Redundant representations in macaque retinal populations are consistent with efficient coding

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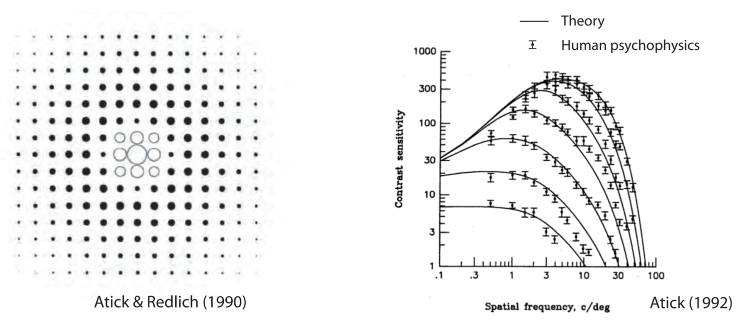
Summary

- Retinal populations transmit ~80% of the information achievable, given population size, total output power, and total synaptic strength.
- Efficient coding accurately predicts the underlying structures of cone projective fields as well as those of retinal ganglion cell (RGC) receptive fields.
- Information conveyed by receptive field outputs is substantially redundant in both RGC and efficient coding populations.

Background

Earlier studies

- Efficient coding: transmitting maximum amount of information subject to neural resource constraints.
- Simplifying assumptions in the earlier studies (Atick & Redlich, 1990; van Hateren, 1992):
  - Neural resource: total output power
  - Transform: convolutional



=> hampering a comparison to physiological data, because in the retina,
- input-to-output cell ratio is not 1:1
- cone photoreceptor mosaic is irregular
- retinal ganglion cell (RGC) receptive fields are inhomogeneous

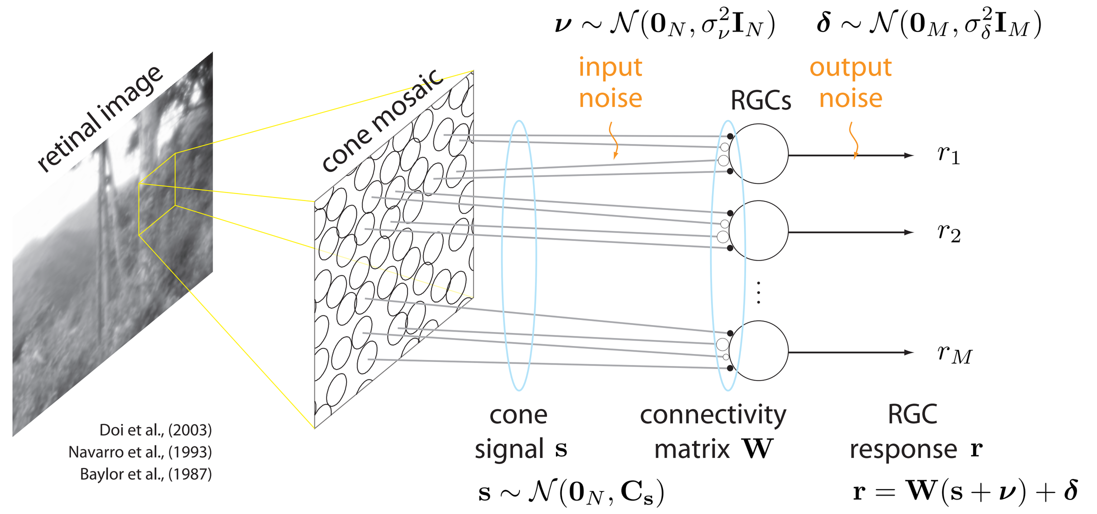
- Relaxing those assumptions (Doi et al., COSYNE 2008; see also Campa et al., 1995):
  - Neural resource: total output power and *neural population size*
  - Transform: *any* linear transform
- A direct comparison to physiological data (Doi et al., COSYNE 2010a):
  - Moderate match
- The solution varies significantly with the neural resource constraints (Doi et al., COSYNE 2010b).

