Quantitative Analysis of Cooperation and Structure in the Cat Striate Cortex

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We have examined the information contained in the non-Poisson firing and joint activity of groups of cells in the primary visual cortex of the cat. 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 microelectrode array pneumatically inserted to a depth of 0.6 mm in three cats.

The information difference between responses to drifting gratings of different orientations was quantified using information-theoretic distances (*KL distance*). The KL distance indicates the performance expected from an optimal classifier in discriminating two responses. When testing small (<10º) orientation differences, the KL distance depended on the temporal resolution of response sampling and increased when including response history (up to about 10 ms), indicating that the temporal structure of responses at that scale is dependent on orientation. Joint activity (i.e., cooperation) across neurons also magnified KL distance for small orientation differences. Cooperation increased as larger populations of cells were sampled jointly (up to at least 6 cells), permitting discrimination of angular differences that were invisible to individual cells. The dependency or synchrony among cells was orientation-dependent and more selective than the average firing rates. Larger orientation differences (>10º) can be discriminated easily on the basis of the independent spike counts. 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.

We also quantified response differences using ad-hoc distances based on *a priori* defined metrics (Victor JD and Purpura KP, *J Neurophysiol* 1996). Metric distances were calculated based on the spike count, spike times, or spike-to-spike intervals. We calculated the information on orientation provided by each of the metric distances. 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. Analysis 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).

The temporal structure of the responses influences synchrony and cooperation across the population of cells. Groups of cells synchronize only when the orientation-dependent time shifts are initially in phase. Synchrony is then preserved by interval-based organization in the form of bursts of spikes and gamma oscillations. 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.