The retinal basis of vertebrate color vision

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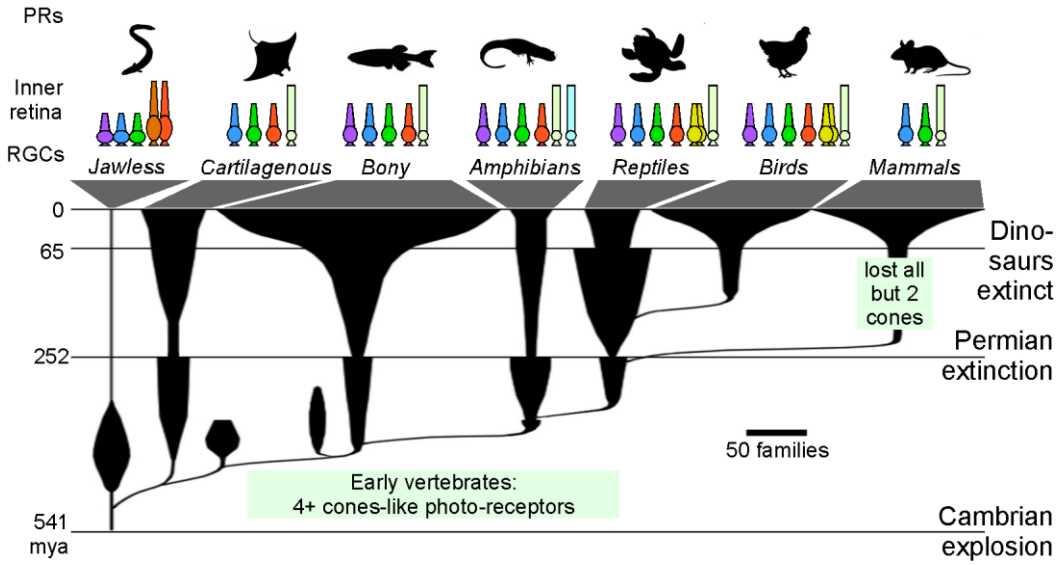
Graphical Abstract



SUMMARY

Vertebrate color vision is evolutionarily ancient. Jawless fish evolved four main spectral types of cone photoreceptor, almost certainly complemented by retinal circuits to process chromatic opponent signals. Subsequent evolution of photoreceptors and visual pigments are now documented for many vertebrate lineages and species, giving insight into evolutionary variation and ecological adaptation of color vision. We look at organization of the photoreceptor mosaic and the functions different types of cone in teleost fish, primates, and birds and reptiles. By comparison less is known about the underlying neural processing. Here we outline the diversity of vertebrate color vision and summarize our understanding of how spectral information picked up by animal photoreceptor arrays is adapted to natural signals. We then turn to the question of how spectral information is processed in the retina. Here, the quite well known and comparatively 'simple' system of mammals such as mice and primates reveals some evolutionarily conserved features such as the mammalian Blue^{ON} system which compares short and long wavelength receptors signals.

We then survey our current understanding of the more complex circuits of fish, amphibians, birds and reptiles. Together, these clades make up more than 90% of vertebrate species, yet we know disturbingly little about their neural circuits for colour vision beyond the photoreceptors. Here, long-standing work on goldfish, freshwater turtles and other species is being complemented by new insights gained from the experimentally amendable retina of zebrafish. From this body of work, one thing is clear: The retinal basis of colour vision in non-mammalian vertebrates is substantially richer compared to mammals: Diverse and complex spectral tunings are established at the level of the cone output via horizontal cell feedforward circuits. From here, zebrafish use cone-selective wiring in bipolar cells to set-up color opponent synaptic layers in the inner retina, which in turn lead a large diversity of color-opponent channels for transmission to the brain. However, while we are starting to build an understanding of the richness of spectral properties in some of these species' retinal neurons, little is known about inner retinal connectivity and cell-type identify. To gain an understanding of their actual circuits, and thus to build a more generalised understanding of the vertebrate retinal basis of color vision, it will be paramount to expand ongoing efforts in deciphering the retinal circuits of non-mammalian models.

Introduction

'…the 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*. Ch. 6.'

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 saw that measurement of the spatial location and the spectral composition of a light are fundamentally incompatible, and proposed trichromacy as the best compromise (Mollon 2003). Young also recognised that the spectrum extends to wavelengths beyond the range that humans can see. We do not know if Young directly influenced Darwin, but the idea that living organisms are imperfect was a mainspring of his theory of evolution (Darwin 1859), because natural selection could not change a perfect mechanism.

As an easily recognised character, 19th century evolutionary biologists took a keen interest in animal and plant coloration (Cronin 1991, Prum 2012). Why, for example, are some animals camouflaged when others have conspicuous coloration, and why do the sexes sometimes differ in their appearance? If coloration evolved by natural selection the same would apply to color vision. Wallace (Wallace 1879), noting the colors of foods eaten by different animals, observed that primates alone amongst mammals have 'tolerably perfect' color vision, and that this was 'probably inferior to that of birds'. We now know that most mammals have two spectral types of cone photoreceptor, many primates have three, and birds have four or five (Fig. 1).

The stimulating influence of Darwinism on research into animal color vision is exemplified by Darwin's friend and neighbour John Lubbock, a politician and gentleman naturalist, whose finding that ants moved their pupae away from UV light was the first demonstration that an animal could see beyond the human visible spectrum (Lubbock 1882). Later Lubbock found that water fleas (*Daphnia*) prefer yellow light to white independently of intensity, and argued that this behaviour can be regarded as color vision (Kelber & Osorio 2010, Lubbock 1889).

Color vision remains a powerful system for investigating how animal senses evolve under natural selection. Photoreceptor spectral tuning is known for many species, and there is a direct relationship between the genotype (the opsin DNA sequence)

and the photopigment spectral sensitivity. In addition, we can record the reflectance spectra of objects encountered by an animal in its daily life, and estimate receptor responses to them, thereby specifying the signals available to the brain. A wealth of studies on opsin evolution, and the ecological influences on photoreceptor spectral sensitivities (Bowmaker 2008, Osorio & Vorobyev 2008), is complemented by behavioral tests which show how photoreceptor signals are used for color and luminance vision (Kelber et al. 2003). In parallel, physiological studies of the retina have addressed questions about selective wiring, chromatic opponency and other aspects of color processing beyond the receptors, especially in mice and primates. In the future it will be important to extend retinal physiology across vertebrate phylogeny, especially to branches such as teleost fish and birds, which feature rich spectral receptor complements, and make much use of color vision (Fig. 1).

Behavioural study of animal color vison

Until about 1980 psychophysical studies of human and animal color vision often had differing objectives, exemplified in key texts by Wyszecki and Stiles (1982) *Color Science*, and Jacobs' (1981) *Comparative Color Vision*. For humans the existence of color vision is not in doubt, and researchers were interested in mechanisms, starting with trichromacy and chromatic opponency, and extending to color constancy, color categorization and color appearance (Brainard & Stockman 2010, Gegenfurtner & Kiper 2003, Wyszecki & Stiles 1982). In animal research early work such a Lubbock's (Lubbock 1889) findings on *Daphina* posed the question of whether a simple response to the spectral composition of a light can be described as color vision. We have no access to *Daphnia's* (or any other species') experience of color, so studies focussed on whether a given species had color vision (Jacobs 1981). Usually these entailed training an animal to associate a reward with a particular spectrum, and then testing it against a range of greys. According to this criterion a wide range of animals tested see color (Kelber et al. 2003). Studies have also measured color discrimination thresholds, either for the wavelength difference between two monochromatic lights ($\delta\lambda$), or of monochromatic light added to an achromatic background (spectral sensitivity) (Kelber et al. 2003). More recently interest has moved to questions about 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 the ways in which specific sets of receptors serve particular behaviours (Orger & Baier 2005, Zimmermann et al. 2018).

For non-human species it has however not been possible to use psychophysical methods to determine the spectral sensitivities of the color mechanisms (i.e. photoreceptors), which underpins work on human color vision (Wyszecki & Stiles 1982). Research therefore benefits greatly from direct measurement of photoreceptor spectral sensitivities (Part 1), because spectral stimuli can then be defined in terms of receptor excitations. An important empirical finding is that color discrimination thresholds can often be predicted from receptor responses by assuming that they are set by noise arising from photoreceptors in (unspecified) in chromatic opponent channels, disregarding the achromatic/luminance signal (Olsson et al. 2018, Vorobyev & Osorio 1998). If this 'receptor noise' model describes experimental data this implies that the use of receptor signals is ideal, so it is not possible to make inferences about post receptoral mechanisms from experimental data. Conversely, deviations from the predictions of the model can give insight into higher level mechanisms, such as color categorization and generalization (Baddeley et al. 2007).

Part 1: Photoreceptors

Evolution of photoreceptor spectral sensitivities

Ecological study of photoreceptor spectral sensitivities began in the 1930's with the 'sensitivity hypothesis', which proposed that fish sensitivities match the ambient illumination (Clarke 1936, Collin et al. 2009, Loew & Lythgoe 1985, Luk et al. 2016). This subject is now grounded in evolutionary genetics, and has gone on to examine the relation of receptor sensitivities to reflectance spectra of objects relevant to a given species as well as to illumination (Davies et al. 2012, Lind et al. 2017, Nathans et al. 1986, Ödeen & Håstad 2003, Osorio & Vorobyev 2008). Here we give a brief background.

Visual pigments are G-protein coupled receptors, known as opsins, which bind a chromophore, namely retinal or a related carotenoid molecule (Arshavsky et al.

2002). Spectral tuning of the pigment is defined as the probability that a photon of a given wavelength incident on the molecule is absorbed by the chromophore to initiate the light response. This tuning is affected by the amino acid residues at key sites on the opsin protein (Patel et al. 2018, Porter et al. 2007, Wilkie et al. 2000, Yokoyama 2000). Opsin spectral tuning has only one degree of freedom, and is normally specified by the value to peak absorbance, λ_{max} (Govardovskii et al. 2000, Patel et al. 2018).

Photoreceptor spectral sensitivities should ideally be measured from intact eyes, and *in vivo* electrophysiological recordings are common in arthropods (Autrum & Zwehl 1964), but the anatomy of the vertebrate eye makes such recordings difficult, so most studies measure visual pigment spectral absorbance by spectrophotometry of an isolated cone's outer segment (Bowmaker 1984), or infer it from the DNA sequence (see above).

Comparative studies of vertebrate opsin and photoreceptor spectral sensitivities find a striking combination of evolutionary conservatism and adaptive change (Lind et al. 2017, Osorio & Vorobyev 2008). Some 500 million years ago the jawless fish which were ancestral to modern vertebrates evolved four classes of cone opsin, designated SWS1 ('UV/Violet'), SWS2 ('Blue'), MWS/RH2 ('Green') and LWS ('Red') (Bowmaker 2008, Davies et al. 2012, Lamb 2013, Okano et al. 1994, Yokoyama 2000). Rod (RH1) opsins probably evolved from the RH2 opsins after the lineages of contemporary jawed vertebrates (gnathostomes) and lampreys (agnathans) diverged, so early gnathostomes saw the world through four sets of cone photoreceptors, and one rod. Contemporary vertebrates retain different subsets of the four cone pigment families, as well as rods (Fig. 1). For example, whereas most mammals have only LWS and SWS1, many teleost fish, amphibians, reptiles and birds have the full ancient complement. Animals that live in dim conditions or in open water, including various fish, penguins, burrowing snakes and nocturnal mammals, typically have fewer spectral photoreceptor types (Bowmaker 2008, Davies et al. 2012). Groups that have reduced their cone-complement to but a single class, or even none, include marine mammals, like whales and seals, as well as many sharks (Griebel 2002, Griebel & Peichl 2003, Meredith et al. 2013, Theiss et al. 2012), and also smaller terrestrial species like beavers or racoons (Peichl 2005). In teleosts and primates the number of opsin genes is increased by gene duplication (Chinen et al.

