

Colour Vision in Birds

Comparing behavioural thresholds
and model predictions

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<p>Abstract</p> <p>Birds use colour vision for many biologically relevant behaviours such as foraging and mate choice. Bird colour vision is mediated by four types of single cones, giving them an extra dimension of colour information compared to trichromatic humans. The cone photoreceptors of birds have coloured oil droplets that are assumed to increase the discriminability of colours in bright light at the cost of dim light sensitivity. In this thesis I present four studies where we have trained chickens to perform colour discrimination and tested the limits of their behavioural performance. In paper I we tested how small colour differences chickens can discriminate. This allowed us to test the predictions of the most well established model for bird colour vision, the receptor noise limited model. There was a reasonably good fit between model and behaviour. Furthermore, we tested in how dim light chickens could discriminate colours and found that the intensity threshold was affected by the colour difference between the stimuli and their intensity. In Paper II we continued testing colour discrimination in dim light and tested the hypothesis that chickens sum the signals from many photoreceptors to increase contrast sensitivity at the cost of spatial resolution in dim light, so called spatial pooling. We used food containers covered with larger, smaller, more or fewer colour patches. Supporting the hypothesis, the containers covered by more colour could be discriminated in dimmer light. In Paper III we tested colour constancy, the ability to maintain colour perception in different spectral illuminations that would otherwise confuse colour perception. Our aim was to find the largest illumination change that chicken colour constancy could tolerate. We found that chicken colour constancy could tolerate larger illumination changes when discriminating stimuli that were more different from each other. In paper IV we continued the work on colour constancy but allowed the chickens to use relative colour learning, which was specifically excluded in paper III. In Paper IV we found that their colour constancy could tolerate larger illumination changes. In nature relative colour cues are available and may be an important aspect of colour learning and perception. These results suggest that such cues can make colour constancy more robust to larger illumination changes. In both experiments chicken colour constancy was improved if they were adapted for 5 minutes in the tested illumination before performing the discrimination task. We compared the illuminations for which chickens retained colour constancy, to the difference between natural illuminations and we can conclude that chickens are well equipped to maintain accurate colour perception when changing between habitats in the wild. Objects are detected both by their chromatic and achromatic contrasts. The receptor noise limited model can be used to predict discriminability through both chromatic and achromatic vision. To use the model reliably its assumptions and predictions must be compared to behavioural results. This has been done for the chromatic version of the model but not the achromatic. In Paper V we compiled all known chromatic and achromatic contrast detection thresholds, and used them to derive the limiting noise level to be used when predicting visual discrimination in a range of animals. We discuss the limitations of using modelling in the wild such as the need to consider the spatial pattern of the stimuli and the light intensities in which the modelling occurs.</p>		
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*To everyone that helped and contributed to this work and to all
of you that supported and believed in me*

”Det går inte att bromsa dig ur en uppförsbacke”

-Sally Santesson, spelad av Maria Lundqvist i TV-serien ”Sally”

”You can’t use the breaks to get over a hill”

-Sally Santesson, played by Maria Lundqvist in the TV-series ”Sally”

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Original papers and manuscripts

Paper I - **Olsson, P.**, Lind, O. and Kelber, A. 2015. Bird colour vision: Behavioural thresholds reveal receptor noise. *J. Exp. Biol.* 218, 184-193

Paper II - **Olsson, P.**, Wilby, D. and Kelber, A. Spatial summation improves bird colour vision in dim light. Manuscript to be submitted to *Vision Res.*

Paper III - **Olsson, P.**, Wilby, D. and Kelber, A. 2016. Quantitative studies of animal colour constancy – chicken as model. *Proc. R. Soc.* in press. doi: 10-1098/rspb.2016.0411

Paper IV - **Olsson, P.** and Kelber A., Relative colour cues improve colour constancy in the chicken. Manuscript to be submitted to *J.Exp. Biol*

Paper V - **Olsson, P.**, Lind, O. and Kelber, A. Parameter estimation and limitations for modelling achromatic and chromatic discrimination in visual ecology. Manuscript to be submitted to *Behav. Ecol.*

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Author contributions

Paper I. PO developed the experimental design, performed the experiments, analysed the data with contribution from OL and AK and wrote the manuscript with feedback from OL and AK.

Paper II. PO had the initial idea for the experiment, developed the experimental design, performed the experiments, analysed the data with contribution from DW and AK and wrote the manuscript with feedback from DW and AK.

Paper III. PO developed the experimental design, performed the experiments, analysed the data with contribution from DW and AK and wrote the manuscript with feedback from DW and AK.

Paper IV. PO developed the experimental design, performed the experiments, analysed the data with contribution from AK and wrote the manuscript with feedback from AK.

Paper V. PO had the initial idea for the experiment, developed the modelling with input from OL and AK, and wrote the manuscript with feedback from OL and AK.

Papers which are not part of the thesis

Lind, O., Mitkus, M., **Olsson, P.** and Kelber, A. 2013. Ultraviolet sensitivity and colour vision in raptor foraging. *J. Exp. Biol.* 216,1819-1826

Lind, O., Mitkus, M., **Olsson, P.** and Kelber, A. 2014. Ultraviolet vision in birds: the importance of transparent eye media. *Proc. R. Soc. B.* 281, 20132209

Wilby, D., Toomey, M., **Olsson, P.**, Fredriksen, R., Cornwall, C., Oulton, R., Kelber, A., Corbo, J. and Roberts, N. 2015. Optics of cone photoreceptor in the chicken (*Gallus gallus domesticus*). *J. R. Soc. Interf.* 12,20150591

Olsson, P., Mitkus, M. and Lind, O. 2016. Change of ultraviolet sensitivity in growing eyes of chicken and quail. *J Comp. Physiol.* 205, 329-335

Svensk sammanfattning

Fåglar har relativt stora ögon för sina kroppsstorlekar och syn är en kostsam sinnesförmåga, speciellt för flygande djur eftersom stora ögon medför extra vikt. Man kan därför anta att fåglar använder synen för viktiga beteenden. De flesta fåglars färgseende är tetrakromatiskt, vilket innebär att fyra typer av fotoreceptorer bidrar till deras färgseende. Det innebär att deras färgseende har en extra dimension av information jämfört med människans trikromatiska färgseende. Fåglar använder sitt färgseende för många biologiskt viktiga beteenden såsom att hitta mat och för sociala interaktioner som att utvärdera partners. Dock vet vi lite om var gränserna för deras färgseende ligger, hur lika färger kan de diskriminera och i vilka ljusmiljöer kan de urskilja färger?

Vi har använt beteendestudier och matematisk modellering för att hitta gränserna för kycklingars färgseende och utvärderat vilka fysiologiska mekanismer som kan underligga dessa gränser.

I manus I så har vi testat hur små färgskillnader kycklingar kan urskilja genom att träna dem att associera matbehållare med en viss färg med en matbelöning och testat hur ofta de väljer den tränade färgen jämfört med matbehållare av en otränad färg. Vi jämförde deras förmåga med människans och såg inga tydliga skillnader mellan kycklingar och människor. Vi drar slutsatsen att fåglars förmåga att urskilja färger är begränsat av högre brus än människans. Vi undersökte också i hur mörka miljöer de kunde urskilja färger och fann att ju mer olika färgerna var, desto mindre ljus behövdes för att särskilja dem.

För att se färg i mörker verkade fåglarna använda sig av spatial summering, det vill säga de lägger ihop signalerna från många fotoreceptorer för att stärka färgsignalen i utbyte mot en något sämre synskärpa. I manus II så testade vi detta antagande genom att använda matbehållare som täcks till olika stor grad av färg. Om spatial summering är viktig för att tillåta färgseende i mörka miljöer bör de behållare som har täcks till större grad av färg kunna urskiljas i mörkare miljöer. Detta var precis vad vi fann, därmed kan vi dra slutsatsen att spatial summering är viktigt för fåglars mörkerseende. Fåglar som har en tappdominerad näthinna och är aktiva mest under dagen, skulle eventuellt kunna se färg i mörkare miljöer än nattaktiva fåglar med en stavdominerad näthinna!

I manus III undersökte vi kycklingars förmåga att se färg i ljusmiljöer där färgen på belysningen förändrades. Färgseende baseras på att jämföra de spektrala signalerna från olika objekt, men den spektrala signalen beror både på hur objektet

reflekterar ljus av olika våglängder och på den spektrala sammansättningen (färgen) av belysningen. Det klassiska exemplet är att den spektrala signalen från en banan i en röd belysning som rent fysiskt är mer lik en orange färg än en gul. Trots det så uppfattar vi att bananen är gul även i den röda belysningen. Detta fenomen kallas färgkonstans och betyder att färguppfattningen är den samma trots att belysningen förändras. Vi testade hur färgkonstans fungerar i olika typer av belysningar hos kycklingar. Vi tränade kycklingar att välja en orange färg framför en gul och en röd färg i en vit belysning och testade dem i rödare belysningar. Fåglarna kunde fortfarande välja rätt färg i dessa belysningar och vi tolkade det som att de har färgkonstans. Hur mycket belysningsförändring deras färgkonstans tolererade berodde hur de tränats och på hur stor skillnaden mellan färgerna de diskriminerade var, stora färgskillnader tolererade större belysningsförändringar.

I manus IV upprepade vi försöken i manus III men tränade kycklingarna att antingen föredra en orange framför en gul färg eller en grön framför en blå. Därmed kunde kycklingarna använda den relativa färgskillnaden, t.ex. alltid välja den rödare färgen för att göra rätt val. En strategi som inte fungerade för att välja rätt i manus III. När relativa färgsignaler kunde användas behöll kycklingarna sin färgkonstans i rödare miljöer än vad de kunde i försöken i manus III. Relativa färgsignaler förbättrar färgkonstansen. Relativa färgsignaler är vanliga, till exempel hos frukter och bär som signalerar sin ätlighet med typiska färger som alltid ses i relation till den vanligtvis gröna bakgrunden.

Vi urskiljer objekt från deras omgivning med hjälp av kontrast, och kontraster kan skapas av både kromatiska skillnader och akromatiska skillnader. För att förutspå vad fåglar kan urskilja så använder vi en modell (*Receptor Noise Limited model*), som baseras på de spektrala känsligheterna hos djurets fotoreceptorer och hur mycket neuronalt brus (slumpmässig variation i nervsignaler som stör informationsflödet) det finns i synsystemet. I manus I kunde vi kalibrera denna modell med våra beteendedata, det vill säga hur mycket brus måste vi anta att det finns i synsystemet för att förklara den minsta färgskillnaden som kycklingarna kunde diskriminera, deras färgdiskrimineringströskel. Detta var första gången som det gjordes för objekt färger, dvs. färger som reflekterar ljus. Denna modell fungerar bra för att förklara färgdiskrimineringströsklar hos flera djur, som människor, bin och fåglar. På senare år har modellen utökats för att förutspå akromatisk diskriminering. Tyvärr, har den i detta fall inte kalibrerats mot diskrimineringströsklar som faktiskt finns.

I manus V så sammanställer vi alla beteendetrösklar som finns och konverterar dessa till brusantaganden som kan användas för att förutspå kromatisk och akromatisk diskriminering. Arbetet som redovisas i manus V visar hur viktigt det är att fler djurs diskrimineringströsklar testas experimentellt för att vi bland annat ska kunna använda synmodellering för att göra förutsägelser om vilka signaler som vi kan mäta i naturen som fåglar faktiskt kan upptäcka och som är relevanta för fåglarna.

