The Retinal Basis of Vision in Chicken

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SUMMARY

The Avian retina is far less known than that of mammals such as mouse and macaque, and detailed study is overdue. The chicken (*Gallus gallus*) has potential as a model, in part because research can build on developmental studies of the eye and nervous system. One can expect differences between bird and mammal retinas simply because whereas most mammals have three types of visual photoreceptor birds normally have six. Spectral pathways and colour vision are of particular interest, because filtering by oil droplets narrows cone spectral sensitivities and birds are probably tetrachromatic. The number of receptor inputs is reflected in the retinal circuitry. The chicken probably has four types of horizontal cell, there are at least 11 types of bipolar cell, often with bi- or tri-stratified axon terminals, and there is a high density of ganglion cells, which make complex connections in the inner plexiform layer. In addition, there is likely to be retinal specialisation, for example chicken photoreceptors and ganglion cells have separate peaks of cell density in the central and dorsal retina, which probably serve different types of behaviour.

INTRODUCTION

The *bauplan* of the vertebrate retina emerged over 500 million years ago in the Cambrian period (Lamb, 2019; Lamb et al., 2007). Since then visual systems have changed to match ecological needs, but they retain many common characters including photopigment gene families and retinal circuity. Early vertebrates had rods and four spectral types of cone photopigment. Today, most mammals have rods and two types of cone, whereas birds have rods and five types of cone. These differences probably arose because in their evolution mammals had a period of nocturnality when two types of cone pigment were lost.

Mammal visual systems, including mice, rabbits and primates have been studied extensively, and much is known about signal processing in the mammalian retina (Baden et al., 2020; Demb and Singer, 2015; Seabrook et al., 2017). Comparable research on birds is very limited, despite most having excellent vision. In some species the eyes occupy 50% of the cranial volume (***Figure 1*a;** Endler and Mielke, 2005; Jones et al., 2007; Richard H. Masland, 2008). Behaviours such as flight, bill control and predator detection rely on vision (Martin, 2017), but have different requirements, which leads to interesting questions about retinal specialisation. More generally, how structurally and functionally different are bird and mammalian retinas?

This review shows that the chicken (*Gallus gallus domesticus*) is suited to addressing these questions, in part because it is an established model for eye disease and development (Wisely et al., 2017). Functional understanding of the chicken retina is rudimentary, but a wealth of anatomical studies has begun to chart the morphology and circuitry of retinal neurons. Compared to mammals, the chicken retina is structurally dense; it features many neurons with complex branching patterns that divide both outer and inner plexiform layers into multiple anatomical strata, which presumably have distinct functions. This anatomical groundwork is of great value for future physiological studies.

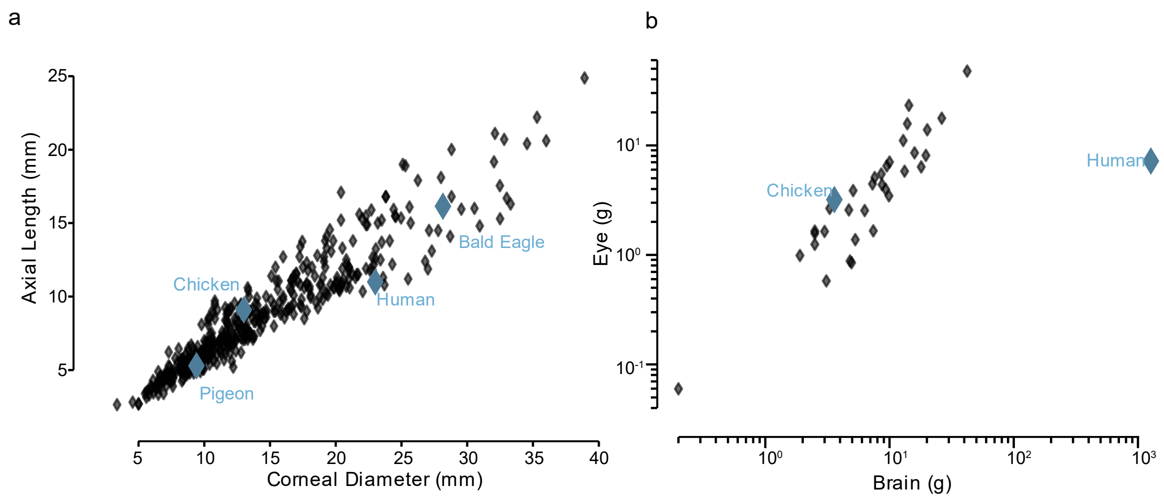

Figure 1|Chicken eye size in relation to other species and in relation to other features of the body a| Comparison of axial length and corneal diameter between different bird species and human. The chicken eye has a medium sized eye when compared to other birds. Data from *(Hall, 2008)* for birds, *(Bhardwaj, 2013)* for human , *(Iribarren et al., 2014)* for chicken. **b|** Comparison between brain weight and eye weight in different bird species, chicken and human. The chicken dedicates a large amount of cardinal volume to its eyes in contrast to humans which have relatively small eyes compared to their brain size.

The Origin of Domestic Chicken

Chickens are domesticated red jungle fowl (*Gallus gallus*), whose natural habitat stretches across Southern Asia and India. Domestication of various jungle fowl subspecies occurred independently in different regions of Southern Asia (Eriksson et al., 2008; Fumihito et al., 1994; Kanginakudru et al., 2008; Storey et al., 2012). Today's commercial poultry, bred for egg or meat production, are genetically diverged from the ancestral jungle fowl (Tadano et al., 2014). There is evidence for positive selection for genes that weaken visual capabilities, so that chickens have 'poor' vision compared to some other birds (Wang et al., 2016). Even so, chickens rely heavily on vision, and their eyes – although of average size - occupy an unusually large proportion of their cranial volume (***Figure 1***a,b**)**.