2003, Nathans et al. 1986). Having multiple opsin genes fish vary pigment expression ontogenetically, sometimes under control of the ambient illumination (Shand et al. 2008, Spady et al. 2006). Normally there are no more than four spectral types of cone in a given retina, each expressing a cone typical opsin gene: L cones ("red", R, LWS opsin), M cones ("green", G, MWS/RH2 opsin), S cones ("blue", B, SWS2 opsin) and UV cones ("ultraviolet", UV, SWS1 opsin). A notable exception is bird/reptile double cones, which express LWS opsin. Finally, vertebrate rods (RH1 opsin) can also contribute to color vision (Part 2), and a second type of rod found in some amphibians (Korenyak & Govardovskii 2013, Yovanovich et al. 2017).

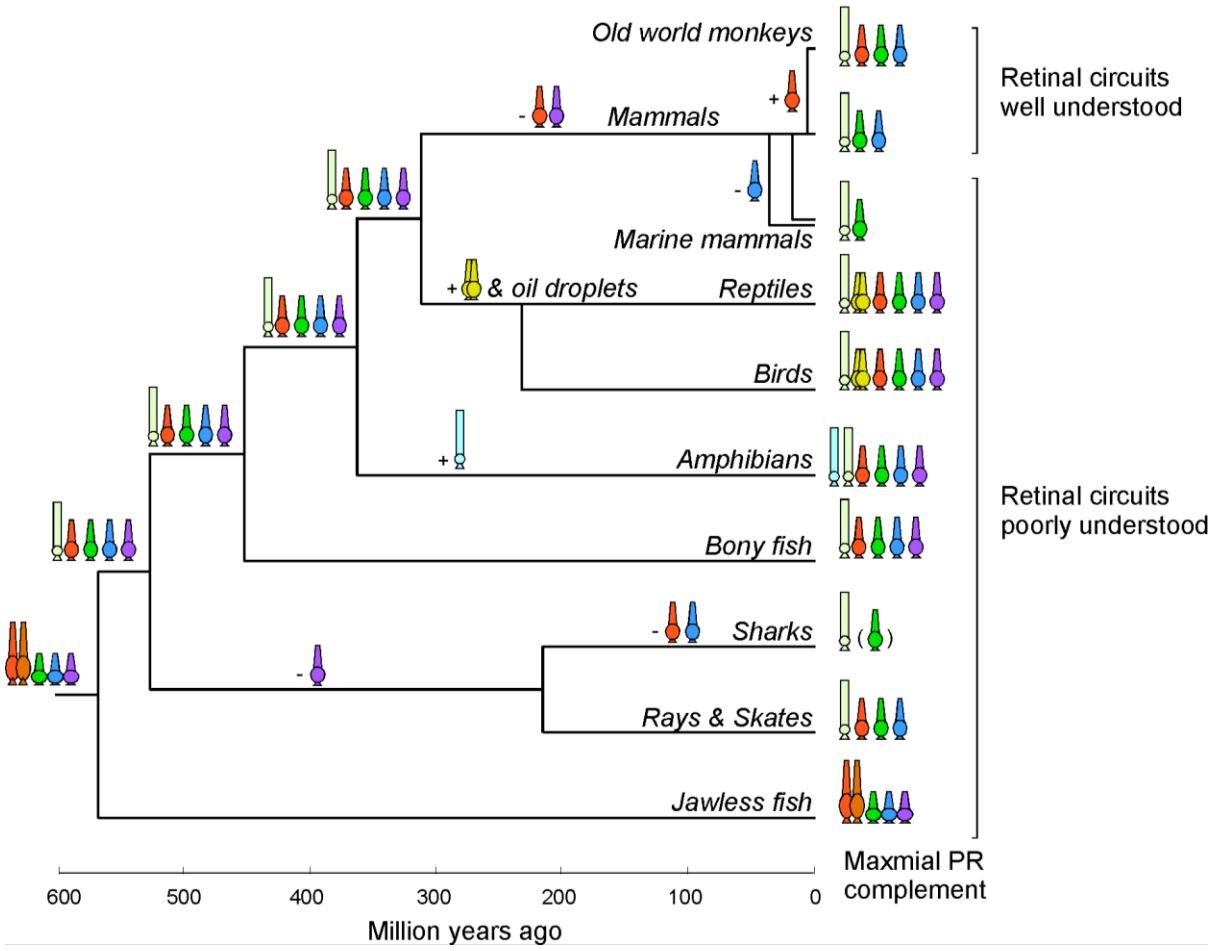


Figure 1 – *Photoreceptor lineages*. The ancient photoreceptor complement present in jawless ancestral vertebrates (leftmost) gave rise to the photoreceptor complements present in jawed vertebrates today (right). Along the way, different lineages added or lost types of photoreceptors at different timepoints. Rods (beige), L-cones (red), M-cones (green), S-cones (blue), UV-cones (purple), "blue" rods (light blue), "double-cones" (yellow). Photoreceptor (PR) complements shown depict the typical maximal diversity in a lineage – often individual groups use fewer.

Spectrally tuning a receptor

While vertebrates inherited the four main opsin families from jawless fish (Collin et al. 2009), they now use varied mechanisms to tune their photoreceptors to suit their lifestyle and habitat. These include (i) genetic changes to the opsin sequence itself, (ii) changing the chromophore, (iii) co-expression of multiple opsins in individual photoreceptors, and (iv) the addition of spectral filters.

In each of the main opsin families amino-acid residues at a few key sites around the binding pocket can vary the pigment's peak sensitivity (λ_{max}) by up to 80 nm (Fig. 2a), and vertebrate visual pigments cover the visible spectrum with λ_{max} as follows: LWS: 490–565 nm, RH2: 480–535 nm, SWS2: 410–490 nm and SWS1: 355–440 nm (Bowmaker 2008, Yokoyama 2000). Some freshwater fish and amphibians extend the LWS peak to around 620 nm by replacing the retinal (A1) chromophore with 3-4 dehydroretinal (A2) (Fig. 2b) (Bowmaker 2008, Enright et al. 2015, Loew & Dartnall 1976). Using this chromophore shift to control spectral sensitivity allows individuals to control spectral tuning, for example to follow seasonal or migratory variation in the light environment. Alternatively, some species co-express more than one opsin in individual photoreceptors to adjust their spectral tuning (Dalton et al. 2014).

Next, although photoreceptor spectral sensitivities depend primarily on their opsin and chromophore, they are modified by spectral absorption in the ocular media. For example, some fish corneas transmit UV while others absorb short wavelengths (Siebeck & Marshall 2001). Spectral filtering is however most significant in those groups whose cone inner segments contain colored oil droplets, namely a lungfish, birds and certain reptiles, including freshwater turtles and lizards (Appudurai et al. 2016, Hart 2001, Loew et al. 2002) (Fig. 2c).

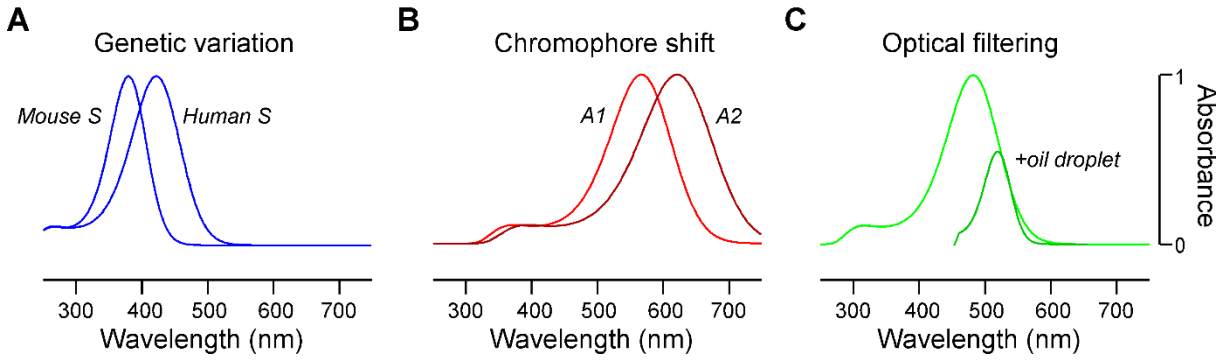


Figure 2 – *Opsin Tuning.* A, Opsins of the same lineage can exhibit different spectral peaks due to differences in the opsin gene sequence – here illustrated for SWS-opsins of mice and men. B, Depending on the chromophore used, the same opsin can exhibit different spectral tunings – here illustrated 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 further be used to shape a photoreceptor's spectral absorbance, here illustrated in for an avian M-cone.

Receptor specialisation and retinal mosaics

The array of photoreceptors in the vertebrate retina has to sample both spatial and spectral signals, and so should reflect the compromises between these roles that suit animals' particular needs, as well as developmental constraints (Rister & Desplan 2011). The following examples from primates, fish, birds and reptiles illustrate some of the organisational principles in photoreceptor function and mosaics in these major vertebrate groups. Part 2 looks further at the particular cases of mouse and larval zebrafish in relation to their retinal circuitry.

1. Old world monkeys

Old-world monkeys are trichromats with opsin spectral sensitivity maxima at about 440 nm (in S/blue cones), 554 nm (in M/green cones) and 565 nm (in L/red cones). As elaborated below (Part 2) this cone-complement produces to two classical spectral channels: the "ancient" blue-yellow axis and a primate-specific red-green axis. A further distinction is made between chromatic and luminance mechanisms (Lee et al. 1990, Livingstone & Hubel 1988, Mullen & Losada 1994). Primates are unusual because the red-green system evolved from the dichromatic ancestral mammalian LWS system by the acquisition of separate L and M cones, without commensurate change in retinal anatomy (Mollon 1989). Wiring of L and M cone outputs is largely non-selective (See Section 2) (Field et al. 2010), and they are integrated to produce a luminance signal which serves many aspects of vision, notably by the parasol ganglion cells, which project to the magno-cellular layers of the lateral geniculate nucleus (LGN). Here, spectral sensitivity differences of the inputs are of no benefit and may corrupt the luminance signal (Gegenfurtner & Kiper 2003, Lee et al. 1990, Osorio et al. 1998). In parallel, chromatic information is transmitted via 'blue-yellow' opponent ganglion cells (Dacey 2000, Dacey & Lee

1994), and 'red or green' midget ganglion cells which project to the parvocellular layers of the LGN (Derrington et al. 1984, Gegenfurtner & Kiper 2003, Lee et al. 2017) (Fig. 3a,b). The midget system, probably evolved as a primate specialisation for spatial acuity, transmits single L and M cone outputs to the brain, where they are integrated by activity dependent plasticity (Doi et al. 2003, Mollon 1989, Wachtler et al. 2007), without specific retinal circuits to separate luminance and red-green chromatic signals. The mosaic of L and M cones is random (Roorda & Williams 1999), but in macaque the S cone array is semiregular (Martin & Grunert 1999). Darwin might have been pleased that anatomically our red-green system seems poorly designed. So far as we know such an arrangement is not present in any other vertebrate visual system, where it is usual to find orderly receptor mosaics driving specialised retinal circuits.

2. Goldfish, zebrafish and triggerfish

Goldfish and zebrafish belong to the carp family (*Cyprinidae*). Adults have four spectral types of cones arranged in a regular mosaic (Engström 1963) with alternating rows of double cones with Red (LWS) and Green (MWS) members, and Blue (SWS2) and UV (SWS1) single cones, giving twice as many Red and Green cones as Blue and UV (Allison et al., Raymond et al. 1993). In goldfish, spectrophotometry of cone outer segments gives respective sensitivity maxima of 623 nm, 537 nm, 447 nm and 356 nm (Palacios et al. 1998). Zebrafish have shorter wavelength peaks at about 565 nm, 477 nm, 415 nm and 360 nm (Meier et al. 2018), but gene duplication allows these fish – like many others – to express different variants in a given cone (Bowmaker 2008, Chinen et al. 2003, Parry et al. 2005).

