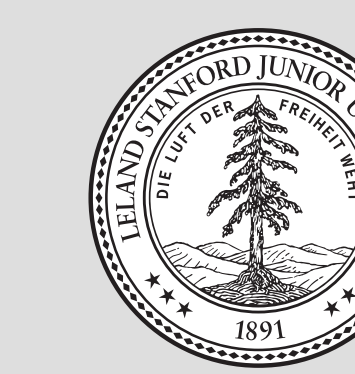


Spatial extent of inputs to primate ganglion cells in natural viewing conditions

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Background

Pseudo-linear encoding models, where the first step is linear summation of the stimulus over space and time, have become the standard for predicting the responses of retinal ganglion cells (RGCs). They have been successful at predicting responses in some cases¹⁻⁵.

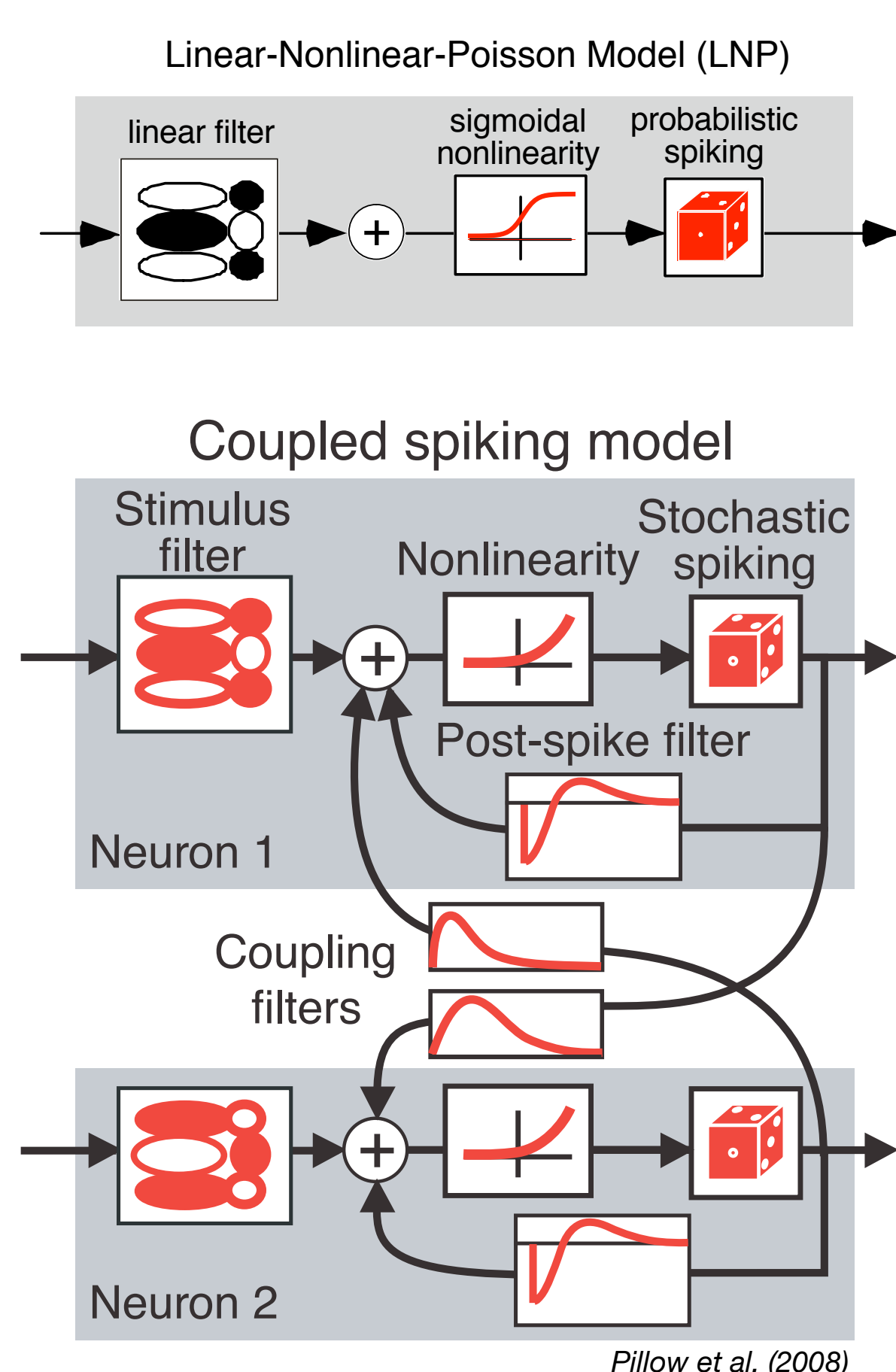
However, it is unclear how accurate this assumption of linearity is, given that there are many known nonlinear mechanisms that contribute to retinal light responses in specific stimulus conditions and cell types⁶⁻⁹. It is unknown whether primate RGCs sum visual inputs effectively linearly under the naturalistic conditions that it evolved to encode.



