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The Retinal Basis of Vertebrate Color Vision

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Abstract

The jawless fish that were ancestral to all living vertebrates had four spectral cone types that were probably served by chromatic-opponent retinal circuits. Subsequent evolution of photoreceptor spectral sensitivities is documented for many vertebrate lineages, giving insight into the ecological adaptation of color vision. Beyond the photoreceptors, retinal color processing is best understood in mammals, especially the blue^{ON} system, which opposes short- against long-wavelength receptor responses. For other vertebrates that often have three or four types of cone pigment, new findings from zebrafish are extending older work on teleost fish and reptiles to reveal rich color circuitry. Here, horizontal cells establish diverse and complex spectral responses even in photoreceptor outputs. Cone-selective connections to bipolar cells then set up color-opponent synaptic layers in the inner retina, which lead to a large variety of color-opponent channels for transmission to the brain via retinal ganglion cells.

1. INTRODUCTION

> [T]he belief that organic beings have been created beautiful for the delight of man…has been pronounced as subversive of my whole theory.
>
> C. Darwin, *Origin of Species*

Study of the evolution and function of animal color vision originates from two nineteenth-century insights into the imperfections of nature. In 1803, Thomas Young found that measurements of the spatial location and the spectral composition of light are fundamentally incompatible, and he proposed trichromacy as the best compromise for human vision (Mollon 2003). Young also proposed that there are wavelengths beyond the spectral range visible to humans, so there is light we cannot see, and there are spectra we cannot discriminate.

We do not know if Young influenced Darwin directly, but the idea that living organisms are imperfect is a mainspring of the theory of evolution (Darwin 1859) because natural selection could not change a perfect mechanism. Animal coloration fascinated early evolutionary biologists (Cronin 1991, Prum 2012). Why, they asked, are some species cryptic when others are conspicuous, and why do the sexes often differ in their appearance? If coloration evolves by natural selection, so too should color vision. Noting the colors of foods consumed by different animals, Wallace (1879) observed that primates alone among mammals have "tolerably perfect" color vision that was "probably inferior to that of birds" (p. 503). We now know that most mammals have two spectral cone types and many primates have three, whereas some fish have four and birds have five (**Figure 1**).

The impetus that Darwinism gave to our subject is exemplified by the work of Darwin's friend and neighbor John Lubbock on the visual behavior of arthropods. Lubbock (1882) first showed that ants move their pupae away from UV light, thereby demonstrating that an animal could see beyond the human visible spectrum. In later work, Lubbock (1889) showed that water fleas (*Daphnia*) prefer yellow to white light regardless of intensity, which he argued could be regarded as color vision (Kelber & Osorio 2010).

Coloration and color vision remain important in evolutionary biology, as an ideal subject for documenting evolutionary variation and adaptation, because photoreceptor spectral tuning is known for many species and there is an unusually direct relationship between an animal's genotype (opsin DNA sequence) and its visual phenotype (photopigment spectral sensitivities). Receptor spectral sensitivities can then be related to an animal's ecological niche and evolutionary history, and by recording the reflectance spectra of objects that an animal encounters in its daily life and estimating its receptor responses to them, researchers can model the adaptive value of different phenotypes (Lind et al. 2017, Osorio & Vorobyev 1996). Behavioral studies complement models by showing how receptor signals are used for color vision (Kelber et al. 2003, Osorio & Vorobyev 2008). Behavioral tests have yielded less insight into color processing beyond photoreceptors. Instead, physiological recording has described the neural mechanisms of chromatic opponency in the retina, especially in mice and primates, and new work is extending retinal physiology across vertebrate phylogeny (**Figure 1**).

Until around 1980, studies of human and animal color vision often had differing objectives, as exemplified by texts such as *Color Science* by Wyszecki & Stiles (1982) and *Comparative Color Vision* by Jacobs (1981). For humans, where the existence of color vision is not in doubt, research was concerned with physiological mechanisms, first trichromacy and chromatic opponency, then extending to color constancy, color categorization, and color appearance (Gegenfurtner & Kiper 2003, Stockman & Brainard 2010). In animals, findings such as those of Lubbock's (1889) study of *Daphnia* posed the question of whether a fixed response to the spectral composition of light can be

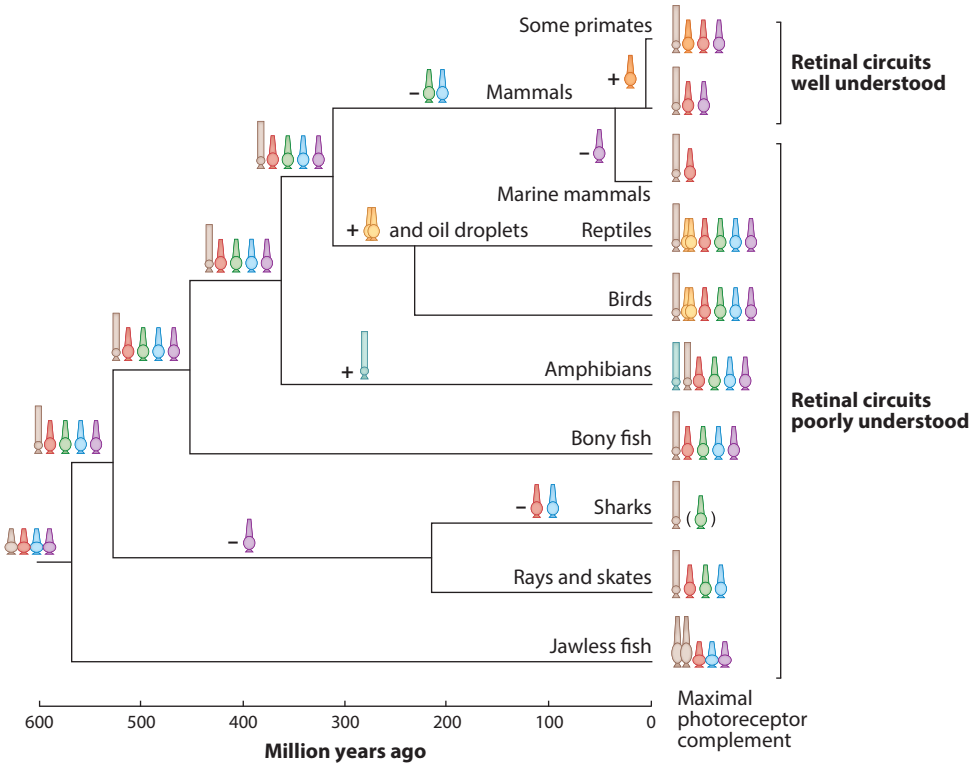

Figure 1

Photoreceptor lineages. The ancient photoreceptor complement of jawless ancestral vertebrates (*leftmost*) gave rise to the photoreceptor complements present in jawed vertebrates today (*right*). At various time points along the way, different lineages added or lost particular photoreceptors: (*beige*) rods, (*red*) L cones, (*green*) M cones, (*blue*) S cones, (*purple*) UV cones, (*teal*) blue rods, (*yellow*) double cones, (*orange*) duplicated L cone in primates. L-type cones of jawless fish (*longer icon*) have a rod-like physiology (Morshedian & Fain 2015). Photoreceptor complements shown depict the typical diversity in a lineage—often, individual groups use fewer.