The presence of four types of cone pigment does not automatically entail tetrachromatic color vision – which requires that four primaries are needed to match any spectrum, but (Neumeyer 1992) showed that a mixture of four monochromatic lights was needed for goldfish to match a white (spectrally flat) light. She also found evidence for three separate chromatic opponent mechanisms by training to single monochromatic lights and testing the intensity ratio of pairs of monochromatic light needed for the fish to make a match. Further, tests under low photopic adapting illumination for discrimination of monochromatic lights ($\delta\lambda$) wavelength also suggest

that goldfish are tetrachromats with sensitivity maxima at about 415 nm, 500 nm and 605 nm (Neumeyer 1986). The long wavelength sensitivity maximum is lost at illumination intensities in the middle of the human mesopic range (Neumeyer & Arnold 1989), when the fish fail to discriminate between 555 nm and 663 nm, implying that signals of the two members of the double cone become functionally coupled. Similarly, zebrafish retain separate double-cone R and G signals in the inner retina (Zimmermann et al. 2018), but their optomotor (movement) response appears to sum R and G signals (Orger & Baier 2005). It is however not clear whether the red+green tuning of the optomotor response is indicative of a general luminance system akin to that in primates. In the fishes natural environment, the main source of optic flow information) is the long-wavelength biased ventral visual field, but the inner retina of larval zebrafish also has several systems with 'fully' achromatic responses that involve all four spectral receptors, rather than 'just' red and green (Zimmermann et al. 2018). Notably, unlike adults, but like in many other vertebrates, larval zebrafish have different density distributions of photoreceptor types in different parts of their eye, presumably to capitalise on different wavelength composition in natural light and different behavioural demands across their large visual field (Zimmermann et al. 2018).

Not all fish are tetrachromats. For example, the triggerfish *Rhinecanthus aculeatus* has three types of photopigment in two types of cones: single cones with a peak sensitivity at 413 nm, and double cones which have two outer segments with sensitivity maxima at about 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 as in the cyprinids this species retains separate double-cone R and G signals.

3. Birds and Reptiles

Birds and many reptiles have four types of single cone and one type of double cone, each of which is associated with a specific type of oil droplet that acts as a spectral filter by cutting off wavelengths below a certain value (Wilby & Roberts 2017). This filtering narrows spectral tuning of the receptor, at the cost of absolute sensitivity (Hart & Vorobyev 2005) (Fig. 2c). Each single-cone type contains a photopigment belonging to one of the four main vertebrate opsin families (Fig. 1) (Bowmaker et al.

1997, Hart & Hunt 2007, Toomey et al. 2015), with two main forms of the UV (SWS1) opsin giving peak sensitivities at about either 365 nm or 410 nm (Kram et al. 2010, Ödeen & Håstad 2003, Wilkie et al. 2000). Bird photoreceptor spectral sensitivities *in vivo* are normally estimated by modelling the sensitivity based on the opsin and oil droplet absorption functions (Hart & Vorobyev 2005, Toomey et al. 2016), which predicts λ_{max} values of 365 nm or 410 nm (SWS1, UV or violet), 440 nm-475 nm (SWS2, blue), 545 nm (MWS, green) and 605 nm (LWS, red). The UV type SWS1 receptors are associated with shorter wavelength SWS2 receptors, whereas the MWS receptor peaks vary little between species. The double cones contain LWS pigments and oil droplets which gives them a spectral sensitivity much like that of human L (red) photoreceptors.

The cone mosaic in the chicken (and other birds) is orderly but less regular than that of fish. The mosaic is consistent with a model where each cone type forms a fairly regular hexagonal array that is independent of each of the other four types (Jiao et al. 2014, Kram et al. 2010). The densities of these arrays differ between cone types. In chicken, double cones represent about 40% of the total, and of the remainder densities fall in the order LWS>MWS>SWS>V/UVS, with the density of LWS cones being about two to four times that of the V/UVS (Hart 2001). There is however substantial variation between species, and across position in the visual field (Hart 2001).

Behavioural tests of color discrimination thresholds in pigeons, parrots and chickens suggest that, like goldfish, birds have tetrachromatic color vision based on the outputs of the 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 likewise imply that chickens have three spectral opponent mechanisms which compare UV vs. S, S vs. (L+M) and L vs. M cones, which is consistent with tetrachromacy (Osorio et al. 1999). Whereas fish double cones contribute to color vision, bird double cones may serve an achromatic system which is used for form and motion vision, resembling the primate luminance pathway (Jones & Osorio 2004). This conclusion is however open to question, for example the fovea of the Harris hawk (*Parabuteo unicinctus*) is free of double cones but has a high spatial acuity and poor color vision (Potier et al. 2018). Similarly, the high acuity lower facing frontal visual field in pigeons, where the birds peck for food, is

dominated by red cones and is probably predominantly luminance sensitive (Remy & Emmerton 1989, Vorobyev & Osorio 1998).

The retinal organisation and receptor spectral sensitivities of anole lizards are essentially identical to those of birds (Bowmaker et al. 2005, Loew et al. 2002), suggesting that this organisation evolved in the common ancestor of the two main lineages of living reptilles. Tests of wavelength discrimination by the freshwater turtle (*Pseudymys scripta*) suggests that, as in birds, four spectral receptor types contribute to color vision (Arnold & Neumeyer 1987, Zana et al. 2001).

Principles of spectral coding

Before turning to the physiology of these systems in the vertebrate retina it is useful to look briefly at underlying principles of spectral coding by photorecptors, and then chromatic oppoency in the retina

When Young suggested that ideally color vision should have an 'infinite' number of spectrally tuned receptors he was unaware of the nature of the spectral stimuli in the natural world. To operate efficiently any coding system should be matched to the characteristics of the signals that it encodes (Barlow 1961, Simoncelli & Olshausen 2001). It follows that the specific set of receptors in a given eye should depend upon the characteristics of the spectra that the animal needs to discriminate. In practice the reflectance spectra of natural materials vary smoothly with wavelength, and this lack of 'spectral detail' means that three receptors capture a large proportion of the available spectral information (Maloney 1986, Vorobyev et al. 1997). In addition, the spectra of many biological pigments tends to vary more at long than at short wavelengths. Consequently, primate trichromacy may in fact be close to the ideal for discrimination fruit and leaves (Osorio & Vorobyev 1996), with the small spectral separation of the L and M receptors well suited to capturing this specific type of spectral information. Similarly, avian color vision with four (single) cone types narrowed by colored oil droplets is well suited to discriminating amongst the reflectance spectra of feathers, which can have more spectral variation than most objects (Osorio & Ham 2002, Vorobyev et al. 1998).

Given a set of receptors that are suitably tuned to measure variation in natural spectra, how should their signals then be encoded by the second-stage of color

vision? Having broadly tuned spectral receptors to sample smoothly varying spectral reflectance functions means that outputs of different spectral receptor are highly correlated (Barlow 1982, Maloney 1986, Srinivasan et al. 1982). A general principle of early stages of visual processing is to remove redundancy in neural signals caused by statistical correlations of this kind (Atick et al. 1992, Buchsbaum & Gottschalk 1983). Thus, lateral inhibition, which produces the centre-surround receptive fields of many retinal neurons can be understood as a means of removing spatial correlation (Srinivasan et al. 1982). In the spectral domain at a basic level, correlations in the signal received by distinct spectral cones are removed before any extraction of spectral information. In the retina, this is implemented by ("color")-opponent wiring. Beyond the requirement for some type of chromatic opponency Buchsbaum and Gottschalk (Buchsbaum & Gottschalk 1983) pointed out that for a retina with *n* spectral photoreceptors decorrelation is - under broad assumptions - achieved by *n* mechanisms with spectral responses such that one has no zero-crossings (i.e. responses have the same sign to all wavelengths), the second has one zero crossing (i.e. responses to short wavelengths are of the opposite sign to those to long wavelengths) and the third has two zero-crossings (i.e. responses to medium wavelengths of the opposite sign to those to short and long wavelengths), and so forth. It follows that mechanisms which simply transmit the outputs of a single cone types independently, or multiple signals that have the same number of zero crossings (e.g. B+G vs. R, or G vs R) are likely to be partly redundant.

Part 2: Retinal circuits for color vision.

For photoreceptors we have strong basis for understanding the function and diversity of animal color vision. Behavioural studies show also that the 'second stage' of color processing, involving retinal circuits, is both necessary and sufficient to preserve the spectral information in the photoreceptors, and that there are distinct chromatic and achromatic/luminance mechanisms (e.g. (Vorobyev & Osorio 1998)), but reveal little about specific chromatic mechanisms. To understand how spectral information is used within the retina and beyond research is now combining single synapse-resolution anatomy with direct physiological study. Key questions are: (i) what is the number and nature of opponent mechanisms that compare the outputs of different spectral receptor types, (ii) how is chromatic- and luminance-information

represented, (iii) how do retinal mechanisms contribute to color constancy, an finally (iv) to what extent do different receptor types contribute to distinct retinal pathways. We will now look at the picture that is emerging from this work.

Color opponency in the outer retina

In general, opponency refers to a neural computation that compares the activity in sets of neurons with different tuning to a given stimulus parameter – for example spatial location or wavelength of sound or of light. For color vision, since a single detector cannot differentiate a shift in wavelength from a change in intensity, retinal color or chromatic opponency requires a comparison between at least two spectral receptor types (Hurvich & Jameson 1957, Krauskopf et al. 1982).

In the vertebrate retina color-opponency typically begins through interactions between the photoreceptors themselves, where inhibitory connections are mediated by horizontal cells (Chapot et al. 2017b, Perlman et al. 2009). These large and highly interconnected outer retinal neurons communicate bidirectionally with photoreceptor synapses, which are known as pedicles. Typically, glutamate release from a photoreceptor's pedicle depolarises the horizontal cell, which by a variety of mechanisms then negatively feeds back onto the same pedicle (feedback) as well as to the pedicles of other cones (feedforward) (Thoreson et al. 2008, Twig et al. 2003). Thereby, cones connected via horizontal cells inhibit each other, and since horizontal cells can be electrically coupled, to form a dense functional network (Becker et al. 1998, Cook & Becker 1995), these interactions may occur over wide spatial scales. This general mechanism establishes color-opponent response properties already at the visual system's first synapse. Since two receptors cannot occupy the same retinal location, any form of color-opponency inevitably has a spatial component. In fact, horizontal cells not only set-up opponency in wavelength and space (lateral inhibition), but also decorrelate neural signals in time. For this, horizontal cell interactions with photoreceptors use a wide range of synaptic and other mechanisms to act over different spatial, temporal and chromatic scales (Chapot et al. 2017a, Jackman et al. 2011, Kamermans et al. 2001, Kemmler et al. 2014, Verweij et al. 1996) including a wealth of feedback mechanisms that remain confined to the level of a single pedicle. While it remains largely unclear how local and global horizontal cell interactions exist in parallel (or how switching functions might work), any purely

local interactions by definition cannot transmit signals to neighbouring cones, meaning that color opponency can only be built using global-scale interactions. This global spectral response of a horizontal cell (HC) type, which is readily measured from its soma (Connaughton & Nelson 2010, Kamermans et al. 1991), depends on the specific cone connections made (Dacheux & Raviola 1982, Goodchild et al. 1996, 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 HCs with distinct, cone-selective connectivity patterns and correspondingly complex chromatic properties (Connaughton & Nelson 2010, Kamermans et al. 1991, Packer et al. 2010). As a result, different cone types receive different spectral-contrast surround inhibition. For example, zebrafish have at least three cone-selective and one rod-selective HCs with spectrally mono-, bi- and triphasic response properties (Meier et al. 2018) (Fig. 3c). More simply, primates use a specific HC type to set up a yellow (R + G dominated) surround in blue cones (Crook et al. 2011, Neitz & Neitz 2011, Packer et al. 2010), and rabbit use a similar circuit (Mills et al. 2014) (Fig. 3a). However, how the multitude of horizontal cell connectivity patterns and feedback functions operate to serve - or even interfere with - chromatic processing in the outer retina remains poorly understood in most vertebrate groups.