Purpose of this study

- Include additional constraint of *total synaptic strength.*
- Evaluate how much the constraints could solely explain the retinal data.
- Assess the redundancy of information in neural populations.

Methods

Linear Gaussian model of RGC response



Transmitted information

$$I(\mathbf{s};\mathbf{r}) = \frac{1}{2}\log_2 \frac{|\mathbf{W}\mathbf{C_s}\mathbf{W}' + \sigma_\nu^2 \mathbf{W}\mathbf{W}' + \sigma_\delta^2 \mathbf{I}_M|}{|\sigma_\nu^2 \mathbf{W}\mathbf{W}' + \sigma_\delta^2 \mathbf{I}_M|}$$

Retinal parameters
- cell ratio = 706 : 131 (measured)
- cone signal = 0 dB (assumed)
- RGC response = 10 dB (assumed)

Constraints for optimization

$$(\text{number of neurons}) = M$$

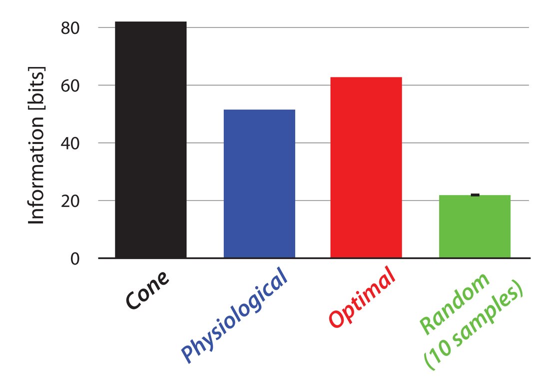
$$(\text{total synaptic strength}) = \sum_{i=1}^{N}\sum_{j=1}^{M} W_{ij}$$

$$(\text{total output power}) = \sum_{i=1}^{M} \mathrm{Var}(r_i) = \mathrm{tr}(\mathbf{W}\mathbf{C_s}\mathbf{W}' + \sigma_\nu^2 \mathbf{W}\mathbf{W}' + \sigma_\delta^2 \mathbf{I}_M)$$

We examine three connectivity matrices.
1. Physiologically measured (Field et al., 2010): $\mathbf{W}_{phy}$
2. Optimal for information transmission subject to all the constraints: $\mathbf{W}_{opt}$
3. Satisfying all the constraints but otherwise random: $\mathbf{W}_{rnd}$

