Colour perception across the species

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Abstract

How different species may be able to perceive colour is explained on the basis of evidence from anatomical and functional studies of visual systems, spectrophotometry, and comparative psychophysics.

Introduction

Without light there is no colour and even when the level of incident light is too low, shades of grey but no other colours are visible. Thus, colour is a percept resulting from a response of the brain to data received by the visual system. Objects emit light of various wavelengths and these can be detected and analyzed precisely by inanimate machines. Therefore colour defined in terms of a physical phenomenon refers to the spectral qualities of the light emitted or reflected from an object or living creature. It can thus be defined and measured precisely with spectrophotometers, which analyze the amount of energy present at each spectral wavelength. With such instruments daylight can be shown to be composed of a continuous range of colours corresponding to different wavelengths of variable intensities, depending on the phase of daylight, while artificial sources are fixed - tungsten light, for example, has a predominant red component and very little blue. The spectral reflectance of an artist's pigment in general has a single broad peak the maximum wavelength of which corresponds to its so-called colour.

The human brain processes signals produced by wavelength mixtures, enabling us to interpret colour signals and giving rise to a psychophysical phenomenon we call colour perception. The perception of colour by a living organism requires both a sensory organ receiving external signals and a brain to process these signals and transform them into meaningful representations. Colour should, however, be distinguished from what we understand as biological colouration, which may be defined as the appearance of a living organism determined by the quality and quantity of light reflected by or emitted from its surface. The concept of biological colouration differs from that of colour since it depends on several other factors, including the relative location of coloured areas on the organism, the quality and intensity of light falling on it, the shape posture and movement of the organism presenting the colouration and, of course, the visual capabilities of the organism looking at it. Since visual systems, defined in terms of light sensitive organs equipped with receptors and mechanisms allowing visual signals to be processed, are not identical in different animal species including fish, birds, non-human and human primates, colour perception is what evolutionary biologists call a species-specific process.

Colour vision in the animal kingdom

Colour perception, like many biological phenomena, is a result of evolutionary pressure. The ability to see colour has evolved, to a greater or lesser extent, in many different species. To be able to distinguish certain colourations from others plays an important part in the processes which ensure survival. Such ability is determined by the anatomy and functional development of the visual system a given species is equipped with. In the animal world, at least forty different types of visual systems exist, the simplest just able to differentiate light from dark, while sophisticated ones can distinguish both shapes and colours, the most complex belonging to the mantis shrimp, a predatory crustacean living on the ocean floor. There is an enormous diversity in both retinal structure and visual neuronal mechanisms across the animal kingdom, with a corresponding diversity in the role of colour vision in animal's perception, behaviour, and interactions with the environment (Land and Nilsson, 2002).

With regard to retinal anatomy, the vertebrate retina is "back to front" i.e. the photoreceptors are located behind a layer of neurons, as opposed to the cephalopod retina, in which the photoreceptors are located in front of the processing neurons, which means that cephalopods do not have a blind spot. Moreover, the cephalopod retina is not an outgrowth of the brain, as in vertebrates, illustrating that vertebrate and cephalopod eyes have evolved separately.

At the start of the 20th century colour vision was thought to be exclusive to man. Now however it is well established that colour vision is widespread in non-human animals, although even among vertebrates, the ability to perceive colour and the spectral range detected varies widely, having evolved several times. Nevertheless, the precise colour perception capabilities of the majority of animal species are still not known, since behavioural or physiological tests for colour vision are not easy to perform. Human colour vision (see later) is made possible by the presence of three types of colour sensitive receptors, a lack of one or other class of colour receptors (cones) provoking deficiencies in colour vision or various kinds of colour blindness. In general terms for all living organisms, if they possess only a single retinal pigment then they will only "see" in monochrome and for even limited colour vision at least two types of cones are required. However the number of retinal pigments in animal species is not limited, as in man, to three. Using behavioural studies and spectrophotometric analysis of light absorbed by animal retina, it can be deduced that four exist in approximately thirty species of birds and five in certain butterflies and many more for sea organisms such as the mantis shrimp and the sea manta, a giant ray (Cronin , Caldwell and Marshall, 2001; Marshall, Cronin and Kleinlogel, 2007). While the human eye cannot detect all of the electromagnetic spectrum emitted by the sun, notable UV, which is absorbed by the human cornea and optic media, lobsters, gold fish, trout, bees, tortoises, many bird species and rodents such as rats and mice can perceive in this region (Cuthill et al., 2000). At the other end of the spectrum, some species, such as snakes, detect infra-red but these rays are captured by specialized heat sensitive organs and not by the retina.