Inner retina and brain projections.

Beyond spectral opponency at the level of photoreceptors, vertebrates dedicate substantial neural resources to chromatic coding in inner retinal networks (Baden et al. 2018, Dacey 1999, Euler et al. 2014, Jacobs 2008, Neitz & Neitz 2011). The complexity of such pathways varies depending on the animal's photoreceptor complement, but many follow common wiring principles that directly emerge from the necessity of differentially combining two or more spectral input pathways. For example, one key circuit motif takes two different "spectrally-pure" bipolar cell pathways and differentially pools their signals in a postsynaptic ganglion cell, such that one bipolar cell pathway excites the ganglion cell, while the other inhibits it (Fig. 3a) (Dacey & Lee 1994, Mills et al. 2014). The result is a color opponent ganglion cell whose spectral tuning is driven by the tuning of the specific bipolar cell pathways

that it combines. A well-studied example of such a circuit forms part of the ancient mammalian “blue-green system” (i.e. S vs L/M cone) which is conserved across mice, guinea pigs (Yin et al. 2009), ground squirrels (Sher & DeVries 2012) and rabbits (Mills et al. 2014) all the way to primates (Dacey & Lee 1994). For some species, including mice, ground squirrel, rabbits, guinea pigs and various primates, key anatomical connections are known. For example, mice have only one type of chromatically pure ‘blue^{ON}’ bipolar cell dubbed Type 9 (Behrens et al. 2016, Breuninger et al. 2011), which makes specific dendritic contacts only with blue cones, thereby ensuring a blue-centre response. Mouse type 9 bipolar cells, like all mammalian On-bipolar cells, express metabotrophic glutamate receptor mGluR6 on their dendrites, which results in a sign-inversion of the blue^{OFF} cone signal into a blue^{ON} signal at the level of the bipolar cell (reviewed in (Euler et al. 2014)). Accordingly, type 9 bipolar cells provide a blue^{ON} center response to their direct postsynaptic partners. Green^{OFF} antagonism to this blue mechanism is provided by another type of bipolar cell, perhaps the green-cone-biased Type 1 Off bipolar cell (Behrens et al. 2016). While the specific putative retinal ganglion- and/or amacrine cells completing such a circuit remain elusive in mouse, such cells are known in rabbits, guinea pigs and primates (Dacey & Lee 1994, Mills et al. 2014, Sher & DeVries 2012, Yin et al. 2009). For example, in primates, the small bistratified RGC selectively collects blue^{ON} and red/green^{OFF} inputs from different bipolar cells across its two respective dendritic arbours in the inner plexiform layer of the retina (Calkins et al. 1998, Crook et al. 2009, Dacey & Lee 1994, Zrenner & Gouras 1981). Notably, some mammals such as the cone-dominated ground squirrel use at least two green-cone selective BCs - an On and an Off variant (Li & DeVries 2006) - to give additional options for building color opponent ganglion cells (Fig. 3a).

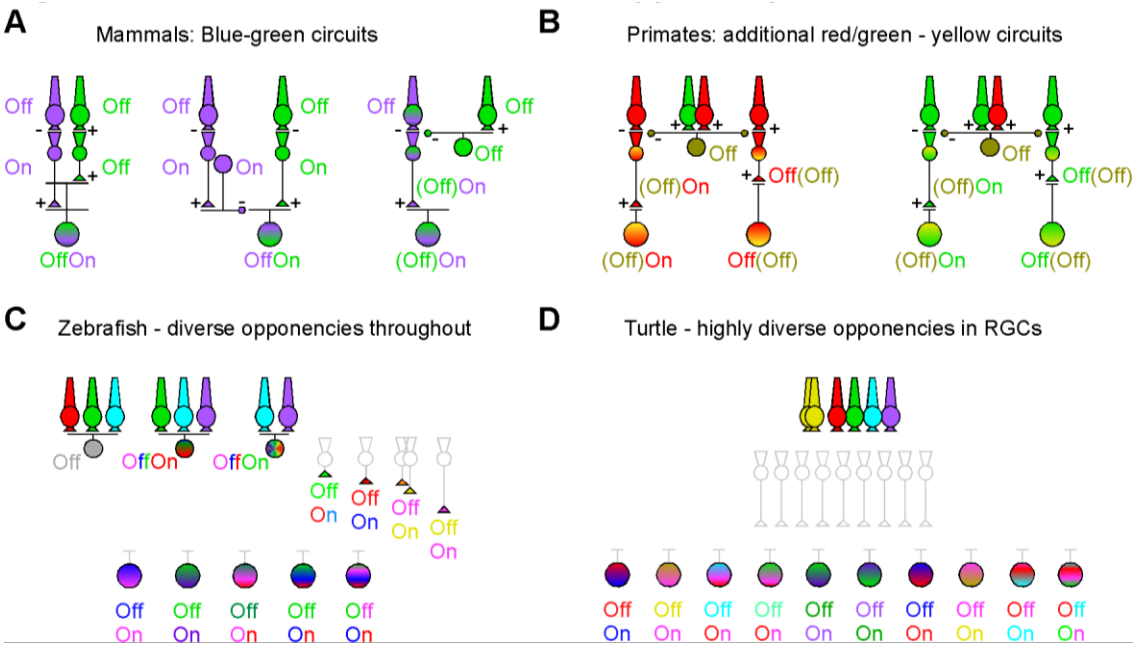


Figure 3 – *Circuit Motifs for Retinal Color Opponency*. A, blue-green (S-M) opponent circuits in mammals. Blue- and green-cone selective On- and Off-bipolar cells, respectively, can be differentially combined via a bistratified retinal ganglion cell (left). Similarly, sign inversion can occur via an S-On amacrine cell leading onto a monostratified retinal ganglion cell (centre). Moreover, sign inversion can occur in the outer retina via a green-dominated horizontal cell feeding into a blue-selective bipolar cell pathway (right). Reviewed in (Neitz & Neitz 2011). B, Primates can build red-yellow (left) or green-yellow (right) opponent midget circuits by pooling a red-green non-selective surround into individual red- or green cones by way of a horizontal cell. Reviewed in (Dacey 1996, Neitz & Neitz 2011). C, Zebrafish use at least three types of cone-selective horizontal cells to differentially poor across their tetrachromatic cone-complement. From here, retinal bipolar cells build diverse color-opponent responses at the level of their presynaptic terminals in the inner retina, and retinal ganglion cells show diverse and often complex chromatic opponencies. However, beyond photoreceptor connectivity patterns (see below) the specific functional and anatomical circuit principles that generate many of these responses are largely unknown. Reviewed in (Meier et al. 2018). D, Turtles are reported to combine their five cone-types into highly diverse retinal output channels that carry at least 12 color opponent signals to the brain (Rocha et al. 2008), but knowledge on the chromatic basis of turtle inner retinal circuits remains sparse.

Case studies of retinal circuits

The 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 specialisations, and at times ‘unusual solutions’

that need to be considered when aiming to synthesise known details of their circuits into a bigger picture. Here, we offer a brief introduction to some of these peculiarities.

Color processing in the peculiar retina of mice

Like all sensory systems, the mouse retina is exquisitely adapted to the mouse's sensory-ecological niche. As a crepuscular species that spends much time underground, mice are often active in the dim light, and rods make up >90% of all mouse photoreceptors - a proportion similar to that in primates including humans. Nonetheless, mice have a well-developed dichromatic cone system based on a UV cone (λ_{max} 360 nm) and an M cone (λ_{max} 508 nm) (Nikonov et al. 2006). As in primates, long-wavelength (M) cones outnumber short-wavelength (blue/UV) ones by over 10:1 (Wässle et al. 2009). In view of the greater abundance of green photons compared to blue/UV in natural light (Párraga et al. 1998), this makes sense, and much mouse vision uses a predominant green-driven luminance signal. The preponderance of green cones means that for color vision it is very important to build cone-selective circuits for the sparse blue system, but less important for the green system. Assuming equal gain of green and blue cone inputs (but see (Baden et al. 2013, Breuninger et al. 2011)) any randomly connecting bipolar- or horizontal cell will be green biased, simply because there are more green cones. This situation is complicated by a distinctive feature of the mouse retina: the dorso-ventral blue-green S-opsin co-expression gradient in "genetic M-cones" (Applebury et al. 2000, Baden et al. 2013, Roehlich et al. 1994, Szél et al. 1992). The ventral mouse retina, which views the sky, is dominated by M-cones that co-express both M- and S-opsins. Indeed, direct spectral sensitivity recordings from ventral co-expressing presumed M-cones reveal a short wavelength bias (Baden et al. 2013, Chapot et al. 2017a), implying that that the S-opsin co-expression is dominant, converting M-cones into 'functional S-cones'. Importantly, this co-expression ceases approximately at the visual horizon, leaving the dorsal retina - looking at the ground - with 'pure' green cones, expressing the LWS opsin interspersed with 'pure' blue cones.

The opsin co-expression gradient has several functional consequences for mouse color vision. Perhaps most importantly, the standard blue-green opponent system cannot work in the ventral retina as it does in the dorsal retina. At the very least, the

green signal is contaminated by enhanced blue sensitivity, and more likely the green component will be almost abolished. Given only traditional cone circuits, the ventral mouse retina would be color blind, but behavioural evidence is to the contrary (Denman et al. 2018). In fact, the mouse retina seems to use “green” rods to build opponency against the S-biased ventral M-cones (see below).

Next, an interesting type of spectral opponency arises at the boundary between the blue-dominated ventral retina and the green-dominated dorsal retina. Here large-field retinal ganglion cells that span both zones almost invariably receive a chromatically mixed input signal, which leads to centre-surround chromatic antagonism in ganglion cells near the visual horizon, without the need for any wiring specificity (Chang et al. 2013).

Overall, mice probably use a subset of the mammalian inner retinal pathways for color vision in their dorsal retina of those which have been characterized in other rodents, lagomorphs and primates. The presence of the opsin gradient markedly complicates things at the horizon and beyond but opens opportunities for exploiting chromatic contrasts by non-traditional circuit motifs. How these peculiarities translate to the brain and behaviour remains largely unclear (but see (Denman et al. 2018, Tan et al. 2015)). Notably, opsin co-expression gradients occur widely in terrestrial animals (e.g. (Sison-Mangus 2006)), and amongst mammals occur in species as diverse as hamsters and hyenas (Peichl 2005). A common feature of these seemingly disparate species is their need to survey the open sky for birds – be it for predator detection for the hamster or allowing the hyena to predict the location of prey or carrion by spotting vultures. In mice, in addition to shifting the spectral sensitivity of genetic M-cones ventral retina, S-opsin co-expression boosts the detection of achromatic dark contrasts (such as the silhouette of a bird in the sky) (Baden et al. 2013). Similar mechanisms may also be beneficial to hyenas and hamsters.

Color processing in the peculiar retina of trichromatic primates.

