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# Ancestral photoreceptor diversity as the basis of visual behaviour

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Animal colour vision is based on comparing signals from different photoreceptors. It is generally assumed that processing different spectral types of photoreceptor mainly serves colour vision. Here I propose instead that photoreceptors are parallel feature channels that differentially support visual-motor programmes like motion vision behaviours, prey capture and predator evasion. Colour vision may have emerged as a secondary benefit of these circuits, which originally helped aquatic vertebrates to visually navigate and segment their underwater world. Specifically, I suggest that ancestral vertebrate vision was built around three main systems, including a high-resolution general purpose greyscale system based on ancestral red cones and rods to mediate visual body stabilization and navigation, a high-sensitivity specialized foreground system based on ancestral ultraviolet cones to mediate threat detection and prey capture, and a net-suppressive system based on ancestral green and blue cones for regulating red/rod and ultraviolet circuits. This ancestral strategy probably still underpins vision today, and different vertebrate lineages have since adapted their original photoreceptor circuits to suit their diverse visual ecologies.

Many sighted animals use multiple spectrally distinct sets of photoreceptors for vision. The classical explanation for this arrangement is that any one photoreceptor type supports greyscale vision, while the addition of further types then also supports colour vision (Fig. 1a). In this view, the main or only purpose of adding photoreceptor types beyond the first is to enable colour vision. However, it may be time to revisit this textbook narrative.

I posit that before serving as colour channels, photoreceptors are parallel feature channels that differentially support visual–motor programmes. I elaborate the argument on the example of vertebrates, focusing on the ancestral-like state in zebrafish[1] (Box 1). Nevertheless, the same concepts may equally explain circuit architectures of diverse invertebrate eyes (Box 2). In the following, I synergize classical and new evidence on photoreceptors, their downstream circuits and the visual behaviours they support, to motivate an alternative model of circuit architectures in vertebrate eyes (Fig. 1b).

First, I posit that most non-spectral aspects of vertebrate vision are predominately built upon 'ancestral red cones' and rods (see Fig. 1c,d for photoreceptor definitions). In most eutherian mammals, including humans, these make up >99% of all photoreceptors[2]. Ancestral red-cone vision is characterized by high spatiotemporal acuity but low gain, and its original behavioural roles would have included body stabilization and navigation to allow animals to move to optimal places in their environment[3]. In the absence of other cones, this primary red system can support all of vision, and for any vision at all, the presence of ancestral red cones and/or rods is probably non-optional.

Second, 'ancestral UV cones' (typically expressing SWS1 opsin)[4] represent the next most important input system. Opposite to red, ultraviolet (UV) cone vision is characterized by low spatiotemporal acuity at high gain. Most vertebrates, including humans, use at least a dual strategy that combines ancestral red/rod and UV circuits[5,6]. In the water, where vision first evolved, UV circuits would have originally served as a specialized foreground-vision system to detect predators and prey[1], and by comparison to red, perhaps to judge distance[7]. In air, key distinguishing features of UV vision do not apply in the same way as they do in water, and consequently many terrestrial species have reduced UV cone numbers and co-opted aspects of this ancient cone system for other tasks, including colour vision[8,9]. However, some ancestral roles may have been retained. For example, aerial predators are disproportionately conspicuous from below when observed in UV[10,11],

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and correspondingly, mice may use ancestral UV cones to detect birds in the sky[11–15]. Overall, the presence of ancestral UV cones for vision, while optional, is 'strongly encouraged'.

Third, and unlike red and UV, 'ancestral green and blue cones' (typically expressing RH2 and SWS2 opsins, respectively) are inessential as evidenced, for example, by the profusion of vertebrate lineages that have lost them[5,6]. I posit that ancestral green and blue cones present a secondary visual system whose main purpose is not to enable vision per se, but rather to regulate the functions of red and UV circuits. This view is supported, for example, by the net functional opposition of green/blue-cone signals relative to those of red and UV in the visual system of zebrafish[1,7,16,17]. It is also supported by the narrower-than-opsin spectral tuning functions of basic visual behaviours across fish[18,19], amphibians[20] and birds[21]. These and other insights imply that in the intact ancestral circuit, green- and blue-cone circuits suppress and thereby regulate[1] the activity of red- and UV-cone-driven functions.

This alternative view on the original roles of ancestral green/blue cones may also rewrite how we need to think about mammalian circuits for vision. This is because in the absence of such regulatory circuits in their eyes[5], eutherian mammals would have had to evolve new mechanisms to compensate for their loss. Accordingly, a subset of visual circuits in eutherian mammals, including in humans, might exist specifically for this previously unrecognized purpose.

The hypothesized ancestral circuit architecture also means that cone circuits heavily interact throughout the early visual system to invertedly produce complex spectral signals (for example, refs. 17,22,23). I suggest that it is these signals, which emerged as consequence rather than a cause of the underlying circuit architecture, that enabled what today we might call colour vision.

## Opsins, photoreceptors and their wiring

### Opsins and photoreceptor diversity existed before image-forming vision

Opsins, the light-sensing engines of animal eyes, probably emerged some 700–710 Myr ago[24] (Ma; and certainly before 571 Ma[3]), and within an evolutionary eyeblink, opsins were everywhere. So powerful must have been the basic ability for early animals to sense light that the descendants of the first 'sighted' founders established themselves as the dominant animal life form at the time, and indeed, ever since. Opsins also rapidly diversified to give rise to all five major opsin and photoreceptor lineages we still find in the eyes of extant vertebrates today[1,3,5,6] (Fig. 1c). Accordingly, when later our earliest craniate ancestors started to evolve image-forming vision along new locomotor abilities and brains to match the information[1] (Box 1), this would have probably been