Results

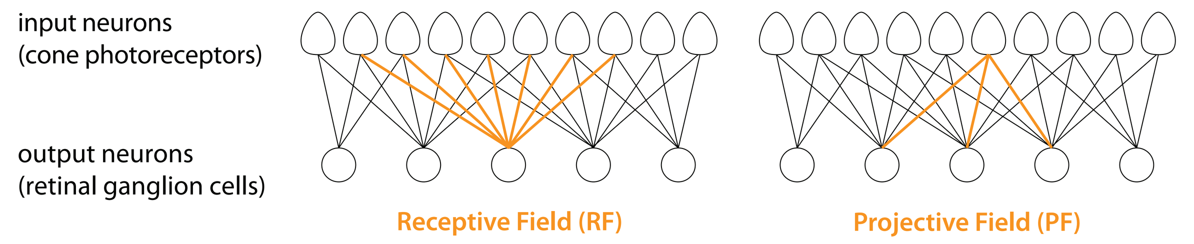
1. Information transmission



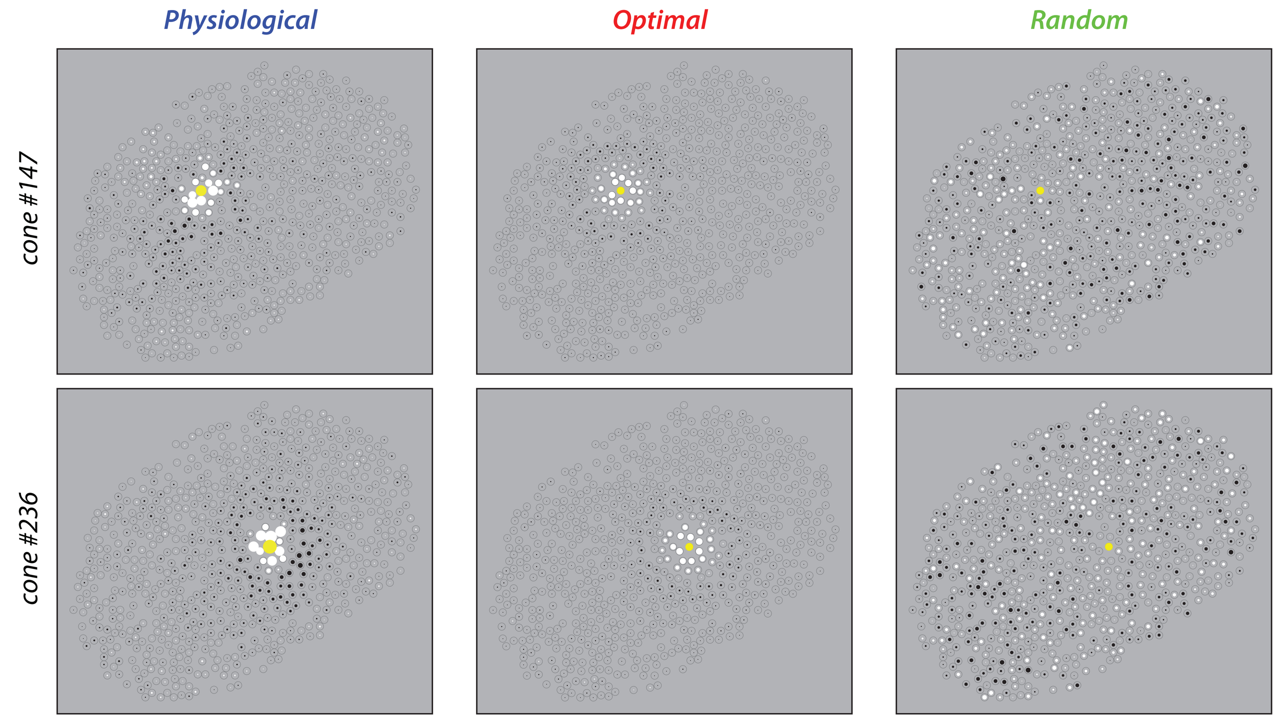
- In spite of the significant reduction of population size from cones to RGCs (~12%), much information is preserved.
- The actual retina ("Physiological") is close to the optimal (~80%).
- ~80% optimality of the retina is observed in three retinal preparations.

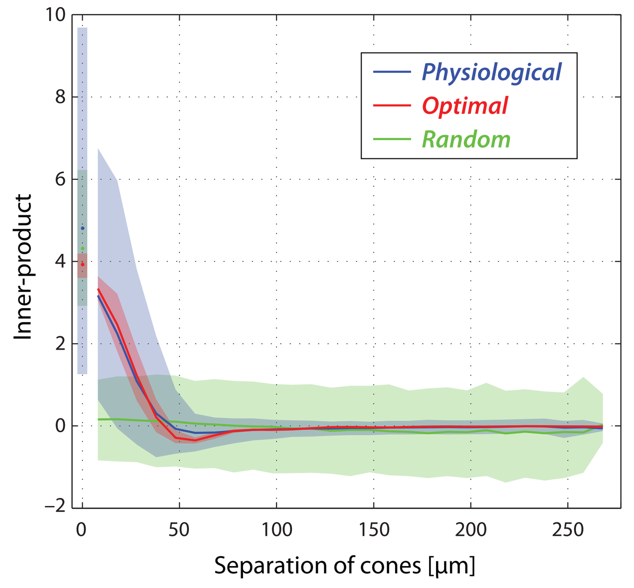
2. Inner-product of projective fields

One can easily observe that W and PW with orthogonal transform P is equivalent in terms of information transmission and neural resources. It implies that there is a continuous (infinite) family of equally optimal W. *How can we compare this to physiologically measured, single connectivity matrix?* The product W'P'PW = W'W is invariant with P, and hence provides a unique prediction. Individual elements of W'W are inner-products of projective fields (Doi et al., COSYNE 2010a).