How accurate are pseudo-linear models in predicting primate ganglion cell responses to naturalistic stimuli?

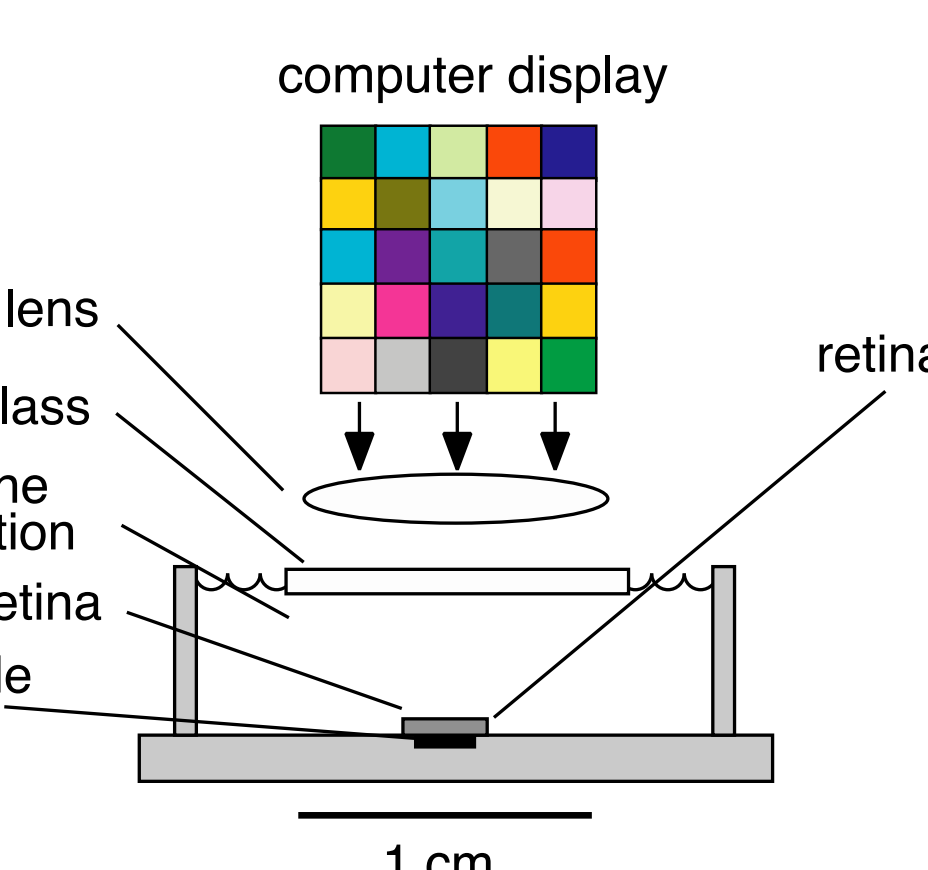
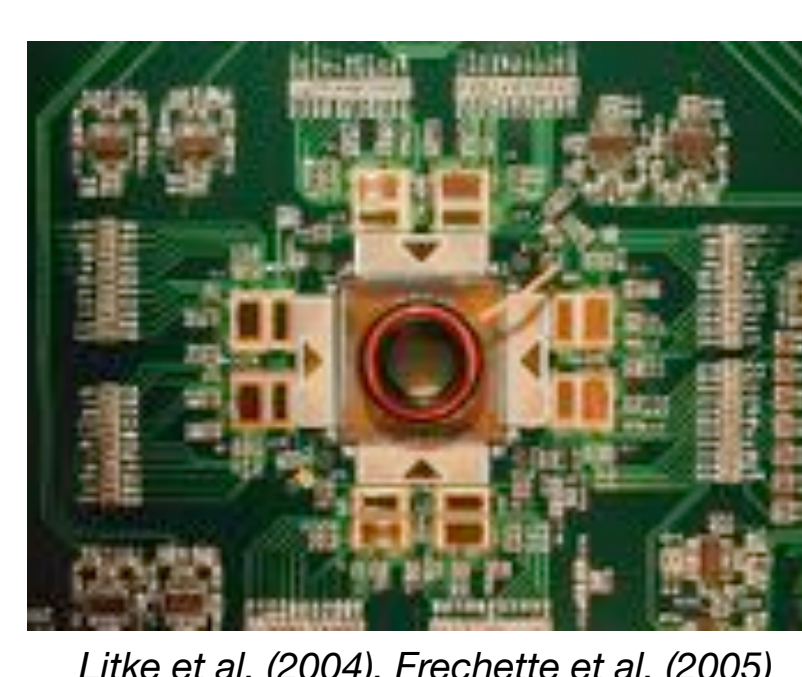
Modeling

