Natural movies evoke responses in the primary visual cortex of anesthetized cat that are not well modeled by Poisson processes
Jonathan L. Baker¹, Shih-Cheng Yen¹, Jean-Philippe Lachaux², Charles M. Gray¹
¹Center for Computational Biology, Montana State University, Bozeman, MT, USA
²INSERM U280, Lyon, France

The responses of striate cortical neurons are often modeled using non-uniform Poisson processes. This model has proved to be a good model of responses to simple, artificial stimuli (Berry et al. 1997; Kara et al. 2000), but several recent studies have suggested that naturalistic stimuli might evoke qualitatively and quantitatively different responses (de Ruyter van Steveninck et al. 1997; Buracas et al. 1998).

We recorded the responses of 50 isolated neurons in the striate cortex of anesthetized cats while presenting repeated naturalistic full-screen movie sequences with frame durations of 35 ms (29 Hz). We compared the spike-count and spike-time variability of the neuronal response across repetitions in each 35 ms window with 1000 sets of surrogate responses generated using a non-uniform Poisson process with a relative refractory period determined from the inter-spike interval histogram of each cell (Berry and Meister 1998). We measured spike-count variability using the Fano Factor (FF), which is the ratio of the variance to the mean of the spike counts across repetitions. We measured spike-time variability by first dividing each 35 ms window into 10 bins, and then ranking the bins in each repetition according to spike counts. Bins with the same spike counts were assigned the mean rank. The probability of getting a rank i in bin j, P(r_i), was then used to compute the entropy. The entropy would be high if spike times were randomly distributed with a frame and low if they were concentrated in a few bins across repetitions. The same spike-count and spike-time variability calculations were applied to the surrogate spike trains, which then allowed us to compute the percentage of surrogates with higher variability, as well as the z-scores of the data compared to the surrogates.

We found spike-count variability in the neural responses to be largely comparable to the surrogate responses, with 4.7% of the windows (with a mean spike count of at least 1) showing lower variability than 95% of the surrogates. At least one of these windows were found in 20% (10/50) of the cells in our database. On the other hand, we found spike-time variability to be much lower than the surrogate responses, with 34.5% of the windows showing lower variability than 95% of the surrogates. At least one of these windows were found in 74% (37/50) of the cells.

We also looked at the firing rate distributions for the cells in our database. When the rate distributions were computed by counting spikes within windows ranging from 25 ms to 250 ms, most of the cells displayed exponential distributions consistent with a Poisson process. This is in agreement with the results of a previous study (Baddeley et al. 1997). We quantified the match by bootstrapping the data, and computing distributions of goodness-of-fit values (i.e. degrees of freedom adjusted R-Square) for an exponential function and a power-law function (which was shown in the study cited above to match the distribution of inter-spike intervals in their data). Only cells that showed significant differences (using the paired t-test) in the distribution of fit values to the two functions, and had mean goodness-of-fit values above 0.75 were accepted as valid matches. Using this criteria with rate distributions computed using windows of 250 ms,
60% (30/50) of the cells displayed distributions consistent with an exponential function, 36% (18/50) of the cells were consistent with a power-law function and 4% (2/50) of the cells were consistent with neither. However, when the rate distributions were computed using the instantaneous firing rate (i.e. the inverse of the inter-spike interval), a much more heterogeneous picture emerged, with only 16% (8/50) of the cells displaying distributions consistent with an exponential function, and 12% (6/50) being consistent with a power-law function. The remaining 36 cells were consistent with neither function. The rate distributions for the surrogates, generated using non-uniform Poisson processes with relative refractory periods, showed similar matches for exponential functions when using windowed firing rates but showed better matches for power-law functions when using instantaneous firing rates (0% (0/50) exponential, 40% (20/50) power, 60% (30/50) neither).

Our results suggest that when stimulated by natural movies, neurons in the striate cortex of the cat exhibited spike time variability that were not well modeled by non-uniform Poisson processes with relative refractory periods. In addition, our analysis of the firing rate distributions revealed a bias towards exponential distributions when using windowed spike counts. A much more heterogeneous picture was revealed when instantaneous rates were used, suggesting that only certain cells in our database truly exhibited exponential rate distributions. Exponential rate distributions have been postulated to indicate that cortical neurons are able to maximize their response entropy (and thus their information content) for a given mean firing rate (Baddeley et al. 1997). Our results suggest that only a subset of cortical cells are consistent with that hypothesis (see also (Treves et al. 1999)). The rate distributions of the surrogates indicate that the addition of a relative refractory period to a Poisson process shifts the firing rate distributions toward power-law functions. However, this shift fails to accurately model the responses of a large fraction of our database, suggesting again that responses to natural movies are not well modeled by non-uniform Poisson processes with relative refractory periods.
Figure 1. Response variability. (Left) The spike count variability in 35 ms windows is shown for all 50 cells in our database. The windows with mean spike counts less than 1 (MSC<1) are plotted in gray while the remaining windows are plotted in black. The windows with spike-count variability lower than 95% of the surrogates are shown in blue (for the windows with MSC<1) and red. (Right) The spike-time variability in 35 ms windows for all 50 cells in our database are plotted as z-scores relative to the spike-time variability of the surrogates. The same color scheme used in the plot on the left is also used here.
Figure 2. Firing rate distributions using windowed spike counts. Firing rate distributions computed using spike counts in 250 ms windows for all 50 cells in our database. Note the log scale on the y-axis. The two red lines indicate the fits to the exponential function (straight line) and to the power-law function (curved line).
Figure 3. Distributions of instantaneous firing rates. Firing rate distributions computed using the inverse of the inter-spike intervals for all 50 cells in our database. Note the log scale on the y-axis. The two red lines indicate the fits to the exponential function (straight line) and to the power-law function (curved line).
Figure 4. Goodness-of-fit values for windowed (left) and instantaneous firing rates (right). The mean fit value from the bootstrap operation for the power-law function is plotted against that for the exponential function for each cell. The cells that showed a significant difference in the distribution of fit values, and had fit values higher than 0.75 are highlighted in red. Red points above the diagonal were significantly better fit by the exponential function while red points below the diagonal were significantly better fit by the power-law function.