Examples of inner-products of PFs for reference cones (yellow)



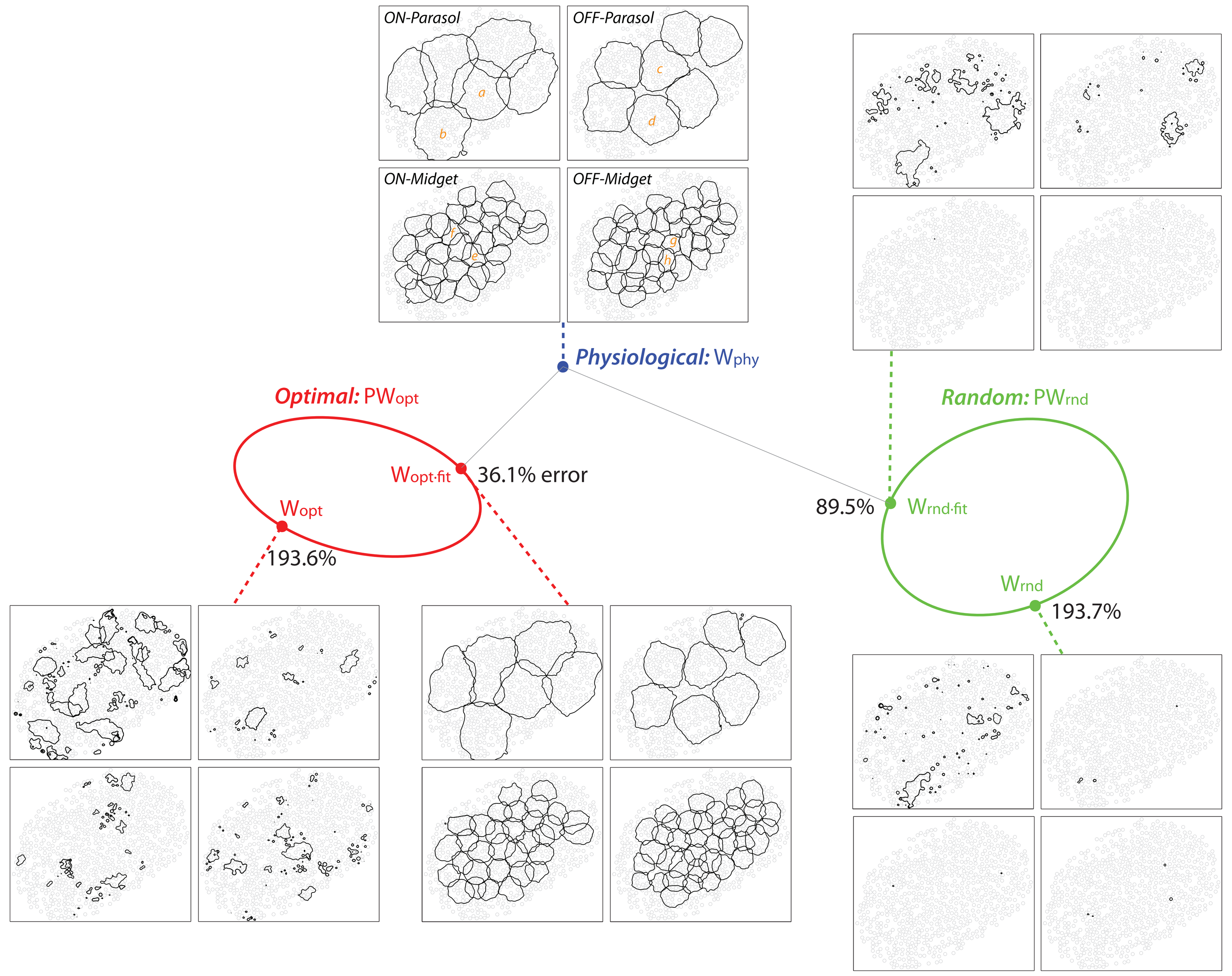


- Inner-products of physiological PFs are well matched to those of the optimal PFs:
  - strongly positive values for nearby cones
  - moderately negative values for surrounding cones