Colour vision in non-primate mammals is a subject of on-going research. It varies considerably between species and often dependant on the nocturnal or diurnal nature of the animal. Much research is currently devoted to elucidating the capacity of colour vision in many different animal species, but there remains a vast number for which little concrete data exist. While certain mammals, such as the shrew (despite reputedly poor sight) and certain squirrel species are considered to be trichromatic, in general non-primate mammals are considered to have relatively limited colour vision. The variation in colour vision results from the fact that the capacity to detect colour has evolved more than once, with gene duplication

for visual opsin pigments (Bowmaker, 1998). In addition, probably because of their nocturnal ancestry, mammals have rod-dominated retinas and many lack cones with long-wave sensitive pigment and therefore have poorer (only dichromatic) colour vision: some species lack cones completely, such as the guinea pig and are thus totally colour blind. Bulls, like many mammals and in spite of the importance of the colour red in bull-fights, are not differentially sensitive to this colour. Similarly, the cat is dichromate with one type of cone sensitive to blue indigo ca 450nm and another to yellow/green ca 556nm, as is also the case for the ferret (Calderone and Jacobs, 2003). Cats do however have more rods (the highly light sensitive receptors) and less cones, giving good night, albeit monochrome, vision. Behavioural studies performed in the 1970's suggested that rabbits have a rather limited capacity to distinguish certain wavelengths, although they can differentiate between green and blue.

Horses also have only dichromatic vision detecting blue and green and the colours based on them (Carroll et al., 2001). The limited colour perception of horses is sometimes taken into consideration when designing obstacles in horse jumping events. Horses, however, have more rods than humans, in addition to twenty fold more rods than cones, giving them better night vision.

A different system has evolved in rats and mice, which have excellent night vision, due to a high number of rods, but reportedly see poorly in colour although both are dichromatic. Both rat and mouse cones co-express two photopigments, one sensitive to wavelengths of ca 510nm and one to ca 360 nm i.e. UV. Their visual systems exploit differences in the spectral absorption properties among the cones, enabling them to make certain dichromatic colour discriminations, which is also the case for gerbils (Jacobs and Williams, 2007; Jacobs, Fenwick and Williams 2001; Jacobs, Williams and Fenwick, 2004; Jacobs and Deegan 2nd., 1994). Both diurnal rodents and rodents which live in almost lightless conditions have been found to have similar colour vision (Williams, Calderone and Jacobs, 2005; Jacobs et al., 2003).

Amongst mammals, primates represent exceptions with regard to colour perception. Sound data confirm the long held suspicion that colour vision in primates including humans, apes, and Old World monkeys is better developed than in other mammals: in spite of data lacking on many species, these are all considered to be trichromatic (Jacobs, 1993). Variations nevertheless exist (Jacobs, 1996; Jacobs and Deegan 2nd., 1999). Variations amongst New World monkeys are even greater, some species being trichromatic while others are only dichromatic (Jacobs and Williams, 2006). In addition, evidence exists that all male New World monkeys are dichromats while, depending on their opsin gene array, individual females can be either dichromatic or trichromatic (Jacobs and Deegan 2nd., 2003; 2005; Rowe and Jacobs, 2004). Some nocturnal species appear to be monochromatic however (Jacobs 1996).

The situation for aquatic mammals is quite different. Many species, including dolphins and seals, and in particular mammals that live in deep water tend to have blue shifted vision compared to that of many terrestrial mammals and are monochromatic (Fasick et al., 1998). This is considered to result from the absence of evolutionary pressure to maintain colour in the dark monochromatic oceanic environment (Newman and Robinson, 2005).