Introduction

The Earth is bombarded by electromagnetic radiation, primarily from the sun. A sliver of the electromagnetic radiation spectrum is available for animal vision and we commonly call this part of the spectrum, light. We characterise the electromagnetic radiation by its wavelength and for humans, visible light is between 400 and 700 nm (Fig. 1).

Light interacts with objects and is reflected in different directions, and in different intensity at different wavelengths from different types of structures and material compositions. This creates a world rich of spatial information, for animals with eyes and nervous systems that can make use of this information (Fig. 1). Eyes appear in the fossil record in the early Cambrian, ca. 530 million years ago, and there exist at least ten different types of eyes (Land and Nilsson, 2012). This work will focus on the camera type eyes of birds.

The eyes of all birds have the same basic structure, but there is variation that presumably reflects their ecological needs (Martin and Osorio, 2008). Large, diurnally hunting raptorial birds typically have very large eyes that require a reduction of the inter orbital septum – the bone between the eyes – that is very thin or even perforated, thus leaving the eye sockets in direct contact (Mitkus, 2015). Owls also have large eyes with very wide pupils that are important for high visual sensitivity, fitting their nocturnal activity patterns. Birds that are less reliant on vision, such as the Kiwi, have much smaller eyes (Martin et al., 2007). Other variation is detected at the retinal level; diurnal birds typically have cone-dominated retinas whereas nocturnal birds have rod-dominated retinas.

Visual systems are generally used for detecting intensity and spectral differences in light reflected from objects in space, and derive a perception of contrasts between them. Contrasts derived purely by a difference in intensity hold no colour information and are called achromatic contrasts. Contrasts derived by spectral difference contain colour information and are called chromatic contrasts.

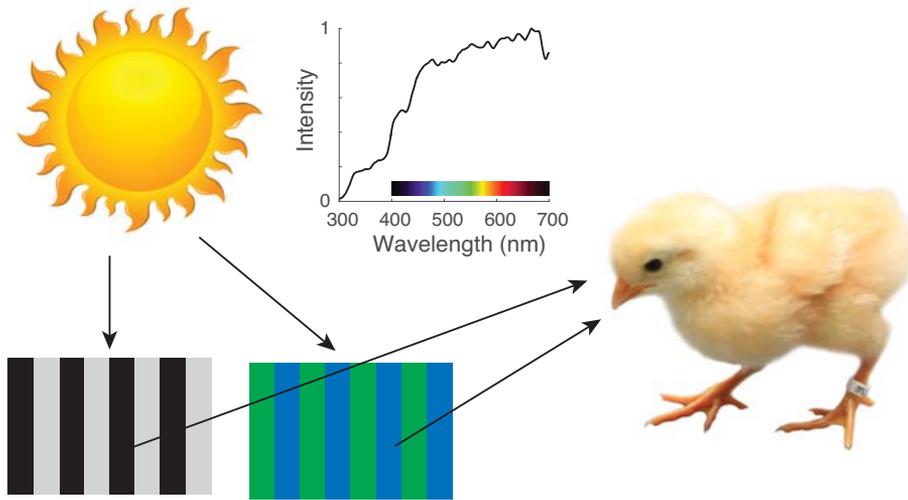


Figure 1. The terrestrial light environment. Sunlight is reflected differently off different objects, which leads to a light environment with spatial information from those objects, such as the achromatic and chromatic grating for the chicken. The graph shows the normalized photon radiance spectrum measured from a white standard placed on the ground on a lightly clouded day in Lund October 2015, at sun elevation 24° . Inserted in the graph is the visual range and a colour perception estimate of trichromatic humans.

Bird colour vision is mediated by four types of cone photoreceptors (Osorio et al., 1999), meaning that birds have an extra dimension of colour information that is not available to us humans that only have three types of cones. Additionally, the cones of bird retinas have strongly pigmented oil droplets that act as ocular filters (Hart, 2001a) and are predicted to increase colour discrimination performance in bright light at the cost of reduced sensitivity in dim light (Vorobyev, 2003). It has also been predicted that these oil droplets aid colour constancy (Vorobyev et al., 1998), the ability to maintain colour perception in spectrally different illuminations (Hurlbert, 2007).

Achromatic vision in birds has been suggested to be mediated by the fifth cone type, the double cone (Campenhausen and Kirschfeld, 1998; Osorio and Vorobyev, 2005; Vorobyev and Osorio, 1998), thereby separating the visual information into different visual channels already at the receptor level.

In this work we have investigated the limits of bird colour vision with behavioural experiments using the chicken as our model. We have compared and analysed their performance with the most established colour vision model for birds, the receptor noise limited model (Vorobyev and Osorio, 1998).

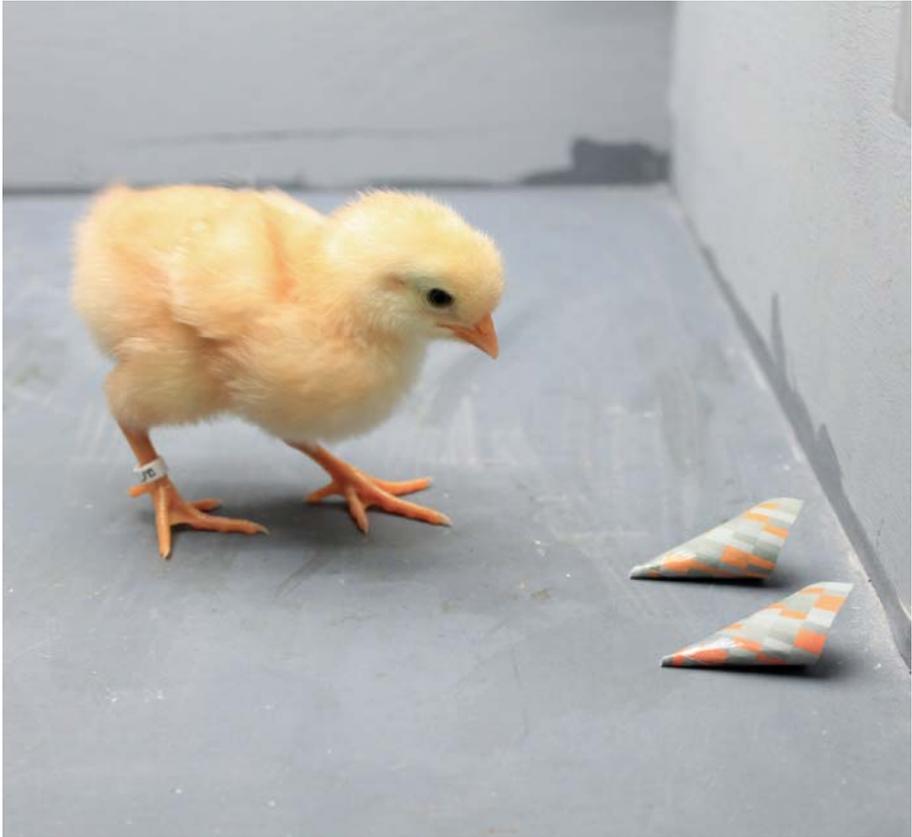
In paper I we tested how good chicken colour vision is, by establishing a behavioural threshold for how similar colours they could discriminate. These behavioural data allowed us to calibrate the parameters used in the receptor noise limited model. In the same study, we determined in how dim light the chickens could discriminate colours. We found that both colour difference and the intensity of the colours affected the intensity threshold of colour discrimination. Bright colours that were more different from each other could be discriminated in dimmer light.

In paper II we continued to study dim light vision and investigated whether birds are summing the signals from many photoreceptors to increase their colour discrimination performance at low light levels. We used stimuli for which variable amounts of spatial summation were predicted to yield different intensity thresholds and performed a behavioural experiment to test the prediction. Indeed, the intensity threshold for colour discrimination was lower for stimuli that had more or larger colour tiles.

In paper III we tested colour constancy, the phenomenon that colour perception remains constant in different spectral illuminations, using several red-shifted illuminations. Our results confirmed that chickens indeed have colour constancy. Furthermore, our aim was to find the limit of how much illumination change chicken colour constancy tolerates. We found that the colour difference between stimuli affected how much illumination change could be tolerated. At very strong shifts in illumination, colour constancy failed.

In paper IV we continued to work on colour constancy, but changed the experiment such that relative colour cues could be used. Instead of learning a specific colour, as in paper III, we allowed chickens to use relative colour cues, e.g. always choosing the 'redder' colour. We found that when relative cues were available the chickens could maintain colour constancy in larger illumination changes than the chickens in paper III. The amount of illumination change, in which the chickens maintained colour constancy, was smaller than the difference between the natural illuminations we modelled.

In nature, animals use both chromatic and achromatic contrasts to detect objects. The receptor noise limited model can be used to predict discriminability via both types of contrasts. In paper V we collected all known chromatic and achromatic detection thresholds and used them to calculate estimates of noise to be used in the receptor noise limited model in a wide range of animals. We discuss some of the problems with performing and interpreting visual modelling, such as the need to consider the spatial structure of the stimuli and the light intensity which is used in the modelling.



Chicken performing the two choice colour discrimination task used in the behavioural experiments of paper I-IV.

Bird eyes

Like other vertebrates, birds have camera type eyes (Fig. 2) (Walls, 1942). Bird eyes are in general large, both in absolute and especially in relative terms compared to other vertebrates (Howland et al., 2004). Large eyes are heavy and therefore disadvantageous for flying. There is also a substantial energy cost associated with large eyes and the nervous tissue required to process the visual information (Moran et al., 2015). The fact that large eyes developed despite these costs is a testament to the importance of visual information for birds.

Optics

Camera type eyes have two main optical structures, the cornea and the lens (Fig. 2) that focus an image on the retina. The corneas of birds have slightly higher refractive indices than water (Avila and McFadden, 2010), therefore corneal optical power is significant in air but weak in water.

The lens has a slightly higher refractive index than the cornea (Avila and McFadden, 2010), but has an interface with the aqueous humour, which has a similar refractive index to water. The difference in refractive index between the lens and the aqueous humour is therefore not as large as that between the air and the cornea. The relative focusing power of the cornea and lens differ between species of birds (Martin and Brooke, 1991).

The combined refractive power of a camera eye can be estimated by creating a schematic eye model, such as the Gullstrand model (Land and Nilsson, 2012). This combined optical system is described by a single focal length. The focal length is defined as the distance from the point of focus, which is the retina (as an emmetropic eye is assumed), to the nodal point. The nodal point is defined as the point in the eye, through which rays of light pass without being refracted.

Generally, larger eyes have longer focal lengths (Hughes, 1977), and thereby create larger images on the retina, which allows for higher spatial resolution. The focal length, together with the diameter of the photoreceptors, determines the acceptance angle of individual photoreceptors (Land and Nilsson, 2012). Longer focal length gives a smaller acceptance angle of the photoreceptor and for a fixed photoreceptor diameter, longer focal lengths lead to higher spatial resolution at the cost of light catch of individual photoreceptors.