Erratum >

described as color vision (Kelber & Osorio 2010). We have no direct access to *Daphnia*'s—or any nonhuman species'—experience of color, so interest focused on whether a given species possessed color vision (Jacobs 1981). Such understanding usually entails training an animal to associate a reward with a particular colorful spectrum and then testing it against a range of grays. According to this criterion, many animals see color (Kelber et al. 2003). Animal studies also measured color thresholds to detect either the wavelength difference between monochromatic lights ($\delta\lambda$) or spectral sensitivity defined as the minimum amount of monochromatic light detectable against an achromatic adapting background (Kelber et al. 2003). More recently, interest has moved to color constancy (Chittka et al. 2014, Dörr & Neumeyer 2000, Olsson et al. 2016), color generalization (Baddeley et al. 2007, Caves et al. 2018, Jones et al. 2001), and how specific sets of receptors serve particular behaviors (Orger & Baier 2005, Zimmermann et al. 2018).

Human color science is underpinned by psychophysical measurements of the spectral sensitivities of color mechanisms (i.e., photoreceptors) (Stockman & Brainard 2010, Wyszecki & Stiles 1982), but such tests are not feasible for nonhuman species. Since approximately 1980, animal research has benefitted greatly from direct physiological measurement of photoreceptor spectral sensitivities, which allow us to specify receptor excitations to spectral stimuli. Moreover, for a range

of animals including insects, birds, mammals, and fish, color discrimination thresholds can often be predicted from receptor responses by assuming that thresholds are set by noise arising from photoreceptors in (unspecified) chromatic-opponent mechanisms (i.e., disregarding the achromatic/luminance signal) (Olsson et al. 2018, Vorobyev & Osorio 1998). When a receptor noise model describes experimental data, the implication is that the use of receptor signals is ideal, so it is not possible to make inferences about postreceptoral mechanisms (see also Chaparro et al. 1993). Conversely, deviations from model predictions can give insight into higher-level mechanisms, such as color categorization and generalization (Baddeley et al. 2007, Caves et al. 2018).

2. PHOTORECEPTORS

2.1. Evolution of Photoreceptor Spectral Sensitivities

Visual ecology began in the 1930s with the sensitivity hypothesis that proposed fish photoreceptor spectral sensitivities match the ambient illumination in their environment (Clarke 1936, Collin et al. 2009, Luk et al. 2016). Since then, visual ecology has extended to questions about photoreceptor evolution in relation to object reflectance as well as illumination spectra (Davies et al. 2012, Lind et al. 2017, Nathans et al. 1986, Ödeen & Håstad 2003, Osorio & Vorobyev 2008). Here we provide a brief background.

Visual pigments are G protein–coupled receptors known as opsins that are bound to a chromophore, namely a retinal or a related carotenoid molecule (Arshavsky et al. 2002). Opsin spectral tuning, which is given by the probability of a photon initiating the light response as a function of wavelength, has only one degree of freedom and is specified by the wavelength of peak absorbance, λ_{max} (Govardovskii et al. 2000, Patel et al. 2018).

Because spectral filtering within the eye modifies photoreceptor spectral sensitivities (**Figure 2**), they are best measured from intact animals. In vivo electrophysiological recordings are common in arthropods (Autrum & Zwehl 1964), but the anatomy of the vertebrate eye makes such recording difficult. Instead, most studies measure visual pigment spectral absorbance by spectrophotometry of isolated cone outer segments (Bowmaker 1984) or infer it from the DNA sequence (see Section 2.2) and then model the effects of spectral filtering to predict the spectral sensitivity in vivo.

Vertebrate opsin and photoreceptor spectral sensitivities exhibit a striking combination of evolutionary conservatism and adaptive variation (Lind et al. 2017, Osorio & Vorobyev 2008).

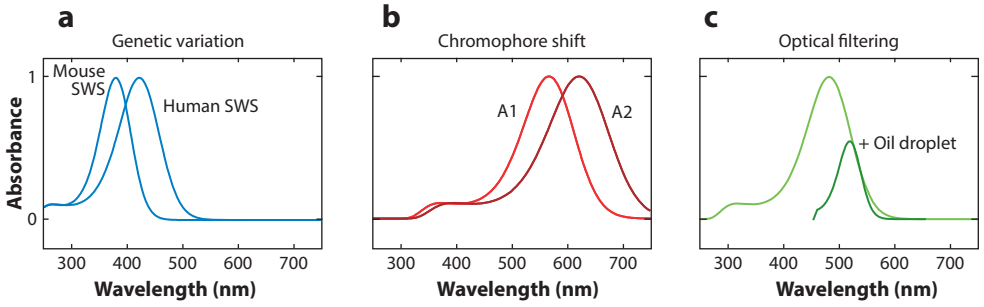

Figure 2

Opsin tuning. (*a*) Opsins of the same lineage can exhibit different spectral peaks owing to differences in the opsin gene sequence; here illustrated for mice and human SWS opsins. (*b*) Depending on the chromophore used, the same opsin can exhibit different spectral tunings; here illustrated for a zebrafish LWS opsin using either 11-*cis*-retinal (A1) or 11-*cis*-3,4-didehydroretinal (A2). (*c*) Addition of filtering media such as oil droplets can also be used to shape a photoreceptor's spectral absorbance; here illustrated for an avian M cone.

Perhaps 500 million years ago, the jawless fish that were ancestral to modern vertebrates evolved four classes of cone opsins, termed SWS1, SWS2, RH2, and LWS (Bowmaker 2008, Davies et al. 2012, Morshedian & Fain 2015, Okano et al. 1994, Yokoyama 2000), which almost certainly resided in four distinct cone types (**Figure 1**). Because the nomenclature of visual pigments and photoreceptor types is inconsistent and potentially confusing, we generally follow the literature we cite but reserve the terms SWS1, SWS2, RH2, LWS, and RH1 for photopigments and their genes, whereas cone types are designated by single letters UV/V, S, M, and L or by color names UV, blue, green, and red. Hence, primate L/red and M/green cones both contain LWS opsins. On occasion, we also specify λ_{max} for the photopigment or photoreceptor (see also Bowmaker 2008). Chromatic-opponent mechanisms are normally designated by conventional color terms such as red–green and blue–green. Color terms do not necessarily correspond to the (English) color term that would best describe the wavelength of peak sensitivity. For example, the primate L cone peak close to 562 nm is yellow not red.

Rod (RH1) opsins probably diverged from RH2 opsins before the lineages of today's jawed vertebrates (gnathostomes) and lampreys (agnathans) separated in the Ordovician period, so early gnathostomes had four cone types and one rod (Lagman et al. 2013). Contemporary vertebrate groups retain different subsets of the four cone pigment families (**Figure 1**). Ancestral bony fish and tetrapods kept all four, but lineages that evolved in dim conditions or in open water, including various fish, penguins, snakes, and mammals, have lost opsin families (Bowmaker 2008, Davies et al. 2012). Groups with only one cone pigment class include many sharks and marine mammals such as whales and seals (Griebel & Peichl 2003, Meredith et al. 2013, Theiss et al. 2012) as well as terrestrial species including beavers and raccoons (Peichl 2005). Jawless fish, teleosts (i.e., most bony fish), and primates increased the number of opsin genes by single-gene and/or whole-genome duplication (Chinen et al. 2003, Lagman et al. 2013, Nathans et al. 1986). Teleosts in particular have multiple paralogous opsin genes in each of the four main families, allowing them to vary pigment expression ontogenetically, typically depending on ambient illumination (Cortesi et al. 2015, Parry et al. 2005, Shand et al. 2008, Spady et al. 2006). Even so, a given retina normally has no more than four spectral cone types, each expressing a typical cone opsin gene: namely, L [red (R), LWS opsin], M [green (G), RH2 opsin], S [blue (B), SWS2 opsin], and UV (SWS1 opsin) (but see Section 3.3.1). The double cones that are present in many teleosts and tetrapods, but not eutherian mammals (**Figure 1**), comprise an electrically coupled pair of cells with two outer segments and two synaptic outputs. The two members of the double cone express different opsins in many teleosts (Section 2.3.2), whereas both members express LWS opsin—as do L-type single cones—in birds and reptiles, giving them five cone types (**Figure 1**).