THE STRUCTURE OF THE CHICKEN RETINA

The vertebrate retina is a complex network, which is organized into functionally distinct layers (***Figure 2***) (Masland, 2001). The chicken follows the common vertebrate retinal organisation, with three nuclear layers: the ganglion cell layer (GCL), inner nuclear layer (INL) and outer nuclear layer (ONL), and three neuropils: the retinal nerve fibre layer (NFL), inner plexiform layer (IPL) and outer plexiform layer (OPL). Signal processing occurs along two major pathways. In the vertical pathway, bipolar cells connect photoreceptors to the retinal ganglion cells whose axons form the optic nerve. Horizontal pathways formed by horizontal cells in the OPL and amacrine cells in the IPL, modulate the vertical pathway, mediating processes such as lateral inhibition and directional selectivity.

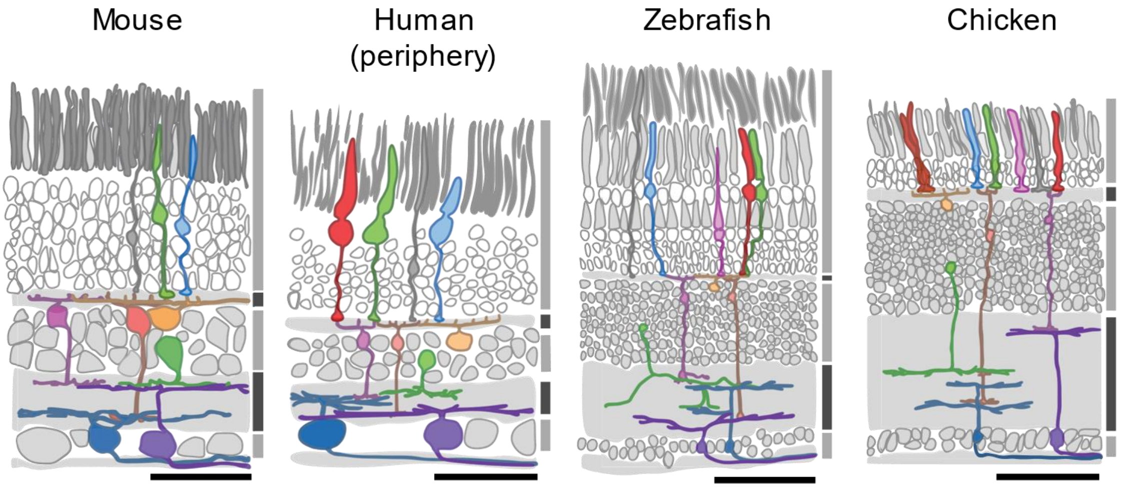

Figure 2| Retina cross section of different vertebrate retinas compared to the chicken retina. The chicken has a relatively large IPL with comparable many neurons in comparison to other vertebrates. Scale bar = 50 µm. Modified from *(Baden et al., 2020)*.

Photoreceptors

Chickens probably have the best studied photoreceptors amongst birds. As in all vertebrates, the photoreceptor somata reside in the ONL, with their photosensitive outer segments embedded in the pigment epithelium, facing away from the light. The inner segments have axons which terminate in pedicles (feet) which connect to bipolar- and horizontal cells in the OPL. Photoreceptor density is not uniform across the visual field, reflecting ecological adaptation. The density is greatest in the area centralis, at about 20,000 cells per mm^2, which is rod-free (da Silva and Cepko, 2017; Morris, 1970; Weller et al., 2009) and decreases linearly with retinal eccentricity to about 8,000 cells.mm^{-2} in the periphery (Bueno et al., 2011). This retinal topography is present in other birds including the pigeon (Querubin et al., 2009), where the maximum cone density is about 30,000.mm^{-2}, falling to about 5,400 cones mm^{-2} in the periphery, and in Australian passerines (Wells-Gray et al., 2016).

Types of Photoreceptors. Based on opsin gene expression, morphology, and function, most studies distinguish six types of visual photoreceptor in birds: four types of single cone, double cones and rods (Bowmaker and Knowles, 1977; Hart, 2001; Okano et al., 1992) (***Figure 3*a**). In the chicken estimates on the relative proportions of these receptor types vary (***Table 1***). In a detailed study of both the central and peripheral retina in multiple individuals Morris (Morris, 1970) found on average, that the central area had 54% single cones, 32% double cones and 14% rods, while the peripheral retina had 37% single cones, 30% double cones and 33% rods. More recently, (López-López et al., 2008) isolated single photoreceptors from the central retina and counted 38% single cones, 44% double cones and 18% rods. Other studies find different relative photoreceptor numbers (Kram et al., 2010; López-López et al., 2008; Meyer and May, 1973; Morris, 1970), which is likely part-explained by differences in the retinal region(s) examined. Generally, the proportion of single cones increases towards the area centralis at the cost of rods while the proportion of double cones is more uniform across the retina. In addition, in chicken retina each cone type forms a loose hexagonal mosaic, which likely originates from lateral inhibition between cones of the same type during development resulting in different exclusion distances between the different types of cones (Kram et al., 2010) ***Figure 3*b**. There is no evidence for interactions between mosaics of different types.

Table 1: Photoreceptor topography in the chicken retina as found in the literature. The relative proportion of different types of photoreceptors as described in different studies are compared. The location refers to the location in the retina from which the retinal probes for the respective studies were taken. Values were rounded to nearest integers.