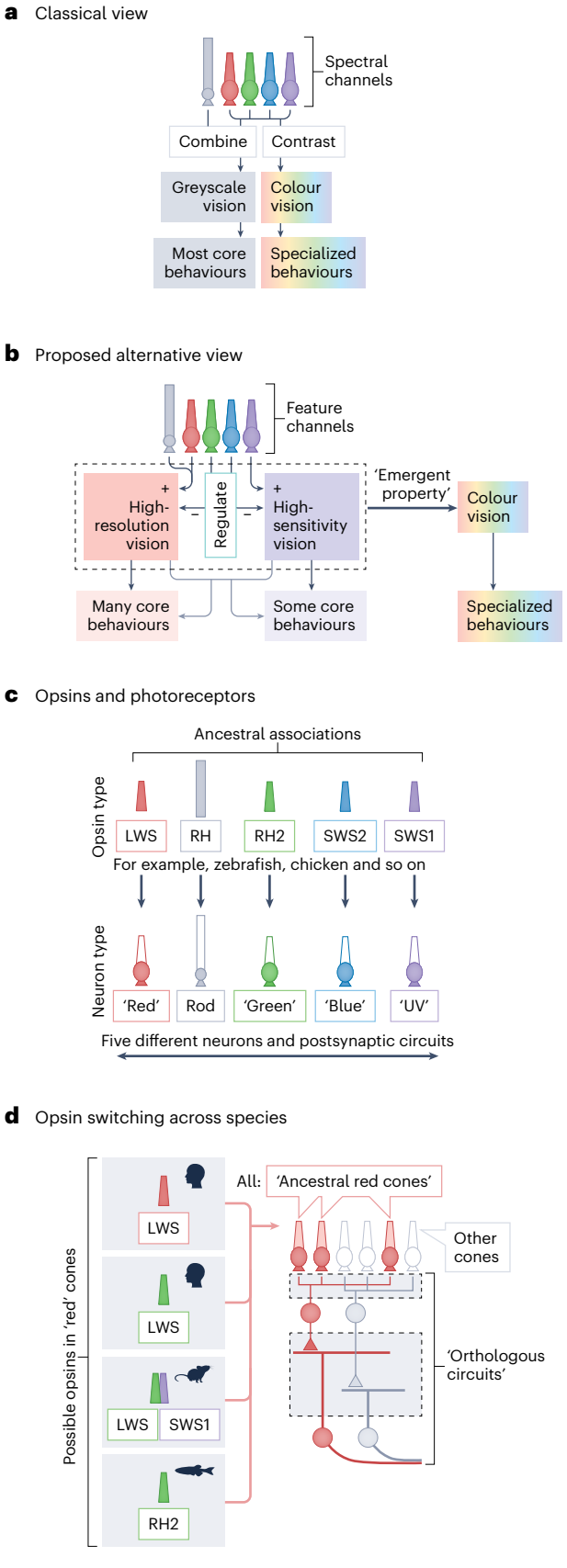


**Fig. 1 | Hypothesis and definition of vertebrate photoreceptors. a**, In the prevailing 'classical' view of retinal organization, photoreceptor signals are pooled to enable greyscale vision and contrasted to enable colour vision. **b**, In the proposed alternative view, different photoreceptor systems are specifically wired to drive or regulate distinct aspects of vision leading to behaviour. Colour vision reflects an emergent property of spectral interactions between cone systems at a circuit level. **c**,**d**, Vertebrate photoreceptor are developmentally, anatomically, molecularly and functionally distinct types of neuron (**c**, bottom). They are traditionally defined and named by their ancestrally expressed opsin[5] (**c**, top). For example, 'ancestral red cones' typically express an LWS opsin and are therefore often called 'LWS -cones'. Other common naming schemes exist in parallel, for example, based on the expressed opsins' spectral sensitivity (for example, 'L/M/S cone' or 'red/green/blue cone' for cones with peak sensitivity at long, mid and short wavelengths, respectively). However, both the spectral sensitivity of opsins themselves, as well as their ancestral associations with specific photoreceptor neuron types, are highly evolvable. Consequently, commonly used naming schemes fail to consistently denote orthologous neuron types across species (**d**). For example, in humans, both 'L/red' and 'M/green' cones refer to the same type of neuron (ancestral red) expressing spectrally distinct variants of LWS opsin[127]. Immediate downstream circuits are 'blind' to this difference[128]. Next, many rodents including mice can co-express an SWS1 opsin alongside LWS[45], and some reef fish and cichlids fish appear to have dropped LWS altogether in favour of an RH2 opsin[44,46,47]. However, in all these cases, the photoreceptor neuron remains 'ancestrally red', and the downstream circuits it serves are, for all we know, orthologous. I will therefore use the term 'ancestral red cone' (and so on, **c**) to specifically refer to the neuron, independent of its expressed opsin(s).

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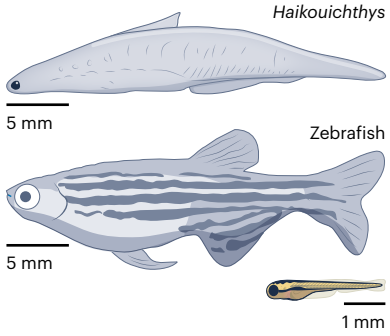
## BOX 1

# Zebrafish vision represents an ancestral-like state

Vertebrate vision evolved in the water, in the well-illuminated daylight shallows of Lower Cambrian coastlines. The fossilized remains of some of the first sighted craniates such as *Haikouichthys* were small, perhaps 3 cm in body length in adulthood[131] (schematic based on same source), and presumably smaller in their juvenile forms. They were approximately fish-shaped, and their heads had holes for lateralized eyes and outlines of an early tectum[132]. Jaws had not yet evolved, but small floating items such as plant matter and small pelagic arthropods could perhaps be visually targeted and ingested. Conversely, early vertebrates also shared their ecosystems with substantially larger and visually hunting invertebrates such as *Opabinia*[133], or diverse radiodonts including *Anomalocaris*[134], the infamous giant of the time. Correspondingly, early vertebrates would have required at least a basic ability to visually detect and consequently avoid threats. While the phylogenetic relation of *Haikouichthys* to modern fish remains debated, their existence strongly suggests that at least some Lower Cambrian craniates had well-developed camera-types eyes. In any case, latest in the subsequent Ordovician and Silurian periods, oceans were teeming with stem vertebrate life where visual navigation, hunting and predator avoidance would have been the norm[135].

Like all extant species, zebrafish are more than 500 Myr removed from these early beginnings. And yet, these small teleosts do resemble several important attributes of our presumed ancestral phenotype. First, zebrafish are diurnal and live in shallow and well-illuminated water of rarely more than half a metre in depth[57]. Second, zebrafish are small: some 3 cm in adulthood, and some 3 mm in their larval stage. Third, soon after hatching and into adulthood, zebrafish visually hunt zooplankton[56,78,111,115]. Fourth, zebrafish are also a prey species, and their eyes and brains comprise a multitude of circuits to visually detect and deal with threats[73]. Fifth, larval zebrafish retain the full ancestral cone complement (red, green, blue and UV), and juveniles and adults in addition feature rods[1].

These similarities compound with practical considerations: zebrafish are probably the most experimentally accessible teleost species that we have access to today, and as a consequence, our current understanding of zebrafish vision[73], including their photoreceptor functions[1], is unmatched amongst aquatic vertebrates. Nevertheless, in time it will be critical to explore which insights gained from zebrafish retinal circuit functions are representative for teleosts in general, and which are specific to their phylogenetic history and/or visual niche.




built on top of pre-existing and functionally diverse photoreceptor lineages. Photoreceptor diversity is therefore fundamentally woven into the very fabric of vertebrate eyes.

### Retinal complexity scales with photoreceptor diversity

While five photoreceptor lineages represent the retina's ancestral state (Fig. 1a–c), different extant species have since lost, modified and/or expanded upon this photoreceptor complement to suit their visuo-ecological niches[1,25] (Fig. 2a). Some species, including some sharks[26], retain only rods for vision in the dark, while others such as many diurnal birds have expanded upon the ancestral state to bring their photoreceptor complement up to seven[8,27]. The loss and gain of photoreceptor types has classically been taken as a signature for a species' ability to detect and resolve spectral contrast (that is, to see 'colour')[5,28]. And yet, beyond detecting ever-increasing nuances in spectral contrasts, the different photoreceptor lineages and their downstream circuits can be intimately linked to more fundamental aspects of vision.

Perhaps most strikingly, the number of a vertebrate's distinct types of photoreceptor is a powerful predictor of their retinal complexity[25,29,30]. For example, the retinas of eagles[31], which are driven by seven photoreceptor types, comprise more than tenfold more neurons per equivalent area compared with the retina of rodents[32], which are driven by three (Fig. 2b). Species differences in cellular density exist throughout all retinal layers; however, they are particularly prominent at the level of the inner retina leading to the retinal output in the form of retinal ganglion cells[25]. The more densely packed inner retinal neurons of birds also tend to be more anatomically complex: for example, murine retinal neurons are mostly mono- or at most bi-stratified[33,34], while avian retinal neurons routinely stratify in three or more retinal layers[27,35]. Taking the numerical density of retinal ganglion cells[36] as a quantifiable (although admittedly crude) proxy of anatomical 'complexity'[25] reveals that this number scales with the number of a species' photoreceptor types as a power law with slope ~2.4 (Fig. 2c). In other words, on average, retinal complexity more than doubles for each added photoreceptor type. At its extremes, species' mean ganglion cell densities span some three log units, from ~25 cells mm$^{-2}$ in the rod-monochromat beluga whale[37], to ~25,000 cells mm$^{-2}$ in some small birds[38] (and up to ~150,000 cells mm$^{-2}$ in their fovea). Importantly, these trends cannot be explained by differences in eye size alone. For example, the eyes of large hummingbirds are approximately the same size as the eyes of mice, and yet they comprise some tenfold higher densities[25,38]. Phylogeny alone also does not explain this trend. For example, closely related species of teleost fish can have drastically different ganglion cell densities[36,39], with rod-only deep-sea species on the low-density end, and cone-tetrachromatic surface-dwelling species on the high-density end[1].

