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Supplemental Data

Cortical Mechanisms of Smooth Eye Movements Revealed by Dynamic Covariations of Neural and Behavioral Responses

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Supplementary Results: Filter extraction using residuals can describe the full relationship between brain and behavior

In our paper, we model the relationship between the residual eye movements and the residual spike trains. We believe such a model to be a most reasonable approximation to the true relationship between neural activity and behavior. Here, we present a simple simulation to justify this stance. We begin by demonstrating how a filter derived from a simulated set of residual eye movements and spike trains can successfully approximate the "true" filter relating brain activity to behavior. Next, we discuss the assumption of linearity that underlies the demonstration, and the effects that common nonlinearities would have for our study.

Our simulation begins with a filter that describes the "true" relationship between brain activity and behavior. This function, plotted as a grey line in Figure S1C, defines the complete relationship between neural activity and eye movements. Next, we design a set of 100 synthetic eye movements with the same statistics as our example set of eye movements from Figure 1. First, we add the mean of the eye movements in Figure 1 to a randomly fluctuating "residual" unique to each trial (Figure S1D). Residuals consist of white noise that has been scaled and smoothed to match the properties of real eye movement residuals. Importantly, as in our data, the magnitude of the residuals changes over the course of the trial. We generate the neural response associated with each complete eye movement by convolving the complete synthetic eye movement on each trial with our filter. The firing rate thus reflects both the mean eye movement as well as the residuals. We then rectify the firing rate on each trial, and convert the rate to Poisson spikes with a maximum instantaneous rate of 50Hz, and a background of 5Hz. Spikes are plotted as a raster in Figure S1B -- compare to Figure 1B.

Figure S1C plots the true filter used to generate the spikes (gray line), and a filter derived from the complete spikes and eye movements, including their means (black ribbon). Both have been normalized so that their dot product with themselves is one, and are thus without units. Due to the strong correlations in the complete eye movement, this procedure yields an incorrect estimate of the true filter. Similar, often more profound, problems arise when attempting to extract the filter from the complete data sets associated with the neurons described in this paper. The correlation coefficient between the true filter and one derived from the full data set is 0.82, and decreases as we increase the number of simulated trials or the firing rate. Figures S1D and S1E plot the residual eye movement and spiking trains derived by subtracting the mean from each. Figure S1F plots the filter derived from these residuals as in the paper (Methods) as a black ribbon, against the "true" filter, both normalized and without units as in Figure S1C. The correlation coefficient between the two for this run of the model is 0.90, significantly greater than the correlation derived from the full data set (t-test, $p < 10^{-8}$). As we increase the firing rate or the number of trials we simulate, the correlation approaches 1.

Supplementary Discussion

In this simulation, we created a model neuron whose firing pattern is generated by a linear filter of the eye movement, followed by a threshold non-linearity. Under these conditions, calculating the neural filter from the residuals produced a better estimate of the true filter than using the complete eye movement. We conclude that if the cell behaves linearly across the range of eye velocities encountered during the trial, a filter derived from the residuals gives an excellent estimate of the true relationship between neuron and behavior. What would happen if the neuron had a more complex relationship to the eyes' velocity?

