

Characterizing neural processing in foveal and parafoveal primary visual cortex Felix Bartsch¹, Bruce G. Cumming², Daniel A. Butts¹

Introduction

• Foveal V1 neurons are seldom studied, primarily due to difficulty measuring and controlling eye position with sufficent accuracy given the small size of foveal receptive fields



• While the center-of-gaze is highly significant behaviorally and dramatically overrepresented in V1, it is expected (though not known) that studies of V1 properties in the parafovea [e.g., 1, 2] should generalize to the fovea.

How does visual processing compare between foveal and parafoveal V1?

Are there differences beyond receptive field scaling?

• Here, we use the Nonlinear Input Model [3], an LNLN cascade, to measure properties of V1 neurons in awake macaques across eccentricites between 0.4 and 16 degrees.

• We use model-based eye-tracking sensitive to ~1 arcmin [4] to allow precise measurements of receptve field propertes and validate model-based measurements with model-independent measures.

Methods

Electrophysiology: Recordings came from two macaques using 24-electrode linear arrays (50 µm spacing, 106 SUs) or a 96-electrode planar Utah array (400 µm spacing, 40 SUs). Animals performed a simple fixation task to obtain a liquid reward upon completion of each 4-second trial.

Stimuli: Uncorrelated random bar patterns ('1D ternary noise') were presented binocularly on CRT monitors, with each pattern lasting 10ms. The bars were oriented close to the cell's preferred orientation. Most experiments were presented at zero disparity, but experiments at >9 degrees eccentricity involved a different dataset where binocular stimuli were presented at randomly selected dispari-



LNLN cascade models fit with the NIM architecture [1] Model parameters were fit using maximum likelihood estimation based on the

eye-tracked stimulus and spike train of each neuron. Hyperparameters, such as the number of excitatory and inhibitory subunits, were estimated via grid search.



Model-based eye tracking [4]

We used the units simultaneously recorded in each experiment to infer the precise position of the eye from moment-to-moment. By integrating probabilistic eye position information over a population of simultaneously recorded neurons, we can infer eye position with roughly 1 arc-min accuracy.







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Receptive field width depends on filter width and spatial scatter





RF size increases wth eccentricity at a rate of 0.17 deg/deg of eccentrcity (R2=0.389)

Position (deg) RF width was measured by averaging the spatial profile of all filters, weighted by each filter's contribution to the model prediction. Scale bar = 0.2 deg.

Spatial scatter increases with eccentricity





As eccentricity increases, average width of model filters increases less than the overall RF width, while the scatter between the filter centroids within each model increases.

High spatial frequency tuning in parafovea

We estimate spatial and temporal frequency tuning of each cell by computing the 2DFFT for each subunit, and taking an average across subunits, weighted by contribution to the model. We find tuning to high SFs in the fovea, but SF preferences in the parafovea decrease very slowly compared to previous results [1].





Models correctly predict SF tuning



We also measure SF tuning through a model-free **forward-correlation (FC)** procedure. We extract the SF spectra of each stimulus frame and compute PSTHs for frames containing power in the upper and lower 30th percentiles for each SF. Subtracting the response to frames with low power at a given SF from the response to frames with high power at that SF gives an accurate estimate of the cell's SF tuning curve.

Spatial scatter at high eccentricities affects responses to gratings

To compare our results to previous studies, we simulate our model's responses to grating stimuli, specifically the magitude of the response to each grating frequency (F1). Grating-predicted SF tuning matches the forward correlation SF tuning in the fovea (<2 deg), but is significantly lower (tested via wilcoxon rank-sum test) in the parafovea.



In this example parafoveal cell, we find an overall F1 preference to low-frequency gratings although individual filters are tuned to high SFs. Because the filters are phase shifted, the responses to high-SF gratings don't sum temporally, while the relatively lower responses to low-SF gratings do sum.

Aligning the filters of this model by phase removes the selectivity to the envelope frequency and reveals the capacity to resolve higher SFs.



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Conclusions

 Model-based measures of V1 tuning provide high-resolution information about the selectivity of V1 receptive fields.

• The increase in RF size with eccentricity is explained by two factors: (1) the increasing width of individual processing elements; and (2) the increasing spatial scatter of these units. This suggests that parafoveal neurons may be able to resolve higher resolution inputs than previously expected.

• This spatial scatter of individual processing elements can result in selectivity to low frequencies in the context of drifting grating stimuli, particularly in the F1 measure, offering an explanation for previously observed "envelope tuning" in V1

• These sensitive measurements across eccentricity rely on a high-resolution model-based eye-tracking algorithm [4].

Necessity of model-based eye-tracking [4]





Our results are facilitated by our eye-tracking algorithm [4], which refines stimuli to reveal smaller RFs, increased filter scatter and higher spatial frequency selectivity in our models.

References

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