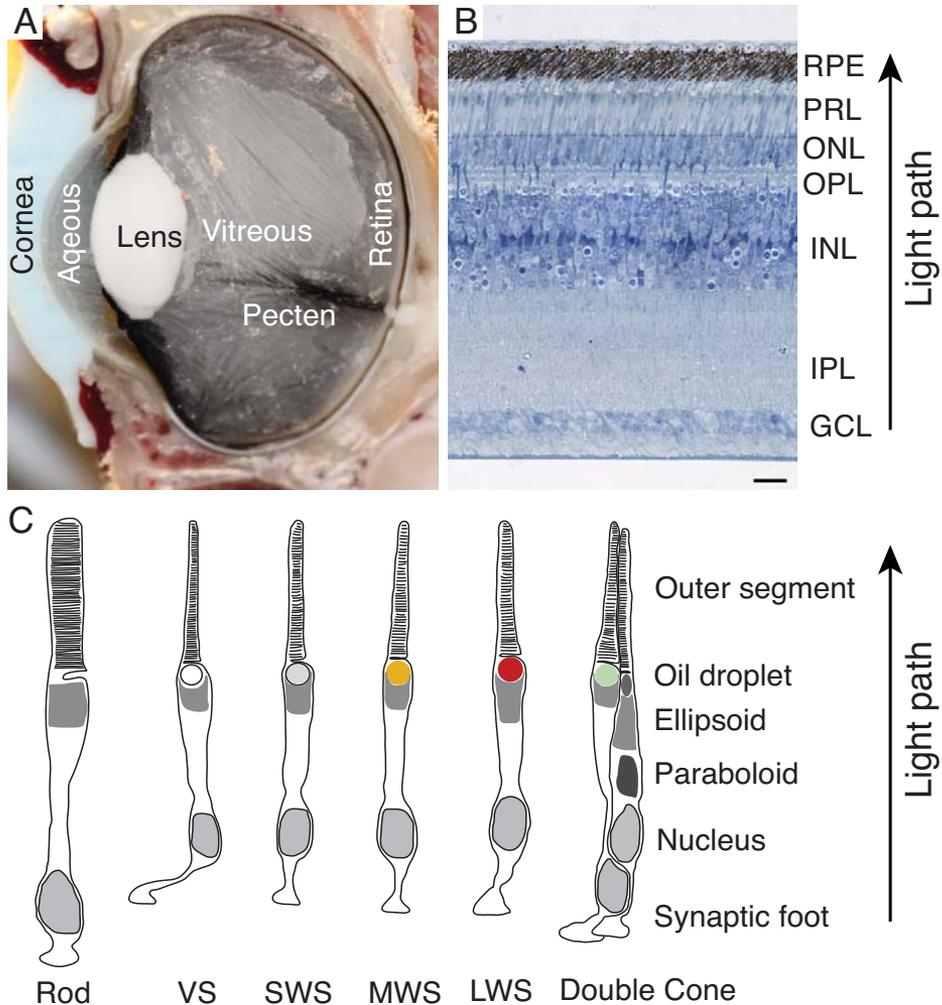


Figure 2. Chicken visual system. **A.** the camera eye of a chicken with annotated structures. The cornea is the eye's interface with the outside world. Between the cornea and the lens there is a fluid filled space, the anterior aqueous humour. Behind the lens is a gelatinous vitreous humour. The retina is located in the back of the eye and the pecten can be seen as the dark protrusion into the vitreous, from the retina. **B.** The chicken retina. Light traverses the whole retinal tissue before reaching the outer segments embedded in the microvilliar processes of the retinal pigment epithelium (RPE). The photoreceptor layer (PRL) contains the photoreceptor cells. The signals transduced in the outer segments of the photoreceptors are transferred at synapses in the outer plexiform layer (OPL) to the bipolar cells located in the inner nuclear layer (INL). The bipolar cells make synaptic contact with the ganglion cells in the inner plexiform layer (IPL). The ganglion cells in the ganglion cell layer (GCL) provide the output signals from the retina to the brain. Scale bar = 20 μ m. **C.** Photoreceptor types of the chicken, located in the PRL in B. There are six types of photoreceptors in the chicken retina. The visual pigments are located in the outer segment of vertebrate photoreceptors. The pigmented oil droplets in the cones act as ocular filters. The ellipsoid is a dense aggregation of mitochondria. The accessory member of the double cone and the rod have paraboloids, which are glycogen-filled organelles (Amemiya, 1975).

Retina

The retina is a multi-layered tissue that is part of the central nervous system. Like in other vertebrates, the retina in birds is inverted. The photoreceptors that capture and transduce the light into electrical signals, are furthest away from the lens in the retina (Fig. 2B). Light must therefore pass through all layers of the retina before it reaches the photoreceptors. As the light passes through the retina it will interact with the retinal tissue and the image may be degraded, resulting in less available spatial information. In mammals, there are blood vessels on the inner surface of the retina that may degrade the image further. Bird retinas are not lined with blood vessels but instead have a pecten, which protrudes into the vitreous from the optic nerve disc (Fig. 2A). The pecten is filled with blood vessels and melanin pigment molecules, and presumably provides nutrients and respiratory function to the inner layers of the retina (Ferreira et al., 2015; Pettigrew et al., 1990).

Closest to the sclera, the fibrous outer layer of the eye globe, is a capillary network of blood vessels called the choroid, which provides nutrients and satisfy the respiratory needs of the outer retina. The retinal pigment epithelium (RPE) is a sheet of cells between the photoreceptors and the choroid that supports many important processes such as absorption of stray light, renewal of visual pigment, outer segment phagocytosis, protection from photo-oxidation and a buffered environment for the photoreceptors (Strauss, 2005). It has finger-like processes that extend to the photoreceptor layer and surround the outer segments. The processes are filled with melanin granules, which can move up and down and thus change the amount of light that reaches individual photoreceptors (Bäck et al., 1965).

Birds have six types of photoreceptors (Fig. 2C), one type of rod, one type of double cone, which does not exist in placental mammals, and four types of single cones (Hart, 2001a). As in many other vertebrates, the rods are likely not involved in colour vision but with their higher sensitivity provide achromatic vision in dim light (Kawamura and Tachibanaki, 2008). Colour vision is mediated by the four single cones (Osorio et al., 1999; Vorobyev and Osorio, 1998). Many vertebrates, except placental mammals, have double cones in their retinas (Walls, 1942) and in birds they are very numerous (Hart, 2001b). It has been proposed that achromatic vision in bright light is mediated by the double cones (Osorio and Vorobyev, 2005). The reasons are their broad spectral sensitivity, which has been found to be similar to the sensitivity of motion sensitive neurons (Campenhausen and Kirschfeld, 1998), their high abundance in the retina (Hart, 2001b) and their lack of participation in colour vision (Vorobyev and Osorio, 1998).

The different photoreceptors types have different spectral sensitivity. The spectral sensitivity refers to the probability to absorb photons of a given wavelength. Each individual photoreceptor cell only mediates a single type response, regardless of the wavelength of the photon absorbed and is therefore

colour blind. Colour is established by the comparison of photoreceptor signals in subsequent cells.

The photoreceptor cells make synaptic contact with horizontal and bipolar cells in the outer plexiform layer (OPL) (Masland, 2001; Smith, 2000). The nuclei of retinal interneurons, the bipolar cells, horizontal cells and the amacrine cells form the inner nuclear layer (INL). Bipolar cells convey the signal from the photoreceptors to the ganglion cells (Smith, 2000). The horizontal cells provide a means of local adaptation. When a given photoreceptor is activated, the horizontal cell with which it has synapses, provides an inhibitory response to the neighbouring photoreceptors (Verweij et al., 1996) and possibly to bipolar cells (Masland, 2012). The horizontal cells are also connected to each other by gap junctions (Smith, 2000) so that a signal in one horizontal cell can spread to the neighbours. The horizontal cells, thereby help adapt the retinal sensitivity to the ambient light levels, which is useful because natural scenes may have large fluctuations in intensity (Masland, 2012). There is a large diversity of amacrine cells in the retina, their function seems to be to modulate the output signal of bipolar cells to the ganglion cells and thereby create the exact response profiles of ganglion cells (Masland, 2012).

The different types of bipolar cells specifically have synapses with specific types of ganglion cells in the inner plexiform layer (IPL) (Euler et al. 2014). The ganglion cells are the cells that provide the output signal from the retina to the brain.

The different types of ganglion cells seem to tile the retina individually such that each visual channel has a full representation of the visual space (Field and Chichilnisky, 2007), some are edge-detectors which are important for high resolution vision, others respond to large or small field motion, for looming targets, or specific directions of movement and some respond to colour (Masland, 2012). The densities and receptive fields of the ganglion cells vary across the retina (Bleckert et al., 2014). For example, around the primate fovea there is a high density of small local edge detector ganglion cells (Dacey and Petersen, 1992), yielding the high acuity of foveal vision.

This information is mainly obtained from mammals, and it is unknown whether the exact same functions of the horizontal and amacrine cells and types of ganglion cells are also found in birds.

Colour vision

Colour vision is found in a large number of animals, mainly belonging to the arthropod and chordate phyla (Kelber et al., 2003). Model calculations suggest that colour vision increases the amount of information that animals can extract from the visual scene in bright light (Vorobyev, 1997). Colour vision requires comparison of the signals from two or more types of photoreceptors with different spectral sensitivity. Multiple photoreceptors with different sensitivity have evolved independently in arthropods and chordates (Porter et al., 2011), suggesting a strong adaptive value for these groups of animals.

Several types of photoreceptors with different spectral sensitivity can also be used for a more fundamental visual problem, the maintenance of lightness constancy in a world of changing illumination spectra (Campenhausen, 1986). For a monochromatic visual system, the same set of objects with different spectral reflectance may not be perceived to have the same relative intensities in different spectral illuminations (Campenhausen, 1986). This may be a big problem as it limits the reliability of visual information.

The early jawless vertebrates appear to have lived in shallow waters, where there is considerable irregularity in the illumination, due to ripples and surface waves. The comparison of signals from photoreceptors with different spectral sensitivities has been proposed to have evolved as a way to filter out this flickering illumination without losing reaction times (Maximov, 2000). These lines of reasoning suggest that spectrally different photoreceptors and the neurons necessary to compare their output signals, evolved primarily as a part of achromatic vision while colour vision followed as a secondary development.

It is suggested that one of the main advantages of colour vision is the recognition of targets on a background of varying intensity. Such as a red fruit against a background of leaves that, because of shadows, vary in intensity (Mollon, 1989). Colour vision also allows for the segregation and identification of objects by their spectral reflectance, which is more informative and robust than their reflected light intensity (Maximov, 2000; Mollon, 1989).

Birds use colour vision to guide many important behaviours such as foraging, communication and partner selection (Bennett and Cuthill, 1994; Bennett et al., 1997; Bennett et al., 1996; Church et al., 1998; Hunt et al., 2001; Maddocks et al., 2001; Siitari et al., 1999).

The colourful displays and plumages of birds were used as inspiration for developing the early models of female mate choice driven sexual selection by Darwin and others, (reviewed by Hill, 2006). However, the prediction that more colourful males would be chosen more often as partners by female birds, was experimentally tested only much later than the models were formulated (reviewed by Hill, 2006). Carotenoids, which are the basis of some of the plumage colours of birds, are only available via the diet (McGraw, 2006). Other factors, such as parasite load and bacterial infections, also affect plumage colour (Hill et al., 2005; Shawkey et al., 2007; Thompson et al., 1997). The colour of the male bird plumage can therefore be an honest signal about his foraging efficiency and health. In accordance with the theory of female choice driven sexual selection, the colour of plumage patches that have been shown to be used in mate choice, have also been found to be more variable (Delhey and Peters, 2008). However, not necessarily more variable in males than in females, suggesting that sexual dichromatism may not be a very precise proxy of sexual selection and that mutual assessment may be more important than realised (Delhey and Peters, 2008).

Spectral sensitivity

The spectral sensitivity of a photoreceptor cell, the likelihood that a photon of a given wavelength will be absorbed, depends on the visual pigment that it expresses and the spectral transmittance of any tissue that is in the light path prior to the visual pigment (Douglas and Marshall, 1999).

