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Origins and objectives of computational diversity in sensory populations

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ABSTRACT

Populations of sensory neurons are not homogeneous. Even neighboring neurons located in the same brain area can process identical stimuli in significantly different ways. Retinal ganglion cells (RGCs) are a prominent example of such heterogeneity — they exhibit diverse properties whose computational role and purpose remain mysterious. In this review, we explore normative theories of neural computation that attempt to explain the origins and role of functional variability in the retina. We first express a general mathematical formulation of normative theories of neural computation and identify components of these theories that can explain the heterogeneity of sensory populations. We then organize existing theoretical studies of retinal coding according to the factors they highlight as explanations of the computational diversity in the retina — the beginning of the visual hierarchy.

1. Introduction

Natural intuition may suggest that, in order to accurately register signals such as images or videos, one may just need to distribute identical sensing units at a desired resolution across the area of an image. Engineered systems are often designed in such a manner; for example, standard digital cameras register images using an array of identical light sensors that uniformly tile the field of view (Ohta, 2020). This design principle aligns with early views on the function of sensory systems when it has been assumed that neurons can be approximated as nearly-identical signal processing devices (e.g. McCullogh & Pitts, 1943). The remarkable capabilities of the brain are, in this view, an emerging property of an intricate network of connections that links approximately identical computational units (Rumelhart et al., 1986).

As has often been the case, this simplified theoretical perspective was challenged by rich and counterintuitive experimental findings. It is now well established that sensory neurons can strongly differ among themselves, even when they belong to the same population and process identical sensory input. This diversity is apparent not only at the higher levels of sensory hierarchies but begins already at the sensory epithelium where the nervous system first registers signals coming in from the external environment. This variability seems to be universal and does not depend on the sensory modality. Neurons that exhibit different functional properties can be found in visual (Vlasits, Euler, & Franke, 2019), auditory (Rhode & Greenberg, 1992), and olfactory (Fleischer, Breer, & Strotmann, 2009) systems, suggesting that the inhomogeneity of sensory populations could be a universal design principle of neural coding.

Retinal ganglion cells (RGCs) are a particularly prominent example of a diverse sensory population that has been extensively studied (Vlasits et al., 2019). Certain properties of RGCs seem to cluster them into distinct groups. For example, it has been suggested that RGCs can be classified into approximately thirty different functional types (Baden et al., 2016) depending on their responses to test stimuli. Other RGC features, such as the shape of the spatial receptive field, vary continuously and cannot be easily discretized (Gupta et al., 2023). Regardless of whether RGCs belong to isolated groups or span continua of encoding properties, their inhomogeneity seems crucial to the organism. The RGC outputs are conveyed further into the brain along the visual hierarchy, ultimately supporting the behavior.

The variability in RGC populations presents a challenge to our desire to understand the nervous system from simple theoretical principles. In order to account for this diversity, sensory coding theories have been developing along with experimental studies. Here, we take a unified mathematical perspective that enables the classification of different sources of diversity in sensory populations. We then review the theoretical literature in an attempt to distill key factors that can contribute to the variability of RGCs and the computational diversity of the retina.

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2. Normative theories of computational diversity in neural populations

In order to gain a quantitative understanding of different functions implemented by a biological system, one needs to solve a hard inverse problem: inferring the evolutionary selection pressures that acted on the studied system, while having access only to its current state. Normative theories of biological function are a class of methods that attempt to solve difficult problems of this kind in a sequence of steps. First, a normative theory postulates what may be the hypothetical objective of the analyzed system. Second, it identifies the parameters relevant for this objective. Third, it derives "ab initio", via mathematical analysis or numerical optimization, parameter values that generate good (sometimes even optimal) performance. In a final step of the analysis, the real parameters of the system studied are compared to the theoretical predictions. If a close match is found, this can be taken as evidence that the evolution and development have guided the analyzed system to implement the postulated objective and achieve a good performance.