Of species studied so far, the best colour vision appears to be found in lower vertebrates such as certain birds, aquatic creatures, and certain insects including butterflies and honeybees. Birds vary according to species in their capacity to sense colour. Diurnal birds tend to have increased ultraviolet sensitivity, with far more cones than rods and their cones are sometimes complex, while nocturnal species such as owls tend towards sensitivity in the lower end of the spectrum, with a relatively high proportion of rods, and are colour-blind. The most acute

avian vision is found in raptors, such as hawks and eagles that rely on their sight to spot prey from altitude. They are bifoviate, increasing the potential number of cones, some of which are double, a phenomenon also observed in fish, amphibians, and reptiles. An eagle has a larger retina than a human with five times more cones and its structure, like that of most birds, is more complex. Many birds have four types of cone making them potentially tetrachromats. Fish appear to have quite well developed visual systems, comparable in some species to those of birds. Some have photoreceptors with peak sensitivities in the ultraviolet range. This may be because they move about in a blue environment and need to contrast food sources or predators against a blue background. Teleostei, regrouping about 23,600 vertebrate species making up 95% of all known fish species, sense red, yellow/green/blue, violet and UV up to 365nm. However, since sea water selectively absorbs longer wavelengths, many fish living below 10 metres see "poorly" in this spectral region. Nevertheless many reef fish species living at this depth emit red fluorescence the origin of which are guanine crystals and do perceive this colour (Michiels et al., 2008).

Amphibians see fairly well in colour with a maximum day vision principally in yellow and at night in green. Colour vision in reptiles is also well developed with turtles able to distinguish between blue, green and orange and lizards between yellow, red, green and blue.

Reptiles have genera that possess rods and four spectral classes of cone each representing one of the five visual pigment families, endowing these species with the potential for tetrachromatic colour vision (Bowmaker, 1998).

Many insects, including butterflies, flies and bees, have colour vision. Butterflies vary widely in their sensitivity to light, and are considered to have the widest visual range of any form of wildlife. The Chinese yellow swallowtail butterfly (Papilio xuthus) has a penta-chromatic visual system, i.e., the eyes contain five different types of cones, sensitive to UV, violet, blue, green, and red wavelength peaks. In nature, these butterflies feed on nectar provided by flowers of various colours not only in direct sunlight, but also in shaded places and on cloudy days. The windmill butterfly (Atrophaneura alcinous) has a visual spectral range from at least 400 nm to 700 nm, while the Sara Longwing butterfly (Heliconius sara) has a range from 310nm to 650nm. Mosquitoes don't see yellow but do perceive violet which is why mosquito traps emit blue to ultraviolet light which attracts these insects. Bees, have complex compound eyes, four visual cells in each ommatidium responding to yellow/green light (530 nm), two responding maximally to blue light (430 nm) and the remaining two responding best to ultraviolet light (340 nm), allowing the honeybee to distinguish colours (except red). However, an additional feature of bee vision is that they are dichroic, i.e. sensitive to polarized light, which would pose a problem in perceiving colour from waxy plant surfaces since this is partially linearly polarized. Bees and many other insects overcome this problem since the majority of their photoreceptors are twisted like a corkscrew which enables them to perceive the same colour in all directions (Wehner and Bernard, 1993).

Comparative psychophysics and the biological significance of colour

Over a century ago, scientists such as J. Lubbock and K. von Frisch developed behavioural criteria establishing that non-human animals see colour. Many animals in most phyla have since then been shown to have colour vision. Colour is used for specific behaviours, such as phototaxis and object recognition, while other behaviours such as motion detection are not dependant on colour. Having established the existence of colour vision, research focussed on the question of how many spectral types of photoreceptors were involved. Recently, data on photoreceptor spectral sensitivities have been combined with behavioural experiments and physiological models to systematically study the next logical

question: "what neural interactions underlie colour vision?" Kelber, Vorobyev and Osorio (2003) give an overview of the methods used to study animal colour vision, and discuss how quantitative modeling can suggest how photoreceptor signals are combined and compared to permit the discrimination of biologically relevant stimuli.