Next to mice, most knowledge about the retinal basis for vertebrate color vision is from trichromatic primates including humans (Dacey 1996, Neitz & Neitz 2011). Like many reptiles and birds and some fish, primates use a specialised acute zone or fovea for high spatial-acuity vision. As with the opsin co-expression gradient in mice,

the primate fovea engenders a range of behavioural and circuit peculiarities. First, since the fovea is only a degree or so across but allows much higher spatial acuity than the rest of the retina, foveated species use specialised eye-movement strategies which result in neuronal and attentional oversampling of the visual world at the fovea (Duncan & Boynton 2003), but, S-cones are absent from the *area centralis* (Roorda & Williams 1999). Consequently, any blue contribution to' chromatic contrasts at the fixation point relies on interpolation, which gives rise to a wealth of popular perceptual illusions. Outside the fovea, primates, like most mammals, have a low blue-cone density alongside a much higher green/red density (Martin & Grunert 1999) to compute long-versus-short chromatic contrasts along a blue-yellow axis. The cone-connectivity patterns of primate bipolar cells are broadly similar to those of mice, including the presence of an S-cone selective On-bipolar cell (Boycott & Wässle 1991, Dacey 1996), but unlike in mice, blue-yellow chromatic circuits are well-characterised for retinal ganglion cells (Calkins et al. 1998, Chichilnisky & Baylor 1999, Dacey 1996, 2000; Neitz & Neitz 2011). This exquisite account from primates, which is complemented by findings in a range of lagomorphs and rodents (see above) dominates the literature about short-versus-long wavelength retinal circuits in vertebrates. While this work provides a solid foundation for blue-green/yellow circuit-motifs in mammals, it is less clear to what extent this translates to non-mammalian groups.

Second, perhaps the most peculiar aspect of trichromatic primate color vision is their green (M) cone. Primate M cone opsin derives from an evolutionarily recent LWS-opsin gene-duplication (Mollon 1989, Nathans 1999), which leads to a fundamental wiring problem. Retinal circuits cannot easily distinguish primate L from M cones (but see (Field et al. 2010)), and thus lack developmentally programmed red- or green-only bipolar cell channels. Instead, chromatic selectivity depends on the presence or 'midget' bipolar- and ganglion cells (Kolb & Marshak 2003), which receive their centre input from a single cone. The surround in turn is spectrally non-selective between red and green. This single-cone-centre wiring motif produces four types of opponent midget signals, red^{ON}-yellow^{OFF}, green^{ON}-yellow^{OFF}, yellow^{ON}-red^{OFF} and yellow^{ON}-green^{OFF} (Fig. 3b), and cone-'clumping' (Hofer et al. 2005) means that this same motif can extend beyond the foveal centre (Martin et al. 2001). However, this strategy defers the disambiguation of red and green signals to the cortex, which

could generate chromatic selective neurons by activity dependent plasticity mechanisms (Doi et al. 2003, Wachtler et al. 2007). As such, unlike other cone-opponent mechanisms, key circuits underlying our ability to distinguish “red” from “green” lie beyond the retina. Interestingly, introducing an additional red-opsin into some mouse green cones leads to apparent trichromatic vision at the behavioural level (Jacobs et al. 2007, Smallwood et al. 2003) (but see (Makous 2007).

Color processing in non-mammalian vertebrates

As we have seen, vertebrates opsins belong to for main families which evolved some 500 million years ago in jawless fish (Collin et al. 2009). Retinal circuitry probably has a similarly conservative *bauplan*, perhaps including chromatic opponent pathways, such as the mammalian blue^{ON} system. However so far knowledge of this aspect of retinal processing is mainly limited to work in teleost fish - notably the cyprinids zebrafish and goldfish, and rainbow trout, e.g. (Meier et al. 2018), Fig. 3c -, reptiles (mostly turtles, Fig. 3d: (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 electrophysiological techniques, which provide detail on single neurons, but have not delivered a comprehensive overview of retinal channels for color vision of any one retina. As such although there are some key studies of the retinal basis of vertebrate color vision (D’Orazi et al. 2016, Li et al. 2009), a coherent picture is yet to emerge.

Nevertheless, it is clear that species with diverse cone types such as the turtle with five cone types and the goldfish with four have a retinal complement of chromatic neurons far exceeding that of mammals - or indeed theoretical prediction (see above). For example, at least 12 color opponent retinal ganglion cells have been described in the turtle (*Trachemys scripta*) (Rocha et al. 2008, Ventura et al. 2001) (Fig. 3d), while teleosts including goldfish, zebrafish, carp and trout display complex chromatic responses even at the level of horizontal cells (Connaughton & Nelson 2010, Kamermans et al. 1991, Meier et al. 2018, Twig & Perlman 2004, Twig et al. 2003). Nonetheless, more coherent picture of the retinal basis for color vision is emerging in at least one tetrachromatic vertebrate: the zebrafish (Fig. 3c).

672 *Color processing in the peculiar retina of zebrafish*

673 Like many shallow-water teleosts, zebrafish use four ancient cone types for color
674 vision: red, green, blue and UV, which in adults form a crystalline mosaic with a
675 stoichiometry of 2:2:1:1, respectively (Allison et al., Engström 1960). Each cone type
676 is genetically distinct, allowing developmentally hardwired retinal circuits (D'Orazi et
677 al. 2016, Li et al. 2009) in any of 24 theoretically possible chromatic combinations (or
678 81 if differentiating On and Off connections). Yet, partly in line with arguments on
679 chromatic redundancy (above), most combinations appear to not be absent. Instead,
680 cone-selective wiring appears to be mainly restricted to spectral 'blocks' rather than
681 'jumps' (Fig. 4). For example, horizontal cell types make selective connections to
682 chromatically neighbouring cones ('blocks'): R+G+B, G+B+U and B+U (Klaassen et
683 al. 2016, Song et al. 2008). In contrast wiring "jumps" (e.g. to R+B but skipping G)
684 are absent. Bipolar cells follow the same principle (Fig. 4b). For comparison, the two
685 cone types of mice and failure to distinguish G and R cones in primates means that
686 also these setups by definition must use blocks ('jumping' requires at least 3 cones)
687 (Fig. 4a). This 'block-wiring principle' of retinal chromatic circuits is untested in any
688 other group, but it is worth noting that on a functional level, bipolar and retinal
689 ganglion cells of non-mammalian species tend to favour long-vs-short wavelength
690 computations, consistent with chromatic block-wiring in the outer retina (Rocha et al.
691 2008, Zimmermann et al. 2018).

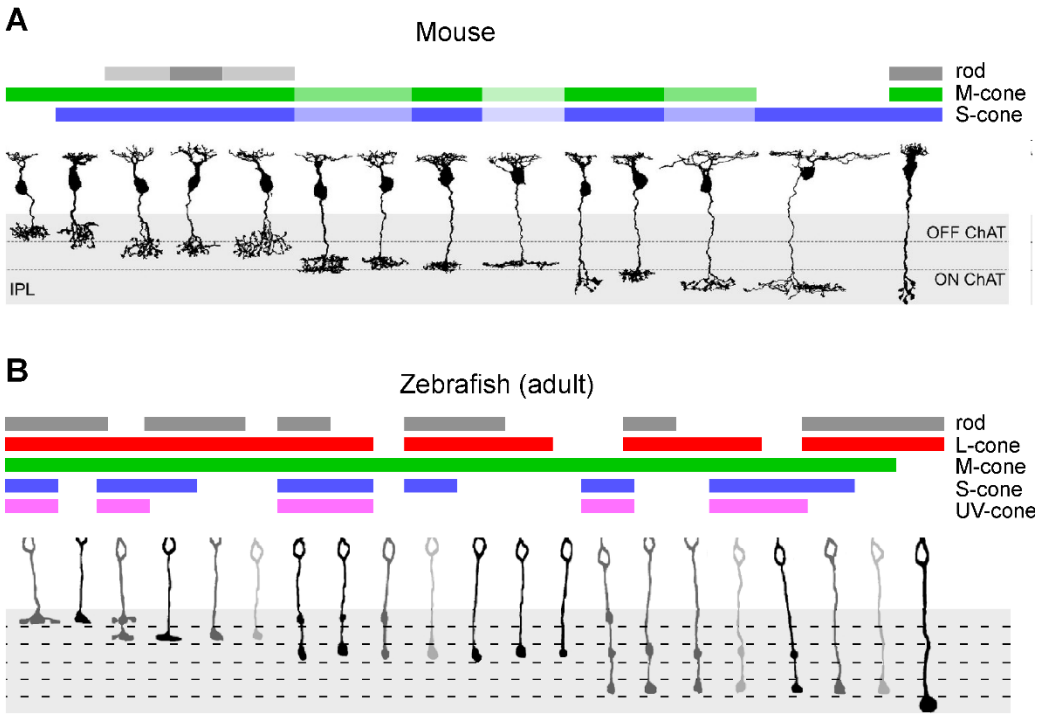


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Figure 4 – *Wiring photoreceptors to bipolar cells*. A, The 14 types of bipolar cells of the mouse retina mostly make cone-type non-selective contacts in the outer retina. Only types 1 (left-most) and 9 (2nd from right) bipolar cells make selective contacts with M- and S-cones, respectively. Rods are contacted by a subset of Off-bipolar cells and rod bipolar cells. Modified from (Behrens et al. 2016). B, Adult zebrafish have 20+ bipolar cells that make diverse sets of contacts across its four cone- and one rod type in the outer retina. Based on (Li et al. 2009).

Simply knowing the anatomical wiring is however insufficient for defining chromatic circuits: After all, opponency requires the combination of differentially tuned pathways with opposite signs, which are difficult to identify from anatomy alone. Here, some understanding of the chromatic physiology of the zebrafish retina is beginning to emerge. Single unit electrophysiological recordings from throughout the zebrafish retina from horizontal cells to ganglion cells, all reveal a rich complement of chromatic opponencies (Connaughton & Nelson 2010, 2015; Klaassen et al. 2016, Torvund et al. 2017).

Regional specialisations in juvenile zebrafish retina

Even if retinal circuits for color vision of the adult zebrafish are reasonably typical of teleosts of similar habitat and lifestyle, whether the same circuitry is present in the larva remains unknown. Building on the wealth of single-cell physiology from both adults and larvae, a recent survey used 2-photon calcium imaging to record the chromatic response properties of some 4,000 larval zebrafish bipolar cells (Zimmermann et al. 2018). Eight-day post fertilization zebrafish larvae have about 10,000 cones in each retina, and single-synapse resolution functional measurements can be made *in vivo*, in any part of the eye. The survey revealed that chromatic processing in the inner retina of larval zebrafish is not only very rich indeed, but perhaps more intriguingly, differs dramatically across the visual field. For example, at the visual horizon bipolar cells encode several varieties of mostly short-vs-long wavelength chromatic opponency while the temporo-ventral retina that views the world just above the horizon in front of the animal, was dominated by UV^{ON} responses despite the presence of all cone-types in this part of the eye. In addition, ventral visual circuits, which survey the sky through Snell's window, were all but color-blind, probably because there is little chromatic information here. This forms an

interesting parallel with the mouse, where cone-only dichromacy also disappears above the horizon.

Where present, in larval zebrafish bipolar cells encoding color opponent or chromatically biased physiologies are systematically distributed into specific layers of the inner retina. For example, layers 1 and 3 of the dorsal retina were dominated by RG vs BU and R vs GBU color opponent responses. Accordingly, retinal ganglion cells that project specifically to these layers should inherit a similar physiology (Connaughton & Nelson 2015, Meier et al. 2018), thus leading to color opponent brain projections that are established already at the second synapse of the visual system. This is corroborated by bipolar recordings in other non-mammalian retinas: mudpuppies, turtles, goldfish and giant danio (*Devario aequipinnatus*) all have fully color opponent bipolar cells (Stell 1978, Werblin & Dowling 1969, Wong & Dowling 2005, Yazulla 1976). Clearly much color opponency is already present at the level of the input to retinal ganglion cells.

Rod-based color vision

Rods are generally inactive at high (photopic) light levels, but in mesopic conditions, when both rod and cone systems are simultaneously active, rod-cone chromatic antagonism can occur. This co-activity regime of rods and cones 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 green cones. Accordingly, rod-driven networks can provide green antagonism. In the ventral mouse retina, this system appears to be exploited by at least one type of retinal ganglion cell (Joesch & Meister 2016), and it seems likely that further circuits in both mice and other species use rod signals (Baden et al. 2016, Field et al. 2009, Reitner et al. 1991). Rod-cone opponency might support some form of color vision in cone-monochromats such as most sharks, marine mammals and or racoons (Griebel & Peichl 2003, Oppermann et al. 2016, Peichl 2005, Von Schantz et al. 1997). However, since most cone-monochromats use green cones which overlap strongly in spectral sensitivity with rods, it remains unclear how much chromatic contrast might be available. Beyond building rod-cone opponent networks, some species even feature two types of spectrally distinct rods, and there is evidence for rod-rod

759 opponency allowing color vision at low light levels (Denton & Wyllie 1955, Hailman
760 1976, Korenyak & Govardovskii 2013, Yovanovich et al. 2017).