The linear-nonlinear Poisson model (LNP) is one of the simplest and easiest to use models, and has been shown to work fairly well. However, it does not capture correlated firing or precise spike train structure, which can be captured by more accurate generalized linear models (GL). However, making these models flexible enough to work for natural scenes and still computationally tractable has proven difficult.



Methods

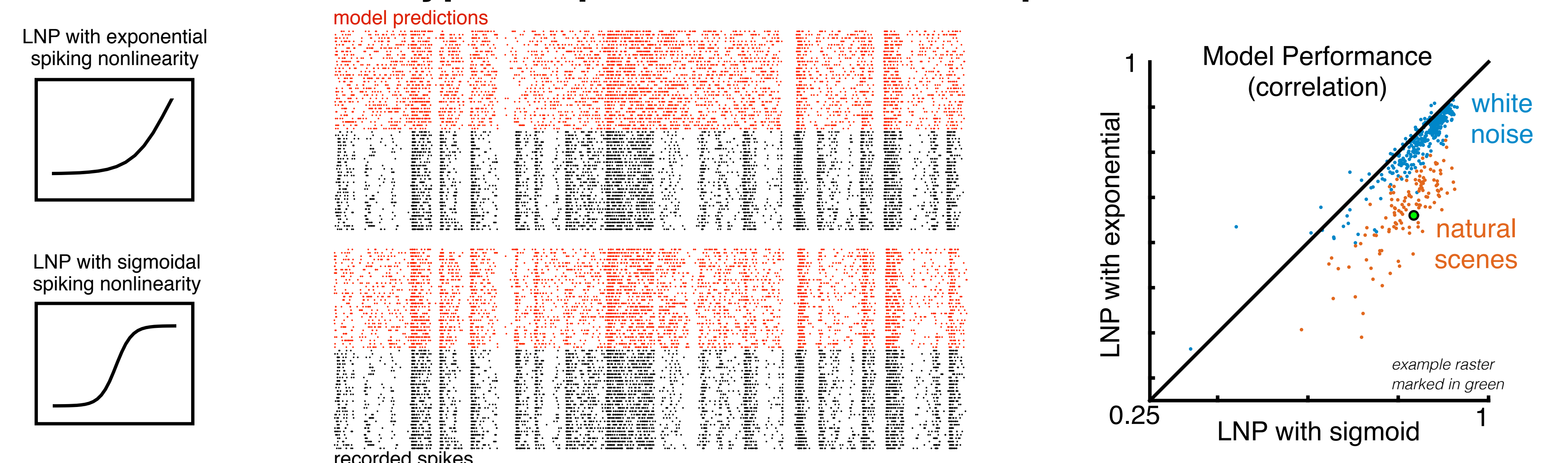
Large-scale multielectrode recordings were performed in peripheral macaque retina *ex vivo*.