A perhaps more plausible explanation for the intimate relationship between a retina's anatomical complexity and its number of photoreceptor channels is that the added circuit complexity is required to usefully process the signals from the extra photoreceptors (Fig. 1b). While adding photoreceptors and downstream circuits does present the possibility to augment spectral resolution, it seems implausible that this benefit alone should necessitate a more than doubling of the retina's neuronal real estate per extra cone type (Fig. 2c). Rather, it suggests that the addition of extra photoreceptor types can bring about functional benefits that go beyond the addition of spectral nuance.

### Some photoreceptor types are more expendable than others

The next puzzle piece comes from considering which photoreceptor lineages are present or absent across different vertebrates. Relative to the full ancestral complement of four cones plus rods, many lineages have reduced their photoreceptor complements, and these patterns of loss are non-random[1,5,6] (Fig. 2a). Loss of ancestral blue and/or green cones is common as, for example, in eutherian mammals, sharks, frogs

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## BOX 2

# Lessons from invertebrates

While this Perspective's central argument focuses on vertebrate eyes, many parallels can be drawn to visual systems of invertebrates. For example, crustacean decapods and their eyes also first evolved in the water, but their descendants soon took onto the land and into the air, for example, in the case of extant insects[92]. The ancestral visual archetype of crustaceans is a crystalline compound eye, as famously preserved in the fossils of trilobites, or of the world's first apex predators such as the five-eyed opabinia[133] or the three-eyed radiodonts[136]. The lateral compound eyes of today's aquatic crustaceans, such as crabs, closely resemble this external ancestral form[137]. Each facet comprises multiple photoreceptor neurons that express some or all of five ancestral rhabdomeric opsin families: LW1, LW2, MW1, MW2 and SW (that is, long/mid/short-wavelength selective)[138]. Usually, these photoreceptors exist at fixed stoichiometry, with mid/long photoreceptors underpinning much of widefield motion vision, while short-wavelength receptors link with threat detection[139,140].

In some cases, anatomically, spectrally and presumably also functionally distinct extra sets of photoreceptors have appeared. The most infamous example of such additions is probably the case of mantis shrimps[141]. Their globular and 'archetypical' compound eyes are complemented by a spectrally diverse band of 12 extra photoreceptor types that should, in theory, deliver some of the best colour vision of any animal. And yet, the shrimps' behaviourally determined spectral discrimination thresholds are surprisingly poor[142], hinting that this spectral capacity might be used for tasks other than traditional colour vision. One such task might be a spectral approach to distance estimation (Fig. 3), which might also link with the mantis shrimps' ecology as ferocious ambush predators.

Outside the water, spectral photoreceptor diversity soon exploded[28], with a pinnacle probably in butterflies[143]. And yet, the basic organization of photoreceptors within and across facets never fundamentally changed: whether in the water or in the air, crustacean decapods consistently use both long- and short-wavelength receptors to differentially drive diverse core visual behaviours. In fact, opsins expressed in the photoreceptors of winged insects derive from just two of the ancestral crustacean lineages (LW2 and SW) and, in most cases, both lineages are preserved. For example, in the eyes of fruit flies[144], each facet comprises eight photoreceptors, dubbed R1–8. Of these, R1–6 all mainly express the same mid-wavelength-sensitive Rh1 opsin that is derived from the ancestral LW2 lineage[145]. Their postsynaptic circuits co-wire to drive achromatic vision, including widefield motion circuits for flight control[146]. The remaining R7/8 photoreceptors come in two variants, which together express one of four opsins: Rh3, 4, 5 or 6. Of these, Rh3–5 are short-wavelength sensitive and derived from the ancestral SW opsin lineage (Rh6 derived from LW2). Each of the four RH7/8 variants feed into developmentally hardwired circuits that are distinct from each other, and from those driven by R1–6 photoreceptors[144], and their activity is linked to a myriad of visual behaviours that notably include startle and escape responses[144,147]. Corresponding spectral-to-behavioural links exist in probably all insects[28,92].

Beyond crustacean decapods, invertebrates including spiders, worms or shellfish have evolved a cornucopia of weird and wonderful visual systems, including both compound and camera-type eyes[3,148] as well as countless distributed visual systems[149]. In many cases, more than one photoreceptor system exists, and typically these include at least one mid/long-wavelength-sensitive and one short-wavelength-sensitive type. The main exception is in the case of cephalopods[150]. For what little we understand today, octopuses, cuttlefish and squid just have a single, mid-wavelength-sensitive photoreceptor that is well-tuned to capture most available light—conceptually reminiscent of vertebrate red cones. Under this lens, perhaps cephalopods have taken a visual route that is not all that different from that of primates: one major input system delivering 'general' visual information to a large brain that is evidently well equipped to deal with a very general input strategy.

and in dozens of smaller lineages across the entire vertebrate tree of life[6]. Of these, some species lost only one cone type, and in these cases, blue is often lost before green. Next, additional loss of UV cones is less common, and UV loss rarely[26] precedes the loss of blue/green.

By contrast, no sighted vertebrate is known to have lost both red cones and rods[6]. The only sighted vertebrates that lack ancestral red cones are rod-only species such as some sharks[26] or deep-sea fish[40], and conversely the only species that lack rods always retain red cones (for example, some diurnal lizards, such as chameleons[41]). This highly conserved pattern, which independently occurred in dozens of vertebrate lineages, strongly suggests that there exists a hierarchy in the expendability of photoreceptors: blue/green > UV > red/rod.

Critically, these photoreceptor loss patterns do not match spectral patterns across our planet's diverse visual habitats, and their animals within. For example, a cone-tetrachromat fish transitioning to life at depth where UV and red light does not reach should correspondingly lose its UV and red cones. Nevertheless, lineages almost always lost the blue and/or green cones first, while compensating for the incurred spectral gap by mid-wavelength shifting the red and UV opsins[42,43], or even changing the expressed opsin type(s) altogether (Fig. 1d). Our own eyes have been subject to such a shift: our 'S cones' (commonly referred to as 'blue') are in fact blue-shifted ancestral UV cones (SWS1), not ancestral blue cones (SWS2). Similarly, 'M cones' of mice are mid-wavelength-shifted ancestral red cones (long-wavelength selective; LWS), not ancestral green cones (RH2). In some more extreme cases, cones even appear to have exchanged their 'native' opsin in favour of a different ancestral variant (for example, refs. 44–46). This type of spectral tuning is, for example, common in cichlids[46] and reef fish[47], which appear to routinely express a 'green' RH2 opsin variant in ancestral red cones. Much along the same lines, in mice, ventrally located ancestral red cones co-express the UV cones' SWS1 opsin. This adaptation renders ancestral red cones UV-sensitive for sampling the UV-rich sky; however, critically they coexist with ancestral UV cones, and each cone system serves part-independent postsynaptic circuits.