Visual pigments

The visual pigment is the molecule that absorbs light and initiates the transduction cascade. In vertebrates the visual pigments are located in the outer segments of the rods and cones (Fig. 2C). The visual pigment consists of two molecules, a chromophore and an opsin protein (Land and Nilsson, 2012).

Both the chromophore and opsin molecule determine the spectral sensitivity of the visual pigment. Bird visual pigments all contain the most common chromophore among vertebrates, the vitamin A1-derivative retinal (Hunt et al., 2009). The differences in spectral sensitivity between the visual pigments in birds are thus determined by their different opsins.

The spectral sensitivity of a visual pigment is normally characterised by a single parameter, the wavelength at peak of absorbance (λ_{\max}), since the shape of the sensitivity function is predictable from the peak (Govardovskii et al., 2000; Stavenga et al., 1993).

The ancestor of modern tetrapods likely had a tetrachromatic visual system with five different visual opsins (Bowmaker and Hunt, 2006; Hunt et al., 2009). The short wavelength sensitive 1 (SWS1) opsin is expressed in the ultraviolet or

violet sensitive (UVS/VS) cones. A second short wavelength sensitive (SWS2) opsin produces a long wavelength shifted visual pigment compared to SWS1 and is expressed in the S cones. The Rh2 opsin is expressed in the medium wavelength sensitive M cones. Long wavelength sensitive (LWS) opsin is expressed in the L and double cones. The Rh1 opsin is expressed in the rods. The evolutionary paths of the five vertebrate visual opsins are sketched in Fig. 3. Most known mammals, except monotremes, have lost the SWS2 opsin and all have lost the Rh2 opsin (Hunt et al., 2009). Some primates have regained red-green colour discrimination by a gene-duplication of the LWS opsin (Dulai et al., 1999) and spectral tuning via mutations that have differentiated their spectral sensitivity (Yokoyama et al., 2008). Interestingly, frogs express SWS2 in a second type of rod, the blue rods (Hisatomi et al., 1999), which may provide very dim light colour vision.

Birds are tetrachromats (Hart, 2001a; Osorio et al., 1999; Vorobyev and Osorio, 1998), with the potential exception of owls (Bowmaker and Martin, 1978; Ödeen and Håstad, 2003) and penguins (Bowmaker and Martin, 1985). The vertebrate ancestral state of four cone opsin types is thus retained in most birds. Both members of the double cone express the same LWS opsin as the L single cone, but differ in spectral sensitivity because of the different ocular filters. The spectral tuning of the MWS and LWS opsin based visual pigments seem relatively invariable in birds (Bowmaker et al., 1997).

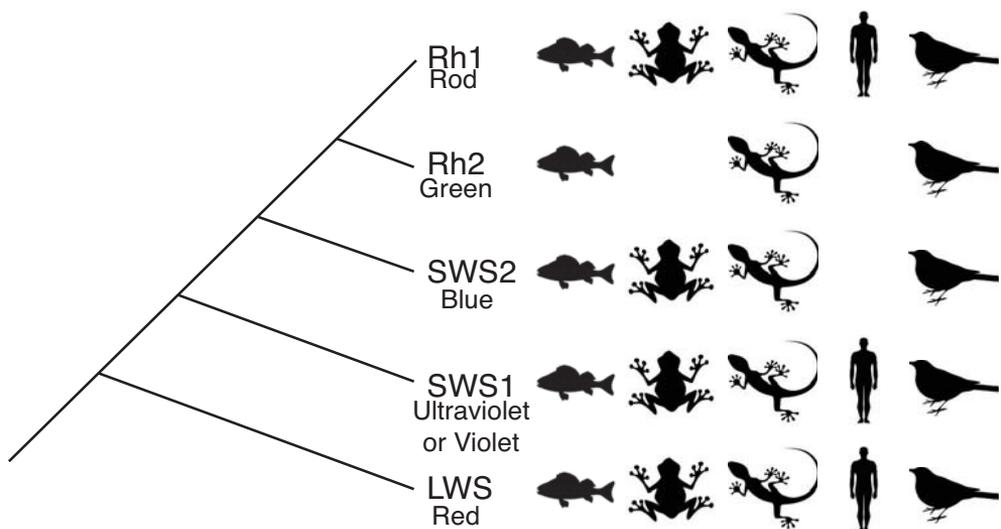


Figure 3. Evolution of vertebrate visual opsins. A cladogram of the evolutionary relationship between and presence of the five different visual opsins in five major groups of vertebrates. Presence is denoted when the opsin has been found in at least one species within a group, and does not mean that all members of the group have the opsin.

The largest variability is found in the visual pigments based on the SWS1 opsin. These come in two general types; the ultraviolet sensitive (UVS) type has a sensitivity maximum, λ_{\max} , between 360-373 nm and the violet sensitive (VS) type has λ_{\max} between 402 and 426 nm (Hunt et al., 2009; Lind et al., 2014). The spectral sensitivity of the SWS2 visual pigment is shifted slightly towards shorter wavelengths in birds with a UVS-type opsin. The spectral tuning of the SWS1 visual pigment is determined at a few key amino acid sites (Wilkie et al., 2000; Wilkie et al., 1998), and the type of visual system has largely been inferred from the genes amino acid sequence (Ödeen and Håstad, 2003; Ödeen and Håstad, 2013; Ödeen et al., 2008). However, recent studies have found a bird with an SWS1 gene indicating a UVS type opsin (M. Toomey and O. Lind, *personal communication*) but with a visual pigment peaking at 399 nm (Baumhardt et al., 2014). This suggests that further comparisons between the genotype and the measured absorbance of the visual pigment should be made, and one should look for additional amino acid tuning sites.

Spectral filtering

The oil droplets of bird cone photoreceptors contain carotenoid pigments that absorb short wavelength light (Goldsmith et al., 1984; Liebman and Granda, 1975). Each type of cone has a specific type of oil droplet with a specific complement of carotenoid pigments (Toomey et al., 2015). There is a red oil droplet in the L cone, a yellow in the M cone, a clear but UV-absorbing oil droplet in the S cone and a transparent oil droplet in the VS/UVS cone (Hart, 2001a; Hart, 2001b).

The oil droplets create a matched filter system with the absorbance of the visual pigments. By absorbing some of the shorter wavelength light and transmitting only light of longer wavelengths, they shift the peak of maximum sensitivity of the cones to longer wavelengths and reduce the overlap in sensitivity between the cone types (Fig. 4). It is suggested that the oil droplets thereby increase the discriminability of colours at the cost of absolute sensitivity (Vorobyev, 2003; Wilby et al., 2015).

The transparent oil droplets in the VS/UVS cones do not seem to contain carotenoids (Goldsmith et al., 1984; Toomey et al., 2015) and do not tune the sensitivity of the SWS1 cones. Instead the transmittance of the ocular media, consisting of the cornea, lens, and aqueous and vitreous humours, determines the sensitivity to ultraviolet (UV) light. All retinal-based visual pigments have some sensitivity to ultraviolet light (Stavenga et al., 1993), also in humans. However, due to pigmentation, our lenses absorb nearly all ultraviolet light (Cooper and Robson, 1969; Van Heyningen, 1971), thus blocking UV light from reaching the retina. However, this is not the case for all animals.

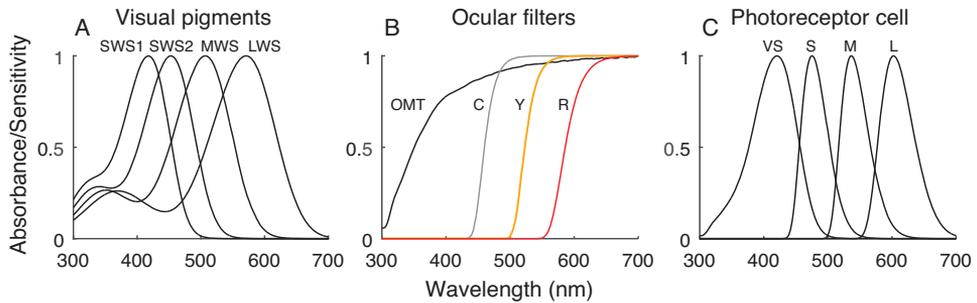


Figure 4. The absorbance of the visual pigments and ocular filters, and the resulting spectral sensitivity of the four single cone types of the chicken. **A.** All four cone visual pigments have overlapping spectral absorbance. **B.** The ocular media transmittance (OMT) determines the sensitivity for the VS/UVS cone type, which does not have a strongly absorbing oil droplet. The clear (C), yellow (Y) and red (R) oil droplets are located in the S, M and L cone respectively. **C.** When the filtering properties of the ocular media and the oil droplets are included the spectral sensitivity of the photoreceptor cells are long wave-shifted, in terms of the λ_{max} , and have reduced overlap in sensitivity.

Biological tissues do not transmit much light below 310 nm, due to the absorbance by aromatic amino acids such as tryptophan, which sets a lower limit to the spectral sensitivity of photoreceptor cells (Douglas and Marshall, 1999; Edelhoch, 1967). If no specific absorbing molecules are present, the amount of UV light transmitted by biological tissues is expected to depend on their thickness (Douglas and Marshall, 1999). This is indeed found in unpigmented fish lenses (Thorpe and Douglas, 1993) and in quail and chicken lenses (Olsson et al., 2016).

Among birds there is a large variability in the amount of UV-light transmitted by the ocular media, but in general the ocular media of UVS birds transmit more UV light than those of VS birds (Lind et al., 2014), as may be expected. Some bird species seem to reduce the amount of ultraviolet light that reaches the retina even further, presumably by having UV-absorbing pigments in the lens or cornea (Lind et al., 2014; Olsson et al., 2016).

Neurophysiology of colour vision

The presence of several photoreceptor types with different spectral sensitivities is critical for colour vision. However, their presence alone does not necessarily mean that they contribute to colour vision. To extract colour information, nervous systems compare the outputs from several receptor types in colour-opponent interactions (Backhaus, 1991; Chittka et al., 1992; Dacey et al., 2013; Lee et al., 2002; Maturana and Varela, 1982; Yazulla and Granda, 1973). A conceptual model for how colour discrimination can occur (Brandt and Vorobyev, 1997) is shown in Fig. 5. Colour-opponent interaction means that a colour-coding

interneuron is inhibited by the input from certain types of photoreceptors and activated by input from other types of photoreceptors.

Neurons with colour-opponency, red-green and blue-yellow, are found in the retina and the lateral geniculate nucleus in humans and other old world primates (Dacey and Lee, 1994; Lee et al., 2002; Livingstone and Hubel, 1988). Several spectral types of colour-opponent neurons have been found in the nervous system of birds (Maturana and Varela, 1982; Yazulla and Granda, 1973), but how the responses of these cells relate to responses of the retinal ganglion cells is unknown.

The way, in which the primate nervous system processes colour information is reviewed by Conway (2009) and Conway et al. (2010), but for other animals much less is known. Birds have retained the original tetrachromatic visual system of the stem amniotes, which makes them, and other animals such as tetrachromatic cyprinid fish, lizard and turtles, interesting for comparative studies on the neurophysiology of colour vision.