Natural scenes consisted of images from the van Hateren database¹⁰ with fixational eye movements simulated by Brownian motion¹¹.

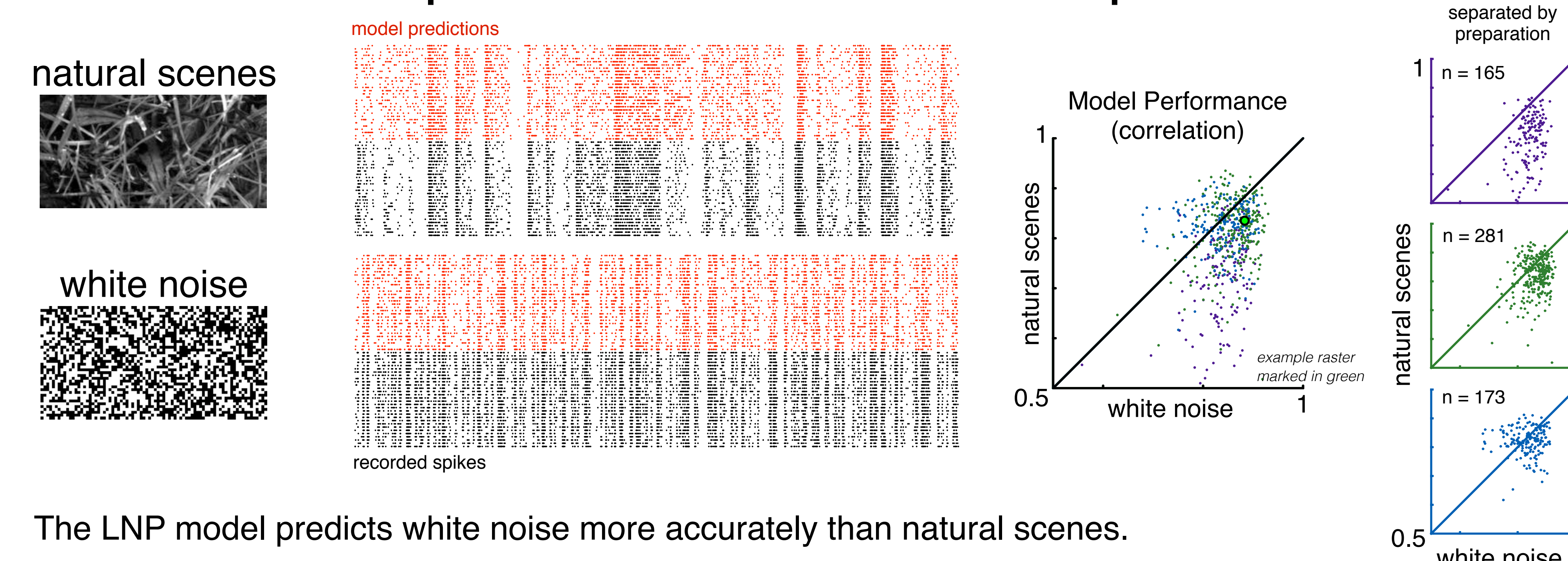
Modeling primate retinal ganglion cell responses to natural scenes using pseudo-linear models

How do different types of pseudo-linear models perform on natural scenes?



