# Neuron

### **Direction-Selective Circuits Shape Noise to Ensure a Precise Population Code**

### **Highlights**

- Direction-selective retinal ganglion cells have correlated response variability
- The "noise correlations" are strongly stimulus dependent
- These correlations are due to common noisy inputs to multiple cells
- Stimulus-dependent correlations provide a 2-fold boost in information transmission

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### In Brief

Direction-selective retinal ganglion cells give noisy responses to stimulation. Zylberberg, Cafaro, Turner, et al. show that stimulus-dependent correlations in this trial-to-trial variability shape the noise so as to significantly reduce its impact on information transmission.





### Neuron Article

### Direction-Selective Circuits Shape Noise to Ensure a Precise Population Code

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#### SUMMARY

Neural responses are noisy, and circuit structure can correlate this noise across neurons. Theoretical studies show that noise correlations can have diverse effects on population coding, but these studies rarely explore stimulus dependence of noise correlations. Here, we show that noise correlations in responses of ON-OFF direction-selective retinal ganglion cells are strongly stimulus dependent, and we uncover the circuit mechanisms producing this stimulus dependence. A population model based on these mechanistic studies shows that stimulusdependent noise correlations improve the encoding of motion direction 2-fold compared to independent noise. This work demonstrates a mechanism by which a neural circuit effectively shapes its signal and noise in concert, minimizing corruption of signal by noise. Finally, we generalize our findings beyond direction coding in the retina and show that stimulus-dependent correlations will generally enhance information coding in populations of diversely tuned neurons.

#### **INTRODUCTION**

Basic biophysical considerations mean that sensory signals are inevitably corrupted with noise. Divergence of these noisy signals to multiple downstream neurons will cause those neurons' response to covary. The noise correlations that result from such common circuit mechanisms can have diverse effects on coding, ranging from redundant codes, in which groups of cells encode less information than would be predicted from studying the individual cells they contain, to synergistic codes, in which they encode more (Averbeck et al., 2006; Hu et al., 2014; Schneidman et al., 2003; Shamir, 2014; Zohary et al., 1994; Romo et al., 2003; Jeanne et al., 2013; Wilke and Eurich, 2002; Wu et al., 2004; Shamir and Sompolinsky, 2004). Understanding the impact of noise correlations on coding is essential for understanding the fidelity with which neural circuits can compute and direct behavior.

Observed noise correlations are diverse in magnitude and structure. In cortex, average noise correlations are often positive, small, and depend on similarities between the cells' tuning to different stimuli (Ecker et al., 2014; Gawne and Richmond, 1993; Bair et al., 2001; Reich et al., 2001; Cohen and Kohn, 2011; Ecker et al., 2010; Shamir, 2014). The small amplitude of noise correlations has been attributed to circuits operating in a balanced state, in which correlated fluctuations in excitatory and inhibitory inputs cancel (Renart et al., 2010; Graupner and Reyes, 2013; Hansen et al., 2012). However, the balanced state does not always hold (Hansen et al., 2012; Cafaro and Rieke 2010), and noise correlations can be guite strong. Moreover, noise correlations can depend on neural firing rate (de la Rocha et al., 2007) and on the stimulus presented (Kohn and Smith, 2005; Cohen and Kohn, 2011; Lin et al., 2015). Because of these issues, the extent of correlations between cells and how those correlations are constrained by the synaptic input cells receive is unclear.

Theoretical work provides guidelines for how noise correlations can affect sensory coding: noise that mimics the signals being conveyed by the population will be deleterious to the population code, whereas noise with different statistical structure than the signal is relatively benign. Most theoretical work considers the case where correlations are constant across stimuli and across neural firing rates (e.g., Zohary et al., 1994; Abbott and Dayan, 1999; Dayan and Abbott, 2001; Panzeri et al., 1999; Oram et al., 1998; Shamir and Sompolinsky 2006; Averbeck et al., 2006; Shamir, 2014). Other work suggests that stimulus dependence can alter the impact of correlations on sensory coding (Josić et al., 2009; Wu et al., 2004; Montani et al., 2007). The importance of this issue is highlighted by studies showing that correlations between cells can be strongly modulated by neural firing rates and stimuli (de la Rocha et al., 2007; Binder and Powers 2001; Franke et al., 2016; Lampl et al., 1999; Samonds and Bonds, 2005; Granot-Atedgi et al., 2013; Ponce-Alvarez et al., 2013; Lin et al., 2015; see also Kohn and Smith, 2005). Previous theoretical work, however, did not isolate the impact of stimulus dependence of the correlations in neural populations from other factors such as the diversity of correlation coefficients across the population (Josić et al., 2009; Wu et al., 2004).

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