Apart from conventional cone-based color vision, rods (RH1 opsin) can contribute to color vision (Section 3.3.6), and some amphibians have two spectral rod photoreceptor types (Korenyak & Govardovskii 2013, Yovanovich et al. 2017). Various recent studies also suggest that melanopsin-based light signals from intrinsically photosensitive ganglion cells contribute to image-based color vision in mice and humans and are likely to be most important at high light levels (Allen et al. 2017, Spitschan et al. 2017, Stabio et al. 2018, Zele et al. 2018).

2.2. Spectrally Tuning a Receptor

Vertebrates tune their photoreceptors by varied mechanisms including (*a*) genetic changes to the opsin, (*b*) changes to the chromophore, (*c*) coexpression of multiple opsins in individual photoreceptors, and (*d*) spectral filters.

Opsin pigments' peak absorbance (λ_{max}) is affected by amino acid residues at a few key sites around the chromophore binding pocket (Patel et al. 2018, Porter et al. 2007, Wilkie et al. 2000, Yokoyama 2000). λ_{max} of the main opsin families varies by up to 80 nm (**Figure 2*a***), measuring as

follows: 490–565 nm for LWS, 480–535 nm for RH2, 410–490 nm for SWS2, and 355–440 nm for SWS1 (Bowmaker 2008, Yokoyama 2000). Some freshwater fish, amphibians, and turtles extend the LWS peak to approximately 620 nm by replacing the retinal (A1) with three to four dehydroretinal (A2) chromophores (**Figure 2*b***) (Bowmaker 2008, Enright et al. 2015, Loew & Govardovskii 2001). This chromophore shift allows a fish to alter photoreceptor spectral sensitivities, especially in the long-wavelength range, for example, in response to seasonal or migratory variation in the light environment. Alternatively, some species adjust their spectral tuning by expressing more than one opsin in individual photoreceptors (Dalton et al. 2014).

Next, photoreceptor spectral sensitivities are modified by spectral absorption in the ocular media. For instance, not all fish corneas transmit UV (Siebeck & Marshall 2001). Spectral filtering is most significant in groups whose cone inner segments contain colored oil droplets, namely lungfish, many amphibians and reptiles, and birds (Appudurai et al. 2016, Hailman 1976, Hart 2001, Loew et al. 2002) (**Figure 2*c***).

2.3. Receptor Specialization and Retinal Mosaics

The photoreceptor array in a vertebrate eye samples both spatial and spectral signals, so its organization should reflect compromises between these functions, dependent on species ecology and developmental constraints (Brainard 2015, Rister & Desplan 2011). The following examples from primates, fish, birds, and reptiles illustrate some organizational principles in photoreceptor function and mosaics, while Sections 3.3.1–3.3.5 look at the retinal circuitry of mice, primates, and larval zebrafish.

2.3.1. Old World monkeys. Old World monkeys typically have photoreceptor spectral sensitivity maxima at approximately 440 nm (in S/blue cones), 534 nm (in M/green cones), and 565 nm (in L/red cones). The primate red–green system evolved from the ancestral mammalian LWS system when duplication of (or allelic variation in) the opsin gene gave rise to separate L and M cone pigments without commensurate changes in retinal anatomy (Mollon 1989), so the wiring of L and M cone outputs is largely nonselective (Field et al. 2010) (Section 3). Thus, L and M signals are combined to produce a luminance signal (Lee et al. 1990, Mullen & Losada 1994), where the spectral sensitivity difference between L and M cone inputs is of no benefit and may be deleterious (Brainard 2015, Gegenfurtner & Kiper 2003, Lee et al. 1990, Matthews et al. 2018, Osorio et al. 1998). Chromatic information is transmitted via at least four types of blue–yellow ganglion cells (Marshak & Mills 2014) (Section 3.3.2) as well as midget ganglion cells, which transmit single L and M cone outputs to the brain (Derrington et al. 1984, Gegenfurtner & Kiper 2003, Lee et al. 2010, Lee et al. 2018) (**Figure 3*a*,*b***). The absence of specific retinal circuits suggests that activity-dependent plasticity is important in producing red–green chromatic mechanisms (Benson et al. 2014, Doi et al. 2003, Mollon 1989, Wachtler et al. 2007). In Old World primates, the retinal mosaic of L and M cones is random (Roorda & Williams 1999), but at least in macaque, the S cone array is semiregular (Martin & Grunert 1999).

Darwin might have been pleased by the apparent anatomical deficiencies in the red–green system of trichromatic primates, when other vertebrates have orderly receptor mosaics driving specialized retinal circuits (but see Brainard 2015, Manning & Brainard 2009).

2.3.2. Goldfish, zebrafish, and triggerfish. Goldfish and zebrafish belong to the carp family, *Cyprinidae*. Adults have a regular mosaic of four spectral cone types comprising alternating rows of double cones with red (LWS) and green (RH2) members and single blue (SWS2) and UV (SWS1) cones (Allison et al. 2010, Engström 1960, Raymond et al. 1993), so red and green cones outnumber blue and UV cones by 2:1. In larval zebrafish, the relative densities of different photoreceptor

