

Quantitative Analysis of Cooperation and Structure in the Cat Striate Cortex

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We applied information-theoretic methods to multi-electrode array recordings in the primary visual cortex of cats to quantify the cooperation and temporal structure that arises in the responses to drifting sinusoid gratings. When testing small differences in orientation ($<10^\circ$), the temporal structure and joint firing can contribute information for discriminating responses. The contributions from joint firing proportionally increase with larger populations of cells. We find that the independent rates of individual cells can essentially represent coarser orientation differences. The orientation of the visual stimulus can determine the timing of the response onset, which can generate synchrony across the cortical circuit. Further structure in the responses in the form of intervals also depends on orientation and maintains multi-unit response coordination. We believe that cortical synchronization reliably propagates visual information with greater efficiency and supports greater precision and complexity.

1. Introduction

We have studied the role of temporal coordination and neural cooperation among the responses of visual cortical cells in discriminating the angle and/or direction of motion of visual stimuli (Samonds et al. 2003, 2004; Samonds and Bonds 2004a,b). Even among small populations of cells, we find substantial cooperation and structure among the responses that are potentially useful for making very small discriminations in the orientation of the stimulus. The cooperation grows with sample size, at least within our limited population, suggesting the possibility of large information advantages from the network as a whole. The cooperation develops out of temporally structured input to the cortex and is maintained by the orientation-dependent non-Poisson interval structure in the responses.

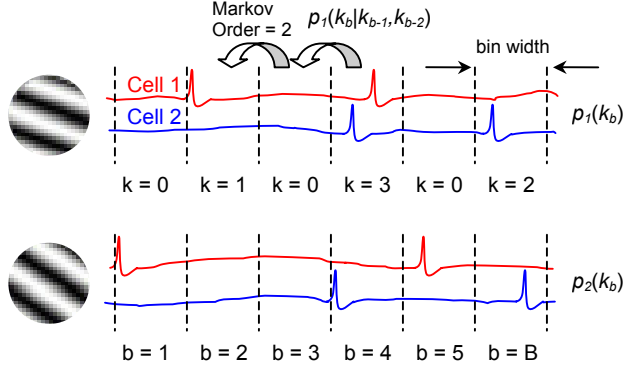
We recorded from *area centralis* in area 17 of ten adult cats paralyzed and anesthetized with propofol and N_2O . Forty-four single-units were resolved from multi-unit recordings at varying cortical depths in seven cats. Twenty-two to 25 single-units were recorded simultaneously using a 5x5 Bionics microelectrode array pneumatically inserted to a depth of 0.6 mm in three additional

cats. We presented approximately 500 repetitions of 2-second drifting sinusoid gratings, varying the orientation in 2° increments with all other grating parameters fixed.

Taking the view of discrimination as a classification problem in the context of the stochastic nature of neurons, we implemented a set of information-theoretic tools to quantify response differences. The Kullback-Leibler (KL) distance makes no assumptions about the nature of the neural code and is ideal for testing population coding (Johnson et al. 2001). Measuring the information from metric-based distances allowed us to test and compare the reliability of single-cell response properties such as firing rate, spike timing, and spike-to-spike intervals (Victor and Purpura 1996, 1997). Lastly, we quantified temporal structure and cortical synchrony using rate-normalized “effective connectivity” measurements (Aertsen et al. 1989).

2. Temporal Structure in the Spike Train Depends on Orientation

The information difference in responses to drifting gratings of different orientations was quantified using an information-theoretic distance (*KL distance*) (Cover and Thomas 1991; Johnson et al.



$$D(P_1 || P_2) = \sum_{b=1}^B \sum_{k=0}^{K-1} P_1(k_b) * \log_2 \frac{P_1(k_b)}{P_2(k_b)}$$

FIGURE 1: Schematic of estimating types and calculating the KL distance between two responses. Probabilities are calculated from hundreds of stimulus repetitions.

2001; Samonds et al., 2003, 2004). The KL distance indicates the performance expected from an optimal classifier in discriminating two responses (Johnson et al. 2001). An increase in KL distance is proportional to an exponential decrease in misclassifying the two responses (Johnson et al. 2001).