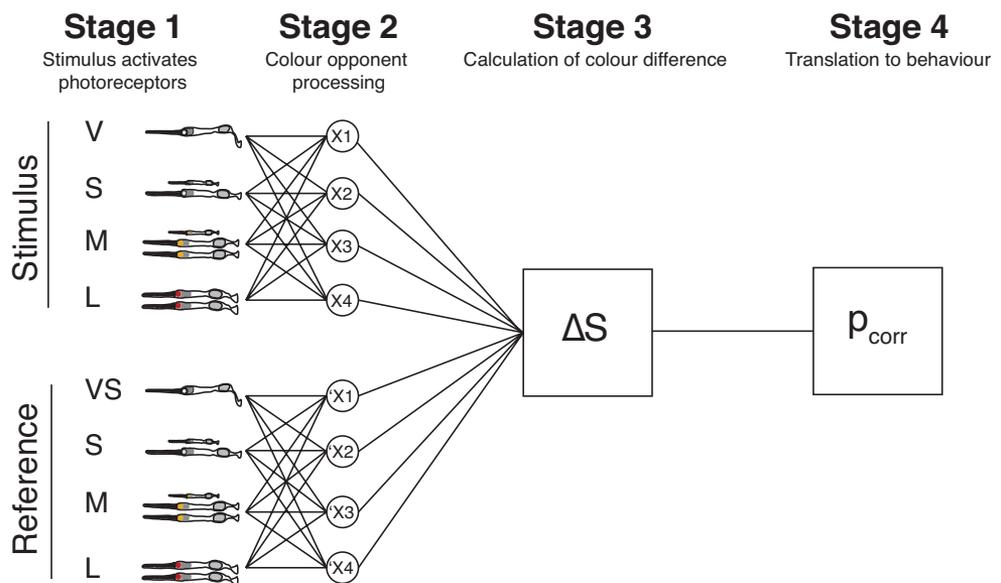


Figure 5. Four stage model of colour discrimination. In stage 1 the stimuli give rise to photoreceptor responses, which are compared in colour-opponent interactions in stage 2. The opponent signals from both stimuli are compared to give rise to a perceptual distance, ΔS , between the two stimuli in stage 3. The ΔS correlates to a behavioural response in the animal, a probability to make a correct choice. Adapted from (Brandt and Vorobyev, 1997).

Behavioural tests and mathematical models of colour vision in birds

Behavioural tests of colour vision

Determining colour vision behaviourally requires either training, such as Karl von Frisch's pioneering experiments with bees (Frisch, 1914) or exploiting some form of natural behaviour, such as landmark learning to find the position of the home nest (Somanathan et al., 2008). The critical test is to show that the animal uses the spectral information of a stimulus independently of intensity (Kelber et al., 2003).

Many behavioural studies have shown colour vision in birds, using a number of different types of experiments. Colour matching experiments exploit the fact that a spectral stimulus coded by n types of receptors can be matched by a specific mixture of n other monochromatic lights (Kelber et al., 2003). Colour matching experiments have been performed with pigeons (Palacios and Varela, 1992; Palacios et al., 1990) and budgerigars (Goldsmith and Butler, 2005).

In wavelength discrimination, the ability to discriminate monochromatic lights independent of their intensity is determined. At any given wavelength the smallest wavelength difference ($\Delta\lambda$) that can be discriminated is reported. Wavelength discrimination tests have been performed with pigeons and hummingbirds (Blough, 1972; Emmerton and Delius, 1980; Goldsmith et al., 1981).

In grey card experiments animals are often trained to respond to a specific colour, printed on a card for example, and in a test they have to discriminate that coloured card among several grey (achromatic cards) of varying intensities. Grey card experiments have been performed with great tits, pied flycatchers, jays and little owls (Derim-Oglu and Maximov, 1994; Hertz, 1928a; Hertz, 1928b; Plath, 1935), reviewed by Kelber et al. (2003). A modified version of the grey card experiment was instrumental in showing that chickens use at least three types of colour-opponent interactions to mediate colour vision (Osorio et al., 1999).

In spectral sensitivity tests animals are trained to respond to large field monochromatic lights presented on a background. The intensity of the monochromatic light is reduced, until the response disappears or is statistically not different from chance. The inverse of the weakest intensity they respond to, the

sensitivity, at a given wavelength is presented. Spectral sensitivity tests have been performed with budgerigars, pekin robins, chickens and pigeons (Chavez et al., 2014; Goldsmith and Butler, 2003; Lind et al., 2013a; Maier, 1992; Prescott and Wathes, 1999; Remy and Emmerton, 1989).

Together, these studies have convincingly shown the tetrachromatic nature of bird colour vision.

Mathematical models of colour vision

Mathematical models can be used to make predictions about the visual performance of animals and to estimate colour perception. Models can be very useful because they provide a means of pursuing biological questions in animals where we may not be able to perform behavioural experiments. Moreover, comparing model predictions and behavioural results can help us to understand the underlying neural mechanisms of colour vision. In models of colour vision, we typically use geometrical spaces to visualize colour differences and estimate perception (Fig 6) (Kelber and Osorio, 2010; Kelber et al., 2003; Renoult et al., 2015). In these colour spaces, colours are represented as points, and their loci in the space are determined by their relative activation of different photoreceptors. The distance between the points in the space is an estimate of their perceived difference. There are many types of colour spaces that use different metrics to calculate colour coordinates and distances (Backhaus, 1998; Renoult et al. 2015).

Receptor sensitivity space

In a receptor space, a stimulus is represented as a vector, V , and each axis corresponds to the excitation of a single receptor channel or type (Backhaus, 1998; Kelber et al., 2003). The direction of the vector, corresponding to its chromaticity (colour), is determined by the activation of the different photoreceptor types. Intensity can be expressed as the length of the vector. For an animal with n receptor types used for colour vision, the corresponding receptor space has n dimensions. A monochromat has a receptor space represented by a single line and cannot distinguish between intensity differences and spectral differences. A dichromat has a two-dimensional receptor space (Fig. 6B), which can potentially separate intensity and chromaticity, though for a dichromat there is no meaningful distinction between chromaticity and spectral purity, or saturation in human terms (Kelber and Osorio, 2010). A trichromatic animal has a three-dimensional receptor space. The receptor space of a tetrachromatic bird has four dimensions, which is impossible to illustrate.

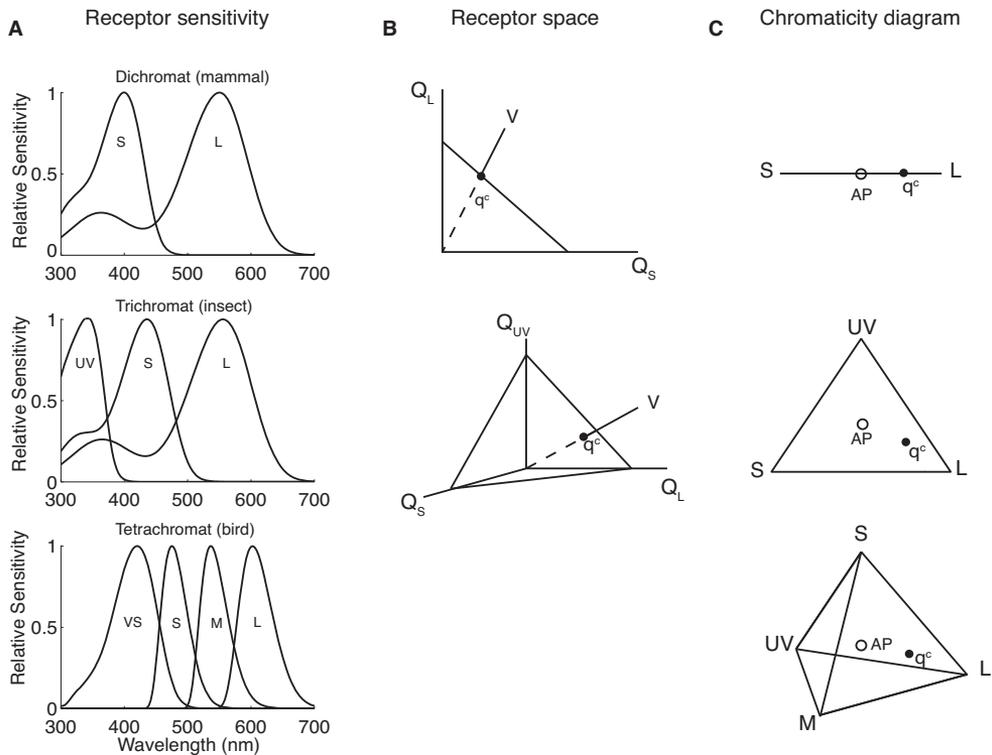


Figure 6. Receptor spectral sensitivities, receptor spaces and chromaticity diagrams of different visual systems. **A.** The receptor sensitivities determine which wavelengths a receptor will respond to. **B.** A receptor space for an animal with n types of receptors has n dimensions; each axis in the space represents a receptor. Colours in a receptor space are represented by a vector (V), the direction of the vector represents the chromaticity of the colour, and intensity can be approximated by the sum of activation of all receptors. **C.** In a chromaticity diagram a colour is represented as a point, its colour locus (q^c) is determined by $n-1$ coordinates for a system of n number of receptors. Each coordinate is determined by the response of a receptor to the stimulus, normalised to the response of all receptors. This means that the intensity cue is removed. Adapted from Kelber et al. (2003).

Chromaticity diagram

A chromaticity diagram differs from a receptor space in that it disregards the achromatic dimension of colours (Kelber et al., 2003). The dimensionality of a chromaticity diagram is $n-1$ for an animal with n receptor types coding for colour and a given colour is represented as a point; its locus has $n-1$ coordinates. Each coordinate represents the quantum catch, Q , of one of the receptors, normalised to the response of all receptors (Eqs. 1 and 2), so that the sum of all coordinates for any colour locus is always 1. The chromaticity diagram of a dichromatic animal has one dimension, comparing the signal of two receptor types at each end of a line axis (Fig. 6C). A trichromatic animal's chromaticity diagram has two

dimensions. A tetrachromatic animal, like a bird, has a three-dimensional chromaticity diagram.

The point in the diagram where all receptor responses are equal is the achromatic point (AP in Fig. 6); the distance from this point determines the spectral purity of the colour.

For a tetrachromatic animal a given stimulus has three coordinates in a chromaticity diagram, which are calculated as

$$x, y, z = \frac{1}{\sqrt{2}}(q_4 - q_3), \frac{\sqrt{2}}{\sqrt{3}}\left(q_2 - \left(\frac{q_3+q_4}{2}\right)\right), \frac{\sqrt{3}}{2}\left(q_1 - \left(\frac{q_2+q_3+q_4}{3}\right)\right) \quad (\text{Eq. 1}),$$

$$q_i = Q_i / \sum_{i=1}^4 Q_i \quad (\text{Eq. 1.1}).$$

Q refers to the quantum catch of a receptor of type i , which is calculated as

$$Q_i = k_i \int_{300}^{700} R_i(\lambda) S(\lambda) I(\lambda) d\lambda \quad (\text{Eq. 2}),$$

where R is the sensitivity of a photoreceptor of type i , S is the reflectance of the stimulus and I is the intensity of the illumination. The term k is an adaptation factor, calculated as the inverse of the quantum catch from the background as

$$k_i = \frac{1}{\int_{300}^{700} R_i(\lambda) S^b(\lambda) I(\lambda) d\lambda} \quad (\text{Eq. 3}),$$

where S^b is the reflectance of the background.