Reference	Location	Single cones in %	Double cones in %	Rods in %
(Kram et al., 2010)	Periphery	59	41	
(Morris, 1970)	Central	54	32	14
	Periphery	37	30	33
(López-López et al., 2008)	Central	38	44	18
(Meyer and May, 1973)	Temporal (Segment 3)	23	45	32
	Periphery	20	40	40

Single cones. The four types of single cones each contain one of four different opsins, which are classified by their genetic family as long wavelength-sensitive (LWS), rhodopsin-like 2 (RH2), short wavelength-sensitive 2 (SWS2) and short wavelength-sensitive 1 (SWS1) (Bowmaker, 2008; Hart, 2001; Okano et al., 1992; Yokoyama, 2008, 2002) (***Figure 3a***). In the chicken, the wavelengths of their absorption maxima (λ_{max}) are 570 nm, 508 nm, 455 nm and 419 nm respectively (Bowmaker and Knowles, 1977; Okano et al., 1989). Single cone nomenclature is either based on the λ_{max}, or on the name of their opsin. LWS cones express the LWS opsin, middle-wavelength-sensitive (MWS) cones express RH2, SWS cones express SWS2, and violet-sensitive (VS) cones express SWS1 (***Figure 3a***). The four different cone types mean the chicken can see light from about 370 nm – 700 nm, ***Figure 3c***), and probably give chicken tetrachromatic vision (Kelber, 2019; Olsson et al., 2015; Osorio et al., 1999).

Birds can be categorized as UV-sensitive or VS-sensitive based on the SWS λ_{max}. Chicken SWS λ_{max} is typical for VS-birds, which also includes pigeons, domestic turkey and the common peafowl (***Figure 3c***). In contrast, UV-sensitive birds, for example the common starling and the common blackbird, have a UV-shifted SWS1 (λ_{max} ~ 370 nm) and SWS2 opsin variants (Hart, 2001), while λ_{max} of RH2 and LWS opsins are similar across both groups.

Double Cones. Double cones consist of two electrically coupled cells, and are present in fish, reptiles, monotremes and birds, but not eutherian mammals. Avian double cones comprise a principal member and a smaller accessory member (Smith et al., 1985), both of which express the LWS opsin (***Figure 3***). This contrasts with double cones in some fish where the two members express different opsins, and spectral opponent interactions between the outputs of the two members of the double cone are possible (Meier et al., 2018; Pignatelli et al., 2010). The function of bird double cones is debated. One hypothesis posits that they serve luminance pathways, but not wavelength discrimination (Jones and Osorio, 2004; Sun and Frost, 1997; v. Campenhausen and Kirschfeld, 1998; Olsson et al. 2015). Consistent with this hypothesis, double cone terminals are connected to rods via horizontal cells (see below). However, double cones are absent from the raptor fovea (Potier et al., 2018), which suggests that single cones can serve luminance vision.

Rods. Few studies specifically concern chicken rods. Like other vertebrates, they contain the photopigment RH1 (Bowmaker and Knowles, 1977), and they are used for vision in dim light (Schaeffel et al., 1991).

Optical Properties of Chicken Photoreceptors. Because photoreceptors act as light guides their specific morphology and refractive index differences within the cells and with the external medium affect their absolute, angular and spectral sensitivities (Westheimer, 2008). Chicken cone outer segments are about 1.5 µm in diameter and average 30 µm in length. Immediately distal to the outer segment two high refractive index organelles, an ellipsoid body and an oil droplet, alter sensitivity by guiding (or focussing) light onto the outer segment (Wilby et al., 2015; Wilby and Roberts, 2017). The ellipsoid body is an accumulation of mitochondria (Wilby and Roberts, 2017), while oil droplets can be pigmented in which case they act as a long pass filters (Stavenga and Wilts, 2014; Wilby et al., 2015; Wilby and Roberts, 2017). In chicken, the T-type oil droplets present in VS cones are unpigmented, while the other cones each contain a specific type of carotenoid pigmentation. The oil droplets are known as C-type (SWS cone), Y-type (MWS cone), R-type (LWS cone) and P-type (double cone)

(***Figure 3*d**) (Toomey et al., 2015). In the accessory member of the double cone, some studies report a P-type droplet, and others find no oil droplet (López-López et al., 2008). The presence of a specific oil droplet in each cone type means that is relatively straightforward to identify them in unstained tissue.

Oil droplet pigments modify cone spectral sensitivities by absorbing light wavelengths below a certain value. Modelling by Wilby and colleagues (Wilby et al., 2015; Wilby and Roberts, 2017) predicts that in chicken the transparent T-type oil droplet enhances the absolute sensitivity of the VS cone whereas pigmented oil droplets on the other single cones narrow absorption spectra at the expense of absolute sensitivity (compare ***Figure 3*c** and **e**).

Although oil droplet pigments seem to be fixed (but see (Toomey et al., 2015)) the pigment density varies considerably between species and within eyes, in some cases under direct environmental control (Hart et al., 2006), thereby setting the trade-off between absolute sensitivity and spectral tuning to suit the ecology of each photoreceptor. (This could explain differences in reported oil droplet colours as summarized by (López-López et al., 2008)). In addition, oil droplet absorption spectra vary across the visual field, with C- and P-type oil droplets in the ventral retina having a significantly higher cut-off wavelength than in the dorsal area. In the pigeon oil droplets pigmentation show a somewhat similar division with a dorsal red field (containing more red oil droplets) and a ventral yellow field. The cut off wavelength in the red field is 10 nm longer than the yellow field (Bowmaker, 1977).