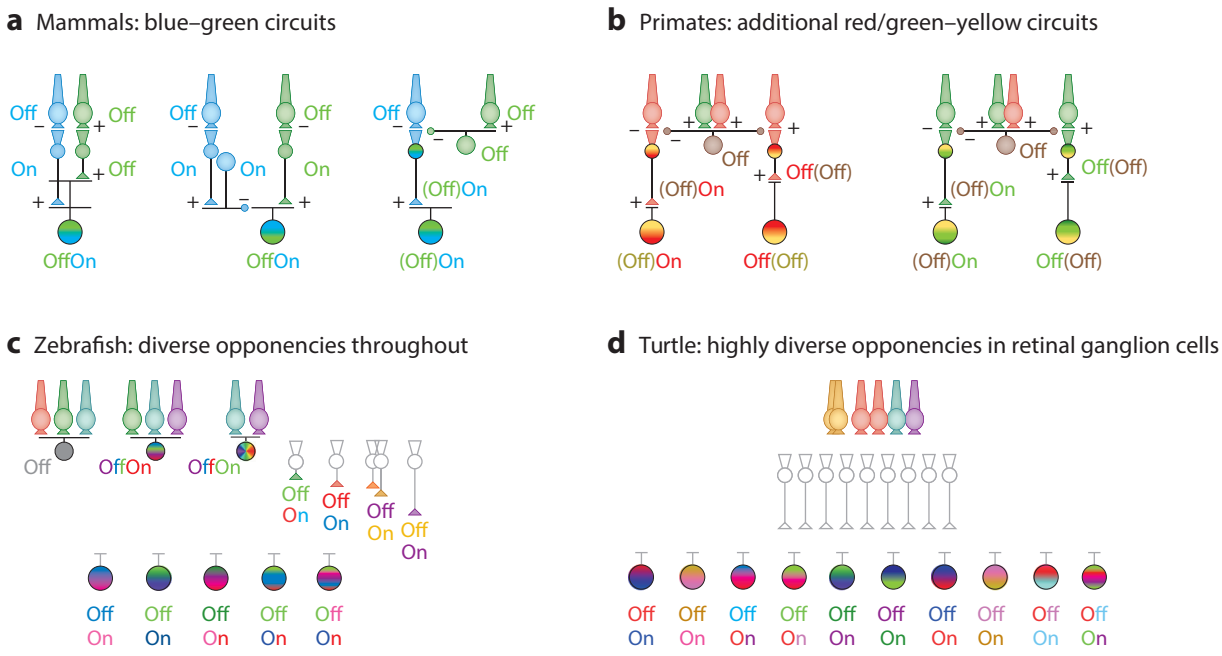

Figure 3

Circuit motifs for retinal color opponency. (*a*) Blue–green (S–M) opponent circuits in mammals. Blue and green cone–selective On and Off bipolar cells, respectively, are differentially combined via a bistratified retinal ganglion cell (*left*). Similarly, sign inversion can occur in the inner retina via an S–On amacrine cell leading onto a monostratified retinal ganglion cell (*center*) or in the outer retina via a green-dominated horizontal cell feeding into a blue-selective bipolar cell pathway (*right*) (reviewed in Lee et al. 2010). (*b*) Primates build red–yellow (*left*) or green–yellow (*right*) opponent midget circuits by pooling a red–green nonselective surround into individual red or green cones via a horizontal cell (reviewed in Dacey 2000, Lee et al. 2010). (*c*) Zebrafish outer retina has at least three types of cone-selective horizontal cells that differentially integrate their four cone types. In the inner retina, retinal bipolar cells build diverse color-opponent responses at their presynaptic terminals, and retinal ganglion cells have diverse and often complex chromatic opponencies. Beyond photoreceptor connections (Section 3.3), the functional and anatomical circuit principles that generate many of these responses are little known (reviewed in Meier et al. 2018). (*d*) Turtles are reported to combine their five cone types into diverse retinal outputs transmitting at least 10 color-opponent signals to the brain (Rocha et al. 2008).

types vary across the retina (Zimmermann et al. 2018) (Section 3.3.4). Goldfish cone sensitivity maxima are approximately 623 nm, 537 nm, 447 nm, and 356 nm (Palacios et al. 1998). Zebrafish have shorter wavelength peaks at approximately 565 nm, 477 nm, 415 nm, and 360 nm (Meier et al. 2018), but these values may not be fixed, as gene duplication allows zebrafish to express different opsin variants in a given cone (Chinen et al. 2003) (Section 2.1).

The presence of four cone pigment types does not automatically entail tetrachromatic color vision, which requires four primaries to match any spectrum. However, Neumeyer (1992) found that goldfish require a mixture of four monochromatic lights to match (spectrally flat) white. The author further found evidence for three chromatic-opponent mechanisms by training fish to single monochromatic lights and then testing the intensity ratio of pairs of monochromatic light the fish needed to make a match. Goldfish color vision seems to vary with light level: In low photopic conditions, goldfish have three wavelength discrimination ($\delta\lambda$) optima at approximately 415 nm, 500 nm, and 605 nm, which is consistent with tetrachromacy (Neumeyer 1986). However, at lower light levels in the human mesopic range (Neumeyer & Arnold 1989), goldfish color vision probably becomes trichromatic, as these fish fail to discriminate between 555 nm and 663 nm, implying that the outputs of the two members of the double cone are combined.

Evidence for flexible use of double cones is also seen in zebrafish, which retain separate double-cone red and green signals in the inner retina (Zimmermann et al. 2018), but the optomotor (movement) response of larval zebrafish sums red and green signals (Orger & Baier 2005). It is unclear whether R + G tuning of the zebrafish optomotor response is indicative of a general luminance system akin to that of primates (Lee et al. 1990, Mullen & Losada 1994). In the zebrafish natural environment, the main source of optic flow is the long-wavelength-biased ventral visual field, but the larval zebrafish inner retina has several systems with fully achromatic responses that involve all four spectral receptors, rather than just red and green (Zimmermann et al. 2018) (Section 3.3.4).

Not all fish are tetrachromats. For example, the triggerfish *Rhinecanthus aculeatus* has three photopigment types in two cone types: single cones with peak sensitivity at 413 nm and double cones that have two outer segments with sensitivity maxima at approximately 480 nm and 528 nm (Cheney et al. 2013, Pignatelli et al. 2010). Color discrimination tests find that triggerfish are trichromats (Champ et al. 2016), implying that, like cyprinids, they retain separate double-cone red and green signals.

2.3.3. Birds and reptiles. Birds and many reptiles have four types of single cones, each of which has photopigment from one of the four main vertebrate opsin families, and one type of double cone (**Figure 1**) (Bowmaker et al. 1997, Hart & Hunt 2007, Toomey et al. 2015). Each cone type contains a specific type of colored oil droplet that narrows spectral tuning at the cost of absolute sensitivity (Hart & Vorobyev 2005, Wilby & Roberts 2017) (**Figure 2*c***). Birds have two main forms of the UV/violet (SWS1) opsin with λ_{max} at approximately either 365 nm or 410 nm (Hart 2001, Kram et al. 2010, Ödeen & Håstad 2003, Wilkie et al. 2000). Modeling bird photoreceptor spectral sensitivities in vivo from opsin and oil droplet absorption functions (Hart & Vorobyev 2005, Toomey et al. 2016) gives λ_{max} values of about 365 nm or 410 nm (SWS1, UV, or violet), 440–475 nm (SWS2, S), 545 nm (RH2, M), and 605 nm (LWS, L). S receptors typically have a shorter wavelength peak when they are associated with cones containing UV (365nm) versus violet (410) SWS1 pigment, whereas M receptor peaks vary little between species (Hart & Vorobyev 2005). Double cones contain LWS pigments and oil droplets that cut off only UV light, giving them a spectral sensitivity similar to that of human L cones.

The cone mosaic of chickens (and other birds) is orderly but less regular than that of fish. Tessellation is consistent with a model where each cone type forms a fairly regular hexagonal array that is independent of all the other four types (Jiao et al. 2014, Kram et al. 2010). This arrangement allows the relative numbers of different cone types to vary flexibly between species and within eyes. In chickens, double cones represent approximately 40% of the total, and the densities of single cones follow the order L > M > S > V/UV, with the density of L cones being approximately four times that of V/UV cones (Hart 2001). The ranking of cone densities in other birds is similar to that in chickens, but there is substantial variation between species as well as with location in the visual field (Hart 2001).

Behavioral tests of color discrimination thresholds in pigeons, parrots, and chickens suggest that they, like goldfish, have tetrachromatic color vision based on four single cones (Goldsmith & Butler 2003, Olsson et al. 2015, Vorobyev & Osorio 1998). Tests with stimuli designed to reveal interactions between specific pairs of cones imply that chickens have spectral-opponent mechanisms comparing UV versus S, S versus (L + M), and L versus M cones (Osorio et al. 1999). The spectral sensitivities of motion and form suggest that bird double cones serve an achromatic system resembling the primate luminance pathway (Jones & Osorio 2004, Olsson et al. 2018), but this conclusion is open to question. For example, the fovea of the Harris hawk (*Parabuteo unicinctus*) lacks double cones, but behaviorally, *P. unicinctus* has high spatial acuity for achromatic gratings (62 cycles per degree) as well the highest spatial resolution reported for any color vision, at

approximately 22 cycles per degree for an isoluminant red–green grating (Potier et al. 2018). Similarly, the pigeon lower-facing frontal visual field, which has high spatial acuity in behavioral tests, is dominated by red cones, and its spectral sensitivity is similar to that expected for an achromatic system (Bloch & Martinoya 1982, Remy & Emmerton 1989, Vorobyev & Osorio 1998).