Receptor noise limited (RNL) model

The most well established colour vision model for birds is the Receptor Noise Limited (RNL) model, postulated by Vorobyev and Osorio (1998). In this model, calculations of the difference between colours is based on three assumptions: (i) in a system of n receptor channels colour is coded by $n-1$ non-specified opponent mechanisms, (ii) these opponent mechanisms give zero signal for stimuli that differ only in intensity and (iii) thresholds are set by noise (sometimes expressed as a Weber fraction) in the receptor mechanisms, not by the opponent mechanisms themselves. A representation of the steps of this model can be seen in Fig. 5. The model calculates a perceptual distance or difference between stimuli, ΔS , which for a tetrachromatic animal, such as a bird, is calculated as

$$\Delta S^2 = \frac{(\omega_1\omega_2)^2(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2(\Delta f_4 - \Delta f_2)^2 + (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2)^2 + (\omega_2\omega_3)^2(\Delta f_4 - \Delta f_1)^2 + (\omega_2\omega_4)^2(\Delta f_3 - \Delta f_1)^2 + (\omega_3\omega_4)^2(\Delta f_2 - \Delta f_1)^2}{(\omega_1\omega_2\omega_3)^2(\omega_1\omega_3\omega_4)^2(\omega_2\omega_3\omega_4)^2} \quad (\text{Eq. 4}),$$

where Δf_i is the signal in a receptor channel of type i , and ω is the Weber fraction for a receptor channel of type i . The receptor channel signals are expressed as Weber contrasts, which are calculated as

$$\Delta f_i = \ln \left(\frac{Q_i \text{ stimulus 1}}{Q_i \text{ stimulus 2}} \right) \quad (\text{Eq. 5}),$$

where Q is calculated as in equations 2 and 3.

The Weber fraction, ω , for a given receptor channel i is calculated as

$$\omega_i = \frac{\sigma_i}{\sqrt{\eta_i}} \quad (\text{Eq. 6}),$$

where σ refers to the standard deviation of the noise within a photoreceptor of type i and η refers to the relative abundance of the receptor type. The model thus assumes that the impact of noise can be reduced in the different cone channels proportionally to the relative abundance of that cone type in the retina. The noise in the channel of the most abundant photoreceptor type thus is lower than the noise in the other channels. The perceptual distance or difference between stimuli, ΔS , is expressed in Just Noticeable Differences (JND), and colour differences equal to or larger than 1 JND are assumed to be discriminable.

This model was created to predict spectral sensitivity data (Vorobyev and Osorio, 1998). However, as it describes general colour mediating processes in animals and is apparently successful in describing colour thresholds, it was quickly adopted to model discrimination of object colours, such as avian plumage spectra (Vorobyev et al., 1998).

Since then the model has been frequently used to estimate the discriminability of colours in the eyes of birds, in many ecological contexts. Such as predatory-prey interactions (Håstad et al., 2005; Lind et al., 2013b; Marshall et al., 2016; Siddiqi et al., 2004), perception of other bird plumage or skin colours (Delhey et al., 2012; Jones and Siefferman, 2014; Lind and Delhey, 2015; Sato et al., 2015; Vorobyev et al., 1998) and a host's ability to discriminate a brood parasites eggs from the hosts own eggs (Feeney et al., 2014).

Comparing the predictions of the RNL model and behavioural thresholds (Paper I)

To make reliable predictions of the discriminability of colours, we must calibrate the mathematical models to behavioural results. The RNL model has been shown to predict colour discrimination thresholds in behavioural spectral sensitivity tests

quite well, in budgerigars, pigeons and the pekin robin (Lind et al., 2013a; Vorobyev and Osorio, 1998), and in bees and humans (Vorobyev and Osorio, 1998; Vorobyev et al., 2001). However, the predicted thresholds for the types of colours that occur in nature, reflecting object colours, have not previously been compared to behavioural thresholds.

In paper I, we performed an experiment where we used the receptor noise limited model with the chicken's spectral sensitivity and the noise estimates from the budgerigar and the pekin robin (Lind et al., 2013a; Vorobyev and Osorio, 1998), to predict colour discrimination thresholds of reflecting object colours in the chicken. Then we trained chickens to discriminate the colours in order to find a behavioural threshold and compare it with model predictions. The stimuli consisted of printed patterns of achromatic grey tiles of varying intensity interspersed with tiles of a given colour. The printed patterns were folded into food containers and the chickens were trained to peck at containers of a rewarded colour to get food, a method inspired by a previous experiment (Osorio et al., 1999). We tested one group of chickens with one series of orange-yellow colours and another group with a series of green-blue colours.

We found that the RNL model predicted colour thresholds well, as a similar Weber fraction could be used to describe the smallest discriminable chromatic contrast in both series. However, we needed to assume a lower noise level than that suggested for the pekin robin and the budgerigar, almost by a factor of 2, in order to consolidate model predictions and behavioural thresholds.

The predictions of the receptor noise limited model have been shown to fail at lower light levels, presumably due to an increase in visual noise, invalidating the Weber fraction used in bright light (Lind et al., 2013a). Therefore, it is valuable to determine the operating range of colour discrimination to understand visual ecology and function, and in which conditions reliable model predictions can be made.

Over a range of relatively bright intensities the sensitivity of the budgerigar visual system has been found to scale with the intensity of the background, in accordance with Weber's law (Lind et al., 2013a). In paper I, we also tested the thresholds of colour discrimination in dimmer light. We found that the discrimination thresholds were the same in bright light (200-300 cd m⁻²) and in light levels corresponding to sunrise and sunset (ca. 10 cd m⁻²). We conclude that Weber's law holds for chickens and the same limiting noise level, or Weber fraction, can be used down to these light levels. Human colour discrimination thresholds have also been found to be unaffected by light intensity down to similar light levels (Brown, 1951; Yebra et al., 2001).

At even lower light intensities than this colour discrimination is still possible, as reviewed in detail in the next chapter. However, the same contrasts cannot be detected and the same Weber fraction cannot be used to predict discrimination thresholds.

The problem of a variable light environment

Colour vision in dim light (Paper I & II)

The intensity of light changes over the course of the day by a factor of 10^8 (Land and Nilsson, 2012). In dim light, the ability of visual systems to detect contrasts is reduced due to the fact that there is an increase in noise (Land and Nilsson, 2012). Photons arrive at the eye and are absorbed by the photoreceptors stochastically, a process that can be described by Poisson statistics (De Vries, 1943; Rose, 1942). For a given average sample of N photons the associated noise, the photon-shot noise, of the sample is \sqrt{N} . The signal to noise ratio is N/\sqrt{N} , meaning that at high intensities with high numbers of photons, the contribution of photon-shot noise relative to the signal is small. But at dimmer light levels, the relative contribution of photon shot-noise increases, formulated as the Rose – de Vries law (De Vries, 1943; Rose, 1942; Rose, 1948).

The sensitivities of visual systems in dim light have been shown to follow the expectation of being limited by photon-shot noise both in invertebrates (Howard and Snyder, 1983) and vertebrates (Shapley and Enroth-Cugell, 1984). Photon-shot noise is unavoidable for visual systems, but there are strategies for reducing its effect. The signals from several photoreceptors can be pooled, or summed over time and space (Barlow, 1958; Donner, 1987; Stöckl et al., 2016; Warrant, 1999). This will increase the signal-to-noise ratio and contrast detection in dim light at the cost of reducing the spatial and temporal resolution.

In dim light, the signal-to-noise ratio remains higher if the signals from photoreceptors are summed into one channel, such as in achromatic vision, than if the signals are divided into several channels and compared in chromatic opponent interactions. Therefore, it is expected, that the higher dimensionality of colour vision, the worse the colour discrimination will be in dim light (Vorobyev, 1997). Spectral contrasts, resulting from the physical reflecting properties of objects, are unaffected by light levels. Therefore, colour vision could be as useful in dim light as in bright light, and it is important to know the limits of colour vision to know in which ecological conditions colour-guided behaviours can still be performed.

Some animals can see colour in extremely low light levels, such as nocturnal hawkmoths (Kelber et al., 2002). These insects have superposition eyes that are optically well suited for high sensitivity and nocturnal activity patterns. Nocturnal colour vision has also been found in the Indian carpenter bee (Somanathan et al., 2008), an insect with apposition eyes, which are optically less suited for high sensitivity. It has been found that the Indian carpenter bees have exceptionally wide rhabdoms that increase the quantum catch of the individual photoreceptors (Somanathan et al., 2009) and may compensate, to a degree, for the apparent disadvantage of apposition compound eyes. Nocturnal helmet geckos have rod-free retinas with extremely wide cone photoreceptors and a large pupil diameter in dim light allowing them to use colour vision in dim moonlight (Roth and Kelber, 2004).

The high dimensionality of bird colour vision and their strongly absorbing oil droplets imply that bird colour vision should be exceptionally poor in dim light (Vorobyev, 1997; Vorobyev, 2003; Wilby et al., 2015). The intensity thresholds of bird colour vision have only been studied in three species: blue tits, budgerigars and Bourke's parrots (Gomez et al., 2014; Lind and Kelber, 2009b; Lind et al., 2013a). Their intensity thresholds ($0.05\text{-}0.4\text{ cd m}^{-2}$), have been found to be higher compared to other species (Fig. 7). Suggesting that they can discriminate colours down to intensities equivalent to very bright moonlight or slightly brighter.

In paper I we tested the intensity threshold of colour vision in the chicken and found that stimuli with higher chromatic contrast and stimuli with higher intensity were discriminable in lower light intensities. This suggests that it is important to account for the chromatic contrast between stimuli and their intensity when comparing the intensity thresholds across experiments. A more general expression of the intensity thresholds of colour discrimination could include the intensity of the stimuli in addition to the illumination.

The intensity threshold for discrimination of orange-yellow colours was somewhat lower in the chicken (0.025 cd m^{-2}) compared to the intensity thresholds found for other birds. However, the intensity thresholds for the discrimination of green-blue colour stimuli in the chicken, (0.08 cd m^{-2}) was more similar to the thresholds found for other bird species with similar colours (Gomez et al., 2014; Lind and Kelber, 2009b). Lower intensity thresholds for the brighter, orange-yellow, colours were also found with human subjects. The same phenomenon was also found among hawkmoth and human subjects earlier (Kelber et al., 2002).

We modelled the intensity thresholds for colour discrimination in the chicken using the receptor noise limited model. The results suggested that photon-shot noise and dark noise, caused by spontaneous activity in the photoreceptor, such as internal visual pigment isomerisations indistinguishable from real photon absorption (Baylor et al., 1980; Rieke and Baylor, 2000), were important in determining the intensity thresholds. Our model calculations also suggested that spatial summation must occur to reach the observed intensity thresholds, similar to

what has been suggested by others (Kelber et al., 2002; Roth and Kelber, 2004; Somanathan et al. 2008).

In paper II, we tested the hypothesis that spatial summation allows chickens to maintain colour vision in dim light. We tested the intensity threshold for colour discrimination using stimuli with fewer or more, and differently sized colour tiles. If spatial summation is important, the stimuli with larger and more colour tiles should be discriminated in lower intensities. Additionally, using these stimuli could help us to understand the range of spatial summation possible for the visual system. The results supported the hypothesis that spatial summation is important for determining the intensity threshold of colour discrimination. We found lower intensity thresholds using the stimuli with more or larger colour tiles. However, beyond a certain number or size of colour tiles, there was no further decrease in intensity threshold. This suggests that the intensity threshold in the dimmest light levels is set by a limit to spatial summation or by dark noise.