  - near-zero values for more distant cones
- Random PFs are very different.

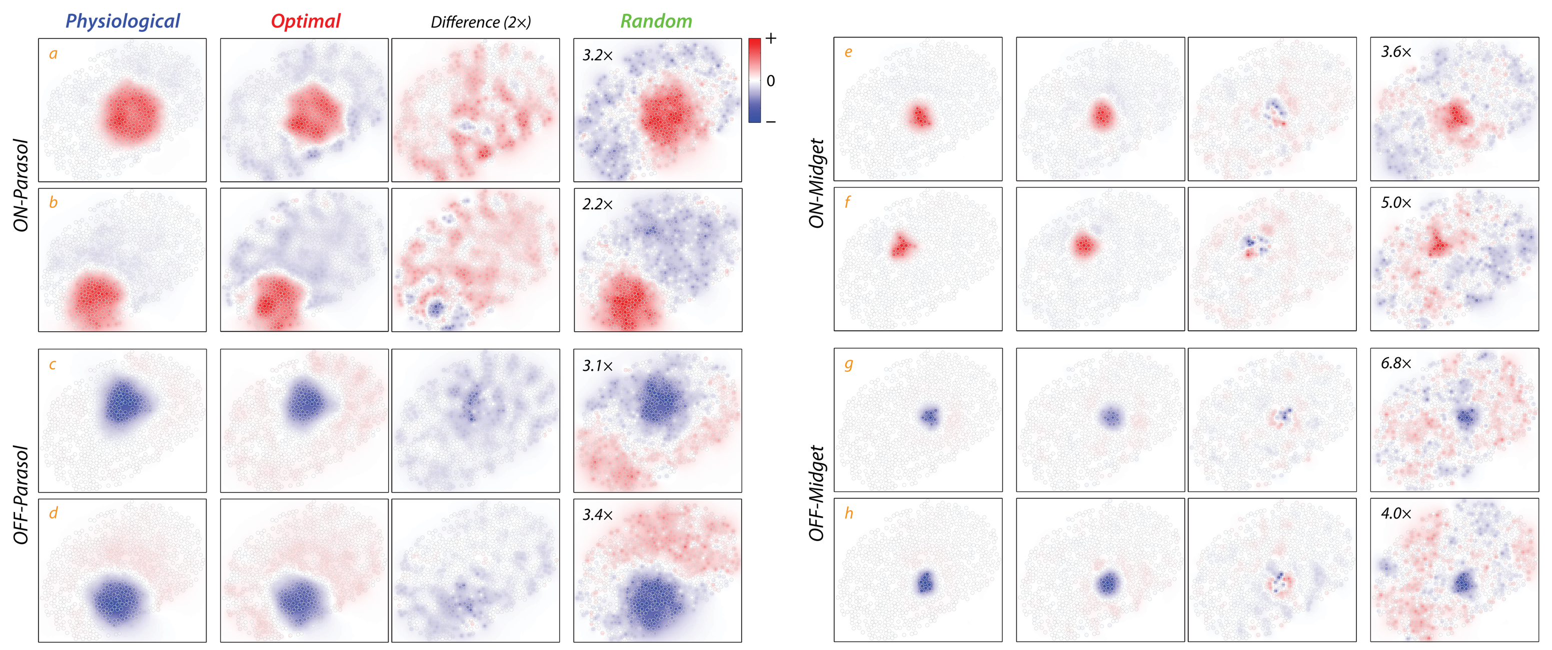
This distance dependence can be summarized for all cones by plotting the inner-product as a function of cone separation (left plot).