To characterize each of the steps described above mathematically, let us consider the example of an individual RGC. Here, the aim of the normative analysis is to understand the computation performed by the neuron when mapping stimuli s (e.g. natural images) on responses r (e.g. firing rates). Each neuron can be characterized by a vector of parameters θ_n. These parameters may determine the spatial receptive field, the nonlinear response function, or other properties, depending on the focus of the analysis. We note that θ_n is, in principle, a vector of multiple parameters; however, for simplicity, we use the vector notation $\vec{\theta}$ only to describe the parameters of a neural population. The crucial component of a normative theory is the utility function $U(\theta_n; r, s)$ that specifies the putative objective of the neuron. Frequently, the utility function incorporates a constraint term that expresses limitations of resources or energy faced by the sensory system. In such a scenario, the utility function can take the form $U(\theta; r, s) = U_{obj}(\theta; r, s) - \lambda C(\theta; r, s)$, where U_{obj} is the utility related only to the computational objective, the function C determines the type of the constraint and the parameter λ its strength.

Because the utility function embodies a hypothesis about the function of the studied system, its choice and design are critical. Historically, two broad conceptual approaches for generating hypotheses about the computational objectives of sensory neurons and related utility functions have developed (Turner, Sanchez Giraldo, Schwartz, & Rieke, 2019). The first approach focuses on encoding stimulus features that support specific behavioral goals, such as the detection of prey (Lettvin, Maturana, McCulloch, & Pitts, 2007). The second approach accentuates the importance of more general objectives of neural computation, such as the amount of information that neurons convey about stimuli (Barlow et al., 1961). Both approaches are closely related and can generate utility functions for parameters of sensory systems. The higher value of utility implies a better performance of the neuron.

The final component of our setting is the joint distribution of stimuli and responses $p(s, r)$. This distribution fully characterizes the statistics of stimuli processed by the neuron in the natural environment as well as the input and output noise. Example factors that shape the stimulus distribution can include the level of contrast in the animal's surrounding or the position of the receptive field within the visual field. Noise statistics can, in one example, depend on the strength of the stimulus (e.g. the light level) relative to the strength of the noise intrinsic to the biophysical properties of the neuron.

The resulting general form of normative analyses of neural systems can be therefore summarized in a compact, mathematical form:

$$\theta_n^* = \arg\max_{\theta_n} \left\langle U(\theta; r, s) \right\rangle_{p(r,s)} \tag{1}$$

where θ_n^* is the normative prediction (e.g. optimal receptive field) that maximizes the utility function (e.g. information transmitted in bits) averaged across all possible stimulus response pairs.

Differences between neurons in a sensory population such as the RGCs can be explained by changes in different components of the normative framework in Eq. (1): objectives represented by different utility functions U (Fig. 1a, left), stimulus and noise statistics $p(r, s)$ (Fig. 1a, middle) or collective optimization of a population of cells described by parameters $\vec{\theta}$ to solve the same task (Fig. 1a, right). In the following sections, we review normative studies of sensory coding in the retina and classify them according to which of the components of the normative framework they rely on to explain a diversity of retinal neurons.

3. Diverse objectives of sensory coding

Perhaps the most intuitive explanation of the neural heterogeneity in the retina is that different cells encode different features of the stimulus. In the normative view, these encoded stimulus characteristics determine the utility functions U_n of each neuron (we index individual neurons with n). If neurons within the population encode different stimulus features, the optimal parameters θ_n will also vary from cell to cell, even if stimulus statistics and noise levels remain fixed (Fig. 1b, top row, left and middle panels).

This view goes back to early research on retinal coding, when it was suggested that neurons in the frog's retina detect stimulus features of immediate behavioral relevance such as the position of insects in the field of view (Lettvin et al., 2007). This early intuition is apparently supported by more recent findings that identified numerous functional RGC types (Baden et al., 2016; Koch et al., 2004). Each of these types could, in principle, correspond to a different behaviorally relevant feature that is extracted from the image and sent for further processing. In one example, a recently discovered RGC type encodes transitions from green-dominated to UV-dominated visual contexts, which may be elicited by head movements from ground to sky (Höfling et al., 2024).