There is variation within the standard vertebrate photoreceptor classes, including specially tuned receptors in mice, primates and zebrafish (Baden et al., 2013; Baudin et al., 2019; Sinha et al., 2017; Yoshimatsu et al., 2019). In the chicken a morphological study by Mariani and Leure-Dupree, (1978) recognised straight and oblique subtypes of single cone, with straight cones having a relatively short vertical axon, while the axon of the oblique cone projects more horizontally into the OPL. López-López and co-workers (López-López et al., 2008) found 36.5% straight and 1.5% oblique cones (relative to double cones and rods) in the central field of the retina. Wai and co-workers (Wai et al., 2006, 2002) found two types of single cone, one having blade like outer segments and the other longer outer segments and rod like inner segments. The same study (Wai et al., 2006, 2002) also described three variants of double cone. This subject needs further investigation, but as few studies distinguish cone morphologies we retain the common classification of six receptor types in the chicken.

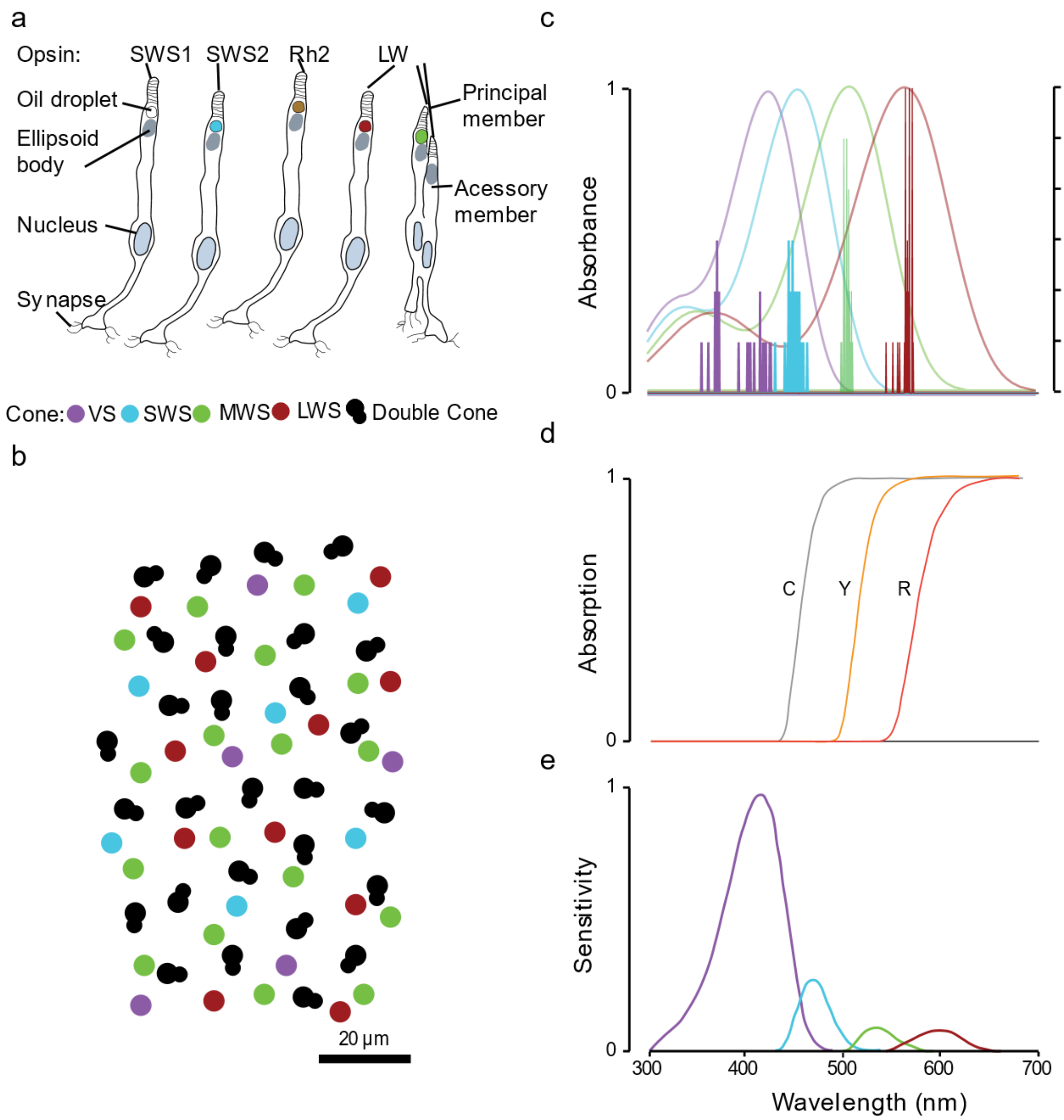

Figure 3|The basis of chicken colour vision. Redrawn and modified from *(Kelber, 2019)*. **a|** Chicken have 5 different types of single cone and a rod photoreceptor. Cones have oil droplets and ellipsoid bodies which modify the effective opsin spectra **b|** Cone mosaic in the retina as described by *(Kram et al., 2010)*. Different cone types form independent mosaics with different sized exclusion zones **c|** Absorption spectra of chicken opsins calculated based on λ_{max} values summarized in *(Hart, 2001)* and using the opsin temple from *(Govardovskii et al., 2000)*. In comparison, the histogram shows λ_{max} values for different other birds. Bin size of the histogram = 0.5nm. **d|**

Absorption of the 3 pigmented types of colour oil droplets found in the chicken as described by *(Olsson et al., 2015)*. The pigments effectively act a long pass filters **e|** Simulated cone sensitivities based on modelling the light path through the ellipsoid body, oil droplet and outer segments *(Wilby et al., 2015; Wilby and Roberts, 2017)*. The VS cone is the most sensitive by far, the effect of the oil droplet narrows the spectra which show little overlap with each other.