Comparative psychophysics addresses questions about how colour perception influences behaviour in the different species. Does a bull get enraged by the colour of a red cape or by its movements? Do colourations help bees to discriminate flowers which are plump with nectar from others? Do specific colourations help a cat detect prey more rapidly? What do animals see when they detect colour and do they actually perceive colour? While no one knows exactly what animals see or perceive, there are several aspects of these questions that can and indeed have been explored. Firstly, we need to know how their visual systems work from a physiological point of view and also the spectral sensitivities of the photo-pigments, which have been reviewed above. More important, however, is the question of how an animal's brain processes colour signal inputs. Many scientists working in the field think that animals "understand" little of what they see, just as humans rarely "understand" abstract paintings, even though they may respond emotionally to and "appreciate" what they see.

Although we know that visual abilities differ among animals, there is an important distinction between detecting properties of the light that illuminates the retina, and understanding what is actually "out there".

Since animals cannot answer questions about the colours they perceive, research scientists have had to develop experiments in which animals are trained to make selective behavioural choices on the basis of colour. Such experiments are not straightforward. If an animal's food is always placed under a red square rather than a green square, if both squares are otherwise identical from all points of view and re-positioned randomly over time, and if the animal still and consistently keeps looking under the red square when it is hungry, we still may not conclude that it is capable of distinguishing what we perceive as red from what we perceive as green. And why not? The discrimination may be mediated by differences in perceived brightness, rather than color, as with a human dichromat. Only if luminance is randomized away as a nuisance variable can the conclusion be drawn – and this has to be done without using a photometer, since doing so assumes that cats have the same spectral sensitivity for luminance as us, which is false (Mello, N and Peterson, N. 1964. "Behavioral evidence for color discrimination in the cat'. Journal of Neurophysiology, 27, 323-333). Yet, what we know about colour perception in the animal kingdom pales in comparison to that yet to be discovered.

Thirty years ago virtually everything known about primate colour vision derived from psychophysical studies of normal and colour-defective humans and from physiological investigations of the visual system of the macaque monkey, the most popular human surrogate for this purpose. The years since have witnessed much progress toward the goal of understanding this remarkable feature of primate vision. Among many advances, investigations focused on naturally occurring variations in colour vision in a wide range of nonhuman primate species have proved to be particularly valuable. Results from such studies (Jacobs, 2008) were central to expanding our understanding of the interrelationships between opsin genes, cone photopigments, neural organization, and colour processing. This work also generated valuable insights into the evolution of colour perception. Latanov, Leonova, Evtikhin, and Sokolov (1997) studied colour discrimination using an instrumental learning paradigm in monkeys (Macaque rhesus) and fish (Carpio cyprinus L). Confusion matrices composed of probabilities of instrumental responses were treated by factor analysis. The spherical structure of perceptual colour space revealed in both species was found to be similar

to that in humans, corresponding to "red-green," "blue-yellow" and the neuronal channels signalling for "brightness" and "darkness".

The dance of the honeybee has been researched extensively, and we have a relatively good understanding of the colour vision of bees and related insects. Mosquitoes and flies have been studied because of their role in spreading diseases, and it has been shown that they are attracted or repelled by specific surface colours, and by specific coloured sources of light. Interestingly, the surface colours they prefer do not necessarily correlate with the light source colours that attract them. Studying colour perception in birds is also quite challenging. Observations clearly demonstrate that different species are attracted to bird feeders of particular colours, and that changing the colour of ambient light can trigger early breeding, or alter fertility rates, by mimicking the change of seasons. It is as hard for us trichromats to imagine how birds perceive colour as it is for a colour blind person to imagine full colour vision: it is simply outside our experience. Some species which we see as having identical male and female plumage differ when viewed by ultraviolet light - a difference which the birds themselves are capable of perceiving. Butterflies also perceive colourations and often identify each other quite easily by their ultraviolet markings. The male and female little sulphur butterflies (*Eurema lisa*) differ only in the ultraviolet region, with males being strongly ultraviolet reflective and females not.

