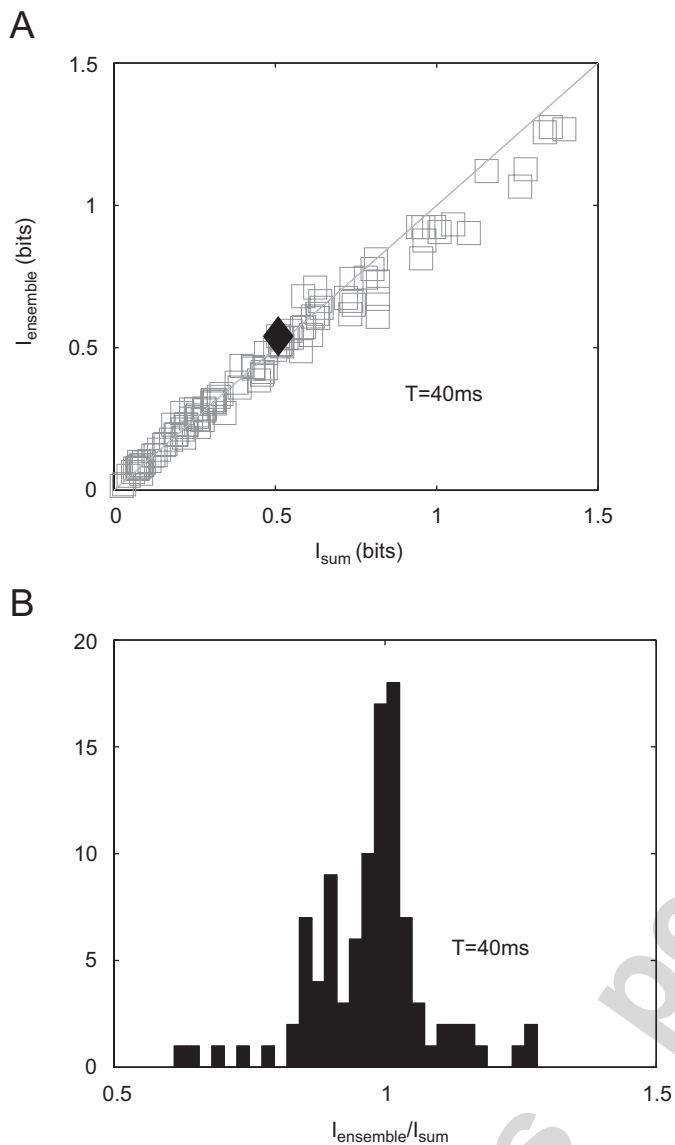


Fig. 4. Information adds approximately linearly across cells. (A) The total (ensemble) information available for each pair is plotted against the sum of the information available from each cell constituting the pair ($n = 102$ pairs). Redundant points lie below the diagonal. The black diamond indicates the pair shown in Figs. 1–3. (B) Histogram of the total (ensemble) information available for each pair divided by the sum of the information from each cell.

synergistic: the ensemble mutual information (I_{ensemble}) grows more rapidly with the time window over which spikes are counted than does the sum of the single cell information values (I_{sum}). Fig. 2 also shows that pooling spikes across cells (I_{pooled}) leads to a drop in information (see Section 5).

We analyzed the degree of synergy (redundancy) of direction coding at a fixed time window of 40 ms, for 102 pairs of cells in V1. The fractional degree of synergy (defined as $1 - I_{\text{sum}}/I_{\text{ensemble}}$) was on average to -0.02352 ± 0.005 (s.e.m.). Our findings (Fig. 4) lead to the conclusion that information about direction essentially

summates across pairs of neurons as it would if the neurons were actually independent, although they are substantially correlated. This is an example of *informational independence*, even though there is substantial *response dependence* [19] between these cells.