Lizards, along with snakes and tuatara (Lepidosauria), probably lack true rods but have retinas and receptor spectral sensitivities that otherwise closely resemble those of birds (Bowmaker et al. 2005, Loew et al. 2002), suggesting that this organization evolved before their lineage diverged from that of birds approximately 250 million years ago. The freshwater turtle (*Pseudemys scripta*) has a very similar arrangement but with red-shifted A2-based pigments (Loew & Govardovskii 2001). Its wavelength discrimination ($\delta\lambda$) functions imply that, as in birds, four spectral receptor types contribute to color vision (Arnold & Neumeyer 1987, Zana et al. 2001).

2.4. Principles of Spectral Chromatic Coding

Young's argument that color vision ideally should have an infinite number of spectrally tuned receptors does not take account of the variation present in natural spectra. We now know that the performance and optimal design of a sensory system is conditional on the characteristics of the signals that it encodes (Barlow 1961, Simoncelli & Olshausen 2001). Specifically, the spectra that an animal sees will affect the performance of different eye designs, dependent on the number of receptor types and their spectral tuning (**Figure 2**) as well as on limitations imposed by the available light (photon catch) and other sources of receptor noise (Lind et al. 2017, Olsson et al. 2018, Osorio & Vorobyev 2008). The dominant factor is that reflectance spectra of natural materials vary smoothly with wavelength and, more generally, have a limited number of degrees of freedom. This lack of spectral detail can be contrasted with spatial images where increasing resolution normally yields more information. Thus, Maloney (1986) found that two principal components explain almost 99% of the spectral variance in a data set of natural reflectance spectra, though this proportion would probably be lower for more colorful spectra used in displays by animals and plants (Osorio & Vorobyev 2008). It is more difficult to account for the specific spectral tuning of photoreceptors. A priori one might expect sensitivity maxima to be evenly spaced across the visible spectrum with limited overlap—as they are in birds (Section 2.3.3)—but the particular spectral characteristics of natural pigments such as chlorophyll, melanin, and carotenoids mean that specifying spectral statistics, for example, as smoothed (low-pass-filtered) spectral white noise (Barlow 1982), is not straightforward. Consequently, evaluation of spectral coding in biological vision has been empirical, based on simulations of photoreceptor responses to ensembles of specific objects of interest such as flowers, fruit, or feathers (Osorio & Vorobyev 2008) or using hyperspectral imaging (Benson et al. 2014). For example, the spectra of many biological pigments vary more at long versus short wavelengths, so biasing spectral sampling to long wavelengths is beneficial. As such, primate trichromacy, with closely spaced L and M receptors, may be nearly ideal for discrimination of fruit and leaves (Osorio & Vorobyev 1996). Similarly, avian color vision with four (single) cone types narrowed by colored oil droplets is suited to discriminating among feather reflectance spectra (Osorio & Vorobyev 2008, Vorobyev et al. 1998).

Principles of coding efficiency also apply to the early neural (second) stage of color vision. The responses of different spectral receptors to natural spectra are highly correlated (Barlow 1982, Maloney 1986), and early sensory processing likely removes redundancy due to statistical correlations of this kind (Atick et al. 1992, Srinivasan et al. 1982). For example, lateral inhibition, which produces the center-surround receptive fields of many retinal neurons, reduces spatial correlation (Srinivasan et al. 1982), whereas spectral domain, chromatic-opponent coding reduces spectral correlations. Under broad assumptions about spectral signal statistics, for a retina with n

spectral photoreceptors, decorrelation is achieved by *n* mechanisms with spectral responses such that the first has no zero crossings (i.e., an achromatic mechanism with responses of the same sign to all wavelengths), the second has one zero crossing (i.e., an opponent mechanism with short-wavelength responses is opposite to mechanisms with long-wavelength responses), and the third has two zero crossings (i.e., an opponent mechanism with medium-wavelength responses is opposite to mechanisms with short- and long-wavelength responses), and so forth (Buchsbaum & Gottschalk 1983, Ruderman et al. 1998). Conversely, mechanisms that simply independently transmit the outputs of a single cone type or multiple chromatic mechanisms with the same number of zero crossings (e.g., B + G versus R, G versus R) are likely to be redundant (see also Section 3.3.5). We next consider how such principles apply to vertebrate retinas.

3. RETINAL CIRCUITS FOR COLOR VISION

For photoreceptors, we have a strong framework for understanding the first stage pertaining to the function and diversity of animal color vision. Behavioral evidence shows that the second stage of color processing involving retinal circuits is sufficient to preserve spectral information in the photoreceptors and that there are distinct chromatic and achromatic/luminance mechanisms (Chaparro et al. 1993, Mullen & Losada 1994, Vorobyev & Osorio 1998), but it has revealed little specific detail about these mechanisms. To understand spectral processing in the retina and beyond, research is now combining single-synapse-resolution anatomy with physiological recordings. Key questions are as follows: (*a*) What is the nature of opponent mechanisms, and how many are there? (*b*) How is chromatic and luminance information represented? (*c*) To what extent do different receptor types contribute to distinct retinal pathways?

3.1. Color Opponency in the Outer Retina

Opponency refers to a neural computation that compares the activity in neurons that differ in their tuning to a given stimulus parameter—for example, spatial location or acoustic frequency. For color vision, a single detector cannot differentiate a wavelength shift from a change in intensity. Thus, color or chromatic opponency requires comparison between at least two spectral receptor types (Krauskopf et al. 1982).

Vertebrate color opponency begins in the outer retina where horizontal cells mediate inhibitory interactions between photoreceptors (Chapot et al. 2017b, Perlman et al. 2009). Cones inhibit each other via horizontal cells, which are large, highly interconnected neurons that communicate bidirectionally with photoreceptor synapses known as pedicles. Typically, glutamate released from a pedicle depolarizes the horizontal cell, which by various mechanisms feeds back negatively onto the same pedicle (feedback) and onto pedicles of other cones (feedforward) (Thoreson et al. 2008, Twig et al. 2003). Feedback confined to a single pedicle coexists with lateral interactions, which allow color-opponent responses to emerge at the visual system's first synapse. Since two receptors cannot occupy the same retinal location, color opponency inevitably has a spatial component. Horizontal cells can be electrically coupled to form a dense network (Becker et al. 1998, Cook & Becker 1995) interacting with photoreceptors over different spatial, temporal, and chromatic scales via a range of synaptic and other mechanisms to mediate opponency in wavelength and space (lateral inhibition) and to decorrelate neural signals in time (Chapot et al. 2017a, Jackman et al. 2011, Kamermans et al. 2001, Kemmler et al. 2014, Verweij et al. 1996).

