One of the primary goals in neuroscience is to figure out simple principles that explain how nervous systems are organized. One of the most successful theories in this vein states that sensory systems should remove redundancies in their inputs to optimize the information they process5. This *efficient coding hypothesis* provides us with a mathematical framework to understand how neurons *should* encode information, which can then be experimentally tested against how neurons *actually* do so. Over the past 60 years, efficient coding has successfully explained many experimental findings in different sensory modalities such as vision4, 8, 13, 18, 19, 24, audition15 and touch17. This hypothesis has been especially successful in the retina, where it can explain many features of retinal encoding such as center-surround receptive fields and ON-OFF pathways2-4, 8, 13. However, we are still lacking efficient coding predictions for how the retina processes complex features of the visual world such as color and motion. My work will tackle this problem and replicate how the retina integrates redundant inputs across different color channels (Aim 1) and across time (Aim 2). These results will allow us to understand how much of retinal physiology can be explained by efficient coding principles.

Retinal processing of visual information follows a well-known structure7, 12: First, photoreceptors transform light from the outside world into electrical activity. They then send this information to bipolar cells, and bipolar cells send this information to retinal ganglion cells (RGCs). These RGCs are the visual inputs to the cortex and send projections to the thalamus through the optic nerve. A lot of work has characterized how these RGCs respond to visual stimuli7, 9, 14. RGCs are separated into two different pathways (ON and OFF), and each neuron within a pathway processes a small region of visual space - its receptive field. Within a pathway, neurons have receptive fields that cover distinct regions of visual space to form a ‘mosaic’ that tiles the entire retina. RGCs in the ON and OFF pathways respond most strongly to small light and dark spots, respectively. This is because their receptive fields have a center-surround organization: ON RGCs encode light in the center and dark in the surround, and vice-versa for OFF RGCs.

Early theoretical work has explained how this center-surround organization arises from efficient coding principles, both for achromatic and for color inputs2, 3. This early work made many simplifying assumptions, such as an infinite number of neurons and linear output responses (i.e. negative firing rates). While these assumptions help make the problem mathematically tractable, such models are too simple to explain the details of retinal physiology. More recent work has leveraged machine learning to make efficient coding models with more biologically realistic constraints, such as non-linear output responses and a limited number of neurons10, 11, 13. These new models explain why RGCs are separated into different subtypes, with neurons within a subtype forming a mosaic. However, the inputs to RGCs are much more complex than static achromatic images – RGCs receive input images from multiple color channels, and visual scenes are usually in motion. While efficient coding can predict how the retina should process achromatic stimuli, its predictions for color and motion processing – two crucial aspects of natural stimuli – involve strong mathematical constraints which are difficult to relate to retinal physiology1, 10, 21. To close this gap, I will use more general efficient coding models to explain how RGCs process color information (Aim 1) and motion (Aim 2). I will take advantage of the established collaboration between my supervisor and Dr. Greg Field from UCLA in studying how efficient coding models relate to experimental data10, 11. This collaboration also opens the possibility to test the predictions of our model against new experimental data.

**Aim 1:** Expand efficient coding models to encompass chromatic information

Color is a crucial aspect of how we perceive the visual world. Encoding colors starts at the level of cone photoreceptors in the fovea of the retina, which come in three types (Long (L), Medium (M), and Short (S), roughly encoding red, green and blue stimuli, respectively)6. This color information is ultimately encoded by RGCs, with different types integrating cone inputs differently. Most of RGCs (~90% in the fovea and ~ 45% in the periphery) are midget cells7, which mostly encode a combination of L and M cones. In the fovea, these cells are ‘red-green opponent’ and encode a contrast between L and M inputs6, 7. In the periphery, these midget cells are not red-green opponent but instead sum L and M cones inputs7, 16. Why midget cells use different coding strategies for the fovea and for the periphery is still unclear. We hypothesize those different strategies have to do with the ratio between RGCs and cones in the fovea versus the periphery. While the periphery has more cones than RGCs, the opposite is true for the primate fovea, with approximately 3 RGCs for every cone26. Here we will test that hypothesis by building an efficient coding model for chromatic natural images (Figure 1). The inputs to this model will be the LMS cone responses to a series of natural images. We will then filter these responses through three different spatial filters (one for each cone), which are summed and then followed with an output non-linearity. The weights of the filter will be fit to optimize the mutual information between the cone inputs and the RGC outputs. Consistent with efficient coding principles, there will be a constraint on the total firing rate across all neurons2, 10, 11, 13. To model the center versus the periphery, we will change the number of outputs RGCs relative to the number of input cones. Preliminary results suggest that if we keep the RGCs-cone ratio to 1:1, efficient coding predicts that L and M inputs should be summed. We will next test if we can replicate chromatic receptive fields in the fovea by building efficient coding models with a 3:1 RGCs-cones ratio. We will also test whether we can replicate receptive fields of RGC types other than midget cells, such as parasol and bistratified cells. Completion of this aim will allow us to assess whether efficient coding can accurately explain how the retina encodes chromatic information.

**Aim 2:** Expand efficient coding models to explain why some RGCs are motion-selective

Visual scenes are typically in motion, either because of objects moving or optic flow from our own movements. The primary visual cortex has historically been thought to be where direction selectivity begins, with some neurons having stronger responses to one direction of motion (e.g. left to right) compared to its polar opposite (e.g. right to left)22, 23. However, it is now known that direction selectivity occurs as early as the retina, with several subtypes of retinal ganglion cells (RGCs) being direction-selective20, 25. However, it is not known whether or how efficient coding principles can explain this finding. My lab previously studied efficient coding in spatiotemporal receptive fields10, but this study made strong assumptions (independently processed spatial and temporal information) that preclude encoding visual motion. To test whether we can explain motion-selectivity in RGCs from efficient coding principles, I will build an efficient coding model that estimates receptive fields in which space and time are processed together. This model will be conceptually similar to the one from Aim 1, where the inputs to model RGCs come from multiple channels, each of which representing a different latency. Completion of this aim will solve efficient coding for motion in natural images, which we will be able to compare to experimental data from both the literature and from our collaboration with Greg Field at UCLA.

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