4. Contrast coding

In the previous section, we studied the coding of information about visual stimulus direction by pairs of neurons, motivated by the directional dependence of response synchronization. However, the contrast of the stimulus can also modulate the synchronization between pairs of neurons [7]. In Fig. 5 we analyse the degree of synergy (or rather redundancy) for the neural coding of contrast by a somewhat stereotypical V1 pair. Fig. 6 shows the picture over the entire population of 71 pairs for which contrast data were available. In almost all cases ($17.24 \pm 0.2\%$) redundancy was observed.

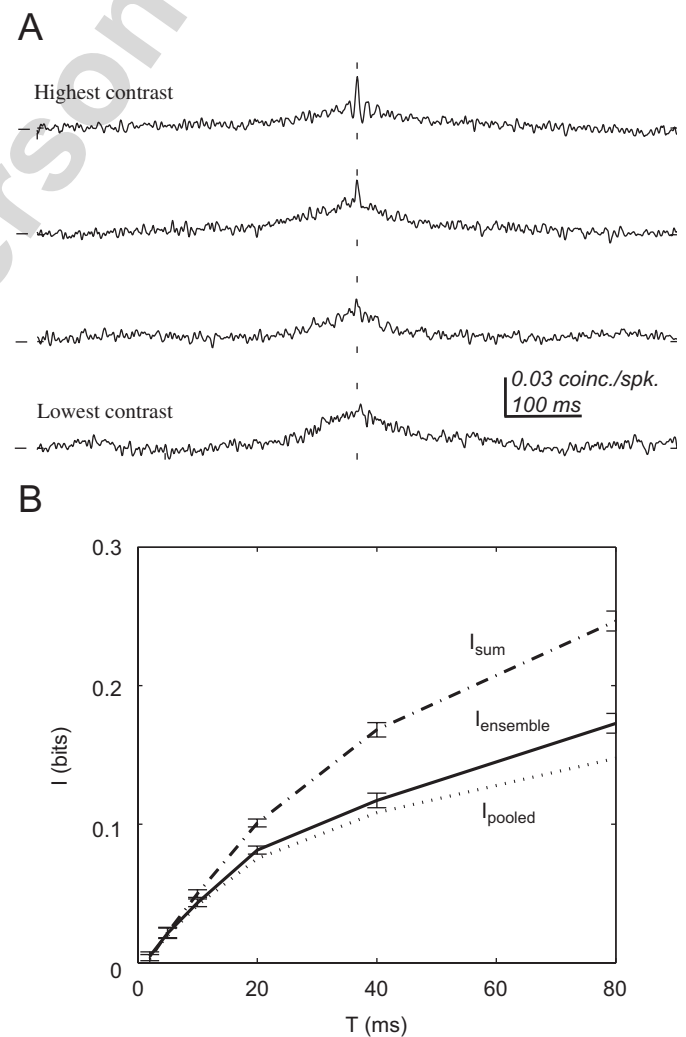


Fig. 5. Coding of contrast by a stereotypical pair of V1 neurons. (A) Cross-correlograms for each of four contrast values. (B) Information analysis results.