Spectral responses of each horizontal cell type depend on its cone connections (Connaughton & Nelson 2010, Dacheux & Raviola 1982, Goodchild et al. 1996, Kamermans et al. 1991, Li et al. 2009) as well as the type and gain of each connection (Baden et al. 2013, Breuninger et al. 2011, Chapot et al. 2017a). Many species, especially those with more than two spectral cone types, feature

multiple types of horizontal cells with distinct, cone-selective connections and correspondingly complex chromatic properties (Connaughton & Nelson 2010, Kamermans et al. 1991, Packer et al. 2010). As a result, surround inhibition varies in its spectral composition. Zebrafish have at least three types of cone-selective and one type of rod-selective horizontal cell with mono-, bi-, and triphasic spectral responses (Meier et al. 2018) (**Figure 3*c***). More simply, a specific horizontal cell in primates sets up a yellow (R + G dominated) surround in blue cones (Crook et al. 2011, Lee et al. 2010, Packer et al. 2010), and a similar circuit is found in rabbits (Mills et al. 2014) (**Figure 3*a***). How horizontal cell connectivity patterns and feedback mechanisms serve—or interfere with—chromatic processing in the outer retina is poorly understood for most vertebrate groups.

3.2. Inner Retina and Brain Projections

Beyond the photoreceptor level, chromatic processing is prominent in vertebrate inner retinal networks (Baden et al. 2018, Dacey 2000, Euler et al. 2014, Lee et al. 2010). The form of these systems surely depends on an animal's photoreceptor complement, but common wiring principles emerge from the need to differentially combine two or more spectral inputs. In one key circuit motif, two spectrally pure bipolar cell pathways connect to a postsynaptic ganglion cell, one excitatory and the other inhibitory (**Figure 3*a***) (Dacey & Lee 1994, Marshak & Mills 2014, Mills et al. 2014), to produce a color-opponent ganglion cell. A well-studied example is part of the ancient mammalian blue–green system (i.e., S versus L cone). This circuit is shared by mice, guinea pigs (Yin et al. 2009), ground squirrels (Sher & DeVries 2012), rabbits (Mills et al. 2014), and primates (Dacey & Lee 1994), and key anatomical connections are known for rodents, rabbits, and primates. Mice have only one type of chromatically pure blue^{ON} bipolar cell, termed type 9 (Behrens et al. 2016, Breuninger et al. 2011), whose dendrites exclusively contact blue cones, thereby ensuring a blue-center response. Type 9 bipolar cells, similar to all mammalian On bipolar cells, express the metabotropic glutamate receptor mGluR6 on their dendrites, which results in a sign inversion that converts the blue^{OFF} cone signal into a blue^{ON} bipolar cell response (reviewed in Euler et al. 2014). Accordingly, type 9 bipolar cells provide a blue^{ON} center input to their postsynaptic partners. In mice, another bipolar cell, perhaps the green cone–biased type 1 Off cell (Behrens et al. 2016), supplies green^{OFF} antagonism to this blue signal. The retinal ganglion and/or amacrine cells completing the circuit remain elusive in mice, but they probably include the melanopsin-containing M5 cell in which there is a blue + green + (weak) melanopsin On center response, which is opposed to a green-dominated surround (Stabio et al. 2018). More typical blue^{ON} cells are known in rabbits, guinea pigs, and primates (Dacey & Lee 1994, Mills et al. 2014, Sher & DeVries 2012, Yin et al. 2009). Primates have at least four types of yellow versus blue ganglion cells (Marshak & Mills 2014, Lee et al. 2010) including two blue^{OFF} cells, but best known is the small bistratified retinal ganglion cell that selectively integrates blue^{ON} and red/green^{OFF} inputs from different bipolar cells across its two respective dendritic arbors in the inner plexiform layer (Calkins et al. 1998, Crook et al. 2009, Dacey & Lee 1994, Zrenner & Gouras 1981). Notably, the ground squirrel uses On and Off green cone–selective bipolar cells (Li & DeVries 2006) that provide additional options for building color-opponent ganglion cells (**Figure 3*a***).

3.3. Case Studies of Retinal Circuits

Precise anatomical and functional wiring motifs for retinal color-opponent circuits remain little known in all but a few species, notably primates, mice, and zebrafish, each of which has specific retinal specializations and at times unusual solutions that need to be considered when aiming to synthesize the known details of their circuits into a bigger picture. Here, we introduce some of these peculiarities.

3.3.1. Color processing in the peculiar retina of mice. The mouse retina is exquisitely adapted to its sensory-ecological niche. As a crepuscular species that spends much time underground, mice are often active in dim light, and >90% of their photoreceptors are rods—a similar proportion to the human retina. Nonetheless, mice have a well-developed dichromatic cone system based on a UV (SWS1) blue cone (λ_{max} 360 nm) and an M (LWS) green cone (λ_{max} 508 nm) (Nikonov et al. 2006). M cones outnumber UV cones by more than 10:1 (Wässle et al. 2009), perhaps because of the greater abundance of green versus UV photons in natural illumination (Párraga et al. 1998), and much mouse vision uses a mainly M cone–driven luminance signal. Given the preponderance of green cones, color vision cone-selective circuits are more important for the sparse blue system than for the green system. Similarly, if we assume equal gain of green and blue cone inputs, any randomly connecting bipolar or horizontal cell will be green biased (but see Baden et al. 2013, Breuninger et al. 2011).

Matters are complicated because the mouse dorsal retina—looking below the visual horizon—has pure green cones interspersed with pure blue cones, but a dorsoventral SWS1 opsin coexpression gradient—looking above the horizon—is found in genetic M cones, which therefore coexpress LWS and SWS1 opsins (Applebury et al. 2000, Baden et al. 2013, Roehlich et al. 1994, Szél et al. 1992). The short-wavelength bias of the most ventral (upward-looking) M cones (Baden et al. 2013, Chapot et al. 2017a) implies that SWS1 opsin expression is dominant. This shifts the spectral sensitivity in genetic M cones of the ventral retina, thereby boosting the detection of achromatic dark contrasts, such as a bird silhouette (Baden et al. 2013). Similar opsin coexpression gradients appear in mammals as diverse as hamsters and hyenas (Peichl 2005) as well as in all species that survey the open sky for birds (e.g., rodents detecting predators, hyenas finding carrion by spotting vultures).

The opsin coexpression gradient has several consequences for mouse color vision. Notably, the standard blue–green opponent system cannot work in the ventral retina as it does in the dorsal retina because the green signal is either contaminated by blue sensitivity or, more likely, almost abolished. Given the standard opponent circuits, mice would be color-blind above the horizon, but behavioral evidence suggests otherwise (Denman et al. 2018), in part because green rods oppose S-biased ventral M cones (see below). An interesting type of spectral opponency also arises at the boundary between the blue-dominated ventral retina and the green-dominated dorsal retina. Here, large-field retinal ganglion cells span both zones and receive a chromatically mixed input, which lacks specific wiring yet produces center-surround chromatic antagonism near the visual horizon (Chang et al. 2013).

Overall, mice probably have a subset of the inner retinal pathways in their dorsal retina that squirrels, lagomorphs, and primates use for color vision, but at and beyond the horizon, they sense chromatic contrasts via nontraditional circuits. How these peculiarities translate to the brain and behavior remains an outstanding question (Denman et al. 2018, Tan et al. 2015).