The above types of tweak in opsin sequence and expression, alongside chromophore shifts, are the primary mechanisms by which animals adjust their spectral sensitivity to current visual needs[5]. They are relatively easily achieved and undone by evolutionary processes, and, correspondingly, are common across visual systems[5,6]. By contrast, ancestral photoreceptor loss is irreversible, and not used for this purpose (Fig. 2a).

### Rods supplement ancestral red-cone circuits for low-light vision

Rods are often considered separately from cones, tasked with taking over all of achromatic vision in low-light conditions when cone circuits fail to operate[48]. Supporting this view, rods are exceptionally light-sensitive, anatomically and molecularly distinct from cones,

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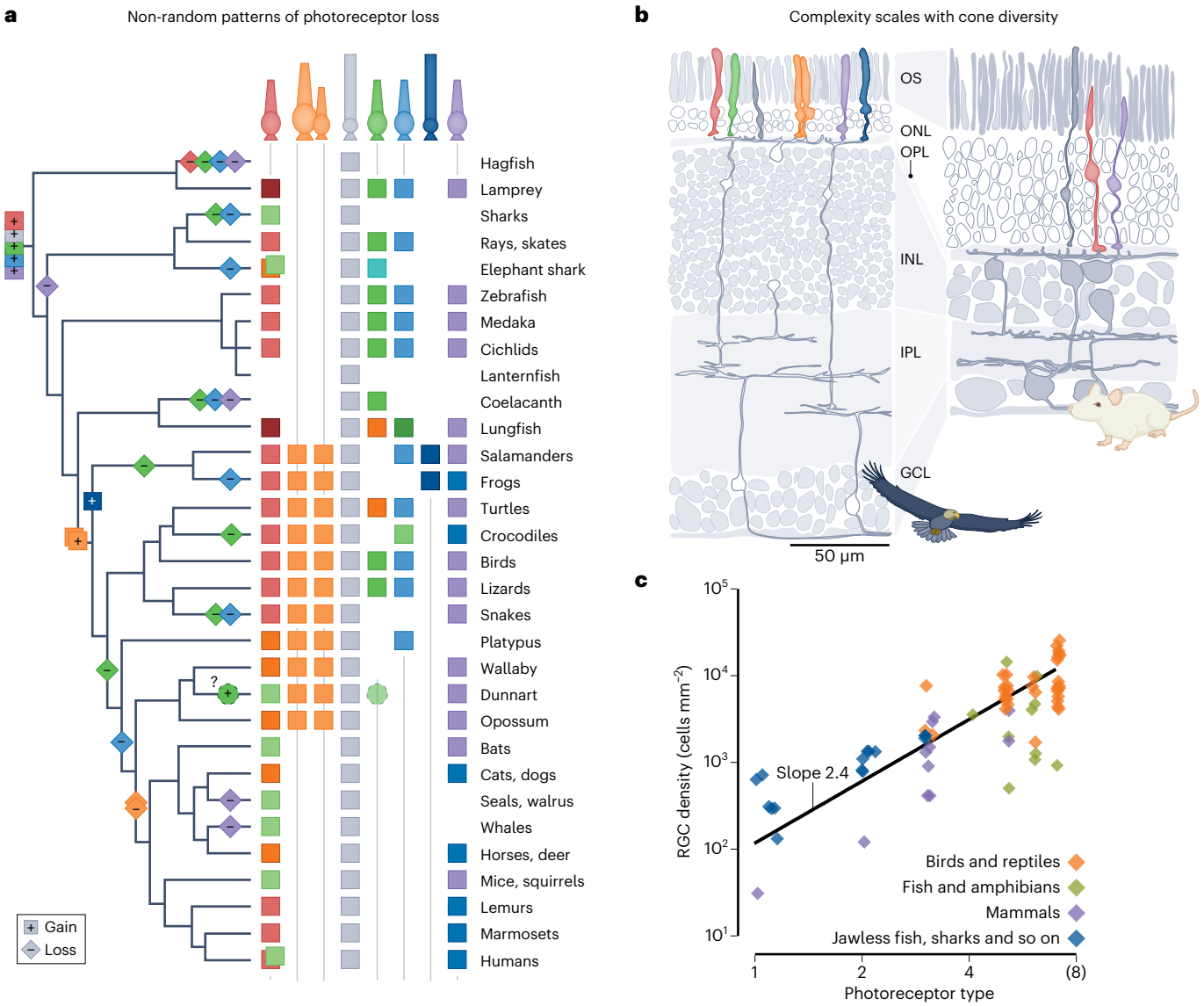


**Fig. 2 | Retinal architecture across species. a**, Vertebrate phylogeny and typical maximal photoreceptor complement (based on ref. 6 and updated by literature elaborated throughout the text). Key inferred photoreceptor loss and duplication events are indicated. Note that most non-eutherian tetrapods (amphibians, reptiles, birds and non-eutherian mammals) have double cones, a new photoreceptor system that probably appeared with the emergence of vertebrates on land. Many amphibians have an additional 'blue rod' (expressing the blue cone's SWS2 opsin—note that in classical literature these are sometimes called 'green rods' in reference to their appearance in histological sections). Within each photoreceptor lineage, the approximate spectral tunings of currently expressed opsins are indicated by their shading. For example, the human ancestral UV cones express a blue-shifted SWS1 opsin, while mouse ancestral red cones express a green-shifted LWS opsin (Fig. 1c,d). Note that the indicated opsin inventories for some species remain speculative (for example, for dunnarts, see refs. 129,130). **b**, Scale-matched schematics of typical avian and rodent retinal cross section (based on ref. 25) with photoreceptors and archetypical retinal circuit architectures indicated. Note neuronal density differences across all retinal layers. OS, outer segments; ONL, outer nuclear layer; OPL, outer plexiform layer; INL, inner nuclear layer; IPL, inner plexiform layer; GCL, ganglion cell layer. **c**, The mean density of retinal ganglion cells (RGCs) across species scales as a slope 2.4 power law with the number of distinct photoreceptor types present (replotted based on data from ref. 25). Panel **b** adapted with permission from ref. 29, Elsevier.

and rod signals predominately reach the retinal output indirectly by hijacking cone-dominated circuits[48]. However, this understanding of rod circuits is overwhelmingly based on work in eutherian mammals, where most cones are red[33]. This body of work can therefore not easily inform about rods' ancestral wiring logic.