3. Best-fitting receptive field population

To compare W in a more conventional manner with receptive fields, we sought P so that PW fits best to the physiological W. This quantifies how the family PW could possibly be close to the physiological W.



Detailed comparison of physiological, best-fitting optimal, and best-fitting random receptive fields (RFs).



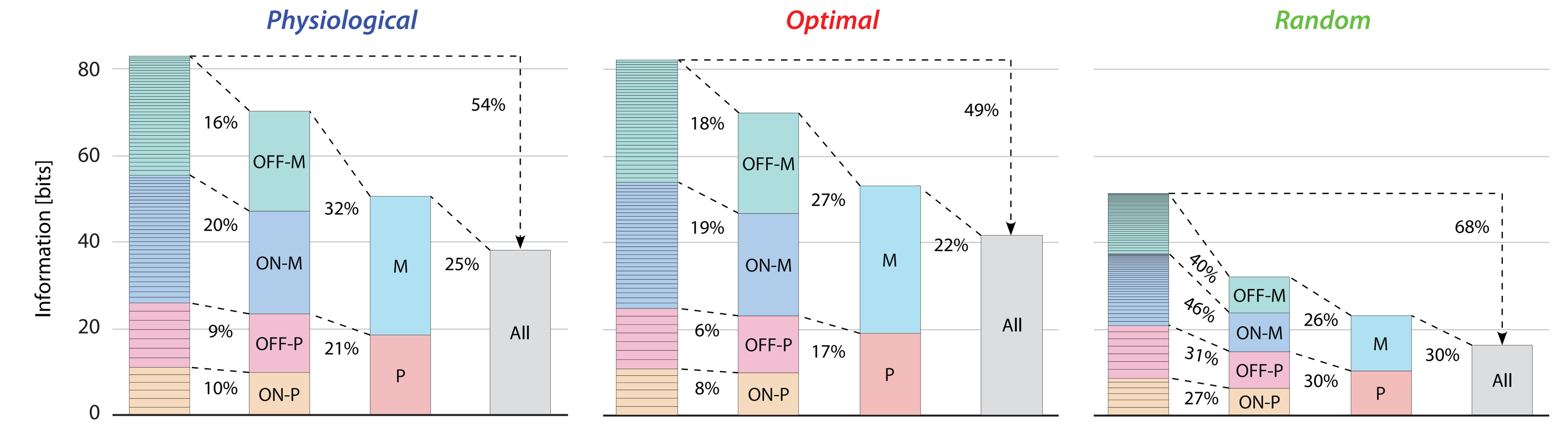
- The best-fitting optimal RFs are very similar to the corresponding physiological RFs in their amplitudes and shapes, but with a slightly stronger surround.
- The best-fitting random RFs are very different from corresponding physiological RFs in their amplitudes, and here they are individually scaled by matching the peak values to those of physiological RFs, just for visibility (scaling factors indicated). Note that the scaled RFs violate the power and the synaptic constraints by the factor of square of scaling factor, and they should not be considered as a legitimate solution.
- A best-fitting random RF exhibits, in addition to the obvious difference of the amplitude, much stronger surround; furthermore, in Midget cells, there are various structures in the surround that are absent in the physiological RFs.