We break down the responses to two different stimuli into discrete bins (typically ranging from 2-6 ms) and assign each bin a letter depending on which cells fired within the bin (fig. 1). The number of possible letters increases exponentially with the number of cells. We then calculate a probability for each letter for each bin across the stimulus duration from stimulus repetitions (the estimated probability distribution is referred to as a type). With two types, we can calculate the KL distance (fig. 1). We add the KL distance from bin to bin as an accumulated distance. To account for any serial dependencies, we substitute the original types with conditional types. The conditional-based KL distance uses a Markov chain of letter probabilities dependent on the probability of letters in previous bins (fig. 1).

We tested small ($<10^\circ$) and large ($>10^\circ$) differences in grating orientation. For small differences in orientation, the KL distance depended on the temporal resolution of response sampling and increased when including response history (Markov order = 1; 4-12 ms), suggesting that the temporal structure of responses within this brief window is dependent on the orientation of a visual

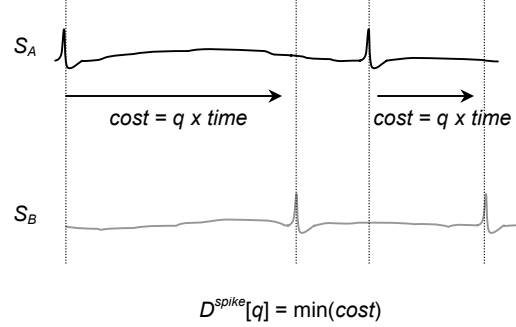


FIGURE 2: Metric-based distances calculate a cost of translating one spike train (S_A) into another spike train (S_B). The cost can account for shifts in time scaled by q (inversely related to the precision of the structure).

stimulus (Samonds et al. 2003).

We also quantified response differences using ad-hoc distances based on *a priori* defined metrics. Metric distances were calculated based on the spike count, spike times, or spike-to-spike intervals (Victor and Purpura 1996, 1997). We calculate a cost of translating the response to one stimulus into the response to another stimulus (fig. 2). First, we add to the cost the number of added or deleted spikes. Then, the total amount of shifted time or change in intervals (depending on the metric) is multiplied by a cost-scaling variable q and added to the total cost. As q increases, the precision of the temporal code increases. The distance is the minimum total cost of translating the response (fig. 2). We calculated the information about orientation provided by each of the metric distances from our stimulus repetitions. Again, we found the temporal structure (both precise spike times and intervals) to be informative for smaller orientation discriminations while the spike count was proportionally more informative for larger orientation discriminations (Samonds and Bonds 2004a).

Direct observation of the responses reveals that rotation of the grating produces clear time shifts in the response structure even when there is little or no change in the spike count or little inherent temporal organization of the spike train (complex cells) (Samonds and Bonds 2004a). We measured almost no spike timing information after shifting responses in phase. Larger orientation differences ($>10^\circ$) can be discriminated easily based on the independent spike counts (Samonds et al. 2003; Samonds and Bonds 2004a).

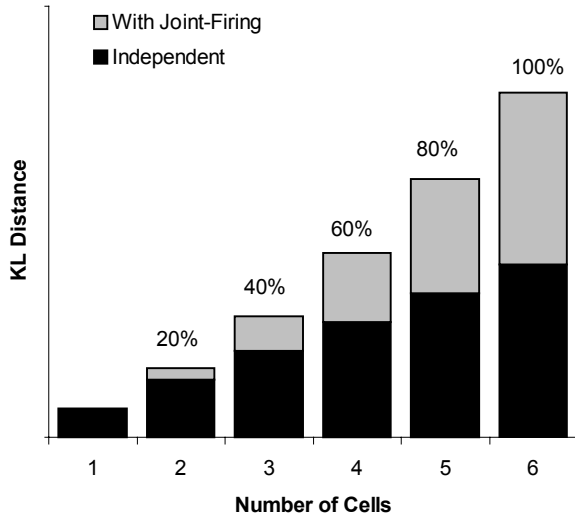


FIGURE 3: Cooperation (the percent gain when incorporating joint-firing into the KL distance with respect to the independent KL distance) increases with larger populations of cells.

3. Cooperative Discrimination of Orientation

We quantify the cooperation among pairs of cells and small populations of cells (≤ 6 cells) by comparing the ensemble KL distance (fig. 2) to the sum of the independent KL distances. The independent KL distances are calculated for the responses to each individual cell in the population. An independent KL distance can only test for two possible letters—the cell fired within the bin or did not. The percent difference of the ensemble KL distance with respect to the independent KL distance is the *synergy*. We call positive synergy *cooperation*, zero synergy *independence*, and negative synergy *redundancy*.