Over millions of years, sea creatures have developed a range of light reflectance properties. One example is the large variation in the patterns and colours of fish inhabiting the world's coral reefs. Attempts to understand the significance of the colouration have been made, but all too often from the perspective of a human observer. A more ecological approach requires us to consider the visual system of those for whom the colours were intended, namely other sea life. A first step is to understand the sensitivity of reef fish themselves to colour. Physiological data has revealed wavelength-tuned photoreceptors in reef fish, and provided behavioural evidence for their application in colour discrimination. Using classical conditioning, freshly caught damselfish were trained to discriminate coloured patterns for a food reward (Siebeck, Wallis, and Litherland, 2008). Within 3-4 days of capture, the fish selected a target colour on over 75% of trials. Brightness of the distractor and target were systematically varied to confirm that the fish could discriminate stimuli on the basis of chromaticity alone. The study demonstrated that reef fish can learn to perform two-alternative discrimination tasks, and provided the first behavioural evidence that reef fish have colour vision. Fishes such as members of the billfish family also appear to perceive colourations. These highly visual predatory teleosts inhabit the open ocean. Little is known about their visual abilities in detail, but previous studies indicated that these fish were likely to be monochromats. However, there is evidence of two anatomically distinct cone types in billfish. The cells are arranged in a regular mosaic pattern of single and twin cones as in many fishes, and this arrangement suggests that the different cone types also show different spectral sensitivity, which is the basis for colour vision. First measurements using micro-spectrophotometry (MSP) revealed peak absorption of the rod pigment at 484 nm. When hunting, billfish such as the sailfish flash bright blue bars on their sides, which also reflects UV light at 350 nm as revealed by spectrophotometric measurements. Billfish lenses generally block light of wavelengths below 400 nm, presumably rendering the animal blind to the UV component of its own body colour. Interestingly, at least two billfish predatory species have lenses transmitting light in the UV waveband and are therefore likely to perceive a large fraction of the UV peak found in the blue bar of the sailfish (Fritsches, Partridge, Pettigrew and Marshall, 2000). Wavelength discrimination ability of the goldfish has also been investigated on the basis of a behavioural training technique in the UV spectral range (Fratzer, Dörr and Neumeyer, 1994). First, spectral sensitivity was determined for two fishes to adjust the monochromatic lights (between 334 and 450 nm) to equal subjective brightness.

The results of the wavelength discrimination experiment showed that, independent of which wavelength the fish were trained on, the relative choice frequency reached values above 70% only at wavelengths longer than 410 nm. Wavelength discrimination between 344 and 404 nm was not possible. These observations cannot be explained on the basis of the cone sensitivity spectra alone. Instead, inhibitory interactions, which suppress the short wavelength flanks of the short-, mid-, and long-wavelength sensitive cone types in the UV range, may have to be proposed.

Kitschmann and Neumeyer (2005) demonstrated that goldfish are able to categorize spectral colours after habituation to a specific training wavelength. Subsequently, Poralla and Neumeyer (2006) trained goldfish on more than one wavelength to prevent very accurate learning. In one experiment goldfish were trained on six adjacent wavelength bands with equal numbers of rewards, and, thus, equal numbers of learning events. Generalization tests showed that some wavelengths were chosen more often than others, indicating that certain spectral ranges are either more attractive or more easily remembered than others. This is a characteristic of the "focal" colours or centres of colour categories in human colour perception and the findings in goldfish may thus be interpreted accordingly. There appear to be four categories in spectral ranges approximately coinciding with the maximal sensitivities of the four cone types, and three categories in-between. Experiments with two training colours have shown that there seems to be no direct transition between categories analogous to human "green" and "red", but that there is a colour analogous to human "yellow".

However, visual systems sensitive to colour are confronted with the fact that the external stimuli are often ambiguous because they are subject to constant variations of luminance and spectral composition. Furthermore, the transmittance of the ocular media, the spectral sensitivity of visual pigments and the ratio of spectral cone types are also variable. This results in a situation where there is no fixed relationship between a stimulus and a colour percept. Colour constancy has been identified as a powerful mechanism to deal with this set of problems, but is active only in a short-term time range. Changes that cover longer periods of time require additional tuning mechanisms at the photoreceptor level or at post-receptor stages of chromatic processing. Colour constancy, due both to receptor adaptation and to neural mechanisms (e.g. Arend & Reeves, 1986), has been identified as a powerful mechanism to deal with this set of problems, but is active only in a short-term time range, typically under 2 minutes.