In non-mammalian species, rods remain tightly associated with red-cone circuits, despite the widespread availability of other cone types. For example, the teleost homologue of the mammalian rod bipolar cell, which presents the first processing stage of the so-called primary rod pathway, connects exhaustively and exclusively with rods and red cones[49,50]. Rod signals also reach inner retinal circuits by electrical coupling to cones (secondary pathway), and by direct innervation of cone bipolar cells (tertiary pathway)[48]. The secondary pathway remains poorly understood outside mammals; however, the tertiary pathway in both zebrafish[49] and chickens[35] further points to a specific association of rods and red-cone circuits: zebrafish rods directly feed into nearly half of the ~20 cone bipolar cell morphotypes, and in all cases, these bipolar cells are also strongly connected to red cones[49]. Moreover, red cones and rods systematically co-target the same layers of the inner retina, and this innervation pattern is anticorrelated to that of the other three cones. Conceptually the same pattern also exists in chickens; however, in their case the red-opsin-expressing double

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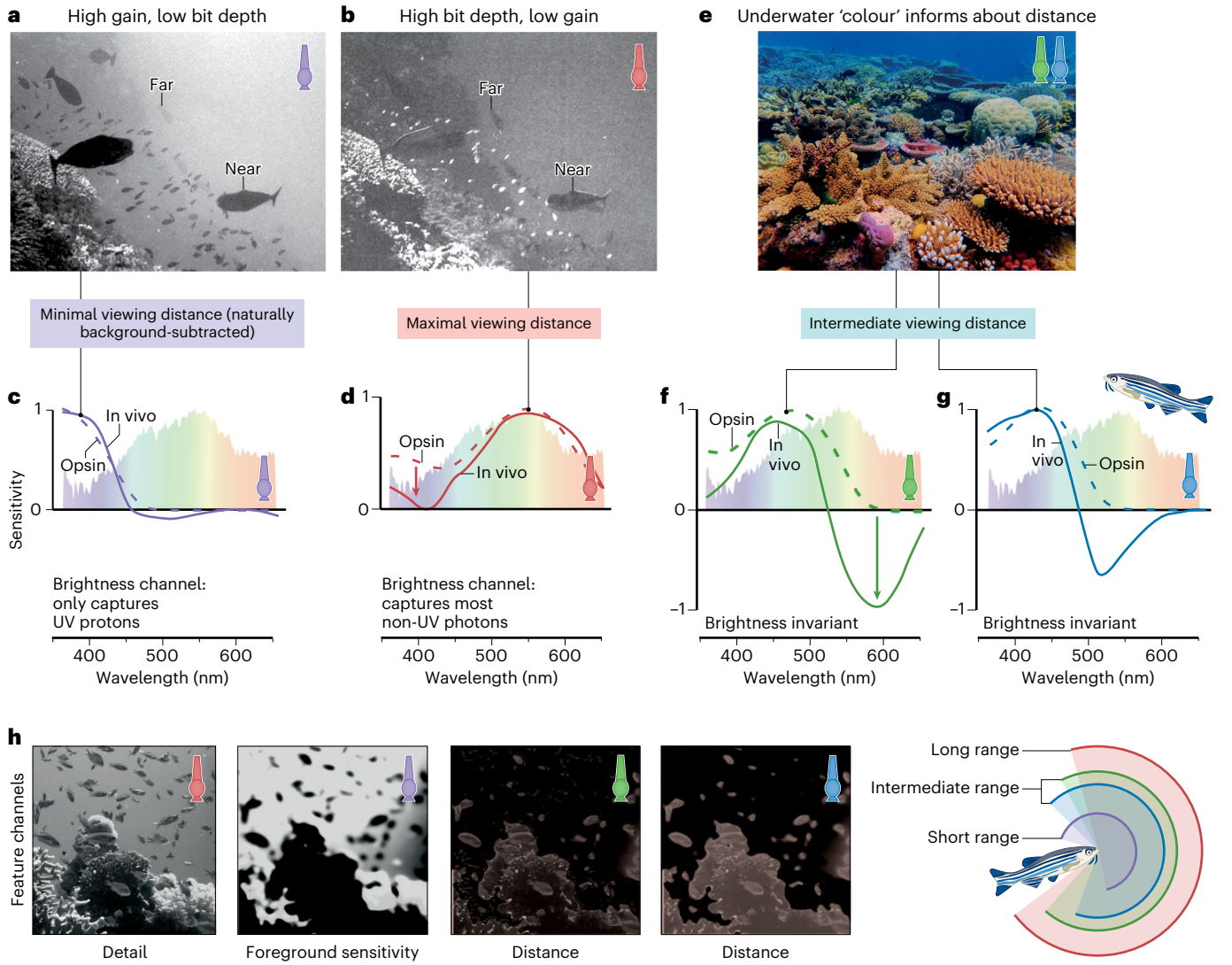


**Fig. 3 | Cones as feature channels. a**,**b**, Coral reef photographed through a UV filter (**a**) and a long-wavelength filter (**b**, modified from ref. 4). Note the UV channel's space lighting, which obscures the background but brings out silhouettes in the foreground. **c**,**d**, Measured in vivo spectral sensitivity functions of ancestral UV (**c**) and red (**d**) cones in larval zebrafish (solid lines, based on ref. 16) and their underlying opsins (dashed lines). A representative mean spectrum of natural sunlight in the zebrafish natural habitat is shaded into the background (based on ref. 57). **e**, Underwater 'colour' photograph taken on a coral reef. Note how spectral detail fades with distance. Credit: Lea McQuillan/500px/Getty images. **f**,**g**, As in **c**,**d**, but for ancestral green (**f**) and blue (**g**) cones, respectively (modified from ref. 16). **h**, Conceptual summary of cones primarily serving as feature channels (left) that in addition operate over different visual distances (right). Panels **a**,**b** adapted with permission from ref. 1, Elsevier; panels **f**,**g** adapted from ref. 16; panel **h** adapted with permission from ref. 7, Elsevier.

cones[27,35] appear to have partially taken over this job from the ancestral red cones. The co-wiring of rods and double cones in the avian retina is also in agreement with their outer retinal anatomy: unlike in mammals[33] or fish[49], the avian outer retina is tri-layered[27,51], with rods and double cones innervating layer one, while ancestral red/green and blue/UV single cones innervate layers two and three, respectively. Avian rods are also connected to double cones via horizontal cells[27]. Moreover, chickens retain a transcriptomic signature of the ancestral rod bipolar cell[52]; however, despite available connectomic data, no anatomical counterpart has been identified[35]. This hints that in chickens, rods primarily feed into the retina via their many direct connections to (double) cone bipolar cells, while the ancestral primary rod pathway may have been anatomically rearranged and co-opted for new purposes. This view is also anecdotally supported by the presence of a transcriptomic signature for rod bipolar cells in the nearly rod-less anole lizard[53]. Returning to the red-cone-dominated mammals, even here rods retain a weak selectivity for red- over UV-cone circuits. For example, mouse A-2 amacrine cells, integral components of the primary rod pathway[48], selectively avoid the processes of the UV-cone-exclusive[33,54] type-9 bipolar cells[55]. Taken together, rods therefore do not indiscriminately associate with any cone, but specifically extend red-cone-associated circuits for vision at low light.

## Photoreceptors are ancient feature channels and not colour channels

### Underwater where vision first evolved different wavelengths provide different types of behaviourally relevant information

UV light is rapidly absorbed and scattered in the water[4], meaning that it can only deliver foreground information[4,7,56] (Fig. 3a). By contrast, longer-wavelength light penetrates deeper and can therefore provide

information about the background (Fig. 3b). Ancestral UV and red cones, respectively, are best positioned to represent these two types of information[16] (Fig. 3c,d): the UV-foreground effect rapidly deteriorates with increasing wavelength, meaning that only UV cones can use it. The natural foreground enhancement largely obviates the need for complex background subtraction[56], which immediately predisposes UV-cone circuits for nearby object vision tasks, such as prey detection and predator avoidance. Conversely, in zebrafish at least, the ancestral red cone's spectral sensitivity function[16] provides a close match to the total availability of natural light in shallow water[57]. Red cones are therefore inherently predisposed for enabling high-spatiotemporal-detail vision. In line, prey capture is intimately associated with UV cones in zebrafish[11,16,19,56,58], trout[59] and sunfish[60], while widefield motion vision tasks probably use red cones[18,61]. Accordingly, the opsin-inherited spectral sensitivities of ancestral red versus UV cones lend themselves to reporting fundamentally distinct aspects of underwater vision. It seems plausible that stem vertebrates would have used the same strategy.