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762

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REFERENCES

Allison WT, Barthel LK, Skebo KM, Takechi M, Kawamura S, Raymond PA. Ontogeny of cone photoreceptor mosaics in zebrafish. *J. Comp. Neurol.* 518(20):4182–95

Applebury M., Antoch M., Baxter L., Chun LL., Falk J., et al. 2000. The Murine Cone Photoreceptor: A Single Cone Type Expresses Both S and M Opsins with Retinal Spatial Patterning. *Neuron*. 27(3):513–23

Appudurai AM, Hart NS, Zurr I, Collin SP. 2016. Morphology, Characterization and Distribution of Retinal Photoreceptors in the South American (Lepidosiren paradoxa) and Spotted African (Protopterus dolloi) Lungfishes. *Front. Ecol. Evol.*

Arnold K, Neumeyer C. 1987. Wavelength discrimination in the turtle Pseudemys scripta elegans. *Vision Res.*

Arshavsky VY, Lamb TD, Pugh EN. 2002. G proteins and phototransduction. *Annu. Rev. Physiol.* 64:153–87

Atick JJ, Li Z, Redlich AN. 1992. Understanding Retinal Color Coding from First Principles. *Neural Comput.*

Autrum H, Zwehl V v. 1964. Die spektrale Empfindlichkeit einzelner Sehzellen des Bienenauges. *Zeitschrift f??r Vergleichende Physiol.*

Baddeley RJ, Osorio D, Jones CD. 2007. Generalization of Color by Chickens: Experimental Observations and a Bayesian Model. *Am. Nat.*

Baden T, Berens P, Franke K, Román Rosón M, Bethge M, Euler T. 2016. The functional diversity of retinal ganglion cells in the mouse. *Nature*. 529(7586):345–50

Baden T, Schubert T, Berens P, Euler T. 2018. The Functional Organization of

797 Vertebrate Retinal Circuits for Vision. *Oxford Res. Encycl. Neurosci.*

798 Baden T, Schubert T, Chang L, Wei T, Zaichuk M, et al. 2013. A tale of two retinal
799 domains: near-optimal sampling of achromatic contrasts in natural scenes
800 through asymmetric photoreceptor distribution. *Neuron*. 80(5):1206–17

801 Barlow HB. 1982. What causes trichromacy? A theoretical analysis using comb-
802 filtered spectra. *Vision Res.*

803 Barlow HBH. 1961. Possible principles underlying the transformation of sensory
804 messages. In *Sensory Communication*, pp. 217–34

805 Becker D, Bonness V, Mobbs P. 1998. Cell Coupling in the retina: Patterns and
806 Purpose. *Cell Biol. Int.* 22(11–12):781–92

807 Behrens C, Schubert T, Haverkamp S, Euler T, Berens P, et al. 2016. Connectivity
808 map of bipolar cells and photoreceptors in the mouse retina. *Elife*. 5:1206–17

809 Bowmaker JK. 1984. Microspectrophotometry of vertebrate photoreceptors. A brief
810 review

811 Bowmaker JK. 2008. Evolution of vertebrate visual pigments. *Vision Res.*

812 Bowmaker JK, Heath LA, Wilkie SE, Hunt DM. 1997. Visual pigments and oil
813 droplets from six classes of photoreceptor in the retinas of birds. *Vision Res.*

814 Bowmaker JK, Loew ER, Ott M. 2005. The cone photoreceptors and visual pigments
815 of chameleons. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav.*
816 *Physiol.*

817 Boycott BB, Wässle H. 1991. Morphological classification of bipolar cells of the
818 primate retina. *Europ.J.Neurosci.* 3:1069–88

819 Brainard DH, Stockman A. 2010. Colorimetry. In *OSA Handbook of Optics (3rd*
820 *Edition, M. Bass, Ed)*

821 Breuninger T, Puller C, Haverkamp S, Euler T. 2011. Chromatic bipolar cell
822 pathways in the mouse retina. *J. Neurosci.* 31(17):6504–17

823 Buchsbaum G, Gottschalk a. 1983. Trichromacy, opponent colours coding and
824 optimum colour information transmission in the retina. *Proc. R. Soc. Lond. B.*
825 *Biol. Sci.* 220(1218):89–113

826 Calkins DJ, Tsukamoto Y, Sterling P. 1998. Microcircuitry and mosaic of a blue-
827 yellow ganglion cell in the primate retina. *J. Neurosci.* 18(9):3373–85

828 Caves EM, Green PA, Zipple MN, Peters S, Johnsen S, Nowicki S. 2018.
829 Categorical perception of colour signals in a songbird

830 Champ CM, Vorobyev M, Marshall NJ. 2016. Colour thresholds in a coral reef fish.
831 *R. Soc. Open Sci.*

832 Chang L, Breuninger T, Euler T. 2013. Chromatic Coding from Cone-type
833 Unselective Circuits in the Mouse Retina. *Neuron*. 77(3):559–71

834 Chapot CA, Behrens C, Rogerson LE, Baden T, Pop S, et al. 2017a. Local Signals in
835 Mouse Horizontal Cell Dendrites. *Curr. Biol.*

836 Chapot CA, Euler T, Schubert T. 2017b. How do horizontal cells 'talk' to cone
837 photoreceptors? Different levels of complexity at the cone-horizontal cell
838 synapse. *J. Physiol.* 595(16):5495–5506

839 Cheney KL, Newport C, McClure EC, Marshall NJ. 2013. Colour vision and response
840 bias in a coral reef fish. *J. Exp. Biol.*

841 Chichilnisky EJ, Baylor D a. 1999. Receptive-field microstructure of blue-yellow
842 ganglion cells in primate retina. *Nat. Neurosci.* 2(10):889–93

843 Chinen A, Hamaoka T, Yamada Y, Kawamura S. 2003. Gene duplication and
844 spectral diversification of cone visual pigments of zebrafish. *Genetics*.

163(2):663–75

Chittka L, Faruq S, Skorupski P, Werner A. 2014. Colour constancy in insects

Clarke GL. 1936. On the Depth at Which Fish Can See. *Ecology*. 17(3):452–56

Collin SP, Davies WL, Hart NS, Hunt DM. 2009. The evolution of early vertebrate photoreceptors. *Philos. Trans. R. Soc. B Biol. Sci.* 364(1531):2925–40

Connaughton VP, Nelson R. 2010. Spectral Responses in Zebrafish Horizontal Cells Include a Tetraphasic Response and a Novel UV-Dominated Triphasic Response. *J. Neurophysiol.* 104(5):2407–22

Connaughton VP, Nelson R. 2015. Ultraviolet dominates ganglion cell responses in larval zebrafish. *Invest. Ophthalmol. Vis. Sci*, p. 3251

Cook JE, Becker DL. 1995. Gap junctions in the vertebrate retina [review]. *Microsc. Res. Tech.* 31(5):408–19

Cronin H. 1991. The Ant and the Peacock. In *The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today*

Crook JD, Davenport CM, Peterson BB, Packer OS, Detwiler PB, Dacey DM. 2009. Parallel ON and OFF cone bipolar inputs establish spatially coextensive receptive field structure of blue-yellow ganglion cells in primate retina. *J. Neurosci.* 29(26):8372–87

Crook JD, Manookin MB, Packer OS, Dacey DM. 2011. Horizontal cell feedback without cone type-selective inhibition mediates “red-green” color opponency in midget ganglion cells of the primate retina. *J. Neurosci.* 31(5):1762–72

D’Orazi FD, Zhao XF, Wong RO, Yoshimatsu T. 2016. Mismatch of Synaptic Patterns between Neurons Produced in Regeneration and during Development of the Vertebrate Retina. *Curr. Biol.* 26(17):2268–79

869 Dacey DM. 1996. Circuitry for color coding in the primate retina. *Proc.R.Soc.Lond.B.*
870 93(2):582–88

871 Dacey DM. 1999. Primate retina: cell types, circuits and color opponency. *Prog.*
872 *Retin. Eye Res.* 18(6):737–63

873 Dacey DM. 2000. Parallel pathways for spectral coding in primate retina. *Annu. Rev.*
874 *Neurosci.* 23:743–75

875 Dacey DM, Lee BB. 1994. The “blue-on” opponent pathway in primate retina
876 originates from a distinct bistratified ganglion cell type. *Nature*. 367(6465):731–
877 35

878 Dacheux RF, Raviola E. 1982. Horizontal cells in the retina of the rabbit. *J. Neurosci.*
879 2(10):1486–93

880 Dalton BE, Loew ER, Cronin TW, Carleton KL. 2014. Spectral tuning by opsin
881 coexpression in retinal regions that view different parts of the visual field. *Proc.*
882 *R. Soc. B Biol. Sci.* 281(1797):20141980–20141980

883 Darwin C. 1859. On the Origin of Species by Means of Natural Selection

884 Davies WIL, Collin SP, Hunt DM. 2012. Molecular ecology and adaptation of visual
885 photopigments in craniates

886 Denman DJ, Luviano JA, Ollerenshaw DR, Cross S, Williams D, et al. 2018. Mouse
887 color and wavelength-specific luminance contrast sensitivity are non-uniform
888 across visual space. *Elife*. 7:

889 Denton EJ, Wyllie JH. 1955. Study of the photosensitive pigments in the pink and
890 green rods of the frog. *J. Physiol.* 127(1):81–89

891 Derrington AM, Krauskopf J, Lennie P. 1984. Chromatic mechanisms in lateral
892 geniculate nucleus of macaque. *J. Physiol.*

893 Doi E, Inui T, Lee TW, Wachtier T, Sejnowski TJ. 2003. Spatiochromatic receptive
894 field properties derived from information-theoretic analyses of cone mosaic
895 responses to natural scenes. *Neural Comput.*

896 Dörr S, Neumeyer C. 2000. Color constancy in goldfish: The limits. *J. Comp. Physiol.*
897 *- A Sensory, Neural, Behav. Physiol.*

898 Duncan RO, Boynton GM. 2003. Cortical Magnification within Human Primary Visual
899 Cortex Correlates with Acuity Thresholds. *Neuron*. 38(4):659–71

900 Engström K. 1960. Cone types and cone arrangements in the retina of some
901 cyprinids. *Acta Zool*. 41:277–295

902 Engström K. 1963. Cone types and cone arrangements in teleost retinae

903 Enright JM, Toomey MB, Sato SY, Temple SE, Allen JR, et al. 2015. Cyp27c1 red-
904 shifts the spectral sensitivity of photoreceptors by converting Vitamin A1 into A2.
905 *Curr. Biol.* 25(23):3048–57

906 Euler T, Haverkamp S, Schubert T, Baden T. 2014. Retinal bipolar cells: Elementary
907 building blocks of vision. *Nat. Rev. Neurosci.* 15(8):

908 Field GD, Gauthier JL, Sher A, Greschner M, Machado TA, et al. 2010. Functional
909 connectivity in the retina at the resolution of photoreceptors. *Nature*.
910 467(7316):673–77

911 Field GD, Greschner M, Gauthier JL, Rangel C, Shlens J, et al. 2009. High-
912 sensitivity rod photoreceptor input to the blue-yellow color opponent pathway in
913 macaque retina. *Nat. Neurosci.* 12(9):1159–64

914 Gegenfurtner KR, Kiper DC. 2003. C <scp>OLOR</scp> V <scp>ISION</scp>.
915 *Annu. Rev. Neurosci.*

916 Goldsmith TH, Butler BK. 2003. The roles of receptor noise and cone oil droplets in

the photopic spectral sensitivity of the budgerigar, Melopsittacus undulatus. *J. Comp. Physiol. A*