The view that RGCs encode stimulus features of immediate behavioral relevance can be contrasted with a more "generalist" view of retinal coding — the efficient coding theory (Barlow et al., 1961). In its basic form, the theory postulates that sensory neurons maximize the sheer amount of stimulus information transmitted, subject to metabolic constraints. These two views can be easily reconciled by observing that in order to encode and transmit any behaviorally relevant stimulus feature, a minimal number of specific bits must be encoded (Bialek, Van Steveninck, & Tishby, 2006). For example, to predict future states of the environment that may be important to the organism, the retina should extract only the most predictive bits of the stimulus. In fact, RGCs have been shown to efficiently encode predictive information about features of simple experimental stimuli, such as moving bars (Palmer, Marre, Berry, & Bialek, 2015). In natural environments, this computation would require adaptation to specific features of sensory signals (Salisbury & Palmer, 2016). A coding objective conceptually related to predictive information maximization is encoding surprise, i.e. how much does any given stimulus violate an expected temporal regularity. A particularly strong form of surprise coding is known as the omitted stimulus response, where the cell spikes when the stimulus did not occur but was expected given prior experience (Schwartz, Harris, Shrom, & Berry, 2007). RGCs exhibit a diversity of surprise-related responses, and it has recently been suggested that this diversity may be due to differences in prior expectations of the stimulus sequences that each cell represents (Despotović, Joffrois, Marre, & Chalk, 2024). In general, efficient coding, coding predictive information and related objectives can be coherently expressed as a rich family of utility functions for neural computations (Chalk, Marre, & Tkačik, 2018). It remains to be understood whether the variability of the RGCs could be explained by differences in the predictive computations they perform.

Stimuli processed by the retina are not stationary; they originate from dynamically changing natural environments. To perform any encoding task efficiently, regardless of what stimulus features are encoded, neurons must adapt to such changes (Laughlin, 1989). Interestingly, adaptation dynamics reveal another type of diversity in the