### Photoreceptors are more than just opsins

Next, a myriad of both intrinsic and circuit mechanisms can build upon these opsin-inherited predispositions to consolidate two very different feature channels right at the first synapse of vision[11,13,16,56,58,62–64]. For example, UV cones across species have consistently evolved to trade-off speed for improved sensitivity[56,62,63]. For this, molecular tuning of phototransduction and horizontal circuit feedback control are jointly used to slow down the UV cones' photo-response, promoting temporal signal integration, while enlargement of light-sensitive outer segments and/or optical modifications[65] can further maximize photon capture rate. This 'high-gain low-detail' strategy is well-suited to leverage the high energy but low availability of UV photons. By contrast, longer-wavelength photoreceptors usually evolve to have lower gain, but they are fast, and they often have a strong spatial surround (for example, refs. 13,66). These are all characteristics of a high-detail low-gain strategy, which suits the high availability of red photons. These and other differences also compound with differences in cones' achromatic contrast encoding[10,11,56,67]. For example, in both fish[56,58,67] and mice[11], cones surveying the upper visual world tend to be dark-biased, sacrificing sensitivity for brighter-than-background contrasts. Conversely, cones surveying contrasts from an evenly lit environment tend to be more linear[11].

### Different cones operate over different visual distances underwater

Beyond contributing to shaping the gain, speed, linearity and/or receptive field sizes of different cone types, outer retinal circuits also interconnect cone types to retune their effective spectral sensitivity functions[16,64,68]. For example, in the live zebrafish eye, horizontal cells UV-suppress red cones[16] (Fig. 3d), such that unlike for the respective opsins, red- and UV-cone spectral sensitivity functions have essentially no overlap (Fig. 3c). However, the capacity for spectral retuning is perhaps most critical in the case of the two mid-wavelength cones, green and blue (Fig. 3e–g): both become strongly red-opponent[16], which means that unlike for red and UV cones (Fig. 3c,d), they cannot report image brightness (because the opponent signals cancel under 'white' light[16]). Instead, they report spectral contrast, which might, at first glance, hint at colour processing. However, light becomes rapidly monochromatic with underwater distance[7,69], which means that far-away objects always look colourless (Fig. 3i). Conversely, this also means that the presence of spectral contrast in an underwater image indicates that its source is nearby[7]. The two different spectral zero crossings between green and blue cones almost inevitably result in two distinct distance regimes (Fig. 3f,g), and both are intermediate compared with the long-range non-opponent red channel (Fig. 3b) and the ultra-short-range UV channel (Fig. 3a). Together, the four cones therefore do not primarily report spectral detail: they report spatiotemporal structure within four staggered-distance shells (Fig. 3h, right). When spatially resolved vision first evolved to help our earliest ancestors to navigate their underwater world, the ability to judge distance based on spectral contrast would have probably been a more useful asset compared with the ability to sense 'colour' as we understand it today. In fact, the four ancestral cones might represent vertebrates' original ability to visually judge spatial structure not in two dimensions, but in three. Presumably this would have been possible long before the first appearance of other strategies for this task, such as the use of stereopsis[70] or pictorial cues[71].

Together, cones are therefore far more than colour channels at the whim of their currently expressed opsins. They are feature channels, much like all other neurons of complex visual systems (Fig. 3h). In fact, cones may well be the original feature channels of the vertebrate eye.

## Inner retinal layering links photoreceptors to behavioural circuits

Retinal bipolar cells carry cone signals from the outer to the inner retina[72]. Here, they make layer-specific connections with the dendrites of amacrine cells, the retina's main set of local inhibitory circuits, and with retinal ganglion cells, the eye's sole output to the brain (Fig. 4a). The outputs from many retinal ganglion cells intimately feed into central behavioural circuits[34,73,74] (Fig. 4b,c). Accordingly, cone signals are in effect routed onto distinct behavioural programmes via the layers of the inner retina.

### Behavioural layering

The vertebrate inner retina consistently displays 'behavioural layering'[75], in the sense that the dendrites of behaviourally related amacrine and retinal ganglion cells tend to co-stratify in shared layers[34,74,76]. This organization is perhaps particularly obvious in zebrafish, where the dendrites of retinal ganglion cells associated with widefield motion processing stratify towards the outer edges of the inner retina[57,74,77] (Fig. 4b, yellow), while those associated with prey capture stratify towards the centre[78–80] (Fig. 4b, purple). A very similar organization also exists in mammals: for example, the murine vesicular glutamate transporter 3 (vGluT3) amacrine cell, a central hub for probably all circuits involved in motion processing, stratifies broadly across the centre of the inner retina[81]. Within this vGluT3 plexus, object motion vision circuits stratify in the centre[82], while direction-selective circuits that are associated with optic flow processing stratify at its outer edges[83,84]. This behavioural layering is a perhaps inevitable consequence of wiring economy and the need to locally process visual signals within and across the dendrites of early retinal neurons. However, whether by accident or design, the behavioural layers provide an excellent substrate for bipolar cells to route the combined and/or contrasted signals of different cone types onto specific behavioural programmes.

### Spectral layering

In line with the layered behavioural organization, different types of retinal bipolar cell carry the combined and contrasted signals from different cone types to different depths of the inner plexiform layer[33,35,49,72] (Fig. 4d). This organization leads to 'spectral layering', because bipolar cells inherit their presynaptic cones' distinct spectral sensitivity functions[13,16,17] (Fig. 3c,d,g,f). A functional signature of this effect is readily observed in larval zebrafish (Fig. 4e). For example, in their acute zone[56], many bipolar cell terminals located in the outermost layers mainly respond to long-wavelength stimulation, while those located in central layers tend to be more responsive to shorter-wavelength stimulation[17,22,57] (Fig. 4e, left). This overall organization is surprisingly invariant to pharmacological blockage of inputs from amacrine cells[22] (Fig. 4e, right).

### Contrasting four cones in two steps

The inner retina's spectral layering can be exploited to infer each bipolar cell's effective cone-type contributions. This strategy of 'spectral