Goodchild AK, Chan TL, Grünert U. 1996. Horizontal cell connections with short-wavelength-sensitive cones in macaque monkey retina. *Vis. Neurosci.* 13(5):833–45

Govardovskii VI, Fyhrquist N, Reuter T, Kuzmin DG, Donner K. 2000. In search of the visual pigment template. *Vis. Neurosci.*

Griebel U. 2002. Color Vision in Marine Mammals: A Review. In *The Vienna School of Marine Biology: A Tribute to Jörg Ott*

Griebel U, Peichl L. 2003. Colour vision in aquatic mammals—facts and open questions. *Aquat. Mamm.* 291:18–30

Hailman JP. 1976. Oildroplets in the eyes of adult anuran amphibians: A comparative survey. *J. Morphol.* 148(4):453–68

Hart NS. 2001. The visual ecology of avian photoreceptors

Hart NS, Hunt DM. 2007. Avian Visual Pigments: Characteristics, Spectral Tuning, and Evolution. *Am. Nat.*

Hart NS, Vorobyev M. 2005. Modelling oil droplet absorption spectra and spectral sensitivities of bird cone photoreceptors. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.*

Hofer H, Carroll J, Neitz J, Neitz M, Williams DR. 2005. Organization of the Human Trichromatic Cone Mosaic. *J. Neurosci.* 25(42):9669–79

Hurvich LM, Jameson D. 1957. An opponent-process theory of color vision. *Psychol. Rev.* 64, Part 1(6):384–404

Jackman SL, Babai N, Chambers JJ, Thoreson WB, Kramer RH. 2011. A Positive

941 Feedback Synapse from Retinal Horizontal Cells to Cone Photoreceptors. *PLoS*
942 *Biol.* 9(5):e1001057

943 Jacobs G. 1981. *Comparative Color Vision*. Academic Press

944 Jacobs G. 2008. Primate color vision: a comparative perspective. *Vis. Neurosci.*

945 Jacobs G, Williams G, Cahill H, Nathans J. 2007. Emergence of novel color vision in
946 mice engineered to express a human cone photopigment. *Science (80-.).*

947 Jiao Y, Lau T, Hatzikirou H, Meyer-Hermann M, Corbo JC, Torquato S. 2014. Avian
948 photoreceptor patterns represent a disordered hyperuniform solution to a
949 multiscale packing problem. *Phys. Rev. E - Stat. Nonlinear, Soft Matter Phys.*

950 Joesch M, Meister M. 2016. A neuronal circuit for colour vision based on rod–cone
951 opponency. *Nature*. 532(7598):236–39

952 Jones CD, Osorio D. 2004. Discrimination of oriented visual textures by poultry
953 chicks. *Vision Res.*

954 Jones CD, Osorio D, Baddeley RJ. 2001. Colour categorization by domestic chicks.
955 *Proc. R. Soc. B Biol. Sci.*

956 Kamermans M, Fahrenfort I, Schultz K, Janssen-Bienhold U, Sjoerdsma T, Weiler R.
957 2001. Hemichannel-mediated inhibition in the outer retina. *Science (80-.).*

958 Kamermans M, van Dijk BW, Spekreijse H. 1991. Color opponency in cone-driven
959 horizontal cells in carp retina. Aspecific pathways between cones and horizontal
960 cells. *J. Gen. Physiol.* 97(4):819–43

961 Kelber A, Osorio D. 2010. From spectral information to animal colour vision:
962 Experiments and concepts. *Proc. R. Soc. B Biol. Sci.*

963 Kelber A, Vorobyev M, Osorio D. 2003. Animal colour vision - Behavioural tests and
964 physiological concepts

965 Kemmler R, Schultz K, Dedek K, Euler T, Schubert T. 2014. Differential regulation of
966 cone calcium signals by different horizontal cell feedback mechanisms in the
967 mouse retina. *J. Neurosci.* 34(35):11826–43

968 Klaassen LJ, de Graaff W, van Asselt JB, Klooster J, Kamermans M. 2016. Specific
969 connectivity between photoreceptors and horizontal cells in the zebrafish retina.
970 *J. Neurophysiol.* 116(6):2799–2814

971 Kolb H, Marshak D. 2003. The midget pathways of the primate retina. *Doc.*
972 *Ophthalmol.* 106(1):67–81

973 Korenyak DA, Govardovskii VI. 2013. Photoreceptors and visual pigments in three
974 species of newts. *J. Evol. Biochem. Physiol.* 49(4):399–407

975 Kram YA, Mantey S, Corbo JC, Hart N, Bowmaker J, et al. 2010. Avian cone
976 photoreceptors tile the retina as five independent, self-organizing mosaics.
977 *PLoS One*. 5(2):e8992

978 Krauskopf J, Williams DR, Heeley DW. 1982. Cardinal directions of color space.
979 *Vision Res.* 22(9):1123–31

980 Lamb TD. 2013. Evolution of phototransduction, vertebrate photoreceptors and
981 retina

982 Lee BB, Cooper B, Cao D. 2017. The spatial structure of cone-opponent receptive
983 fields in macaque retina. *Vision Res.*

984 Lee BB, Pokorny J, Smith VC, Martin PR, Valberg a. 1990. Luminance and
985 chromatic modulation sensitivity of macaque ganglion cells and human
986 observers. *J. Opt. Soc. Am. Opt. Image Sci. Vis.*

987 Li W, DeVries SH. 2006. Bipolar cell pathways for color and luminance vision in a
988 dichromatic mammalian retina. *Nat. Neurosci.* 9(5):669–75

Li YN, Matsui JI, Dowling JE. 2009. Specificity of the horizontal cell-photoreceptor connections in the zebrafish (Danio rerio) retina. *J. Comp. Neurol.* 516(5):442–53

Lind O, Henze MJ, Kelber A, Osorio D. 2017. Coevolution of coloration and colour vision? *Philos. Trans. R. Soc. B Biol. Sci.*

Livingstone M, Hubel D. 1988. Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science (80-.).*

Loew ER, Dartnall HJA. 1976. Vitamin A1/A2-based visual pigment mixtures in cones of the rudd. *Vision Res.* 16(9):891–96

Loew ER, Fleishman LJ, Foster RG, Provencio I. 2002. Visual pigments and oil droplets in diurnal lizards: A comparative study of Caribbean anoles. *J. Exp. Biol.*

Loew ER, Lythgoe JN. 1985. The ecology of colour vision. *Endeavour*

Lubbock J. 1882. *Ants, Bees and Wasps. A Record of Observations on the Habits of the Social Hymenoptera*

Lubbock SJ. 1889. *On the Senses, Instincts, and Intelligence of Animals, with Special Reference to Insects. 292 Pages, 118 Figures. London: Kegan Paul, Trench*. London, UK: Kegan Paul

Luk HL, Bhattacharyya N, Montisci F, Morrow JM, Melaccio F, et al. 2016. Modulation of thermal noise and spectral sensitivity in Lake Baikal cottoid fish rhodopsins. *Sci. Rep.*

Makous W. 2007. Comment on "Emergence of Novel Color Vision in Mice Engineered to Express a Human Cone Photopigment" *Science (80-.).* 318(5848):196b–196b

1013 Maloney LT. 1986. Evaluation of linear models of surface spectral reflectance with
1014 small numbers of parameters. *J. Opt. Soc. Am. A*

1015 Martin PR, Grunert U. 1999. Analysis of the short wavelength-sensitive (“blue”) cone
1016 mosaic in the primate retina: Comparison of New World and Old World
1017 monkeys. *J. Comp. Neurol.* 406(1):1–14

1018 Martin PR, Lee BB, White AJR, Solomon SG, Rüttiger L. 2001. Chromatic sensitivity
1019 of ganglion cells in the peripheral primate retina. *Nature*. 410(6831):933–36

1020 Meier A, Nelson R, Connaughton VP. 2018. Color Processing in Zebrafish Retina.
1021 *Front. Cell. Neurosci.*

1022 Meredith RW, Gatesy J, Emerling CA, York VM, Springer MS. 2013. Rod
1023 Monochromacy and the Coevolution of Cetacean Retinal Opsins. *PLoS Genet.*
1024 9(4):e1003432

1025 Mills SL, Tian L-M, Hoshi H, Whitaker CM, Massey SC. 2014. Three distinct blue-
1026 green color pathways in a mammalian retina. *J. Neurosci.* 34(5):1760–68

1027 Mollon JD. 1989. “Tho” she kneel’d in that plaace where they grew...’ . *J. Exp. Biol.*

1028 Mollon JD. 2003. *Introduction: Thomas Young and the Trichromatic Theory of Colour*
1029 *Vision. In Normal and Defective Colour Vision*. Oxord University Press

1030 Mullen KT, Losada M a. 1994. Evidence for separate pathways for color and
1031 luminance detection mechanisms. *J. Opt. Soc. Am. A*

1032 Nathans J. 1999. The Evolution and Physiology of Human Review Color Vision:
1033 Insights from Molecular Genetic Studies of Visual Pigments. *Neuron*. 24:299–
1034 312

1035 Nathans J, Thomas D, Hogness D. 1986. Molecular genetics of human color vision:
1036 the genes encoding blue, green, and red pigments. *Science (80-.).*

1037 Neitz J, Neitz M. 2011. The genetics of normal and defective color vision. *Vision*
1038 *Res.* 51(7):633–51

1039 Neumeyer C. 1986. Wavelength discrimination in the goldfish. *J. Comp. Physiol. A*

1040 Neumeyer C. 1992. Tetrachromatic color vision in goldfish: evidence from color
1041 mixture experiments. *J. Comp. Physiol. A*

1042 Neumeyer C, Arnold K. 1989. Tetrachromatic color vision in the goldfish becomes
1043 trichromatic under white adaptation light of moderate intensity. *Vision Res.*

1044 Nikonov SS, Kholodenko R, Lem J, Pugh EN. 2006. Physiological Features of the S-
1045 and M-cone Photoreceptors of Wild-type Mice from Single-cell Recordings. *J.*
1046 *Gen. Physiol.* 127(4):359–74

1047 Ödeen A, Håstad O. 2003. Complex distribution of avian color vision systems
1048 revealed by sequencing the SWS1 opsin from total DNA. *Mol. Biol. Evol.*

1049 Okano T, Yoshizawa T, Fukada Y. 1994. Pinopsin is a chicken pineal photoreceptive
1050 molecule. *Nature*

1051 Olsson P, Lind O, Kelber A. 2015. Bird colour vision: behavioural thresholds reveal
1052 receptor noise. *J. Exp. Biol.*

1053 Olsson P, Lind O, Kelber A. 2018. Chromatic and achromatic vision: Parameter
1054 choice and limitations for reliable model predictions

1055 Olsson P, Wilby D, Kelber A. 2016. Quantitative studies of animal colour constancy:
1056 Using the chicken as model. *Proc. R. Soc. B Biol. Sci.*

1057 Oppermann D, Schramme J, Neumeyer C. 2016. Rod-cone based color vision in
1058 seals under photopic conditions. *Vision Res.*

1059 Orger MB, Baier H. 2005. Channeling of red and green cone inputs to the zebrafish
1060 optomotor response. *Vis. Neurosci.* 22(3):275–81

1061 Osorio D, Ham a D. 2002. Spectral reflectance and directional properties of
1062 structural coloration in bird plumage. *J. Experimantal Biol.*

1063 Osorio D, Ruderman DL, Cronin TW. 1998. Estimation of errors in luminance signals
1064 encoded by primate retina resulting from sampling of natural images with red
1065 and green cones. *J. Opt. Soc. Am. a-Optics Image Sci. Vis.* 15(1):16–22

1066 Osorio D, Vorobyev M. 1996. Colour vision as an adaptation to frugivory in primates.
1067 *Proc. R. Soc. B Biol. Sci.*