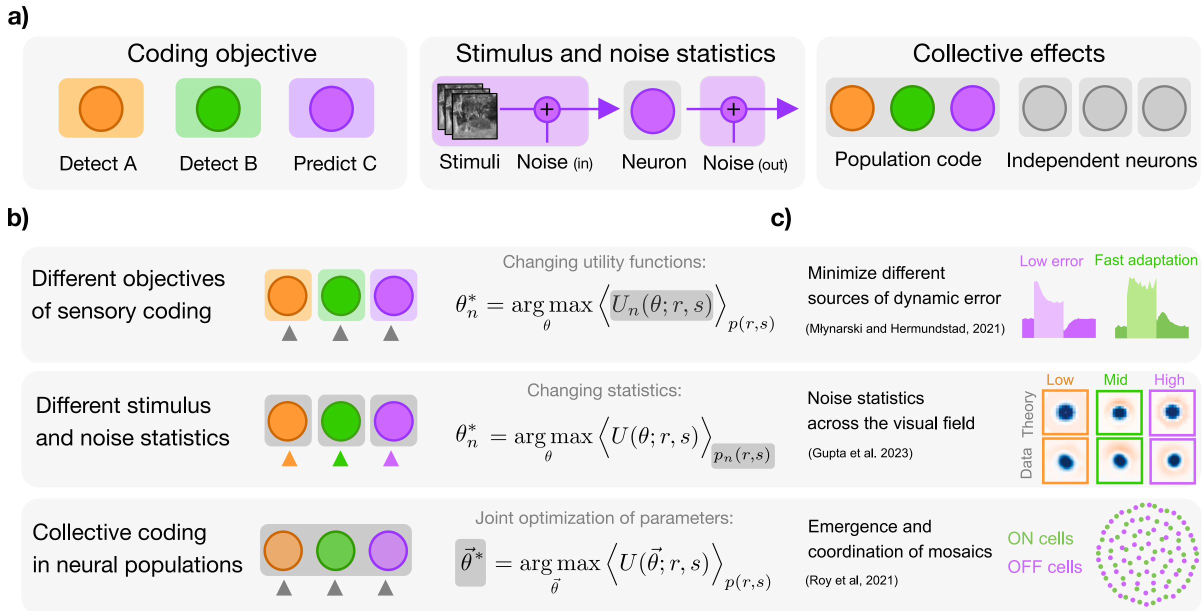

Fig. 1. Theories of functional diversity in sensory populations (a) Three proposed sources of diversity in sensory populations. Left: Individual cells (circles) can belong to different functional types (circle colors) due to differences in coding objectives (denoted by color of rectangles surrounding each cell). Middle: statistics of stimuli and input and output noise (summarized by the color of the triangular arrows) can lead to differentiation of cells that implement the same objective. Right: A population of cells (left; circles belonging to the same population are drawn within the same gray rectangle) that is collectively optimized to encode stimuli can differentiate cell types in scenarios where independent neurons could be identical (right; independently optimized cells are within separate gray rectangles). **(b)** Sources of cell-type diversity and mathematical formulation of optimization objectives. Top: cell types that implement different computations on identical inputs (left) are defined by objective specific utility functions (right, utility function U_n marked with dark gray). Middle: cells with the same objective but different stimulus and noise statistics (left) are optimized to maximize the same utility U but averaged across cell-specific distribution of stimuli and responses $p_n(s, r)$ (right, dark gray). Bottom: populations of neurons are collectively optimized to encode the same ensemble of stimuli (left). This corresponds to joint optimization of a vector of parameters $\vec{\theta}$ (right, dark gray). **(c)** Examples of studies where different sources of computational diversity in the retina where reported. Top: variance (contrast) adaptation responses of simulated neurons that maximize adaptation speed or minimize encoding error (Młynarski & Hermundstad, 2021) reproduce adaptive and sensitizing response dynamics of retinal ganglion cells (Kastner & Baccus, 2011). Middle: shapes of receptive fields of retinal RGCs adapt to the change of signal-to-noise ratio across the visual field (Gupta et al., 2023). Bottom: joint optimization of a neural population predicts emergence and coordinated anti-alignment of mosaics of on and off RGCs (Roy, Jun, Davis, Pearson, & Field, 2021).

retina. Depending on the trajectory of their firing after a change in stimulus contrast, RGCs can be classified as "adapting" or "sensitizing" (Kastner & Baccus, 2011, 2013). Responses to a change in luminance also reveal a rich phenomenology that may be context-dependent (Tikidji-Hamburyan et al., 2015). Importantly, these variable responses are often triggered by identical stimuli, suggesting that neurons may implement different computations. From the computational perspective, adaptation itself posits a nontrivial problem, where cells need to differentiate changes in the stimulus caused by their stochasticity from shifts in the underlying distribution (DeWeese & Zador, 1998). Recent theoretical work has suggested that, in a general case, cells can minimize the error of encoding individual stimuli or detect changes in the underlying distribution (Młynarski & Hermundstad, 2021). These often mutually exclusive objectives can be satisfied to a different degree giving rise to a continuum of utility functions for neural computation in dynamic environments. Model neurons that optimize different utilities along this continuum reproduce adaptive phenomena observed in the retina, such as sensitization or adaptation (Młynarski & Hermundstad, 2021) (Fig. 1c, top). These results suggest that at least some of the RGC diversity can be understood as a solution to navigate the trade-offs between competing sources of encoding error that arise in dynamic, natural environments.