3.3.2. Color processing in the peculiar retina of trichromatic primates. Next to mice, retinal circuits for color vision are best known in trichromatic primates including humans (Dacey 2000, Lee et al. 2010). As with the opsin coexpression gradient in mice, the primate fovea engenders behavioral and circuit peculiarities because S cones are absent from a region approximately 0.25° across in the area centralis (Roorda & Williams 1999, Williams et al. 1981), so any blue contribution to color appearance at the fixation point relies on interpolation. Elsewhere, as in other mammals, the density of S cones is much lower than that of M/L cones (Martin & Grunert 1999), and the cone connectivities of primate bipolar cells broadly resemble those of mice, including an S cone–selective On bipolar cell (Boycott & Wässle 1991, Dacey 2000). Unlike in mice, the blue–yellow chromatic circuits in the primate inner retina are well known (Calkins et al. 1998,

Chichilnisky & Baylor 1999, Dacey 2000, Lee et al. 2010). This exquisite account, complemented by findings from lagomorphs and rodents (see above), dominates the literature on short- versus long-wavelength retinal circuits in vertebrates, but its relevance to nonmammalian groups is unclear.

Perhaps the most peculiar feature of trichromatic primate retina is the presence of separate red (L) and green (M) cones, owing to an evolutionarily recent LWS opsin genetic polymorphism or gene duplication (Mollon 1989). This causes a wiring problem because retinal circuits seemingly do not distinguish L from M cones (but see Field et al. 2010) and thus lack developmentally programmed red or green bipolar cells. Instead, chromatic selectivity depends on the presence of midget bipolar and ganglion cells (Lee et al. 2010), in which the center input is from a single cone, and the surround is spectrally nonselective and depends on the local density of red and green cones in the random cone array (Hofer et al. 2005). This single-cone-center wiring produces four types of opponent midget signals, red^{ON}–yellow^{OFF}, green^{ON}–yellow^{OFF}, red^{OFF}–yellow^{ON}, and green^{OFF}–yellow^{ON} (**Figure 3*b***), that extend beyond the fovea (Lee et al. 2010). This system defers the disambiguation of red and green signals to the cortex, which could generate chromatic-selective neurons via activity-dependent plasticity mechanisms (Benson et al. 2014, Doi et al. 2003, Wachtler et al. 2007), unlike other vertebrate cone-opponent mechanisms that probably start in the retina. These conclusions are reinforced by evidence indicating that the introduction of an additional red opsin into a subset of LWS cones leads to trichromatic vision in human dichromats (Mancuso et al. 2009) and, more surprisingly, in mice (Jacobs et al. 2007; but see Makous 2007).

3.3.3. Color processing in nonmammalian vertebrates. Jawless fish probably evolved retinal circuitry for color vision along with the four vertebrate opsin families some 500 million years ago (Collin et al. 2009). This circuitry probably has a similarly conservative Bauplan, including, for example, a homologue of the mammalian blue^{ON} system. Our knowledge here is limited mainly to teleosts, notably zebrafish, goldfish, and rainbow trout (Meier et al. 2018) (**Figure 3*c***), and a few studies of reptiles, mostly turtles (**Figure 3*d***) (Arnold & Neumeyer 1987, Rocha et al. 2008, Ventura et al. 2001, Zana et al. 2001) and amphibians (Werblin & Dowling 1969). The vast majority of this work has probed retinal function by single-cell electrophysiology, which provides detail on single neurons. Despite some key studies (D'Orazi et al. 2016, Li et al. 2009), this work has not delivered a comprehensive account of color processing of any one retina.

Nevertheless, it is clear that animals such as the turtle with five cone types and the goldfish with four have a retinal complement of chromatic neurons that exceeds not only that of mammals (as one might expect), but also the additional number of opponent mechanisms needed to encode chromatic information (see above). For example, the turtle *Trachemys scripta* has 12 color-opponent retinal ganglion cells (Rocha et al. 2008, Ventura et al. 2001) (**Figure 3*d***), whereas teleosts have complex chromatic responses even in the horizontal cells (Connaughton & Nelson 2010, Kamermans et al. 1991, Meier et al. 2018, Twig & Perlman 2004, Twig et al. 2003). However, a fuller picture of the retinal basis for color vision is emerging in the zebrafish (**Figure 3*c***).

3.3.4. Color processing in the peculiar retina of zebrafish. Like their goldfish relative, zebrafish may well be tetrachromats (see Section 2.3.2). In adult zebrafish, the red, green, blue, and UV cones form a crystalline mosaic with relative densities of 2:2:1:1. Each cone type is genetically distinct, allowing developmentally hardwired retinal circuits (D'Orazi et al. 2016, Li et al. 2009) in any of 80 (i.e., $3^4 - 1$) theoretically possible chromatic combinations. Single-cell electrophysiology in zebrafish retina ranging from horizontal cells to ganglion cells reveals a rich complement of chromatic opponencies (Connaughton & Nelson 2010, 2015; Klaassen et al. 2016; Torvund et al. 2017). Yet, recordings from approximately 4,000 bipolar cell synapses in zebrafish larvae

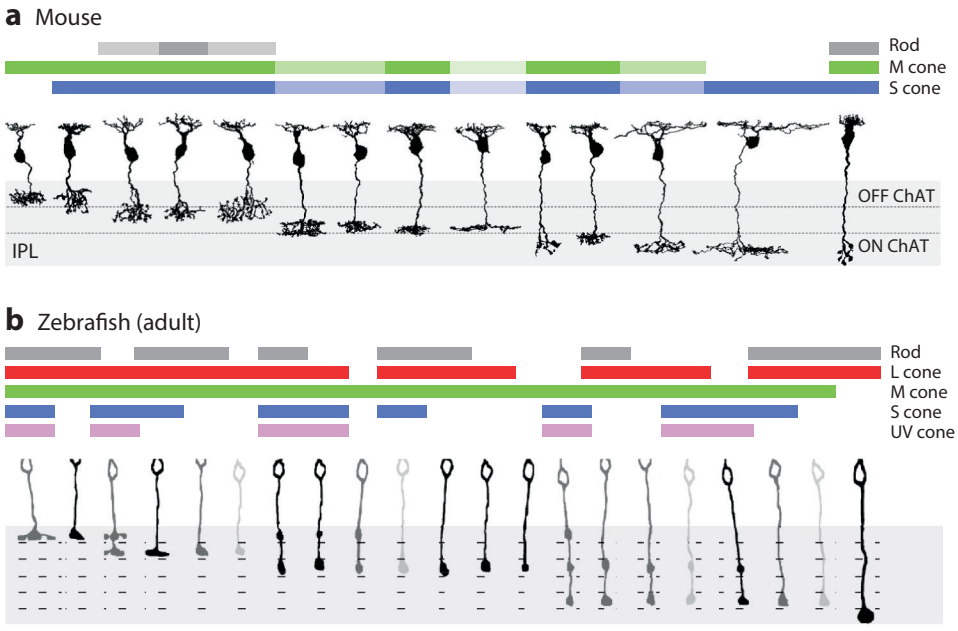

Figure 4

Wiring photoreceptors to bipolar cells. (*a*) The 14 mouse bipolar cell types make mostly cone-type nonselective contacts in the outer retina. Only types 1 (*leftmost*) and 9 (*second from right*) bipolar cells make selective contacts with M and S cones, respectively. Rods are contacted by rod bipolar cells and a subset of Off bipolar cells. Panel *a* adapted with permission from Behrens et al. (2016). (*b*) Adult zebrafish have more than 20 bipolar cells that make diverse sets of contacts across the four cone types and one rod type in the outer retina. Panel *b* adapted with permission from Li et al. (2009).