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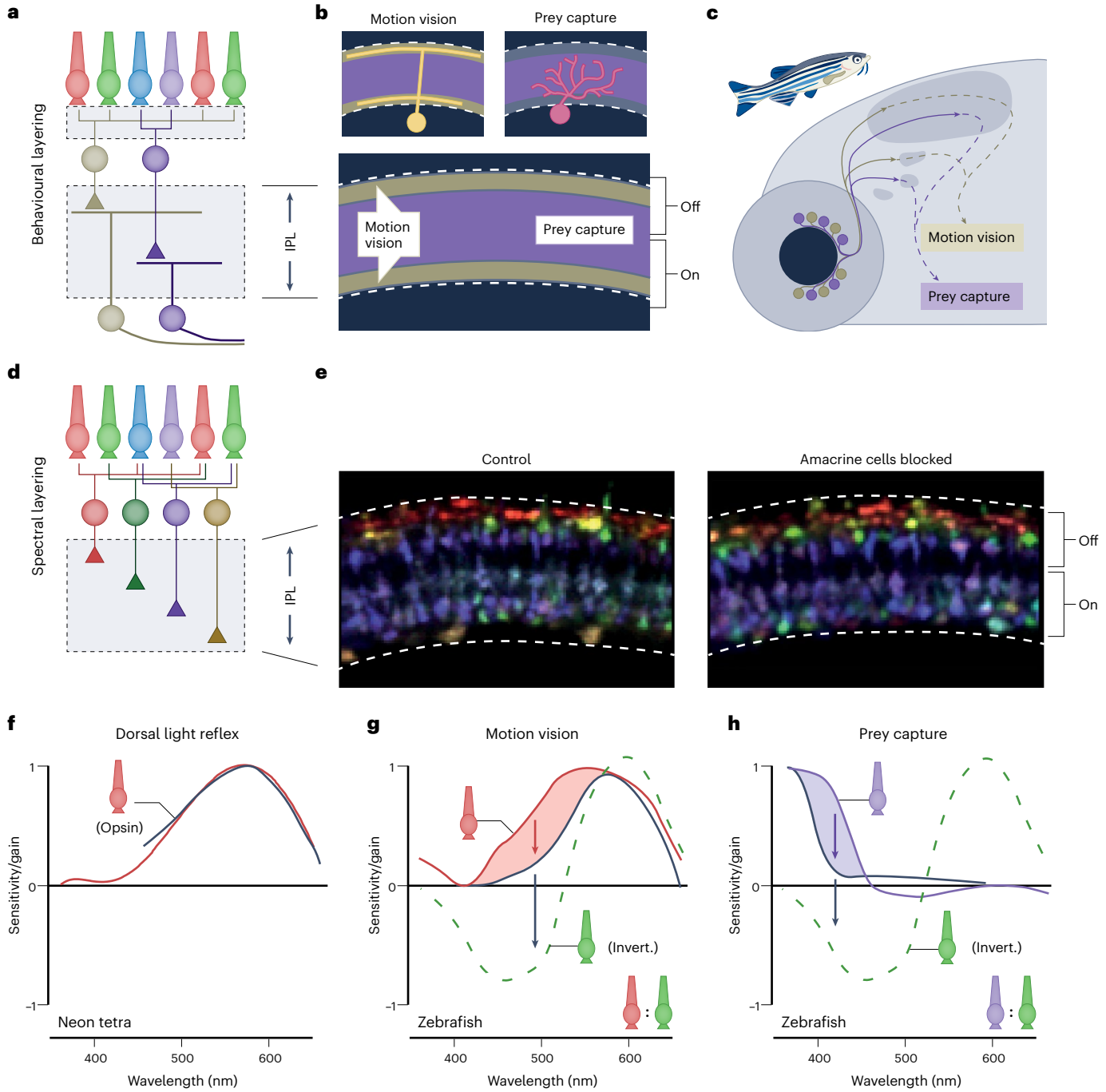


**Fig. 4 | Inner retinal layering and spectral sensitivity functions of visual behaviours. a**–**c**, Schematized retinal (**a**,**b**) and central (**c**) visual circuit architecture, showing typical connectivity from photoreceptors via bipolar cells to ganglion cells. In zebrafish, the dendrites of ganglion cells associated with widefield motion processing and prey capture systematically stratify in the outer and inner layers of the inner retina, respectively (based on ref. 74). The traditional segregation of the inner retina into 'off-layers' and 'on-layers' is indicated in **b**. **d**, As in **a**, illustrating how different bipolar cells can carry diverse cone combinations to different inner retinal layers. **e**, Illustration of **d** from larval zebrafish inner plexiform layer, with bipolar cell synaptic terminals RGB-colour coded by their two-photon responses to flashes of red, green and UV light, respectively (based on ref. 22). Shown is an example from the acute zone under control conditions (left) and after the pharmacological blockage of inhibition from amacrine cells (right). **f**–**h**, Spectral sensitivity functions of behavioural programmes (from refs. 18,19,96) superimposed on sensitivity functions of cones (from ref. 16) that might underlie each behaviour. The dorsal light reflex of neon tetra aligns with the spectral sensitivity of the expressed red opsin (**f**), while the zebrafish optomotor response is tuned notably more narrowly (**g**), which may be explained by a hypothetical red-minus-green-cone circuit. Zebrafish prey capture behaviour is tuned more narrowly than its UV cone and could be explained by a UV-minus-green circuit (**h**). The spectral sensitivity function of green cones is *y*-inverted (invert.) to illustrate its hypothesized opposition to red-cone (**g**) and UV-cone (**h**) circuits.

inference'[17] has yielded insights into how zebrafish cones are functionally routed onto the different layers of the inner retina[17,22,57]. First, it revealed that red-cone contributions dominate bipolar cell functions[17], consistent with red cones representing the most important input channel (Fig. 1b). Second, inner retinal circuits mainly combine the signals from red, green and blue cones, but routinely contrast their combined signals against those of UV cones. Third, the inner retina's 'off-layer' (upper part of the inner plexiform layer; Fig. 3e) mostly

receives sign-conserved (that is, off) inputs, while the 'on-layer' (lower part) receives a surprisingly balanced mixture of both sign-conserved (off) and sign-inverted (on) inputs. Fourth, UV-versus-all contrasting occurs in the inner retina's on-layer. Accordingly, the retina's strategy for differentially combining and contrasting the signals from the four ancestral cones involves only two main steps. First, green and blue cones are individually contrasted against red cones in the outer retina[16], and second, the now combined signals of red, green and blue cones are jointly contrasted against those of UV cones in the inner retina.

Functionally, this circuit architecture effectively splits the four ancestral cones into two opposite systems: red and UV cones provide the retina's principal drive, while green and blue cones counteract this drive (Fig. 1b). This is because green and blue cones are red-opponent (that is, they carry a 'red-inverted' signal; Fig. 3f,g). Summing these red-inverted signals with the non-inverted direct drive from red cones cancels the red component and thereby attenuates the overall signal. Subsequently contrasting the resultant circuits against UV then allows recycling the same system to also regulate the UV channel.

### Amacrine cells mainly serve red- and UV-cone circuits

For contrasting cone signals, horizontal cells underlie step one[16,85], while amacrine cells are obvious candidates for step two[22,86]: as a population, amacrine cells differentially interconnect probably all synaptic terminals of bipolar cells and therefore can—in theory, at least—arbitrarily combine and contrast their signals[87,88]. And yet, zebrafish amacrine cell circuits have surprisingly moderate impacts of bipolar cells' spectral organization[22] (Fig. 4e). This is in stark contrast to the incurred major changes in bipolar cells' spatiotemporal processing and gain when amacrine cells are blocked[22,89]. In fact, zebrafish amacrine cells themselves appear to mainly draw their inputs from only two cone types: red and UV[22]. It seems that amacrine cells are not primarily used for linking cone systems. Instead, they act as functionally cone-type-specific regulatory systems, serving first and foremost red-cone circuits, followed by UV, and then, if at all, green and blue.

## From cones to behaviour

Next, retinal ganglion cells convert integrated signals from bipolar and amacrine cells into a spiking code for transmission to the brain. Central circuits then combine the incoming visual information with inputs from other senses and internal state, ultimately to drive behavioural programmes[73]. However, despite this complexity added beyond the retina, the spectral signatures of the cones that serve distinct visual circuits remain identifiable all over the brain[1,7,90,91], including within the behavioural output[18,19,56,61] (Fig. 4f–h).

In fact most, if not all, visual behaviours are spectral in nature[92]. For example, in humans more than 99.9% of all photoreceptors are either rods or ancestral red cones (LWS), and these two photoreceptor systems differ slightly in their spectral sensitivity[5]. Correspondingly, as light levels decrease and rods take over from cones, humans experience an overall blue-shift, known as the Purkinje effect[93]. This quirk of our own visual system has long been exploited, for example in art[94]. More generally, the intimate link between the eye's spectral sensitivity and behaviour has been recognized for more than two centuries, and systematically exploited to study the functions of eyes and brains[95] since long before the discovery of the action potential or the genetic code.