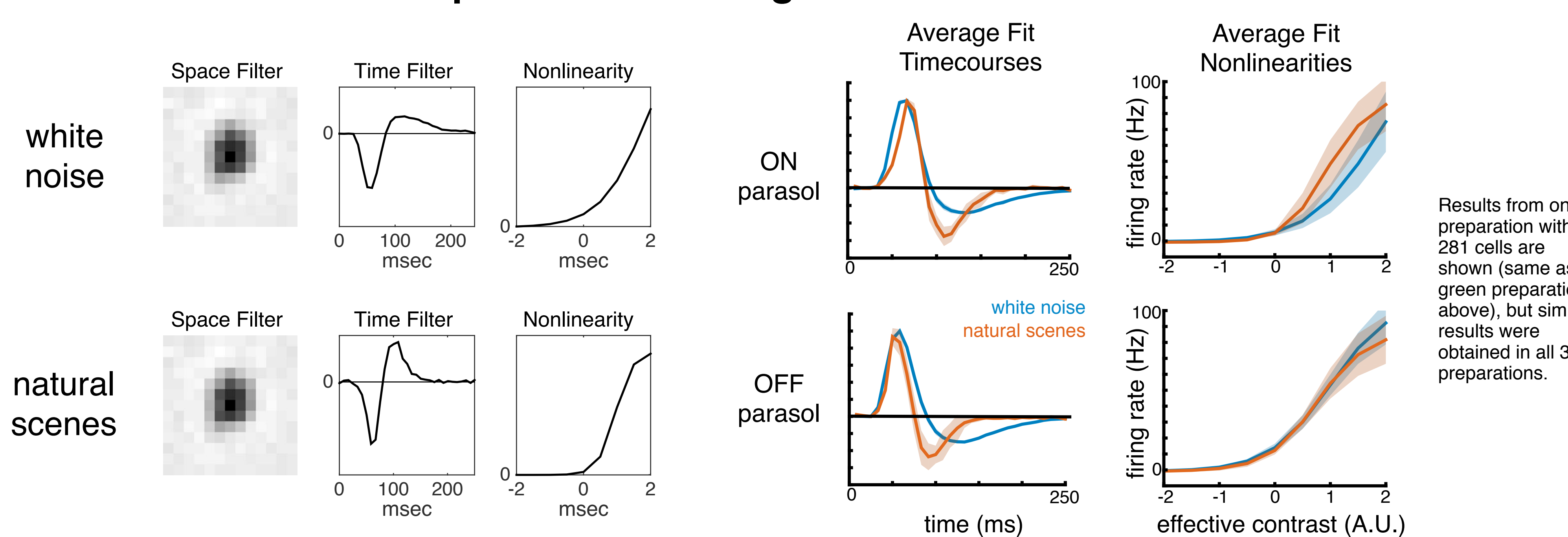
Performance on natural scenes is sensitive to the architecture of the model.

How does model performance on natural scenes compare to white noise?



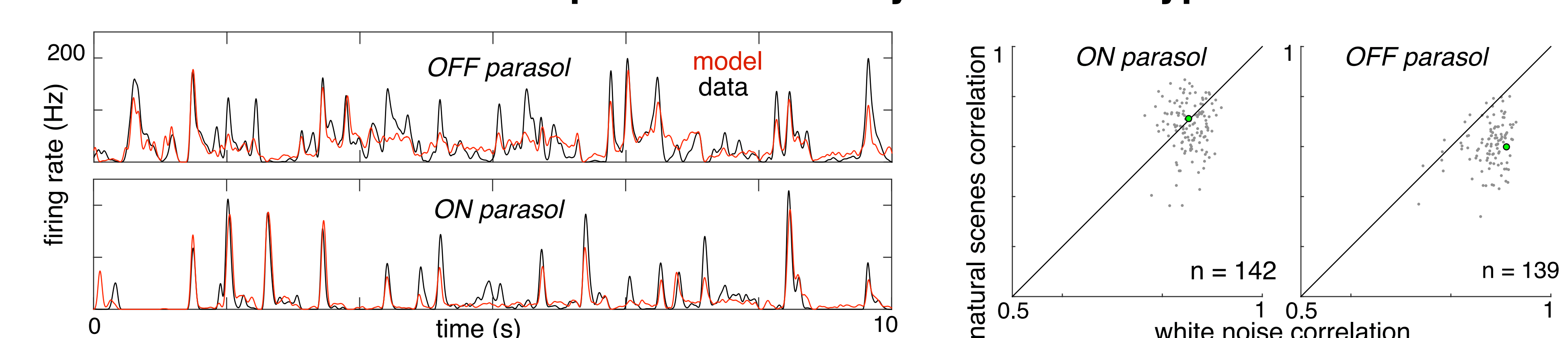
The LNP model predicts white noise more accurately than natural scenes.