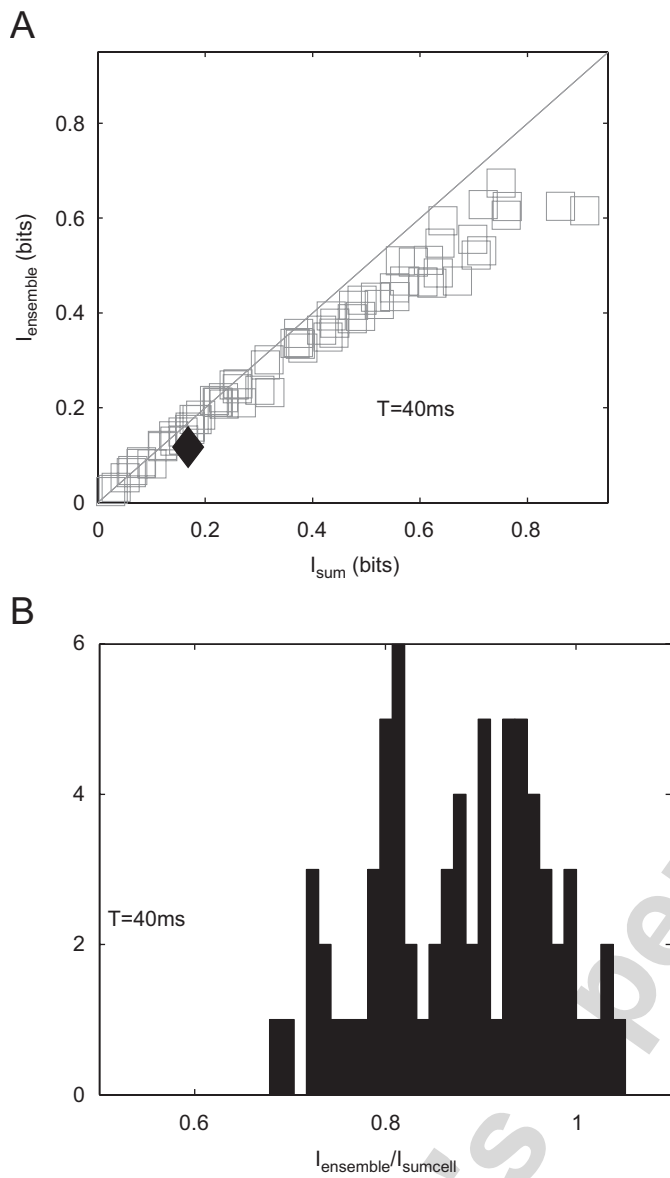


Fig. 6. Coding of contrast is substantially redundant across the entire data set. (A) Comparison of pair and linear summation information values. The black diamond shows the pair considered in the previous figure. (B) Histogram showing the degree of redundancy across the data set.

5. Pooling

Pooling (summing spikes together from a neuronal pool regardless of the cell which fires them) is a popular population decoding strategy [20]. Figs. 3 and 5 both showed a loss of information when the “pooled” code was used, although it was much greater for the example of direction coding. How general was this? Fig. 7 shows that the loss of information due to pooling is generally much greater for direction than for contrast coding.

6. Discussion

We used information theory in order to understand how correlations between the spikes fired by pairs of V1 neurons