4. Diversity of stimulus and noise statistics

Regardless of which stimulus features are encoded by retinal populations, to do so efficiently, neurons need to adapt to the statistics of signals they process (Atick & Redlich, 1992; van Hateren, 1992). At the same time, to transmit information reliably, they need to correct for the input noise that distorts the incoming signals and the output noise that corrupts messages conveyed downstream. The statistical relationship between stimulus and noise is specified by the joint distribution $p(r, s)$ (Fig. 1a, middle panel). Within the normative perspective, this distribution determines the optimal solution θ^* to any encoding objective specified by a utility function U. An important implication for neuronal diversity is that even cells that implement exactly the same computation (e.g. detect the same stimulus feature) can exhibit different properties, if the statistics of their inputs and noise vary (Fig. 1b, middle panel).

The relevance of these theoretical principles for retinal coding has been highlighted multiple times. A now-classical study demonstrated that center–surround receptive fields can instantiate predictive coding, a form of increasing coding efficiency. Predictive coding reduces the dynamic range of the input signal by removing spatially redundant bits of the stimulus and encoding only the spatial change in luminance computed as the difference between the center and surround components of the receptive field (Srinivasan, Laughlin, & Dubs, 1982). Center surround-receptive fields have also been derived from related principles of sensory coding such as redundancy reduction (Atick & Redlich, 1990) and whitening (Bell & Sejnowski, 1997).

This theoretically optimal shape of the spatial receptive fields is a well-known source of diversity in the retina that separates RGCs into two distinct classes. The so-called "on" cells respond to local increases in light intensity, while "off" cells encode a decrease in brightness (Hartline, 1938; Kuffler, 1953). Interestingly, the number of off cells typically exceeds the number of on cells and this asymmetry has been suggested to be a consequence of the "excess of darkness" in natural scenes, where local contrast is more likely to decrease rather than increase (Ratliff, Borghuis, Kao, Sterling, & Balasubramanian, 2010).

According to the spatial predictive coding model, optimal receptive fields are determined by the spatial autocorrelation function, which measures how correlated are activities of neighboring photoreceptors, and the strength of the input noise. These two factors have a similar impact on the shape of the optimal receptive field. When the processed images are smooth and the autocorrelation is long — surrounds of the optimal RGC receptive fields become broad and diffuse to exploit this redundancy. If photoreceptor noise dominates the signal, which is often the case in low-light conditions, the surround also needs to expand spatially to "average out" this variability and to better estimate the underlying image.

Although these theoretical predictions were known for a long time, it was unclear whether the RGCs exploit subtle changes in signal autocorrelation or noise to increase coding efficiency. Such adaptation could happen in time, when the receptive field of a single neuron changes shape in response to e.g. increased noise strength, or in space, where receptive fields vary across the retina driven by spatial inhomogeneities in the statistics of the natural visual field (Abballe & Asari, 2022; Qiu et al., 2021). A recent experimental study was able to simultaneously record activity of thousands of RGCs covering significant fraction of the retinal surface (Gupta et al., 2023). This large-scale recording revealed variation of RGC receptive fields across the visual field. In close agreement with the predictive coding model, receptive fields processing inputs from the bottom of the visual field where the light intensity is low and the RGC input is dominated by noise, had diffuse and shallow surrounds. In contrast, neurons processing input from the upper visual field, where the relative noise strength is much weaker, had sharp, well-defined surrounds (Fig. 1c, middle). Receptive fields varied continuously from upper to lower visual field following a smooth gradient of change with a rapid transition a the horizon line. These results indicate that retinal populations exploit even subtle fluctuations of stimulus and noise statistics giving rise to continuous variability of their functional properties.

5. Diversity as a consequence of collective effects

The theories described above either consider sensory neurons individually or approximate neural populations as collections of independent signal processing units. Although this may be a useful approximation, retinal neurons are not independent; they form networks and encode natural stimuli together. Population coding can be easily expressed within the general normative framework. Instead of optimizing the parameters θ_n of each neuron one by one, one can simultaneously optimize a set of parameters $\vec{\theta}$ that describe an entire population. In such jointly optimized populations, individual cells can complement each other and devote their capacity to encode stimulus features not encoded by their neighbors. Due to such "division of labor" neural heterogeneity can arise even if all neurons share a common computational objective and process stimuli with identical statistics (Fig. 1a, right panel).