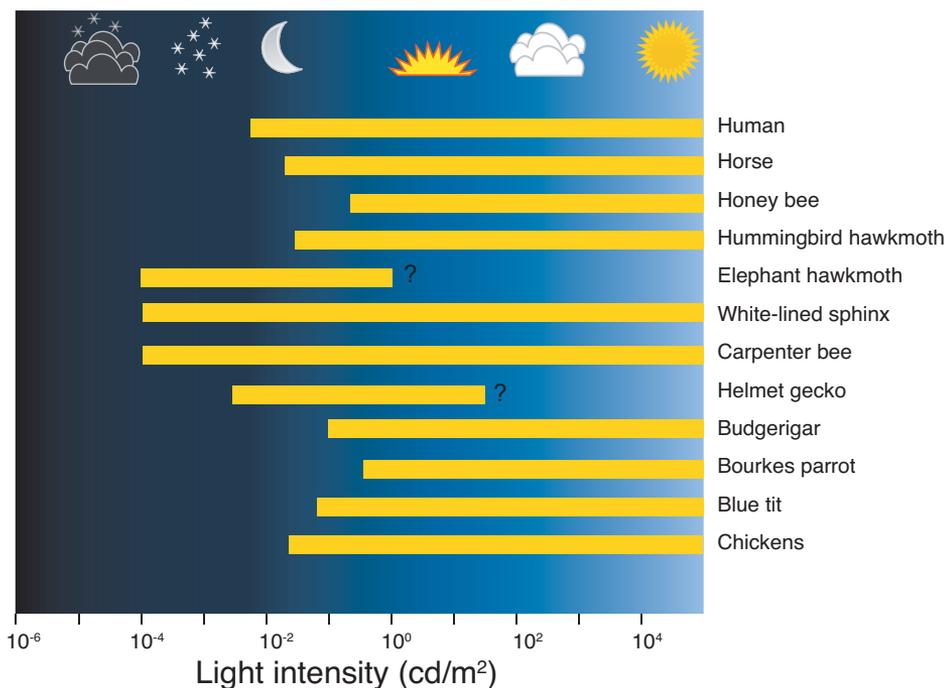


Figure 7. Intensity range for colour vision in different animals. In humans (Paper I; Kelber et al., 2002), horse (Roth et al., 2008), honeybee (Menzel, 1981), hummingbird hawkmoth and White-lined sphinx (Kelber et al., 2002), Indian carpenter bee (Somanathan et al., 2008), Helmet gecko (Roth and Kelber, 2004), Budgerigar and Bourke's parrot (Lind and Kelber, 2009b), Blue tit (Gomez et al., 2014), and the chicken (Paper I). Adapted from Kelber and Lind (2010).

This study is the first to test the hypothesis that spatial summation is important for dim light colour vision directly in non-human animals. If spatial summation is important to maintain colour vision in dim light, it may be expected that nocturnal vertebrates, which typically have rod-dominated retinas, may actually have higher intensity thresholds for colour discrimination than diurnal vertebrates with cone-dominated retinas.

Colour vision in spectrally different environments (Paper III & IV)

Light environments differ both in intensity and in spectral composition. Inside the forest, the downwelling light is filtered through the leaves, resulting in a changed spectral illumination (Endler, 1993). At twilight there is an evident blue shift of the illumination (Fig. 8), and starlight is red shifted (Johnsen et al., 2006). As the radiance spectrum reaching the eyes from a given object is a function of the objects reflectance and the illumination, the changing spectral content of the illumination is a potential problem. A colour learned in one illumination may be perceived differently in another illumination, thereby making colour information unreliable (Chittka et al., 2014).

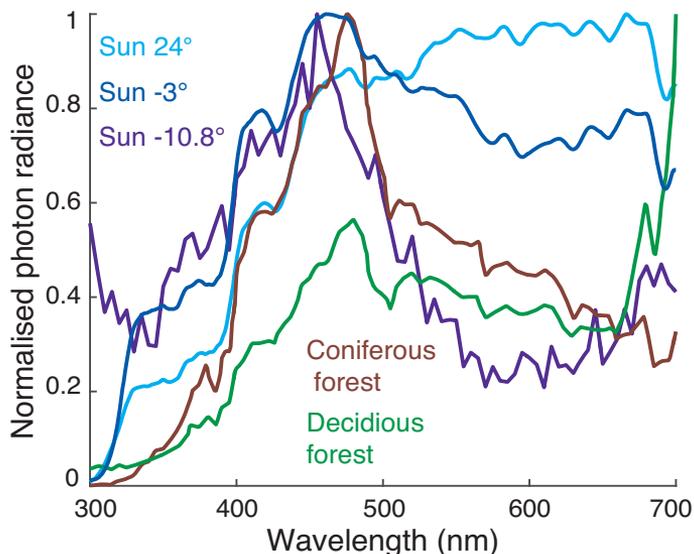


Figure 8. Examples of natural illumination spectra. The sunlight spectra were measured in Lund on a cloudy day at 24° and -3° of sun elevation. The spectrum with sun elevation at -10.8° is taken from (Johnsen et al., 2006) and two forest illumination spectra from (Håstad et al., 2005).

Colour constancy is the phenomenon that colour perception remains constant in different spectral illuminations (Hurlbert, 2007). An example can be seen in Fig. 9. The perceived colour of an apple changes if only the apple is covered by a red patch. When the whole scene is covered by a larger patch of the same red colour, the apple stays green. This example shows two important aspects of human colour constancy: first, there is a spatial interaction that is important and second, colour constancy is not perfect as the colours of the apple in Fig. 9A and C do not appear exactly the same. It is suggested that perfect colour constancy may in fact be maladaptive because the illumination change itself provides information (Smithson, 2005).

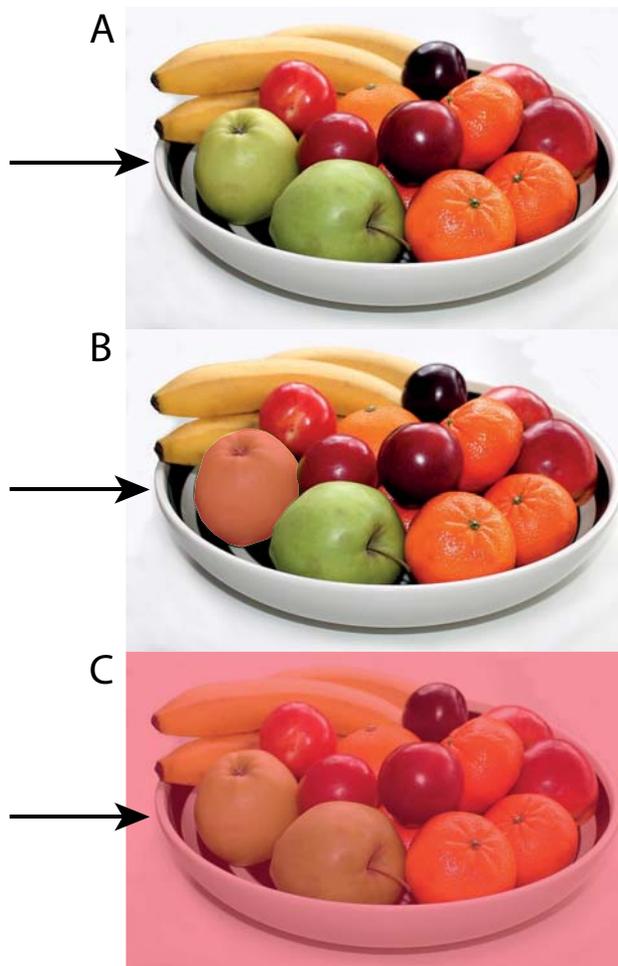


Figure 9. Example of colour constancy. The apple to the left in panel A appears orange when covered by a red patch (B). When the same red patch is extended to the whole scene, the apple again appears green (C).

To achieve colour constancy visual systems must adapt to and discount the illumination change (Hurlbert, 2007). To account for receptor adaptation and colour constancy, visual models typically use a von Kries type of transformation (Kries, 1905), normalising the photoreceptor signals of a stimulus to that of a reference, such as the background (Eq. 3, page 32). It is proposed that photoreceptors with narrow spectral sensitivity should be ideal for colour constancy based on a von Kries type model, as each photoreceptor type can adapt independently of each other (Worthey and Brill, 1986). The oil droplets of the bird retina serve this purpose, their long-pass filter properties create narrow spectral sensitivities with little overlap (Fig. 4, page 27).

Colour constancy is an important and fundamental property of colour vision that should be expected in all animals that rely on colour for important behaviours. Colour constancy has indeed been found in goldfish (Dörr and Neumeyer, 2000; Ingle, 1985), honeybees (Chittka et al., 2014; Neumeyer, 1981; Werner et al., 1988), hawkmoths (Balkenius and Kelber, 2004), swallowtail butterflies (Kinoshita and Arikawa, 2000), toads (Gniubkin et al., 1975), chickens (Katz and Révész, 1921) cats, and non-human primates (for references see Neumeyer, 1998).

Most studies on colour constancy in animals have qualitatively determined that animals remain colour-constant in spectrally different illuminations. Only two studies have tried to quantify colour constancy in non-human animals. Dörr and Neumeyer (2000) studied colour constancy in the goldfish. They trained the goldfish to one colour and tested them with a number of progressively more dissimilar colours, in different illuminations. They analysed the distribution of choices towards the trained and unrewarded colours and used the change in the peak of choice distribution, away from the training colour, to quantify colour constancy in any given illumination. The new position of the peak was compared to the amount of change of the illumination. Werner et al. (1988) studied colour constancy in the honeybee and used a conversion of a human scale to quantify honeybee colour constancy.

In paper III, we developed a different technique to quantify colour constancy in animals. Our aim was to find the limits of chicken colour constancy, in how large illumination changes they remained colour-constant, as opposed to quantifying colour constancy in a given illumination as had been done before. We trained chickens to discriminate colour stimuli in a white illumination and tested their colour discrimination performance in red-shifted illuminations. We created several illuminations that were more and more red-shifted compared to the training condition, and determined how much the illumination could be changed before chickens were unable to discriminate the colours.

We used the receptor noise limited model, calibrated for chicken colour vision as in Paper I, to quantify the difference between illuminations and the difference between colour stimuli.

We confirmed that chickens indeed have colour constancy and found that they could discriminate the colours with larger colour differences in more strongly red-shifted illuminations. The training regimen also affected colour constancy performance such that familiarity with the stimuli improved colour constancy. By adapting the receptor noise limited model to the visual systems of goldfish and honeybees, we determined that chickens remained colour constant in larger illumination shifts than goldfish (Dörr and Neumeyer, 2000), and that the illumination changes in which honeybees had been tested (Werner et al., 1988) were smaller than those in which chickens remained colour constant. However, the limits of honeybee colour constancy may have been underestimated as determination of thresholds was not the specific aim of that study.

To determine that the birds were in fact colour-constant, we designed the experiments in such a way that other cues, such as intensity and the relative colour cue, would not be reliable. We trained the chickens to prefer an orange colour from two unrewarded colours, a 'yellower' and a 'redder' colour. In each two-choice discrimination test, they were presented with the rewarded colour and one of the unrewarded colours. Thereby, the chickens could not use relative colour cues to solve the discrimination task, as in any given presentation the rewarded colour was either the 'redder' or the 'yellower'. In paper IV we repeated the experiment from paper III but allowed the chickens to use relative colour cues to solve the discrimination task. They were trained to discriminate either an orange colour from a yellow colour or a green from a blue colour in a white illumination and tested in red-shifted illuminations.

In nature, relative colour cues are readily available; red berries will, for instance, be 'redder' and reflect more long-wavelength light than a green or brown background, in almost any illumination spectrum. This information may be an important aspect of colour perception and learning. We again tested in how large illumination changes the chickens maintained colour discrimination and found that they tolerated larger illumination changes when relative colour cues were available. This suggests that the learning of such relative colour cues could make colour constancy more robust to larger illumination changes.

