Early visual system neuronal responses: A precise start with an imprecise finish

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Recorded from V1 neurons

Figure 1. Stimuli used when recording from striate neurons. The Walsh pattern stimuli consisted of 8 different Walsh patterns at 5 contrast levels. 8 orientations of gratings at 5 contrast levels were also used. The bars were presented at 8 orientations and 8 contrast levels. Negative contrast indicates the bar as being darker than the background. 32 digitized picture stimuli were also used. A total of 274 stimuli were presented in random order. The gratings, Walsh patterns and pictures were all iso-luminant.
Response latency varies with stimulus

Figure 2. Rastergram display of the responses of a complex striate cell to gratings of different orientations and contrasts. The vertical line indicates stimulus onset. 100 ms pre-stimulus and 300 ms of post-stimulus activity are shown. This cell responded best to gratings at a 45 degree oblique. The low background activity typical of complex cells facilitates detection of trial by trial response latency. The responses to decreasing stimulus contrast (column) clearly show increasing response latency. The increase in response latency with decreased contrast is present for stimuli producing weak responses (e.g. left column) as well as for the responses to effective stimuli (45 oblique orientation). Note also that the response latencies to stimuli producing weak responses at a given contrast are similar to the latencies of responses to effective stimuli at the same contrast (compare 1st and 3rd panel in the top row).
Response latency does not vary with response strength.

**Figure 3. Scatter plot of response latency against response strength.** Response latency of each trial is plotted against the number of spikes in the response. The estimates from stimuli with the highest tested contrast are plotted in black, the estimates from stimuli with the lowest tested contrast are plotted as open circles. It is clear that the stimuli of low contrast produced responses with latencies some 25ms longer than high contrast stimuli. Note that across all trials the lower limit of the response latency is almost constant for both contrast levels despite large changes in the response strength.
Response latency carries information

Figure 4. Average transmitted information about the input stimuli using 3 different codes. The transmitted information from 19 cells (+/- SEM) is shown for each of the four stimulus sets. For all stimulus sets, response latency carries substantial information (compare left and middle bars), and that some of this information is independent of spike count (compare left and right bars).
Figure 5. Information content about stimulus contrast and stimulus pattern of Walsh patterns and grating stimuli. The information about stimulus contrast is shown in the top row. The information about stimulus pattern is shown in the bottom row. Information in responses to Walsh patterns are shown in the left column, information in responses to grating stimuli are shown in the right column. Information content of the dual code of response latency and response strength (Latency + Spikes, right bars) was taken as the total information available about the stimulus attribute (Contrast or Pattern). The latency code (middle bars) carries effectively all the information about stimulus contrast (upper row) while the spike count code (left bars) carries effectively all the information about the stimulus pattern (lower row).
Later spikes carry less information.

Figure 6. Transmitted information from the time of the 1\textsuperscript{st}, 2\textsuperscript{nd} and 3\textsuperscript{rd} spikes. The transmitted information for three codes (Spk = spike count, Lat = time of spike and Spk+Lat = the dual code of spike count and spike time) is shown. The information from the time of a spike decreases as the spike occurs further into the response. The reduction in information available from the time of the spike is reflected in the reduction in the information calculated using the dual code, suggesting that the information loss from later compared to earlier spikes is the information that is independent of the spike count.
Later spikes are more redundant with spike count

Figure 7. Independence index for 1\textsuperscript{st}, 2\textsuperscript{nd} and 3\textsuperscript{rd} spike with spike count.

\[
\text{Independence} = \frac{I_{\text{Dual Code}} - I_{\text{Spike Count}}}{I_{\text{Time of Spike}}}
\]

Independent index for the transmitted information is plotted as a function of spike position within the response. As the spike occurs later in the response, the information carried by its time relative to stimulus onset becomes more redundant with the information carried by spike count.
Examining repeating triplets