Perhaps the simplest form of coordination between RGCs is their spatial arrangement. Too densely placed neurons would sample the visual field in a redundant and inefficient way, while neurons that are far apart from each other could omit relevant parts of the scene. The spacing of the RGC receptive fields appears to match the autocorrelation structure of natural scenes and is optimized to tile the field of view in a way that maximizes the amount of information transmitted (Borghuis, Ratliff, Smith, Sterling, & Balasubramanian, 2008). Collective optimization can also explain the benefits of the separation of RGCs into on- and off-channels. Pairs of simple units that respond to increases ("on") and decreases ("off") of one-dimensional stimuli can transmit the same amount of bits as pairs of units of the same type, but at a lower metabolic cost (Gjorgjieva, Sompolinsky, & Meister, 2014). This principle also generalizes to larger populations of units (Gjorgjieva, Meister, & Sompolinsky, 2019). Going beyond one-dimensional stimuli, an elegant model of population coding demonstrated that on- and off-center receptive fields emerge from statistics of natural images (Karklin & Simoncelli, 2011). These optimal receptive fields tile the image area in a way closely resembling the RGC mosaics. The same efficient population coding model (Karklin & Simoncelli, 2011) reveals surprising emergent properties that are consistent with the intricate architectural characteristics of the RGC populations. Retinal mosaics of on-center and off-center RGCs are anti-aligned to minimize spatial overlap between cells across types (Roy et al., 2021). This property emerges as an optimal solution to information transmission about natural images in certain input and output noise regimes (Jun, Field, & Pearson, 2021; Roy et al., 2021) (Fig. 1c, bottom). In addition to efficiently transmitting natural stimuli, anti-alignment of retinal mosaics can support tasks such as the formation of functional maps in the primary visual cortex (Jang & Paik, 2017). A recent extension of the noisy population model has found that increasing the size of the neural population that encodes natural videos leads to the emergence of novel cell types with distinct temporal and spatial receptive field features (Jun, Field, & Pearson, 2022). A similar result has been obtained using simpler naturalistic pink-noise stimuli (Ocko, Lindsey, Ganguli, & Deny, 2018). These intriguing results suggest that perhaps the diversity of retinal cell types serves the purpose of maximizing information transmission and encoding as many bits of information as permitted by metabolic and anatomical constraints.

A possible source of diversity in neuronal populations originates from changes in metabolic and anatomical constraints and their strength in different parts of the brain. For example, the receptive fields of sensory neurons can be influenced by the activity and connectivity limitations faced by the population. Depending on the type of constraint, such as the sparsity of neuronal connections or spatial locality, receptive fields optimized to accurately encode natural images can take different forms — from Gabor filters reminiscent of the primary visual cortex to features similar to the center surrounding the retina (Doi & Lewicki, 2014). In the primate retina, the receptive field structure is consistent with an information-maximizing neuronal population that is subject to spatial locality constraints and pools inputs from neighboring photoreceptors (Doi et al., 2012).

When considering populations of sensory neurons, one should separate two types of population effects: joint optimization and collective behavior. In the first case, neurons are optimized together, but then they act independently without communicating between themselves. In the second case, neurons actively interact and exchange information when encoding stimuli. Neuronal populations have been shown to act collectively (Ganmor, Segev, & Schneidman, 2015; Schneidman, Berry, Segev, & Bialek, 2006; Tkačik, Marre, Amodei, Schneidman, Bialek, & Berry, 2014), and that they may even exploit neuron-to-neuron interactions as means of encoding natural stimuli (Hoshal et al., 2024). The type of interaction that optimizes information transmission by populations that collectively encode stimuli is strongly dependent on the level of noise (Tkačik, Prentice, Balasubramanian, & Schneidman, 2010) - at high noise levels, populations form "basins of attraction" to correct for random distortions. These theoretical considerations and empirical findings have led to suggestions that populations of retinal neurons form optimal error-correcting codes (Berry & Tkačik, 2020; Prentice et al., 2016). An important feature of population codes is their easy decodability and learnability by downstream circuits (Ganmor, Segev, & Schneidman, 2011). Even though encoding mechanisms may be complex and implemented by heterogeneous neural populations, downstream areas should be able to rapidly decode relevant information and detect changes in the neural representation, which may be an important normative objective. The theoretical principles of collective coding in neural populations and how they can explain neuronal diversity remain an active area of research (Berry, Lebois, Ziskind, & da Silveira, 2019; Schneidman, 2016).

