## Third-Order Edge Statistics Reveal Curvature Dependency

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While neural circuits *in vivo* connect many thousands of different cells, statistical and measurement complexity limit functional data to pairwise interactions. This is especially important in visual cortex, superficial V1, where pairwise edge co-occurances have supported an association field model for long-range horizontal connections (Fig.1(c)). However, how well do such low-order models capture the (higher-order) neural structure? Computationally it is known that such second-order (pairwise) models can account for the mean of the connection distribution, but fail to predict the variance in connections across cells.

We developed a method for estimating a third-order statistic for edge element interactions by conditioning the second-order interaction on a third element. Diffusion maps are used to reveal a global organization of the data, and embedded points that cluster together model the connections.

A significant asymmetry emerges: (i) Excitatory (third-order) connections depend on curvature. This dependence models co-circularity and predicts both the mean and the variance in population statistics of excitatory connections (Fig.1(i)). (ii) Inhibitory connections are more uniformly distributed across orientation and position. Consistent with axonal projections of inhibitory interneurons in V1, there is no dependency on curvature (Fig. 1(g)).

**References** [1] Ben-Shahar, and Zucker, S.W., Geometrical computations explain projection patterns of long-range horizontal connections in visual cortex, *Neural Computation*, 2003, **16**(3), 445 - 476. [2] Coifman, R. et al., Geometric diffusions as a tool for harmonic analysis and structure definition of data: Diffusion Maps, *Proc. Nat. Acad. Sci. (USA)*, 2005, **102**(21), 7426 - 7431. [3] Geisler, et al., Edge co-occurrence in natural images predicts contour grouping performance, Vision Research, 2001, 41(6), 711 - 24.

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Figure 1: Learning excitatory and inhibitory connections between oriented edge filters. (a) Typical black and white image. (b) Thresholded edge responses (color corresponds to orientation). (c) Association field model for interaction: a horizontal edge at the center position is enforced by edges in its neighborhood. All edges have this connection structure and it does not depend on curvature. (d) Co-circular connections for curvature = straight; for small positive curvature (e); and large positive curvature (f). Note the union over these curvature-based connections is the association field (c). (g) Inhibitory connections. Shown is the strength of connection (first eigenfunction) color coded. The (x,y) plane is position; height is orientation. Blue = weak; red = strong. (h) Geometric harmonic embedding of similar edge pairs conditioned on the presence of a strong edge at center location. Clusters indicate connected edge responses. (i) Remapping of clusters from (h) to image coordinates. Note the circular connections (color corresponds to cluster).