In both paper III and paper IV, we found that longer adaptation times made colour constancy possible in illumination changes in which the birds previously had failed. We also used the receptor noise limited model to quantify the difference between natural illuminations in the eyes of chickens. We found that the differences between natural illuminations (Table 1) were smaller than the illumination changes the chickens maintained colour constancy in (10-27 JND). This suggests that chicken colour constancy is well equipped to maintain colour perception and object identification mediated by colour in the different illumination they would experience in the wild, such as a sunlit field, a sunlit patch in a forest, and the spectrum under the canopy.

This method of quantifying colour constancy in animals can be used to compare the limits of colour constancy across species. The receptor noise limited model relates spectral differences between stimuli and between illuminations to the studied animal's visual system and may be the best way to make such cross species comparisons.

Table 1.

Colour difference (JND) between pairs of natural illuminations in the eyes of chickens.

Illumination 1	Illumination 2				
	Sun 11.4° (clear)	Sun 24° (cloudy)	Sun -3° (cloudy)	Rainforest (clearing)	Coniferous forest
Sun 24° (cloudy)	1.1	-	-	-	-
Sun -3° (cloudy)	0.8	0.3	-	-	-
Rainforest (clearing)	2.5	1.7	1.9	-	-
Coniferous forest	10.7	9.8	10.0	10.2	-
Decideous forest	5.6	4.6	4.9	5.0	5.3

Modelling chromatic and achromatic contrast thresholds (Paper V)

Contrasts between objects can result from differences in intensity (achromatic contrast) or differences in their spectra (chromatic contrast). In order to realistically predict the discriminability of stimuli in the eyes of animals, we need to consider both chromatic and achromatic vision. The receptor noise limited model, which has been shown to accurately describe colour thresholds, has been extended to model also achromatic discriminability (Siddiqi et al., 2004). In the achromatic version of the model perceptual distances, ΔS , are calculated assuming a single visual channel as

$$\Delta S = \left| \frac{f_i}{\omega_i} \right| \quad (\text{Eq. 7}),$$

where f_i is the receptor specific signal (Eq. 5, page 33), and ω_i is the limiting Weber fraction. For birds the spectral sensitivity of the double cone is often used.

Since then, many studies have used the receptor noise limited model to predict both chromatic and achromatic contrast detection in many ecological interactions in the eyes of birds. These include predictions of the discriminability of bird plumages (Feeney et al., 2014; Jones and Siefferman, 2014; Tanaka et al., 2011), lizards (Marshall et al., 2016), insects (Barry et al., 2014; Lindstedt et al., 2011; Papiorek et al., 2015), snails (Surmacki et al., 2013) and frogs (Maan and Cummings, 2012; Siddiqi et al., 2004).

As discussed previously, models of chromatic discriminability have been calibrated to behavioural thresholds. However, the achromatic version of the model has not been calibrated to behavioural thresholds.

The best description of an animal's ability to resolve spatial visual information is a contrast sensitivity function. It describes the ability of a visual system to detect contrasts at a given spatial frequency. Spatial frequency is a measure of the detail in an image, and is described in cycles/degree (Land and Nilsson, 2012). In tests of contrast sensitivity, an animal is trained to discriminate grating stimuli, and tested using gratings of different spatial frequency and contrast. In those types of experiments, contrast is measured as the difference in intensity between a dark and bright bar or between an object and the background normalised to the sum of their intensities as

$$C = \frac{I_{stim1} - I_{stim2}}{I_{stim1} + I_{stim2}} \quad (\text{Eq. 8}).$$

For stationary targets, achromatic contrast sensitivity functions typically take a band pass shape (Fig. 10) (Jarvis and Wathes, 2008; Uhlrich et al., 1981). Contrast sensitivity, the inverse of the smallest contrast difference that can be detected, is highest at a medium spatial frequency and lower at higher and lower spatial frequencies. Most birds, for unknown reasons, have lower contrast sensitivity than mammals (Ghim and Hodos, 2006; Hirsch, 1982; Hodos et al., 2002; Jarvis et al., 2009; Lind et al., 2012; Reymond and Wolfe, 1981; Bisti and Maffei, 1974; De Valois et al., 1974).

Contrast sensitivity functions using colour gratings have only been determined for humans (Mullen, 1985) and for budgerigars (Lind and Kelber, 2011), in both cases the functions show a low pass shape and lower resolution than for achromatic contrast, suggesting that chromatic vision is tuned for discriminating larger field stimuli. More often, other measures of chromatic detection thresholds have been used, which were reviewed in the chapter about behavioural tests and mathematical models.

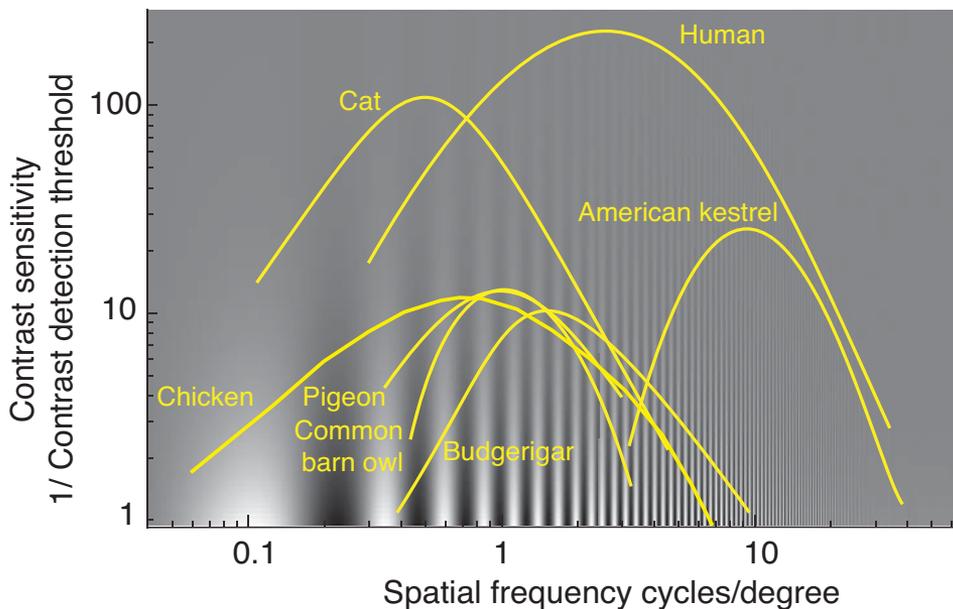


Figure 10. Behaviourally determined achromatic contrast sensitivity functions (CSFs). CSFs determined using two alternative forced choice experiments in humans (Berkley, 1976) and cats (Bisti and Maffei, 1974), and five species of birds: chicken (Jarvis et al., 2009), American kestrel (Hirsch, 1982), budgerigar (Lind et al., 2012), pigeon (Hodos et al., 2002), barn owl (Harmening et al., 2009). The pattern in the background does not directly relate to the scale, it is only used to illustrate increasing spatial frequencies and decreasing contrasts. Courtesy of Mindaugas Mitkus.

In paper V we compiled the measured chromatic and achromatic contrast detection thresholds available in the literature and used these to estimate the equivalent noise or Weber fractions, presumed to limit contrast detection (Lind and Kelber, 2009a; Vorobyev and Osorio, 1998). These estimates should be used as parameters in models of chromatic and achromatic detection.

We also discussed some of the issues in modelling contrast detection thresholds, such as the fact that the spatial structure of the stimulus is often disregarded. As we can see in Fig. 10, the detectable contrast is not the same at all spatial frequencies and therefore the same noise level or Weber fraction cannot safely be used for the modelling of all stimuli. Another limitation is light intensity. In the previous chapters we showed that at lower light levels colour contrast thresholds are higher and this is also true for achromatic vision, e.g. (Jarvis et al., 2009). Unfortunately, there is not yet enough knowledge to understand how to reliably predict an animal's ability to discriminate objects in dim light.

Bird achromatic vision has long been assumed to be mediated by the double cones (Campenhausen and Kirschfeld, 1998; Osorio and Vorobyev, 2005), implying that there is functional separation between achromatic and chromatic vision already at the receptor level. However, behavioural studies have not been able to exclude input from the LWS and MWS cone types to achromatic vision in birds due to the overlap in spectral sensitivity with the double cone (Jones and Osorio, 2004; Lind and Kelber, 2011). Additionally, the foveas of some raptors, where the highest spatial resolution is found, have no double cones (Mitkus, 2015; Reymond, 1985) and very few in others (Mitkus, 2015). The common swift has been found to have no double cones in the retina at all (Oehme, 1962). Taken together, this suggests that double cones do not mediate achromatic vision completely on their own. Double cones constitute a large fraction, ca 40-50% of all cones, in the eyes of many birds (Hart, 2001b). However, if achromatic vision was mediated only by the double cones it would seem that the image would be under-sampled. Why should not at least the L and M cones contribute?

Resolving the issue of how achromatic contrasts are mediated by the bird visual system is a key question for improving our understanding of bird visual ecology.

Concluding remarks

We have used behavioural experiments to find the limits of colour vision in chickens. In paper I and II we studied how similar colours they could discriminate, in how dim light they could discriminate colours and which factors were important for determining these thresholds. The behavioural data were compared with the predictions made by the receptor noise limited model, the best established model for bird colour vision. This allowed us to estimate the noise levels in the visual system of the chicken, both in bright light and in dim light. We found that a lower noise level must be assumed to consolidate behavioural and modelled threshold, compared to previously estimated noise levels for other species of birds. Suggesting that future modelling should include both estimates to assure robustness of model predictions.

To maintain colour vision in dim light, chickens are very likely using spatial summation mechanisms to pool the signals from many photoreceptors to reduce the impact of photon-shot noise. However, spatial summation in colour vision is controversial. In colour vision, the signals from the different cone types must remain separated. How can the information remain separated during spatial summation? Perhaps spatial summation for colour vision only occurs at higher levels than the retina? These are intriguing questions for future studies.

We also tested the impact of different spectral illuminations on colour discrimination in chickens and confirmed that they have colour constancy. Colour constancy is important for animals with colour vision or else colour would be an unreliable cue as the illumination spectrum changes between natural habitats. We determined the limits of chicken colour constancy, how large illumination changes they remained colour constant, and found that it partly depended on the colour difference between the stimuli. Colours that are more different may be discriminated in larger spectral changes of the illumination than more similar colours. The chickens remained colour constant in illumination changes that were larger than the changes between illuminations found in nature. When relative colour cues can be used, colour constancy is extended to even larger changes of the illumination. Many open questions still remain; can our results be safely extended to illumination changes in other direction of colour space? What are the adaptation mechanisms that ensure colour constancy in birds?

Contrast between stimuli can derive either from chromatic (spectral) or achromatic (intensity) differences, or both. The receptor noise limited model can

predict the discriminability of contrasts based on both chromatic and achromatic contrasts. We have reviewed the literature of chromatic and achromatic contrast detection thresholds and used them to estimate the critical parameter for modelling visual discrimination, the noise. We discussed the limitations of visual modelling with the current knowledge. Furthermore, we discussed the separation of chromatic and achromatic channels; which photoreceptors are contributing to which channel? What is the function of the double cone?

This work has extended our knowledge about the limits of colour vision in birds and proved valuable knowledge that can be used to guide future work on studying vision in birds. Furthermore, this work will hopefully guide those who wish to use visual modelling to estimate visual perception both in bright light, dim light and spectrally different illuminations.

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