Figure 8. Searching for repeating triplets. Pairs of inter-spike intervals were examined to see if they repeated within individual spike trains (horizontal bar). Two sets of repeating triplets are illustrated, one identified by red arrows, the other (repeating 3 times) by green arrows.
Information from repeating triplets is redundant with the information from the spike count

Figure 9. Information measures from the number of repeating triplets are inherent in the total spike count. Three measures of the mean information (± SEM) are shown. The information from the total spike count (All Spikes) is higher than the information from the number of repeating triplets (Number of Triplets). If the presence of repeating triplets were independent of the first order statistics of the spike trains then the information from Spikes + Triplets would be the sum of the information from All spikes and the information from the Number of Triplets. The information from a joint code containing all spikes and the number of triplets (Spikes + Triplets) is no different from the information from the spike count (All spikes). Upper: LGN data, ANOVA: Effect of code $F_{[2,42]}=56.1$, $p < 0.0005$. Lower: Primary visual cortical data, ANOVA: Effect of code $F_{[2,36]}=78.5$, $p < 0.0005$. 
The spike count matched model

Figure 10. Modeling V1 responses. Upper: The spike density function calculated from the responses of one LGN neuron to a single, effective stimulus. Lower: Summation of the spike density function from the upper panel gives the cumulative spike function. Normalization gives the cumulative spike probability function, allowing random numbers drawn from a uniform distribution to be transformed into the distribution of spike arrival times given by the spike density function (upper section). To generate a trial with, say, three spikes, 3 uniformly distributed random numbers between 0 and 1 are drawn. These random numbers are then transformed using the cumulative spike probability function to obtain the times at which the spikes will occur in the simulated spike train. The arrows show an example of the transformation of 3 evenly spaced random numbers (y-axis) into the spike times (x-axis) appropriate for the spike density function shown. Note that in the example the spikes in the resulting train are not evenly spaced.
Figure 11. The spike count matched model accurately predicts the number of repeating triplets in neuronal data. Scatter plots of the number of repeating triplets from the spike count matched model against the number of repeating triplets found in the neuronal data on a logarithmic scale are shown. One was added to the number of repeating patterns to allow use of trials where no repeating patterns were present. Mean number of repeating triplets per trial from the spike count matched model and primary visual cortical neuronal data for each stimulus and each of the 19 cells on a logarithmic scale (n=3389). The points from the cumulative spike probability function are scattered around the equality line (diagonal), indicating excellent predictive value of the spike count matched model. 

Inset: Frequency plot of the ratio of the number of repeating spike patterns predicted from by model to that seen in the neuronal data. Note the tight distribution of this ratio about 1.0 obtained using the spike count matched model compared to the flatter distribution extending down to 0.0 from the non-homogenous Poisson process (NHPP) model for the neural data sets.

**Primary Visual Cortex**

$n=3389$

$R^2 = 0.98$

Intercept = 0.002

Slope = 1.012
Predicting “sore thumbs”

Figure 12. The spike count matched model predicts large variability in the number of particular repeating triplet types. The distributions of each repeating triplet type show that the spike count matched model matches the neuronal data including the occasional large numbers of particular triplet types. **Upper**: The number of times each triplet type, defined by the first and second intervals, was found in the responses of one striate cortical neuron to one stimulus. **Lower**: The distributions of expected numbers of repeating triplets from four runs of the spike count matched model. Note the model shows large variability in the numbers of particular repeating triplet types from run to run.
Conclusions

Spike times relative to stimulus onset

- Response latency (time of first spike of response) carries substantial information. Temporal resolution on the order of 1-5 ms
- Times of spikes in later part of response carry information that is also carried by spike count.
- **Initial phase of the response is temporally precise**

Spike times relative to each other

- SCM model allows prediction of temporal patterns
- No evidence that the precise times of spikes relative to each other carry information unavailable from spike count/spike density function (~20 ms precision).
- **The internal structure of responses has little temporal precision**