4. Redundancy of information in neural populations

How redundant are the neural (RGC) representations, and how are they compared with the most efficient representations?
- We are interested in the informational overlap in the neural population, and hence define the redundancy as (Brenner et al. 2000; Machens et al. 2001; Schneidman et al. 2003):

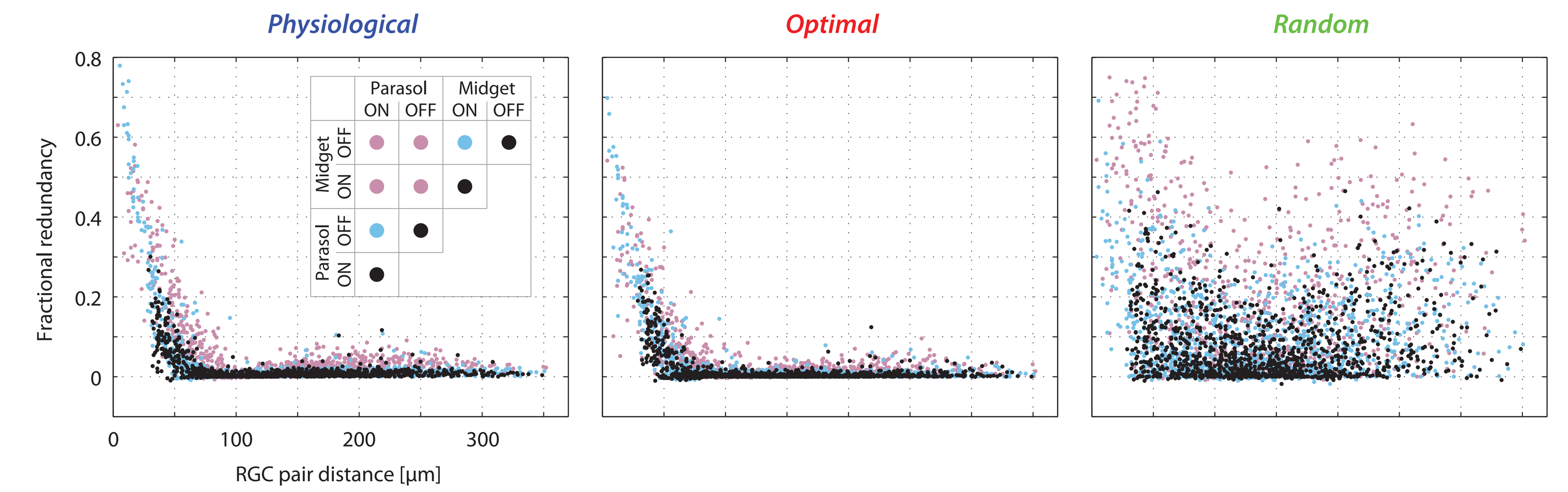
$$\Delta I_{red}(\{r_1, \cdots, r_M\}, \mathbf{r}) = \sum_{i=1}^{M} I(r_i;\mathbf{s}) - I(\mathbf{r};\mathbf{s})$$

- Note: the word "redundancy" is also used to be referred to as "inefficiency", as pointed out in Latham & Nirenberg (2005).



- In physiological case, the redundancy is 54%. The redundancy in the initial cone photoreceptor representation is 77%. The redundancies are significantly reduced in the successive stages in the retina, in accordance with the findings in the auditory system (Chechik et al. 2006).
- This high degree of redundancy is *also* the case for the most efficient, optimal case: 49%. Random case exhibits even higher redundancy.
- It is reasonable to believe that a good portion of this redundancy is caused by our simplifying model assumptions:
  - Compared to a more realistic model with a rectifying nonlinearity, ON and OFF cells within Parasol (or Midget) may be seen to have duplicated representations.
  - Parasol and Midget cells are known to have different temporal, as well as spatial, response properties. Our simplified model assumes instantaneous neural response and hence ignores differences in temporal properties.

Distance dependence of redundancy is found, in accordance with Puchalla et al. (2005).



Appendix: Insensitivity to SNR assumption

We do not have a good estimate of input (cone) and output (RGC) SNRs in the retina, under the linear Gaussian model. We found that our results are robust with SNR assumptions, and hence, our specific selection of SNRs is not crucial for our conclusion.

Transmitted information under ±10 dB SNRs of the default condition (top). The optimality is its ratio to the optimal amount of transmitted information (bottom). Information transmission via physiological connectivity is consistently around 80% relative to the optimal, while random connectivity is always around 40%.