Wagner and Kröger (2005) used the trichromatic blue acara (Aequidens pulcher, Cichlidae) as a model system and studied retinal physiology and visually evoked behaviour after rearing fish for 1-2 years under various conditions, including nearly monochromatic light (spectral deprivation) and two intensities of white light (controls). In general, long-term exposure to long wavelength light had lesser effects than light of middle and short wavelengths. Within the cone photoreceptors, spectral deprivation did not change the absorption characteristics of the visual pigments. In contrast, the outer segment length of middle and long-wave-sensitive cones was markedly increased in the blue reared group. Furthermore, in the same group, a loss of 65% short-wave-sensitive cones was observed after 2 years. These changes were interpreted as manifestations of compensatory mechanisms aimed at restoring the balance between the chromatic channels. At the horizontal cellular level, the connectivity between short-wave-sensitive cones and the H2 cone horizontal cells were affected in the blue light group. Responses of H2 horizontal cells to light were also sensitive to spectral deprivation showing a shift of the neutral point towards short wavelengths in the blue reared group. An intensity effect was found in the group reared in bright white light, where the neutral point was more towards longer wavelength than in the dim light group. Like changes in the cones, the reactions of horizontal cells to spectral deprivation in the long wave domain may be considered to be compensatory. The spectral

sensitivity of the various experimental groups of blue acara in a visually evoked behaviour task revealed that changes in relative spectral sensitivity were too complex to be explained by a simple extrapolation of adaptive and compensatory processes in the outer retina. The inner retina, and/or the optic tectum appear to be involved here, reacting to changes of the spectral environment. Thus in summary, there appears to be considerable developmental plasticity in the colour vision system of the blue acara, where epigenetic adaptive processes at various levels of the visual system respond to the specific spectral composition of the surroundings and provide a powerful mechanism to ensure functional colour perception in different visual environments.

Processes involving an active fine-tuning of photoreceptors and post-receptor processing of chromatic information during ontogenetic development are a general feature of all colour vision systems. These appear to attempt to establish a functional balance between the various chromatic channels. This is likely to be an essential condition for cognitive systems to extract relevant and stable information from unstable and changing environments. Comparisons of functionally important changes at the molecular level in model systems have identified key adaptations driving isolation and speciation. In cichlids, for example, variation in the long wavelength-sensitive opsins appear to play a role in mate choice and variations in colourations of the males, within and among species. To test the hypothesis that the evolution of elaborate colourations in male guppies (*poecilia reticulata*) is also associated with opsin gene diversity, Ward, Churcher, Dick, Laver, Owens, Polack, Ward, Breden and Taylor (2008) sequenced long wavelength-sensitive opsin genes in six species of this family and concluded that enhanced wavelength discrimination may be a possible consequence of opsin gene duplication and divergence in spectral sensivity. This might have been an evolutionary prerequisite for colour-based sexual selection and may have led to the extraordinary colourations now observed in male guppies and in many other species.

Conclusions

Many living organisms clearly appear to detect visual information relative to colour, and are able to perceive differences in colourations. How essential is it for their survival, and is its absence life threatening? Several generalities can be postulated: there exists a strong interdependence between the habitat and/or behaviour patterns of different species and their capacity to perceive colour. For example, flying birds require a comprehensive visual perception in three-dimensional space, while birds that live on seeds and fruits in the forest canopy need to differentiate between green and the colours of their chosen foods. Monkeys need to distinguish between orange fruits and green foliage to find food. Ultraviolet vision as possessed by the kestrel can offer a significant advantage in spotting the traces left by prey, such as urine and faeces. The spectral range of vision of bees and butterflies also extends into the ultraviolet, which could aid them in seeking nectar in flowers they pollinate which have specific ultraviolet patterns. Evolutionary forces have been operational in developing specific characteristics, including particular spectral sensitivities and specific colourations, so that species survive better in a highly competitive environment. Thus, biological colourations may have different functions, but they all represent a means of signalling to members of the same or other species. These functions may be divided into three broad categories - deceptive signalling or camouflage, advertising, and repulsive signalling, discussed elsewhere in great detail (cf Dresp-Langley & Langley, 2006) and leading towards issues about functional aspects of visual perception that have been raised by Gestalt psychologists with regard to processes of perceptual organization (Dresp-Langley, 2015) and figure-ground segregation (Metzger, 1930).

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