How do the model parameters change from white noise to natural scenes?



The temporal filter is more biphasic and the spiking nonlinearity is more saturated for natural scenes.

Does model performance vary across cell types?

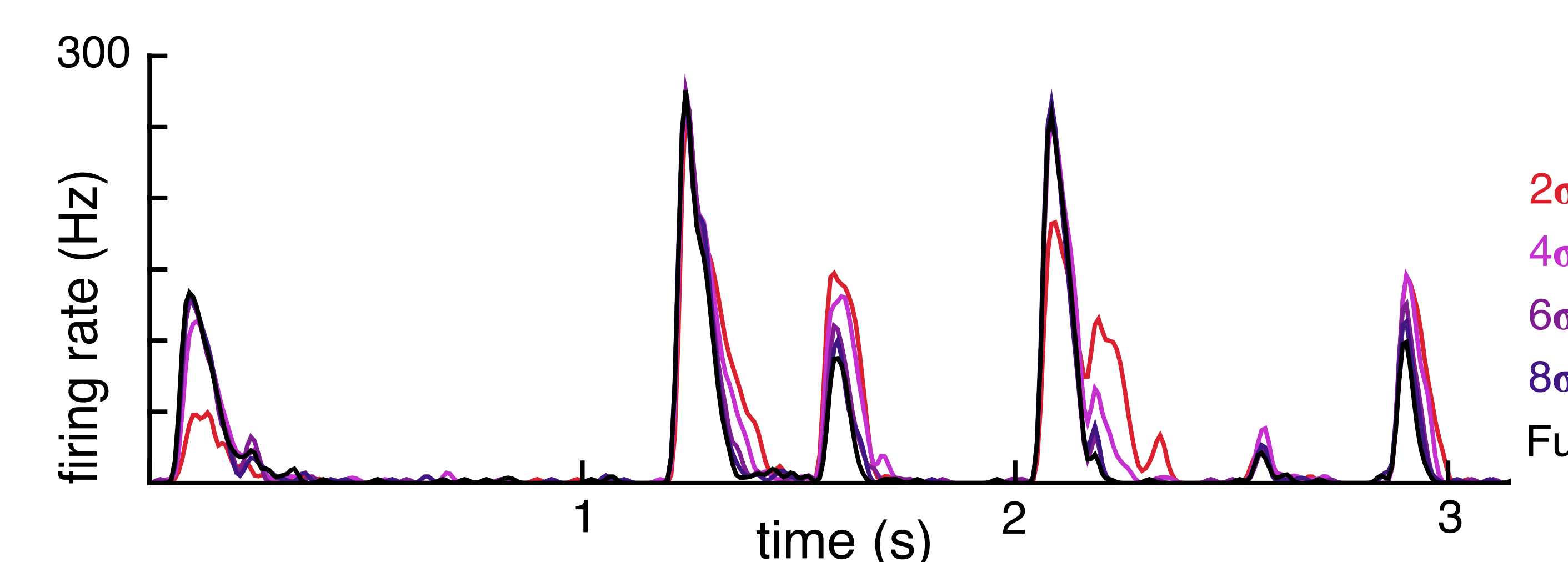
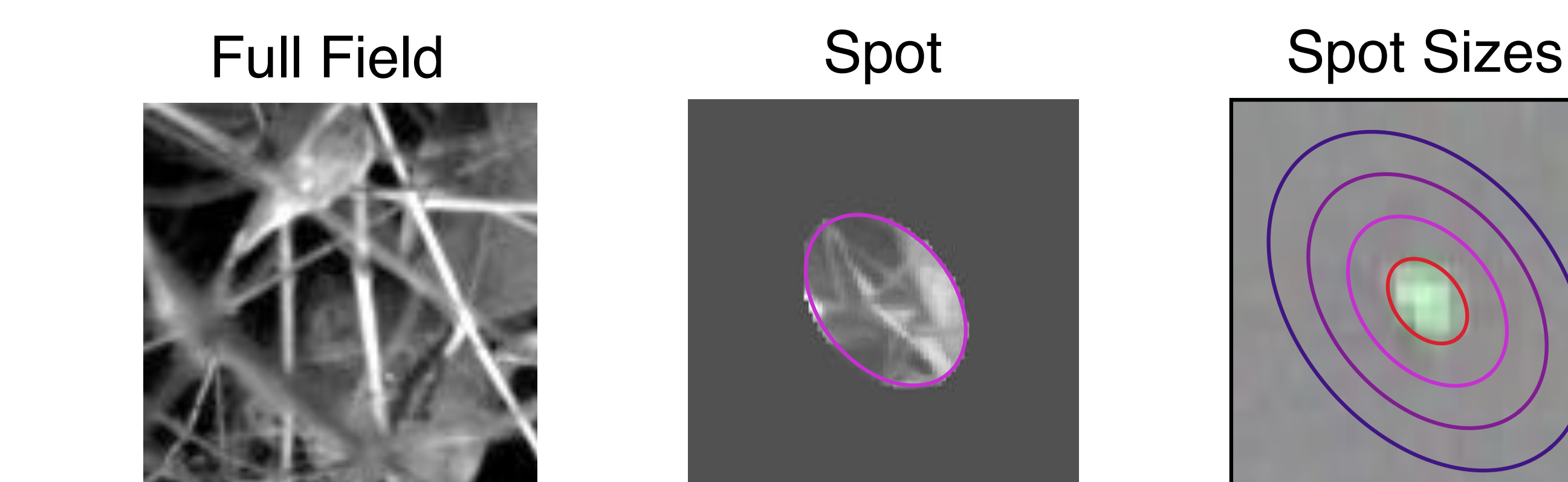