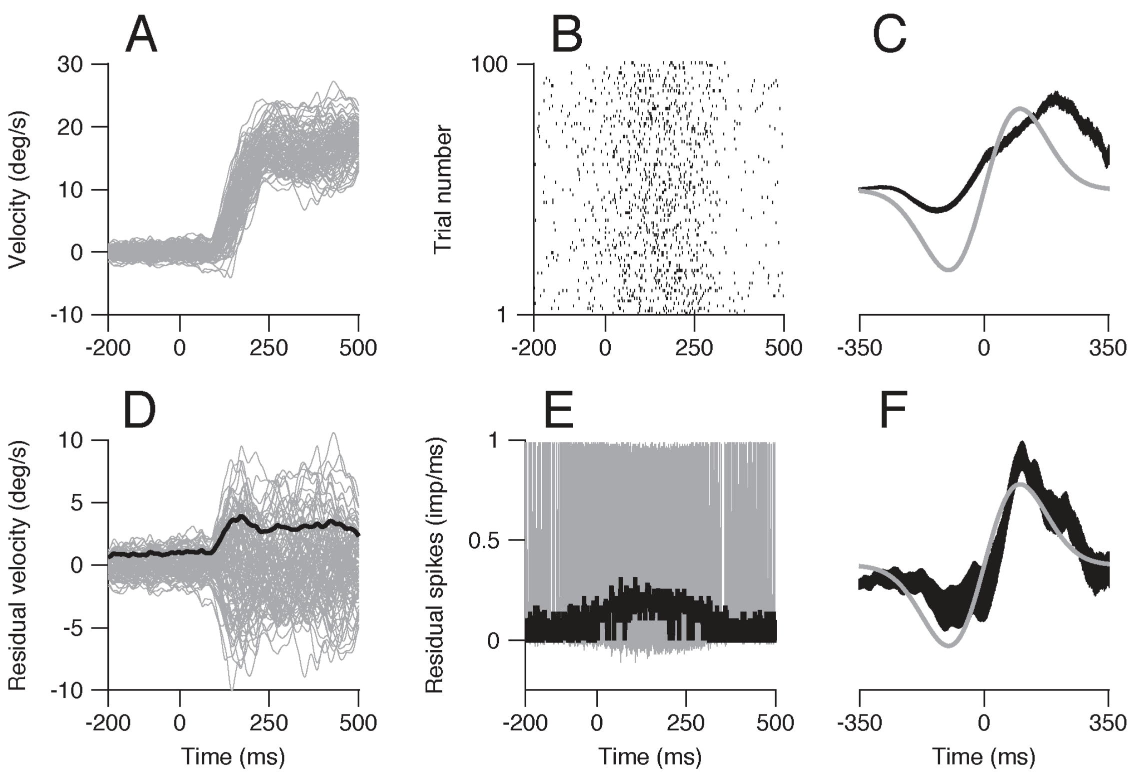
Often, the linear filter that relates stimulus fluctuations to spiking in sensory neurons will change with the mean level of the stimulus (Nagel and Doupe, 2006). To observe how the filter depends on the mean, one can calculate separate filters for distinct periods of low and high stimulus mean. Calculating a single filter for data collected at different means will yield a weighted average of the filters at each mean (each filter will be weighted by the number of spikes it produces). This weighted average will generally have less predictive power than the mean-specific filters on individual stimulus segments, but will generalize better between stimulus conditions.

By analogy with the sensory case, in this study we calculated a single filter for at least two eye movement conditions: initiation of and steady-state smooth pursuit. Given that the inputs to the system are different between the two conditions, the filters relating spiking to movement might be different during these different behaviors, and our procedure would produce an average of these true filters. Whether FEF_{SEM} neurons show this type of nonlinearity is not known, and such an exploration is beyond the scope of this paper. However, even if there exists a more complex relationship between spiking and eye movements, we do believe our filters represent the best possible linear estimate of this relationship for the range of movements we have explored.

As a more complete picture of the relationship between spikes in the FEF_{SEM} and concurrent eye movements emerges, we expect these better models to yield even higher neuron-behavior correlations. Such a finding would imply even lower downstream noise (or even fewer neurons in the active population). Our findings thus stand as a conservative estimate of the strength of the relationship between brain and behavior.

Supplementary Figure Legend

Figure S1: Extracting the filter from the residuals yields an excellent approximation of the "true" filter. **A:** 100 synthetic eye movements, plotted as overlaid grey traces **B:** Synthetic spike trains, each associated with a grey eye movement trace. Spike trains were derived by filtering each eye movement and the "true" filter, then rectifying the resulting firing rate and simulating a Poisson spike train with background of 5Hz and peak activity of 50Hz **C:** The "true" filter, used to generate the firing rate is plotted in grey. The filter relating the full set of eye movements and spike trains is plotted as a black ribbon signifying one standard deviation above and below the mean of 150 estimates. Both filters have been normalized so that their dot product with themselves is one, and are thus without units. **D:** The eye movement residuals are plotted as overlaid grey traces, and their standard deviation is plotted as a black line. **E:** The residual spike trains are plotted as overlaid grey traces, and their standard deviation as a black line **F:** The "true" filter is plotted in grey. The filter relating the eye movement and spiking residuals is plotted as a black ribbon, showing one standard deviation above and below the mean filter. Filters have been normalized as in **C**.



Schoppik et. al. Supplementary Figure 1