OPL projections. Chicken outer plexiform layer (OPL) is divided into three strata, by photoreceptor outputs (Gallego et al., 1975; López-López et al., 2008; Mariani and Leure-Dupree, 1978; Waldner et al., 2019), and horizontal (Fischer et al., 2007; Mariani, 1987; Wahlin et al., 2010) and bipolar cell morphology (Quesada et al., 1988). Double cones and rods project to the first (outermost) stratum, LWS and MWS cones project to the second, and VS and SWS cones to the third stratum (Wahlin et al., 2010). In each case there are stratum-specific connections with subsets of bipolar and horizontal cells ***Figure 4***.

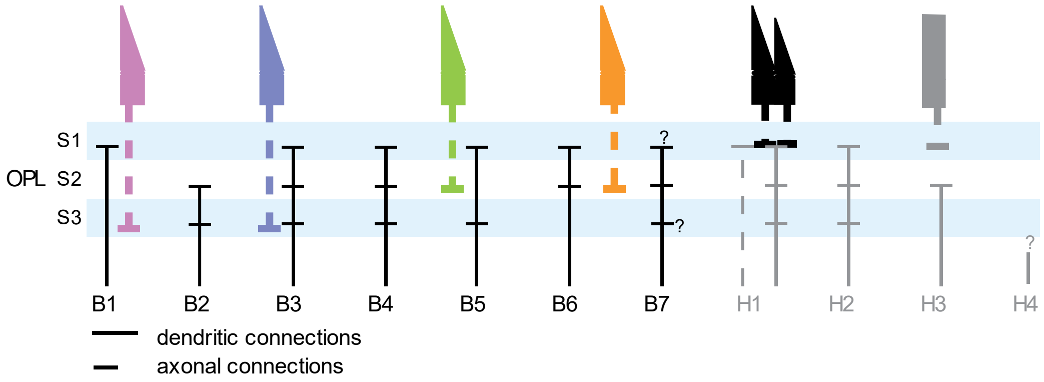

Figure 4| Connections in the chicken OPL. PRs, BCs, and HC, project to one of the 3 strata found in the OPL. PR axonal projections are based on description by *(Waldner et al., 2019)*, colours: VS cone = purple, SWS cone = blue, MWS cone = green, LWS cone = red, double cone = black, rod = grey. BP cell projections are based on description of their dendritic tree by *(Quesada et al., 1988)*. HC projections are based on descriptions by *(Fischer et al., 2007; Mariani, 1987; Wahlin et al., 2010)*.

Horizontal Cells

Horizontal cells (HCs) provide direct feedback and relayed feed-forward connections between photoreceptors, as well as feed-forward connections to bipolar cell dendrites (Chapot et al., 2017; Thoreson and Mangel, 2012). Vertebrates have four major types of HC, of which with some groups such as mammals have a subset (Boije et al., 2016). In pigeon Golgi stains identify all four HC types (Mariani, 1987) (***Figure 5a)***, while in chicken there is morphological evidence for at least three types (Tanabe, 2006) and immunochemical evidence for four (Fischer et al., 2007; Sun and Crossland, 2000; Wahlin et al., 2010). This review follows the HC classification of (Boije et al., 2016), but there is some variation: Type 2 described by (Edqvist et al., 2008; Tanabe, 2006) appears to match type 3 and/or 4 of (Fischer et al., 2007; Mariani, 1987; Sun and Crossland, 2000) and vice versa.

About 50% of chicken HCs are GABA positive, which indicates that GABA is an inhibitory neurotransmitter in the OPL (Araki and Kimura, 1991; Fischer et al., 2007; Kalloniatis and Fletcher, 1993; Sun and Crossland, 2000). Different HC-to-cone interactions have been proposed. Mouse cones lack ionotropic GABA receptors but HC's express them, which suggests that GABA is involved in auto-reception, where GABA acts on the same neuron by which it was released (Chapot et al., 2017). GABA might also be involved in HC inhibitory signalling to bipolar cells (Puller et al., 2014). Unlike mammals, in chicken most GABA positive HCs are also positive for glycine, leading to the suggestion that GABA mediates rapid transmission which is modulated by glycine (Sun and Crossland, 2000) (but see: (Thoreson and Mangel, 2012)).

Type 1 HCs. Chicken type-1 HCs have a narrow dendritic field of about 230 µm^2 with an axon of about 80 µm, which projects to the first OPL stratum. The axon froms synapses with double cones and rods (Tanabe, 2006) while the dendrites from synapses with all five types of cone in all three OPL strata, including synapses with both members of the double cone in a circular terminal (Fischer et al., 2007; Mariani, 1987; Tanabe, 2006). Axon terminals on the principal member of the double cone and on rods are GABA positive, but terminals with accessory member of the double cone are GABA negative (Araki and Kimura, 1991). The fact that double cones synapse with both axons and dendrites of type 1 HCs suggests that the double cones serve two distinct pathways: axon terminals combine double cone and rod signals, while the dendrites combine double and single cone signals.

Chicken type-1 HC resembles the sole type in the mouse, where the axon connects to rods and the dendrites to cones (Chapot et al., 2017). Other vertebrates have an equivalent HC – for example zebrafish type 1 connects to all single cones except UV (Li et al., 2009).

HC type 2. This HC forms a dendritic field of about 700 µm^2, the arborization is mostly flat (stellate) lying in OPL stratum 1, and only slightly deeper than the cell body. A a few branches project to OPL stratum 2, where they connect to MWS and LWS cones (Tanabe, 2006; Wahlin et al., 2010).

HC type 3. Type 3 HCs have a candelabrum-shaped morphology with a dendritic field of about 200 µm^2 in all three OPL strata. These cells connect with the accessory but not the principal member of the double cone (Tanabe, 2006).