Previous work indicates that ON parasols integrate visual inputs more linearly than OFF^{9,12}. A similar asymmetry was observed in 1/3 preparations tested using natural scenes (shown, same as green preparation above).

What effect does peripheral stimulation have on RGC responses under natural viewing conditions?

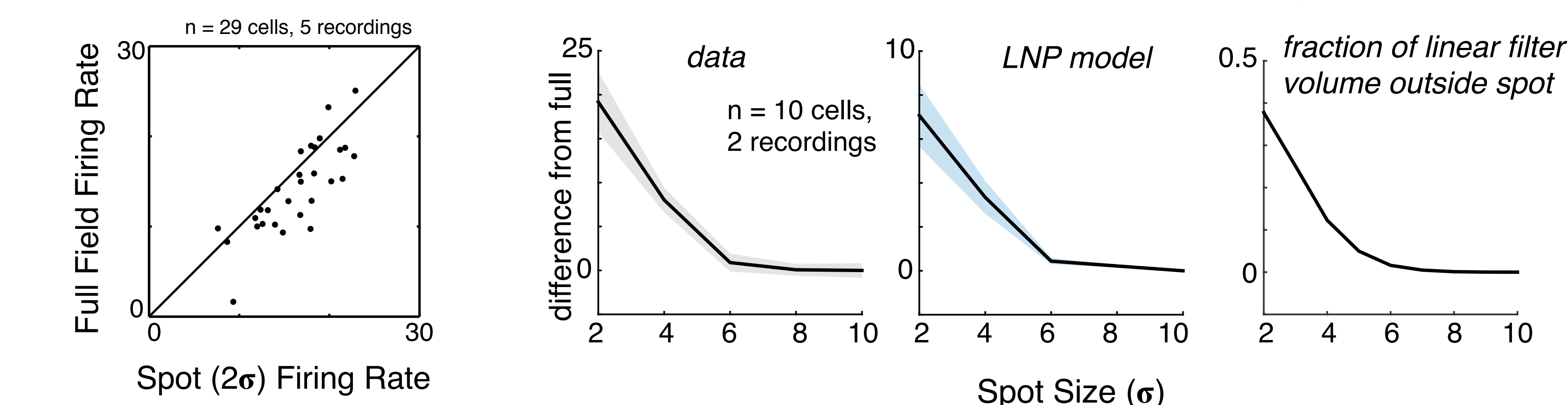
Extra-classical receptive field effects

RGCs can receive peripheral input from outside their classical receptive fields⁸, thought to be transmitted through wide field amacrine cells. How do peripheral stimuli influence responses of primate RGCs in natural viewing conditions? Do we need to include peripheral input in our models?



Consistent with previous findings, the periphery had a mostly suppressive effect.

Surprisingly, this plateau at 6σ can be predicted by the spatial extent of the linear filter (as measured with a white noise stimulus).



The spatial extent of inputs to ON and OFF parasol RGCs can be predicted from the classical receptive field.

References

- Justin Keat, Pamela Reinagel, R. Clay Reid, and Markus Meister. Predicting Every Spike: A Model for the Responses of Visual Neurons. *Neuron*, 30:803-817, 2001.
- E.J. Chichilnisky. A simple white noise analysis of neuronal light responses. *Network: Computation in Neural Systems*, 12:199-213, 2001.
- Liam Paninski. Maximum likelihood estimation of cascade point-process neural encoding models. *Network: Comput. Neural Syst.*, 15:243-262, 2004.
- Jonathan W. Pillow, Jonathan Shlens, Liam Paninski, Alexander Sher, Alan M. Litke, E.J. Chichilnisky and Eero P. Simoncelli. Spatio-temporal correlations and visual signalling in a complete neuronal population. *Nature*, 454:995-999, 2008.