(Zimmermann et al. 2018) reveal that most combinations are not used. Instead, 87% of bipolar synapses were nonopponent, 12% opposed longer- against shorter-wavelength inputs with a single null point on the visible spectrum, approximately 1% had the form (L + S) versus M with two null points, and no synapses had three null points (i.e., UV + G versus B + R) (Buchsbaum & Gottschalk 1983) (see Section 2.4). Much remains to be learned about the organization of color mechanisms in larval zebrafish (see Section 3.3.5), but the finding that little neural bandwidth is devoted to complex spectra suggests that chromatic coding is approximately matched to the spectral statistics of natural images (Maloney 1986, Ruderman et al. 1998) (Section 2.4). Consistent with physiological evidence, cone-selective wiring of horizontal cells is restricted to spectral blocks expected for achromatic and long- versus short-wavelength opponency [e.g., (U + B) versus (G + R)], rather than the jumps [e.g., (UV + R) versus (B + G)] (**Figure 4**) that would be associated with the higher-order chromatic mechanisms (Klaassen et al. 2016, Song et al. 2008). Bipolar cells also follow the same principle (**Figure 4*b***). Apart from zebrafish, this block-wiring principle of retinal chromatic circuits is untested. Yet, bipolar and retinal ganglion cells of nonmammalian species tend to have long- versus short-wavelength responses, consistent with chromatic block wiring in the outer retina (Rocha et al. 2008, Zimmermann et al. 2018).

3.3.5. Regional specialization in juvenile zebrafish retina. Color circuits in adult zebrafish retina may resemble those of other cyprinids and perhaps tetrachromatic vertebrates in general. Whether larval zebrafish have the same circuitry as adults is unknown, but it is becoming clear that

they have elaborate spectral processing, with regional specialization matched to their behavioral needs. Building on the wealth of single-cell physiology from both adults and larvae, a recent survey used two-photon calcium imaging to record the spectral responses of approximately 4,000 larval zebrafish bipolar cells (Zimmermann et al. 2018). Eight days after fertilization, zebrafish larvae have approximately 10,000 cones in each eye, and in vivo single-synapse resolution measurements can be made in any part of the retina. Despite the presence of all cone types, chromatic processing in the inner retina varies dramatically across the visual field. For example, at the visual equator there are several types of bipolar cells, most of which have short- versus long-wavelength chromatic opponency. By contrast, UV^{ON} responses dominate the temporoventral retina, which looks forward and slightly upward. Ventral visual circuits, which view the sky through Snell's window, are all but color-blind, probably because there is little chromatic information in this region of the visual field. This parallels the mouse system, where cone-only dichromacy disappears above the horizon (see Section 3.3.1).

Larval zebrafish bipolar cells with color-opponent or chromatically biased responses are separated into specific layers of the inner retina. For example, RG versus BU and R versus GBU opponent responses dominate layers 1 and 3 of the dorsal retina. Retinal ganglion cells that project to these layers should inherit a similar physiology (Connaughton & Nelson 2015, Meier et al. 2018), so opponent inputs to the brain can be established by the second synapse of the visual system. Bipolar cells in other nonmammalian retinas, including mudpuppies, turtles, goldfish, and giant danio (*Devario aequipinnatus*), have fully color-opponent responses (Stell 1978, Werblin & Dowling 1969, Wong & Dowling 2005, Yazulla 1976).

3.3.6. Rod-based color vision. Rod–cone chromatic antagonism can occur in mesopic conditions, when both rod and cone systems are simultaneously active, and may extend to traditionally photopic levels (Szikra et al. 2014, Tikidji-Hamburyan et al. 2015). Vertebrate rods express RH1 rhodopsin, which in most species is spectrally similar to the RH2 (green) opsin. In the mouse ventral retina, this system appears to be exploited by at least one type of retinal ganglion cell (Joesch & Meister 2016), and further circuits in both mice and other species probably use rod signals (Baden et al. 2016, Field et al. 2009, Reitner et al. 1991). Rod–cone opponency might allow color vision in cone monochromats such as sharks, marine mammals, and raccoons (Griebel & Peichl 2003, Oppermann et al. 2016, Peichl 2005, Von Schantz et al. 1997); however, because their cone spectral sensitivities overlap strongly with rods, little chromatic contrast will be available. Beyond rod–cone opponency, some amphibians have two spectrally distinct types of rods that allow color vision at low light levels (Korenyak & Govardovskii 2013, Yovanovich et al. 2017).

SUMMARY POINTS

1. Vertebrates evolved rod opsin (RH1) and four main genetic families of cone opsin (SWS1 UV/violet, SWS2 blue, RH2 green, and LWS red) before the emergence of jawed fish around 450 Mya. Many lineages, including birds and teleost fish, retain these opsin families, whereas others, including mammals, snakes and elasmobranch fish, have lost one or more families.
2. In teleosts the two members of the double cone often contain different types of photopigment (LWS and RH2), which contribute independently to color vision giving an opponent signal. Avian double cones contain a single type of pigment (LWS) and may serve luminance vision, with the four spectral types of single cone being used for color.

3. The arrangement of the different spectral types of cones varies widely. Many teleosts have a highly regular mosaic of cones, and bird cones retain a degree of order, whereas the array of red and green cones in primates is random.
4. Color vision requires chromatic opponent mechanisms that compare the outputs of different cone types, and this may well involve retinal circuits. Best known is the mammalian blue^{ON} system, which compares SWS1 and LWS cone signals.
5. Different types of horizontal cells mediate chromatic opponency in the outer retina. How these inhibitory interactions finally contribute to color vision remains unclear.
6. In the inner retina, single-cell recordings from a turtle that has four spectral types of cone find at least 12 types of chromatic opponent ganglion cell. In larval zebrafish, most chromatic neurons oppose long against short wavelengths in varying combinations (e.g., LWS versus RH2 + SWS2 + SWS1 or LWS + RH2 versus SWS2 + SWS1).
7. Amongst mammals, the primate L versus M (i.e., red-green system) and mouse ventral retina, which is effectively monochromatic, have unconventional chromatic mechanisms that do not rely on putatively ancient retinal circuits.
8. In larval zebrafish the distributions of the four spectral types of cone across the visual field are not uniform, probably reflecting behavioral specialization. For example, color vision is best in the ventral visual field, and a dorsal frontal area of the visual field is rich in UV cones, probably to aid capture of protozoan prey.

FUTURE ISSUES

1. With the exceptions of the mammalian blue^{ON} circuit and the primate red-green system, spectral processing in vertebrate retina remains largely unexplored. New methods that allow recording from multiple retinal neurons offer the opportunity to open this field. Key questions are the following.
2. Can we identify an ancient set of neural circuits, which evolved in the early tetrachromatic chordates, to complement the five main types of retinal photoreceptor?
3. What are the key functional principles underlying the organization of chromatic coding in vertebrate retinas? For example, principles of coding efficiency predict that an eye with n spectral types of photoreceptor should have an achromatic mechanism, plus $n - 1$ chromatic opponent mechanisms with 1 to n spectral null points, respectively, but physiological evidence from turtle and zebrafish does not seem to conform to this scheme.
4. Do vertebrate retinas have distinct luminance and chromatic circuits?
5. What are the extent and nature of specialization in retinal circuits across the visual field, and how do they complement the variation in absolute and relative densities of different cone types?
6. How are retinal circuits reconfigured to serve color vision over a wide range of light intensities? For example, there is evidence that goldfish are trichromatic in low photopic levels and tetrachromatic in brighter light.
7. How do retinal circuits serve chromatic adaptation and color constancy?

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