1068 Osorio D, Vorobyev M. 2008. A review of the evolution of animal colour vision and
1069 visual communication signals. *Vision Res.*

1070 Osorio D, Vorobyev M, Jones CD. 1999. Colour vision in domestic chicks. *J. Exp.*
1071 *Biol.*

1072 Packer OS, Verweij J, Li PH, Schnapf JL, Dacey DM. 2010. Blue-yellow opponency
1073 in primate S cone photoreceptors. *J. Neurosci.* 30(2):568–72

1074 Palacios AG, Varela FJ, Srivastava R, Goldsmith TH. 1998. Spectral sensitivity of
1075 cones in the goldfish, Carassius auratus. *Vision Res.*

1076 Párraga C a, Brelstaff G, Troscianko T, Moorehead IR. 1998. Color and luminance
1077 information in natural scenes. *J. Opt. Soc. Am. A. Opt. Image Sci. Vis.*
1078 15(3):563–69

1079 Parry JWL, Carleton KL, Spady T, Carboo A, Hunt DM, Bowmaker JK. 2005. Mix
1080 and match color vision: Tuning spectral sensitivity by differential opsin gene
1081 expression in Lake Malawi cichlids. *Curr. Biol.*

1082 Patel JS, Brown CJ, Ytreberg FM, Stenkamp DL. 2018. Predicting peak spectral
1083 sensitivities of vertebrate cone visual pigments using atomistic molecular
1084 simulations. *PLoS Comput. Biol.*

1085 Peichl L. 2005. Diversity of mammalian photoreceptor properties: adaptations to
1086 habitat and lifestyle? *Anat. Rec. A. Discov. Mol. Cell. Evol. Biol.* 287(1):1001–12

1087 Perlman I, Weiner E, Kolb H. 2009. Retinal Horizontal Cells. *Encycl. Neurosci.* 233–
1088 43

1089 Pignatelli V, Champ C, Marshall J, Vorobyev M. 2010. Double cones are used for
1090 colour discrimination in the reef fish, rhinecanthus aculeatus. *Biol. Lett.*

1091 Porter ML, Cronin TW, McClellan DA, Crandall KA. 2007. Molecular characterization
1092 of crustacean visual pigments and the evolution of pancrustacean opsins. *Mol.*
1093 *Biol. Evol.*

1094 Potier S, Mitkus M, Kelber A. 2018. High resolution of colour vision, but low contrast
1095 sensitivity in a diurnal raptor. *Proc. R. Soc. London B Biol. Sci.*

1096 Prum RO. 2012. Aesthetic evolution by mate choice: Darwin's really dangerous idea

1097 Raymond PA, Barthel LK, Rounsifer ME, Sullivan SA, Knight JK. 1993. Expression
1098 of rod and cone visual pigments in goldfish and zebrafish: A rhodopsin-like gene
1099 is expressed in cones. *Neuron*

1100 Reitner A, Sharpe LT, Zrenner E. 1991. Is colour vision possible with only rods and
1101 blue-sensitive cones?

1102 Remy M, Emmerton J. 1989. Behavioral Spectral Sensitivities of Different Retinal
1103 Areas in Pigeons. *Behav. Neurosci.*

1104 Rister J, Desplan C. 2011. The retinal mosaics of opsin expression in invertebrates
1105 and vertebrates

1106 Rocha FAF, Saito CA, Silveira LCL, De Souza JM, Ventura DF. 2008. Twelve
1107 chromatically opponent ganglion cell types in turtle retina. *Vis. Neurosci.*
1108 25(3):307–15

1109 Roehlich P, Van Veen T, Szél A. 1994. Two different visual pigments in one retinal
1110 cone cell. *Neuron*. 13(5):1159–66

1111 Roorda a, Williams DR. 1999. The arrangement of the three cone classes in the
1112 living human eye. *Nature*. 397(6719):520–22

1113 Shand J, Davies WL, Thomas N, Balmer L, Cowing JA, et al. 2008. The influence of
1114 ontogeny and light environment on the expression of visual pigment opsins in
1115 the retina of the black bream, Acanthopagrus butcheri. *J. Exp. Biol.*

1116 Sher A, DeVries SH. 2012. A non-canonical pathway for mammalian blue-green
1117 color vision. *Nat. Neurosci.* 15(7):952–53

1118 Siebeck UE, Marshall NJ. 2001. Ocular media transmission of coral reef fish--can
1119 coral reef fish see ultraviolet light? *Vision Res.* 41(2):133–49

1120 Simoncelli EP, Olshausen BA. 2001. Natural image statistics and neural
1121 representation. *Annu Rev Neurosci*. 24:1193–1216

1122 Sison-Mangus MP. 2006. Beauty in the eye of the beholder: the two blue opsins of
1123 lycaenid butterflies and the opsin gene-driven evolution of sexually dimorphic
1124 eyes. *J. Exp. Biol.*

1125 Smallwood PM, Olveczky BP, Williams GL, Jacobs GH, Reese BE, et al. 2003.
1126 Genetically engineered mice with an additional class of cone photoreceptors:
1127 Implications for the evolution of color vision. *Proc. Natl. Acad. Sci.*
1128 100(20):11706–11

1129 Song PI, Matsui JI, Dowling JE. 2008. Morphological types and connectivity of
1130 horizontal cells found in the adult zebrafish (Danio rerio) retina. *J. Comp. Neurol.*
1131 506(2):328–38

1132 Spady TC, Parry JWL, Robinson PR, Hunt DM, Bowmaker JK, Carleton KL. 2006.

Evolution of the cichlid visual palette through ontogenetic subfunctionalization of the opsin gene arrays. *Mol. Biol. Evol.*

Srinivasan M V., Laughlin SB, Dubs A. 1982. Predictive coding: A fresh view of inhibition in the retina. *Proc. R. Soc. London - Biol. Sci.*

Stell WK. 1978. Inputs to bipolar cell dendrites in goldfish retina. *Sens. Processes*. 2(4):339–49

Szél A, Röhlich P, Caffé AR, Juliusson B, Aguirre G, Van Veen T. 1992. Unique topographic separation of two spectral classes of cones in the mouse retina. *J. Comp. Neurol.* 325(3):327–42

Szikra T, Trenholm S, Drinnenberg A, Jüttner J, Raics Z, et al. 2014. Rods in daylight act as relay cells for cone-driven horizontal cell-mediated surround inhibition. *Nat. Neurosci.* 17(12):1728–35

Tan Z, Sun W, Chen T-W, Kim D, Ji N. 2015. Neuronal Representation of Ultraviolet Visual Stimuli in Mouse Primary Visual Cortex. *Sci. Rep.* 5(1):12597

Theiss SM, Davies WIL, Collin SP, Hunt DM, Hart NS. 2012. Cone monochromacy and visual pigment spectral tuning in wobbegong sharks. *Biol. Lett.* 8(6):1019–22

Thoreson WB, Babai N, Bartoletti TM. 2008. Feedback from horizontal cells to rod photoreceptors in vertebrate retina. *J. Neurosci.* 28(22):5691–95

Tikidji-Hamburyan A, Reinhard K, Seitter H, Hovhannisyan A, Procyk CA, et al. 2015. Retinal output changes qualitatively with every change in ambient illuminance. *Nat. Neurosci.* 18(1):66–74

Toomey MB, Collins AM, Frederiksen R, Cornwall MC, Timlin JA, Corbo JC. 2015. A complex carotenoid palette tunes avian colour vision. *J. R. Soc. Interface*

1157 Toomey MB, Lind O, Frederiksen R, Curley RW, Riedl KM, et al. 2016.
1158 Complementary shifts in photoreceptor spectral tuning unlock the full adaptive
1159 potential of ultraviolet vision in birds. *Elife*. 5(2016JULY):1–27

1160 Torvund MM, Ma TS, Connaughton VP, Ono F, Nelson RF. 2017. Cone signals in
1161 monostratified and bistratified amacrine cells of adult zebrafish retina. *J. Comp.*
1162 *Neurol.* 525(7):1532–57

1163 Twig G, Levy H, Perlman I. 2003. Color opponency in horizontal cells of the
1164 vertebrate retina

1165 Twig G, Perlman I. 2004. Homogeneity and diversity of color-opponent horizontal
1166 cells in the turtle retina: Consequences for potential wavelength discrimination.
1167 *J. Vis.*

1168 Ventura DF, Zana Y, Souza JM de, DeVoe RD. 2001. Ultraviolet colour opponency
1169 in the turtle retina. *J. Exp. Biol.* 204(14):

1170 Verweij J, Kamermans M, Spekreijse H. 1996. Horizontal cells feed back to cones by
1171 shifting the cone calciu,-current activation range. *Vision Res.* 36(24):3943–53

1172 Von Schantz M, Argamaso-Hernan SM, Szél Á, Foster RG. 1997. Photopigments
1173 and photoentrainment in the Syrian golden hamster. *Brain Res.* 770(1–2):131–
1174 38

1175 Vorobyev M, Gumbert A, Kunze J, Giurfa M, Menzel R. 1997. Flowers through insect
1176 eyes. *Isr. J. Plant Sci.*

1177 Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds.
1178 *Proc. R. Soc. B Biol. Sci.*

1179 Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC. 1998. Tetrachromacy,
1180 oil droplets and bird plumage colours. *J. Comp. Physiol. - A Sensory, Neural,*

Behav. Physiol.

Wachtler T, Doi E, Lee TW, Sejnowski TJ. 2007. Cone selectivity derived from the responses of the retinal cone mosaic to natural scenes. *J. Vis.*

Wallace AR. 1879. Colour in nature. *Nature*. 19:501–5

Wässle H, Puller C, Müller F, Haverkamp S. 2009. Cone contacts, mosaics, and territories of bipolar cells in the mouse retina. *J. Neurosci.* 29(1):106–17

Werblin FS, Dowling JE. 1969. Organization of the retina of the mudpuppy, Necturus maculosus. II. Intracellular recording. *J Neurophysiol*. 32(3):339–55

Wilby D, Roberts NW. 2017. Optical influence of oil droplets on cone photoreceptor sensitivity. *J. Exp. Biol.*

Wilkie SE, Robinson PR, Cronin TW, Poopalasundaram S, Bowmaker JK, Hunt DM. 2000. Spectral tuning of avian violet- and ultraviolet-sensitive visual pigments. *Biochemistry*

Wong KY, Dowling JE. 2005. Retinal bipolar cell input mechanisms in giant danio. III. ON-OFF bipolar cells and their color-opponent mechanisms. *J. Neurophysiol.* 94(1):265–72

Wyszecki G, Stiles WS. 1982. *Color Science*. Wiley, New York

Yazulla S. 1976. Cone input to bipolar cells in the turtle retina. *Vision Res.* 16(7):737-IN3

Yin L, Smith RG, Sterling P, Brainard DH. 2009. Physiology and morphology of color-opponent ganglion cells in a retina expressing a dual gradient of S and M opsins. *J. Neurosci.* 29(9):2706–24

Yokoyama S. 2000. Molecular evolution of vertebrate visual pigments

Yovanovich CAM, Koskela SM, Nevala N, Kondrashev SL, Kelber A, Donner K.

2017. The dual rod system of amphibians supports colour discrimination at the absolute visual threshold. *Philos. Trans. R. Soc. B Biol. Sci.*

Zana Y, Ventura DF, De Souza JM, Devoe RD. 2001. Tetrachromatic input to turtle horizontal cells. *Vis. Neurosci.*

Zimmermann MJY, Nevala NE, Yoshimatsu T, Osorio D, Nilsson D-E, et al. 2018. Zebrafish Differentially Process Color across Visual Space to Match Natural Scenes. *Curr. Biol. CB*. 28(13):2018–2032.e5

Zrenner E, Gouras P. 1981. Characteristics of the blue sensitive cone mechanism in primate retinal ganglion cells. *Vision Res.* 21(11):1605–9