The high dimensionality of the response descriptions from the Markov order and the population size can lead to bias problems even with our relatively small populations. Several hundred samples does not allow an adequate estimate of bias with bootstrapping techniques so we replace our independent baseline with a more conservative comparison that is still vulnerable to the same systematic biases as our original ensemble KL distance. We randomly shuffle the responses in order to remove the dependencies among the population of cells and recalculate the KL distance. Both the

shuffled KL distance and independent KL distance lead to qualitatively similar results and conclusions with respect to the properties of population coding described below.

Joint-activity (i.e., cooperation) increased KL distance for small orientation differences (Samonds et al. 2003). As we move from very fine orientation discriminations to coarser orientation discriminations, the population coding fluctuates from largely cooperative to nearly independent (Samonds et al. 2004). Cooperation increased as larger populations of cells were sampled jointly (up to 6 cells), permitting discrimination of angular differences invisible to individual cells (fig. 3) (Samonds et al. 2004). However, the gain in cooperation cannot continue with larger populations indefinitely due to fundamental limits on the incoming information (Johnson 2004). Nonetheless, fig. 3 does suggest there is still potential for greater gains from joint-analysis of even larger neural populations.

The dependency or synchrony among cells was orientation-dependent and more selective than the average firing rates (Snider et al. 1998; Samonds et al. 2003, 2004; Samonds and Bonds 2004b). Information on small angular differences is thus contained in fine structure of the spike train and is markedly enhanced by analysis across groups of cells.

4. Relationships between Temporal Structure and Synchronization

We quantified the synchrony between pairs of cells and the interval structure of individual cells using the rate-normalized “effective connectivity” measurement (Aertsen et al. 1989). Aertsen et al. (1989) derive “effective connectivity” from joint post-stimulus time histogram analysis and the measurement provides a more appropriate auto- and cross-correlation measurement that normalizes for any changes in the firing rate across time and across stimulus variations.

The temporal structure of the responses influences synchrony and cooperation across the population of cells. Synchrony depended highly on whether or not the stimulus was appropriate to generate responses that were initially in phase (fig. 4) (Samonds and Bonds 2004b). Synchrony was only moderately related to the interval-based prop-

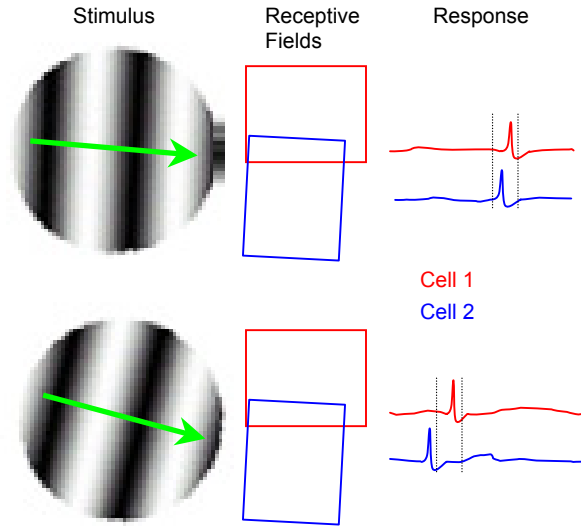


FIGURE 4: The responses of two cells will initially synchronize depending on the relationship between the stimulus and spatiotemporal properties of the receptive fields.

erties of bursts of spikes and gamma oscillations (Samonds and Bonds 2004b). The bursts and oscillation are likely produced from synchronous inputs that produce suprathreshold potentials.

At the same time, the oscillation and bursts are important in preserving the synchronization. All responses with gamma oscillation maintained synchrony across the entire 2-s stimulation period whereas 75% of the responses without gamma oscillation had a slow (seconds) decay in synchrony (Samonds and Bonds 2004b). Bursts can preserve synchrony by preserving timing information with more reliable or effective synaptic connections (Snider et al. 1998).

We conclude that synchrony is fundamental to the representation of structures in the visual environment. Synchrony provides a reliable mechanism to transmit visual information in a chaotic environment and offers an efficient cooperative neural code that we have only begun to explore.

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