Redundant representations in macaque retinal populations are consistent with efficient coding.

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Early investigations of efficient coding with the linear-Gaussian model showed striking similarities to experimental data (Atick & Redlich, 1990; van Hateren, 1992). However, direct comparison with the retinal receptive fields has been hampered by three limitations: (a) Retinal ganglion cells (RGCs) are inhomogeneous, both within and between cell types (e.g., Gauthier et al, 2009), as are their cone inputs, and the input-to-output cell ratio is not 1:1. Most theoretical studies assume homogeneity and a 1:1 cell ratio for analytical tractability (although see Li & Atick (1994), Campa et al (1995), Doi & Lewicki (2007)); (b) RGC receptive fields under photopic conditions should be written in terms of weights on the cone photoreceptors, and these data were obtained only recently (Field et al, 2010); (c) Efficient coding depends on neural resource constraints, and including a cost for synaptic weights significantly alters the solution (Doi et al, 2010a). Together, these advances enable us to conduct a direct comparison, and here we present four results: (1) Retinal receptive fields transmit 74-82% of the information in natural images, relative to the optimal linear-Gaussian solution. By comparison, a weight matrix that produces the same average output power, and has the same average squared weights, but is otherwise random (Wrnd) achieves only 35-38%; (2) Optimal weights mimic retinal weights in generating highly redundant representations of natural images; (3) The optimal weights are non-unique, but the inner-product of projective fields (ipPF) is uniquely constrained (Doi et al, 2010b), and the optimal ipPF provides a good match to the data; (4) Although the optimal weights are non-unique, a solution that achieves the optimum and best fits the data can be found (Doi et al, 2010b). The error of this solution is 36.1%, significantly smaller than the best-fit error for Wrnd: 89.5±3.2%.

We solve for the receptive field weights that maximize information transmission subject to three neural resource constraints measured from the retinal data: i) neural population size, ii) total bandwidth of neural population (power cost), and iii) total squared weights (synaptic cost). We assume a Gaussian input model whose covariance matches natural images, and additive white Gaussian noise in cone photoreceptors and RGCs.

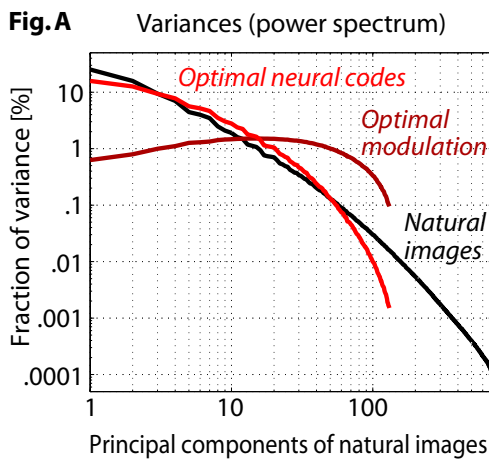**Fig. A** Variances (power spectrum)

Fig. A: Variances of principal components of natural images are highly non-uniform ("Natural images"). The optimal solution modulates ("Optimal modulation") these variances, but the result retains strong non-uniformity ("Optimal neural codes"), and thus significant redundancy. Retinal codes are similarly redundant (data not shown here, because the principal components differ). See (2) in Summary.
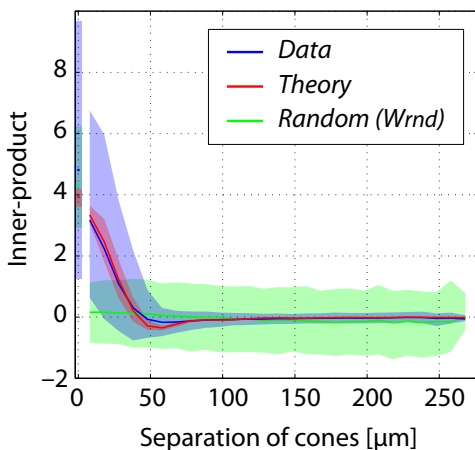
Fig. B: The theory predicts an average ipPF as a function of cone separation that is similar to that computed from the data. ipPF for a random weights matrix Wrnd (that satisfies the same constraints) is quite different. See (3).

Fig. C: Optimal receptive fields (the best-fit solution) are derived *simultaneously* for all four cell types with *natural images*. Contours indicate level curves at 30% of the receptive field peak found in the data. Cone mosaic is shown in the background. We reported similar results in Doi et al (2010b), but that didn't include the synaptic cost. This cost changes the solution significantly, providing a better match to the data. See (4).

Fig. B Average and (5,95)-percentiles of ipPF

Fig. C Comparison of an entire population of receptive fields
(ON/OFF-Parasol: yellow/green, ON/OFF-Midget: red/blue)