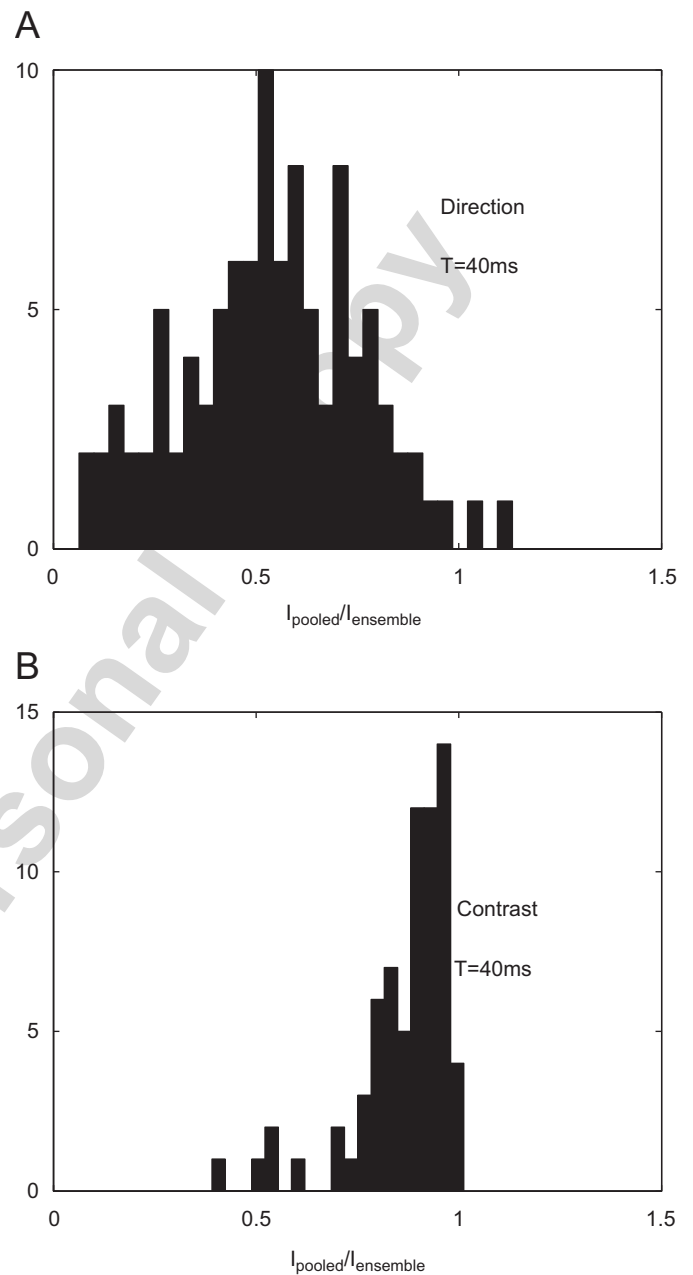


Fig. 7. The effect of pooling (ignoring the identity of the cell which fired each spike train) is a substantial loss of information. (A) Direction coding. (B) Contrast coding.

contribute to the direction and contrast coding. Our main findings were that at timescales of the order of 40 ms, information about direction adds approximately linearly across pairs of cells, whereas information about contrast adds sub-linearly (redundantly). In both cases the responses covary (due to the synchronization), so the neurons are response-independent, but in the first case the neurons are informationally independent also (or approximately so), but in the second case the neurons code redundantly. What is the explanation for this? The neurons generally (although not always) have a substantial overlap in their direction tuning curves (i.e. positive signal

correlation), and also have positive noise correlation due to fine-timescale synchronization of their responses. Information-theoretic analysis predicts that in this regime, if the noise correlation is not stimulus-dependent, then the neurons will interact redundantly [13,14]. If the synchronization is instead stimulus-dependent (as we see here), there is in addition an “extra channel” of information, which makes the stimuli easier to discriminate by an ideal decoder (which takes correlation into account) and makes up for the information lost due to redundancy. This effect can be further analysed in terms of an information component breakdown [16], which is taken up in a separate paper [11]. The contrast data set provides us with a natural control for the direction coding analysis. For contrast, the tuning curves of different neurons in a pair tend to be fairly similar, and synchronization is at lower contrasts less temporally precise. This resulted in a coding regime more similar to the traditional intuition, in which correlations tend to result in redundancy, and thus limit the number of neurons whose outputs could usefully be combined to represent the stimulus variable. The major factors driving the differences in contrast and orientation coding are thus the greater redundancy due to similarity in the tuning curves between pairs of cells for contrast coding, and a slightly lower degree of stimulus dependence in the correlation. The brain could take advantage of the robustness provided by the redundancy in contrast, and the accuracy due to the informational independency in the orientation code. These factors have been explored in more detail by performing an information component decomposition [16], which will be presented in a separate paper.

Our results are roughly in line with previous information analyses that have found the existence of weak synergy or independent coding in V1 [17,6]. One difference between our experiments and these previous studies were that we characterized the complete response characteristics of each neuron in the pair, and generated a set of stimuli which, as far as possible, drove both neurons across their dynamic range, and included stimuli which excited both neurons well. There are also substantial differences in the analyses performed. In our study, we took advantage of recent advances in entropy estimation techniques [12]. This was crucial to the current study, as despite working well for the analysis of single cell recordings, other estimation techniques resulted in significant residual bias with this paired recordings data set.

Destroying the identity of which neuron fired each action potential resulted in a substantial loss in information about stimulus direction. This provokes the question: how could downstream neurons decode/make use of the positive information contribution provided by the stimulus-dependent synchronization? Integrate-and-fire type neuronal operation would effectively pool input spikes regardless of origin, thus being subject to the Zohary et al. [21] limitations on combining information from correlated input neurons. Nonlinear dendritic summation [5] would appear to be a necessary feature of a decoder capable of

making use of the additional information contribution, and thus circumventing the pooling limit.

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