HC type 4. In pigeon, (Mariani, 1987) found a fourth type of HC, which is morphologically similar to type 3, but has a larger dendritic tree. In chicken, immunochemistry (Fischer et al., 2007) finds four types of HC, but the distinction remains unclear, possibly because types 3 and 4 are morphologically similar (Fischer et al., 2007; Sun and Crossland, 2000).

Bipolar Cells

Bipolar cells (BC) dendrites receive input from photoreceptors and horizontal cells in the OPL, and project to distinct layers of the IPL where they synapse with amacrine- and ganglion cells. From RGCs connection patterns Naito and Chen, (2004b) identify eight IPL strata in the chicken, but the literature on chicken amacrine cells typically divides the IPL into five strata (Millar et al., 1985). Typically for vertebrate bipolars (Nelson and Connaughton, 2012), chicken bipolar cells are mostly glutamatergic, and all are GABA negative (Kalloniatis and Fletcher, 1993; Sun and Crossland, 2000).

Eleven types of bipolar cells have been identified in chicken from dendritic tree morphology, without considering axonal projections (Quesada et al., 1988) (***Figure 5*a**). Most chicken BCs are bi- or tri-stratified, as is common in amphibians and teleost fish (Nelson and Connaughton, 2012), but not mammals (Behrens et al., 2016; Euler et al., 2014). How this structural complexity is mirrored in function is a fascinating question.

Bipolar cell dendritic field diameters range from 3 µm (~0.013° of visual angle) to over 25 µm (~0.11° of visual angle), and they can be symmetric or asymmetric. The smallest chicken BCs are midget-like, with dendritic arbors having a morphology consistent with single cone connectivity (Quesada et al., 1988). In primates midget bipolar cells connect individual cones to midget ganglion cells, which allows visual resolution to approach that set by the receptor array (Kolb and Marshak, 2003). In the chicken, it is unknown if BCs with this putative single-cone connectivity form synapses with midget-like ganglion cells in the IPL, or whether these BC's are restricted to the area centralis. Notably, primate midget cells seem to be a derived character (Mollon, 1989), and their evolutionary relationship to avian midget cells is unknown.

Chicken BCs resemble those in other bird retinas. Specifically, in the pigeon Mariani, 1987 described eight different types of BCs many of which resemble chicken BCs, including a midget-like BC. In addition, an interplexiform cell has been described in the pigeon INL. This cell forms medium-field connections between the IPL and OPL, and has been described in a range of non-mammalian vertebrates (Mariani, 1987). Kalloniatis and Fletcher (1993) found a possible interplexiform cell in the chicken retina, but its projections have not been identified.

An interesting feature of avian (and other non-mammalian) BCs is a structure called Landolt's club which is a specialised dendrite that reaches into the external limiting membrane of the retina. This structure links BCs to Muller (glial) cells, and is thought to support the metabolic/nutritional needs of BCs (Quesada and Génis-Gálvez, 1985). These structures, which are also present in most pigeon BCs (Mariani, 1987), might be needed because the avian retina lacks of a vascular system for nutrient transfer (Quesada et al., 1988).