### Red behaviours

One well-conserved visual behaviour of animals is the dorsal light reflex[96,97]. Sunlight tends to come from above, and animals as diverse as squid[98] and humans[99] use this cue to vertically stabilize their body and/or eyes. In fish, the spectral sensitivity function of this reflex can be measured with minimal equipment: it requires only a fish tank, 'coloured' light sources placed on the side and a ruler to measure the fish's resultant body axis relative to vertical. Early behavioural experiments such as these established the dorsal light reflex as one of many originally aquatic visual behaviours that are predominately linked to red cones[96] (Fig. 4f) and rods[100], the principal brightness sensors of the vertebrate eye (Fig. 2). In fact, most major off-circuits of the zebrafish eye[17,22,57,80] and brain[7,90,91] are spectrally consistent with dominant input from red cones alone.

Early links between photoreceptor types and basic behavioural programmes such as dorsal righting may have 'locked' them in place, in the sense that they became non-optional. This is because visuo-behavioural programmes build on each other. For example, reliable eye and body stabilization is a prerequisite for robust motion vision: the ground is usually the most stable visual landmark in shallow water, and consequently, zebrafish optomotor circuits take most of their input from the lower visual field[1,101,102]. However, this strategy only works if the fish is straight. Conversely, the putative absence of a strong link between blue cones and similarly foundational visual behaviours[1] might then render blue cones relatively more expendable (Fig. 2a).

Like the dorsal light response (Fig. 4f), both optomotor and the closely related optokinetic reflexes[103,104] are examples of ancient visual behaviours that are consistently long-wavelength biased, including in mammals[104,105], fish[18,61,106], frogs[20] and birds[21]. However, outside of mammals, the spectral sensitivity functions of these motion systems are systematically too narrow to be explained by inputs from red cones alone. In zebrafish, motion vision circuits are best explained by a putative circuit that subtracts green-cone signals from red[1] (Fig. 4g). Selection pressures that led to this hypothesized ancestral circuit may include 'rippling caustics'[107]: as sunlight enters the water, ripples on the surface are projected onto the seabed as moving brightness patterns. These visual waves will activate red cones much more readily than the approximately brightness-invariant green cones[16]. Green-cone signals may therefore be useful to regulate the gain of the otherwise achromatic motion vision circuits. Such a solution would not require green circuits to be motion sensitive themselves—rather, their suppressive influence could come after a red-motion response has already been extracted. In agreement, spectral signatures for 'red-minus-green' circuits are sparse within the inner retina[17,22,57] where widefield motion signals are first extracted[108] (Fig. 4b), but they are prominent all over the brain[7,90,91,109].

### UV behaviours

On the other end of the spectrum, the issue of rippling caustics is less of a problem for UV cones because the ground is poorly UV reflective. Correspondingly, behaviours linked to UV-cone circuits usually draw on downwelling light[1]. Of these, teleost prey capture[110], with a focus on zebrafish[78,111], is probably the most intensely studied example[16,17,19,56–58,80]. When illuminated by the sun, zooplankton such as paramecia inadvertently give away their position in a bright and moving UV sparkle[56,112], and zebrafish, who like many fish attack from below[19,113], have evolved to exploit this fact of nature. Their acute zone[56,57,74,114] is densely covered in UV cones that are anatomically, molecularly and functionally specialized for prey capture[56,58]. This boosts the cones' sensitivity for UV-bright contrasts more than two orders of magnitude compared with other parts of the eye[56], and this UV dominance propagates all the way across the outer and inner retina[17,22,57,80] into brain circuits[7,90,91] leading to behaviour[19,56,115]. As a result, capture of paramecia prey is preferentially elicited under UV illumination[19,56], and the behaviour plummets to near chance levels when UV cones are genetically ablated[56,115]. Moreover, the behaviour's spectral profile[19] is notably narrower than that of UV cones[16], and this spectral difference is consistent with an inhibitory input from green-cone circuits (Fig. 4h)—reminiscent of the inferred corresponding interaction between red and green cones underlying widefield motion vision (Fig. 4g). In the case of prey capture, this UV sharpening may help fish to distinguish food from inedible floating debris. Alternatively, or in addition, interactions with mid-wavelength cones may support distance estimation[19].

While the link between UV-cone circuits and prey capture in zebrafish may well be representative for ancestral visual hunting

strategies in small aquatic species, including invertebrates (Box 2), prey capture was probably not the first use of UV cones for driving behaviour. More probably, this would have been for detecting threats. For example, the zebrafish visuomotor response is highly responsive to UV light[116]. Perhaps more ancestral still, many small animals including larval zebrafish are negatively phototactic to harmful levels of UV light[117], an ability that does not even require the presence of an eye[118,119] and could thus be substantially older. In fact, long pre-dating bilaterians[120] let alone vertebrates, the first light-sensitive opsins[24] were probably UV-sensitive, because at that time the intrinsically UV-sensitive chromophore was not yet covalently attached to the opsin protein[4]. From here, it is only a small leap of faith to suggest that perhaps the origin of all animal vision was a UV-avoidance circuit in a common neuralian ancestor.

Returning to vertebrates, the high gain of UV cones generally predisposes this channel for supporting threat detection; however, it can be advantageous to additionally recruit red cones for the same task. For example, zebrafish do not only swim away from too much UV light, they also, independently, swim towards long-wavelength light[117]. This combination of UV-negative and red-positive phototaxis establishes a common behavioural axis that allows zebrafish to flexibly seek light environments that are suitable for 'normal vision' without being harmful. Once such cone-to-behavioural circuits are wired up in principle, their cone weights can then be gradually readjusted or even reversed over evolutionary time to suit changing visuo-ecological requirements. For example, many larger species including most frogs seek rather than avoid short-wavelength light[121]. Some even exhibit spectrally bimodal positive phototaxis[122], suggesting that in this case UV- and red-cone circuits act additively. Similarity, the UV-dominant zebrafish visuomotor response can also be elicited at long wavelengths[116], and the dorsal light response is not categorically red-exclusive in all fish[123]. Finally, UV and red cones may also be differentially used for driving common behavioural programmes across different parts of visual space[10,57] or depending on object contrast[80].

Taken together, vertebrate visual behaviours therefore appear to be mainly, and perhaps exclusively, driven by the combined and contrasted signals from red and UV cones alone. By contrast, no basic visual behaviour of vertebrates is known to be primarily driven by ancestral green or blue cones. In zebrafish at least, their strong spectral opponencies render them insensitive to achromatic contrasts[1,16], and this property appears to be exploited to regulate rather than drive visual behaviour.

## Conclusion

Synergizing insights into the distinct sets of challenges and opportunities of vision underwater with our growing understanding of the structure and function of early circuits across a broad range of vertebrates and their behaviours, I have attempted to span an alternative narrative arc that perhaps goes partway to explaining common themes and differences we see across animal eyes today. It is, however, likely, and perhaps inevitable, that some interpretations offered will need to be reconsidered in due time.

Nevertheless, one thing seems clear. Truly understanding the structure, function and dysfunction of eyes, including our own, will also require understanding their ancestry, and it will be very difficult to achieve this without further looking outside eutherian mammals. The time for doing so could not be more opportune: the now widespread availability of powerful 'omics' approaches across essentially all areas of vision science, from anatomy via molecular profiling, neurophysiology, computation and behaviour, is currently facilitating renaissance of interest in some of the traditionally most understudied eyes[16,53,124–126].

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## Competing interests

The author declares no competing interests.

## Additional information

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