6. Towards reconciliation of parsimonious theories and biological diversity

In our attempts to understand the diversity of sensory populations, we are trying to reconcile the desire for conceptual simplicity with the overwhelming complexity of biological systems. Sensory coding in the retina is a perfect model system for developing a principled theoretical understanding of biological diversity. Retinal neurons play a key role in transmitting sensory information, yet they vary in many ways, simultaneously forming seemingly discrete types and continua of properties.

We outlined three key components that may contribute to heterogeneity of neural populations: the computational objective specified by a utility function, statistics of stimulus and noise, as well as population effects. To better reflect the complexity of the real world, these factors can of course be considered simultaneously. In one example the strength of input and output noise determines properties of receptive fields in jointly optimized neuronal populations (Doi et al., 2012; Karklin & Simoncelli, 2011).

Retinal codes are certainly also shaped by evolutionary selection pressures that are not captured by relatively simple objective functions that have been studied to date. For example, to consider behavior, eyes are not passive devices and are actively moved by the organism to sample the visual space (Samonds, Geisler, & Priebe, 2018). Optimization of sensory arrays for systems that sample the environment in "glimpses" that resemble saccadic movements, results in emergence of fovea-like structures reminiscent of organization of the primate retina (Cheung, Weiss, & Olshausen, 2016). At small spatial scales, eye movements can reformat sensory information into a more efficient form (Anderson, Ratnam, Roorda, & Olshausen, 2020; Rucci & Victor, 2015; Wu et al., 2024), and perhaps should be considered jointly with properties of the retinal code. Recent experimental evidence demonstrates that the behavioral state of the animal such as arousal or locomotion can affect the output of the retina by modulating its gain (Schröder et al., 2020). Active behavior and sensor movements should be therefore incorporated into normative theories of sensory processing already at the earliest stages of the visual pathway.

A particularly promising path to reconcile the richness of biological data and the desired theoretical simplicity is the synthesis of normative theories of neural computation with statistical analysis tools. Normative theories can be incorporated into statistical analyzes as very rich and structured priors or inductive biases (Gonçalves et al., 2020; Młynarski, Hledík, Sokolowski, & Tkačik, 2021). This approach can dramatically reduce the amount of data required to fit parameters of biological systems such as receptive fields of an entire population (Qiu et al., 2023). Inductive biases such as the network architecture can also enable predictions about diverse and non-trivial response properties of sensory neurons simply by fitting experimental data (Maheswaranathan et al., 2023). The majority of normative models and theories of sensory coding in the retina rely on relatively simple linear–nonlinear architectures. Although these models generated enormous progress, they do not fully capture the input–output relationship in sensory neurons (Goris, Movshon, & Simoncelli, 2014), in particular in behaving animals (Fu et al., 2024). The synthesis of modern statistical approaches and normative theories can open a way to resolve this important conceptual challenge in the study of sensory coding. At the same time, synthesis of normative theories and statistics permits rigorous tests of the proposed normative explanations that go beyond qualitative comparison of features of computational models and experimental observations (Młynarski et al., 2021).

The diversity and heterogeneity of the nervous system may seem overwhelming even at its earliest stages, such as the retina. Normative theories of neural computation offer a path to taming this apparent diversity by explaining it as a manifestation of relatively few well-interpretable principles.

Data availability

No data was used for the research described in the article.

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