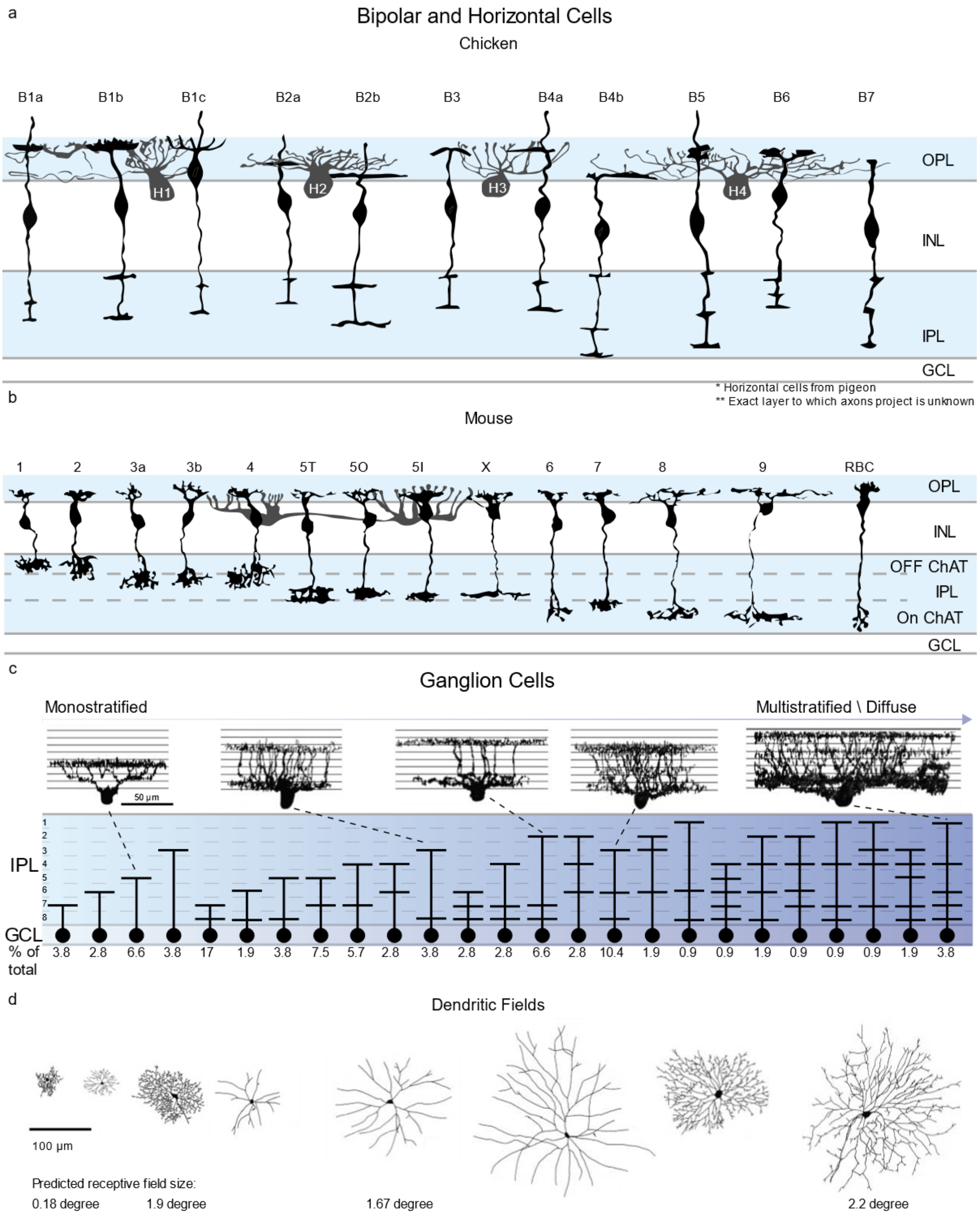

Figure 5| Overview over bipolar-, horizontal-, and ganglion cell morphology. a| BCs and HCs found in the chicken compared to those found in the mouse. Chicken BC are often bi- or tristratified which is uncommon in the mouse. The exact layers to which BC axons project in the chicken are unknown. BC drawings for the chicken were taken from *(Quesada et al., 1988)*, HC drawings were taken from the pigeon *(Mariani, 1987)*, but their morphology is comparable to those found in the chicken. Mouse BCs drawings were taken from *(Behrens et al., 2016)*, HC drawing was taken from *(Wang et al., 2003)*. Cell sizes are not to scale. **b |** Stratification patterns of RGC found in the chicken as described by *(Naito and Chen, 2004a)*. Some example cell morphologies are shown, these are copied from *(Naito and Chen, 2004a)*. Receptive field sizes for these cells were approximated by calculating the angle in the visual field which the dendritic tree potentially sees.

Retinal Ganglion Cells

Amongst vertebrates, birds have a relatively high density of retinal ganglion (RGCs) (***Figure 6***). For example the pigeon (Querubin et al., 2009) has 10,800 RGCs per mm^2 in the fovea and the starling (Dolan and Fernández-Juricic, 2010) 20,000.mm^{-2} compared to 13,500 mm^{-2} in the chicken. Nevertheless, the total of 2.6 (Ehrlich, 1989) to 4.9 million (Naito and Chen, 2004b) RGCs reported for the entire retina (in the right eye, see lateralization) are over double that in humans, despite a smaller ocular diameter. Considering the peak density of PRs and RGCs this would mean that every RGC connects to about 1.5 photoreceptors in the area centralis. RGC density peaks in the area centralis at about 13,500 RGCs mm^{-2} – which is similar to the human parafovea (Quinn et al., 2019). A second, albeit less pronounced region of high density lies in the dorsal retina (10,200 RGCs mm^{-2}). For ground-foraging birds this arrangement allows simultaneous high acuity vision in the lateral/frontal visual field (*area centralis*) and at the location where the bird will peck for food (*area dorsalis*), which is beneficial (Evans and Evans, 1999).

Across the retina, the sizes of RGC somata vary, ranging from 40 to 560 µm^2, with a near linear increase with eccentricity (Ehrlich, 1989; Naito and Chen, 2004a). The same is true for dendritic fields, which from 43 µm to 504 µm in diameter (Naito and Chen, 2004a). Assuming that receptive field size is approximated by the extent of the dendritic tree, RGC receptive field areas range from about 0.18° in the central zone (roughly equivalent to the area centralis (Naito and Chen, 2004a)) to about 2.2° in the peripheral zone of the retina (***Figure* 5d**). Unlike BCs, no single cone (midget-like) RGCs have been found, although the smallest RGCs are expected to exhibit low convergence from BCs.

Chicken RGCs include mono-, bi-, multi-stratified and diffuse types which send dendritic branches into nearly all IPL strata (***Figure* 5c)**. Mono- and bistratified forms are most common, and in general, anatomical RGC-type density appear to be inversely related to the number of innervated strata.

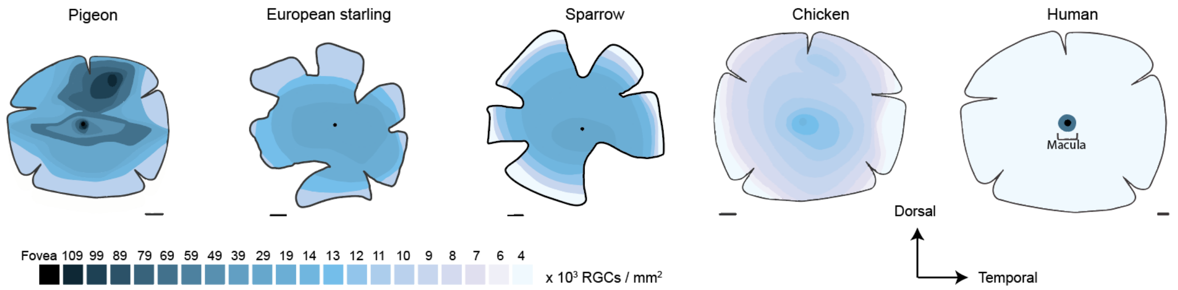

Figure 6| Topography of retinal ganglion cells in different birds compared to human. The average density of RGC in the chicken is much higher compared to the human but relatively low when compared to other birds. The chicken is missing a fovea but has to areas of higher RGC densities, which are found in the central and dorsal retina. Figures reproduced from *(Rodrigues et al., 2016)* and *(Dolan and Fernández-Juricic, 2010)*. Chicken data is based on *(Chen and Naito, 1999)*, pigeon data is based on *(Querubin et al., 2009)*. Scale bar = 2mm.