- Sheila Nirenberg and Chethan Pandarinath. Retinal prosthetic strategy with the capacity to restore normal vision. *Proceedings of the National Academy of Sciences*, 209(37):15012-15017, 2012.
- Hochstein and Shapley. Linear and nonlinear spatial subunits in Y cat retinal ganglion cells. *Journal of Physiology*, 262(2): 265-284, 1976.
- Shapley and Victor. The effect of contrast on the transfer properties of cat retinal ganglion cells. *Journal of Physiology*, 285:275-98, 1978.
- James T. McIlwain. Receptive fields of optic tract axons and lateral geniculate cells: peripheral extent and barbiturate sensitivity. *Journal of Neurophysiology*, 27(6):1154-1173, 1964.
- Maxwell H. Turner and Fred Rieke. Synaptic Rectification Controls Nonlinear Spatial Integration of Natural Visual Inputs. *Neuron*, 90(6):1257-1271, 2016.
- J. H. van Hateren and A. van der Schaaf. Independent component filters of natural images compared with simple cells in primary visual cortex. *Proceedings: Biological Sciences*, 265(1994):359-366, Mar 1998.
- Xutao Kuang, Martina Politi, Jonathan D. Victor, and Michele Rucci. Temporal encoding of spatial information during active visual fixation. *Current Biology*, 22(6):510 - 514, 2012.
- E.J. Chichilnisky and Rachel S. Kalmar. Functional Asymmetries in ON and OFF Ganglion Cells of Primate Retina. *Journal of Neuroscience*, 22(7):2737-2747, 2002.
- Alan Litke et al. What Does the Eye Tell the Brain?: Development of a System for the Large-Scale Recording of Retinal Output Activity. *IEEE Transactions on Nuclear Science*, 51(4):1434-1440, 2004.
- E. S. Frchet, A. Sher, M. I. Givich, D. Petrusca, A. M. Litke, E. J. Chichilnisky. Fidelity of the Ensemble Code for Visual Motion in Primate Retina. *Journal of Neurophysiology*, 94(1):119-135, 2005.

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