Amacrine Cells

Amacrine cells (ACs) laterally connect BCs and RGCs in the IPL. Amacrine cells have diverse structures and functions, and as a class they remain the least understood set of retinal neurons in any species (Masland, 2012). At least thirty different ACs are described in the mammalian retina. A general assumption is that a higher diversity of RGCs leads to a higher diversity of ACs (MacNeil and Masland, 1998; Masland, 2012). Accordingly, chicken should have a sizable diversity of ACs, and several different anatomical and immunohistochemical types have been described. While an account of all known types is beyond the scope of this review, we can highlight few interesting features of chicken ACs.

Following the common vertebrate pattern chicken ACs form a distinct layer in the INL (approximately the bottom half of the INL), typically with larger cell bodies than BCs (Fischer and Stell, 1999; McMains et al., 2011; Millar et al., 1987; Sun and Crossland, 2000; Waldner et al., 2019). Ehrlich, 1989 and Chen and Naito, 1999 suggested that about 30 – 35 % of the cells in GCL are displaced amacrine cells, which since ACs are often GABA positive (Masland, 2012) is in line with findings by (Kalloniatis and Fletcher, 1993) that about 40% of the cells in the GCL are GABA positive. In addition to GABA, avian ACs probably use many other neurotransmitters and modulators including glycine, acetylcholine, substance P, serotonin, nitric oxide and dopamine (Morgan, 1983) – in line with mammalian ACs.

Cholinergic Amacrines. The chicken has at least three different morphological types of cholinergic AC.

Types 1 and 2 are monostratified and connect to BCs, ACs, and RGCs. Type 3 is bistratified and connects to ACs and RGCs in separate IPL strata (Millar et al., 1987). The best known vertebrate cholinergic ACs are starburst amacrine cells which are involved in directional selectivity (Masland, 2012). Millar et al., 1987 found that chicken type 1 AC is morphological equivalent to mammal starburst type-a and type 2 AC is similar to starburst type b, type 3 AC as no known equivalent (homologue) the mammalian retina. A recent study found that acetylcholine gates dendritic spikes in direction selective GCs (Brombas et al., 2017).

Nitrergic ACs. Nitric oxide is a widespread signalling molecule, which acts as a neurotransmitter though not via conventional synapses. (Fischer and Stell, 1999; Wilson et al., 2011) described several different types of nitrergic AC with different stratification patterns. Some are ubiquitous across the retina and others present in specific regions of the retina only. In a recent study, the function of one type of nitrergic ACs in the mouse retina was revealed (Jacoby et al., 2018). This type of AC forms a dense network of gap junctions controlling NO release across the retina. Gap junction coupling is regulated by the NO release of the same cells. Because the NO release of these cells is regulated by light exposure they are effectively coupled in dark conditions and decoupled in the light.

Retinal lateralisation Interestingly, the data on pigeon RGCs presented in Querubin et al., 2009 hints that RGC numbers and density differ between the right and left eyes, although this was not explicitly noted. In the common starling the proportions of the photoreceptor types differ between the two eyes (Hart et al., 2000). Could avian retinas, including in chicken, be functionally lateralised? Chickens tend to use their left and right eyes for distinct subsets of visual behaviours (Dharmaretnam and Andrew, 1994; Vallortigara et al., 2001, 1996). For example, Vallortigara et al., 1996 reported that chicken preferably use their left eye for spatial learning. The extent of structural and functional lateralisation in avian retinas is a fascinating open question, and in any case when working with birds, it is critical to keep note of which eye is being investigated.

RETINAL FUNCTION

There are few detailed studies of chicken retinal processing. Lisney et al., 2012 used electroretinograms (ERGs) to measure the flicker fusion frequency at 105 Hz, which is comparable to the maximum human value of about 95 Hz (Heck, 1957). In another ERG study, (Schaeffel et al., 1991) showed that rods are inactive during the daytime but turned on endogenously at night. Various studies compare ERGs of normal retinae and disease models (Wisely et al., 2017).

Multielectrode arrays (MEAs) record many RGCs simultaneously, but their potential remains underexploited. (Chen, 2003) made the first such recordings in chicken and (Schaeffel, 2017) used an MEA, to show that RGC responses vary with image focus. (Stett et al., 2000) used an MEA to deliver electrical stimuli to specific parts of the retina and in turn measure RGC responses.

Finally, (Shen et al., 2002) used patch-clamp recordings in a study of a new type of GABA receptor in the chicken retina.

CONCLUSION

Birds making an interesting comparison with primates, which have secondarily returned to diurnality, after a ‘nocturnal phase’ in mammal evolution, (Mollon, 1989; Ross, 2000)). As far we can tell, the chicken has a ‘typical’ bird retina. Compared to mammals, the morphology suggests complex and diverse signal processing. The retina contains relatively more neurons in the INL and GCL and a higher degree of stratification in both the OPL and IPL. Chicken photoreceptors have been studied in detail, and there are relevant psychophysical studies, especially of colour vision (Jones et al., 2001; Kelber, 2019; Osorio et al., 1999)). In addition, the chicken is established as a model organism for ocular diseases and development (Wisely et al., 2017). This is helpful because genetic, immunochemical and developmental markers are well established and accessible. All in all, the chicken the most accessible avian model organism today and using its potential is a task for scientists in the future. Birds have highly sophisticated eyes, and the chicken may just hold the key to “solve” the riddle of their function.

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