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Colour and the race for behavioural success: From mate choice to visual art and architecture

Keith Langley

Keywords: Colour; Ornaments; Sexual Traits; Evolution; Colour Vision; Visual Art
Abstract

The influence of evolutionary and environmental pressures on both perceptual capacity and colour trait production is made evident. The functional role of colour in terms of its potential benefits to behavioural success is then made clear, as colour helps ensure the survival of animal species on the one hand, and the intellectual and cultural development of man on the other.

Introduction

The choice of a sexual partner represents an important step towards the most successful propagation of a given species by a sexual process. Successful reproductive sex in animals constitutes a process of combining and mixing genetic traits, often resulting in the specialization of organisms and to form offspring that inherit traits from both parents. Genetic traits, contained within the DNA of chromosomes, are passed on from one parent to another in this process. Because of their motility, animals often engage in coercive sex. While in a large number of essentially monogamous species, such as humans, the selection of a sexual partner is most often mutual, this is far from being the case in many animal species. Both inter and intra-species differences are observed. In many species which are not monogamous, male domination is often determinant. Since certain inherited characteristics may be linked to specifically sex-associated chromosomes, physical differences are frequently observed between the different sexes of an organism. Such secondary sexual traits (i.e. those not strictly linked to the reproductive system) of males in certain species may include greater size compared with females. The expression of such physical traits, examples of which would include antlers, goat horns or hippopotami teeth, can be employed to aggress or to ward off rival males. Biological colourations also often constitute secondary sexual traits. Colour traits are observed in a wide variety of animal species. They have been particularly well studied in birds, where major differences in feather colours of males and females may be observed (Fig. 1). Over recent years an overwhelming bulk of evidence has shown that these differences play a significant role in mate determination, with males frequently displaying these attributes with the aim of attracting a female partner. However, feather colourations may also, in certain species, be employed to impress and repel would-be rivals, which is the case for peacocks. Feather colours of birds are, however, not always specifically sexual traits as both sexes of many bird species possess apparently identical, highly coloured feather patterns. These too may determine mutual mate choice in monogamous birds, such as king and emperor penguins. Thus, since dramatic inter and intra-species differences exist in reproductive behaviour, the role of colour in mate choice has to be considered strictly in the context of individual species and even individuals within the same species, and must not be generalized to all species.

Sexual dimorphism and animal colouration

Secondary sex characteristics constitute sexual dimorphism and can affect the overall size of the animal as well as the colour patterns of their external ornaments. An extraordinary variation of external sexual traits exists in the animal kingdom, from the manes of male lions to the long, often intriguingly complex, coloured feathers of male peacocks, or the brightly coloured feathers of mallard ducks (Fig. 1) and other male birds. In mammals, dramatic examples include the tusks of male narwhals and elephants, enlarged proboscises in male elephant seals and proboscis monkeys, the bright facial and rump coloration of male mandrills, and the horns of goats and antelopes. In many species, in particular polygamous ones, the males are bigger, and this may be put to advantage to gain reproductive access with the females in competition with other male individuals. Well known examples in birds include common pheasants, chickens and Indian pea fowl, which are sexually dimorphic both in size
and colour. Frequently the males have a more colourful appearance (Fig. 1) compared with the females. Cockerels differ from hens not only by a greater size, but also by a larger, more intensely red comb, and better developed and brighter plumage colours, with more conspicuous and impressive tail feathers. Such characteristics have been linked to aggression, or differences in aggressive behaviour between males and females, demonstrated by the combative behaviour of the cockerels. Some mammals also have additional traits like antlers in male deer, for example, which are used in combat between males to win the “right” to mate with female deer. In contrast, most insects and many fish, have larger females, which may result from the fact that bigger ones can produce more eggs. Sexually dimorphic traits are under genetic control, but environmental influences can considerably modify the phenotype and produce intra-specific variations. The production of such features during the development of an animal may be controlled by sex hormones (androgens or oestrogens), as demonstrated by menopausal chicken hens assuming cockerel secondary characteristics. Sexual traits may be either seasonal, like the antlers of male deer or the body colour of male sticklebacks, or permanent.

Secondary sexual traits are classically considered to be derived by sexual selection for traits which give an individual an advantage over its rivals in courtship or aggressive interactions (Darwin, 1971). The evolution of exaggerated secondary sexual traits is not a recent phenomenon. It has been maintained (Tomkins et al. 2010) that the crests of the pterosaur Pteranodon longiceps and the large elaborate back sails of Dimetrodon and Edaphosaurus, the biggest example of sexual dimorphism known in any animal, would function as elaborate sexual signals, suggesting that male Pteranodon competed with each other in battles for dominance using their crests like animals with horns or antlers, or alternatively, that females assessed males on the size of their crests, in a similar way to peahens choosing among a group of displaying males.

Two not entirely incompatible theories have attempted to explain sexual selection of ornamental traits in animals. One, known as the sexy son hypothesis (Weatherhead & Robertson 1979), proposes that this might arise because of some arbitrary female preference that is initially amplified by random genetic drift, eventually being reinforced by active selection for males with the appropriate ornament, synonymous with a male whose genes will produce male offspring with the best chance of reproductive success, a theory implying that a potential mate’s capacity as a caregiver are irrelevant. An alternative hypothesis, the “good genes” hypothesis, proposes that some of the genes that enable males to develop impressive ornaments or fighting ability may be correlated with fitness markers such as disease resistance or a more efficient metabolism. In this context the impressiveness of ornaments can reflect information on immune-competence and general health (e.g. Nolan, Dobson, Dresp, & Jouventin, 2006). The state of a peacock’s plumage, for example, could indicate to a peahen much about whether or not the male has blood parasites, i.e. about health condition and not just “good genes”.

The presumed importance of sexual selection in trait evolution has been questioned on the basis that exaggerated ornaments could represent a handicap to the males that produce them (Zahavi, 1975). While it is true that some traits cost considerably such as a peacock’s tail, and that this may hinder flight, it is nevertheless a fact that without this elaborate ornament success in finding a mate is extremely compromised. White male peacocks for instance rarely find a mate.

**Colour vision**

In order for colour to have a biological meaning, it must be detected and encoded by the visual receptors of a living organism and subsequently processed by its nervous system. Such processing only enables what is commonly called colour perception. The ability to detect,
process, and perceive colour is a consequence of evolutionary pressure. It has evolved, to a
greater or lesser extent, in many different species and is determined by the functional anatomy
and epigenetic development of the visual system of a given species. At least forty different
types of visual system exist in the animal world, the simplest only able to differentiate light
from dark, as in *aplysiae*. The visual brains of higher order species are able to discriminate
both shapes and colours. Enormous diversity in both animal retinal structure and visual
neuronal mechanisms has been observed, with a corresponding diversity in the functional role
of colour vision in animal perception and behaviour (Land & Nilsson, 2002). This diversity
may be explained by the fact that separate evolutionary processes have acted on different
species.

Human colour vision is made possible by the presence of three types of colour sensitive
receptors. If a living organism possesses only a single retinal pigment it will only perceive the
world around in monochrome, and for even very 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. With one more class of cones than man, tetrachromatic animals can
theoretically see twice the number of colours. Microspectrophotometry, a rather complicated
procedure with limited applications has often been employed to test the spectral sensitivity
properties of animal retinas. With this technique and through behavioural studies, it has been
deduced that four exist in approximately thirty species of birds. Some birds have five types of
cone photoreceptor: four single cones and a double cone (Bowmaker et al., 1997). Each
contains a different photopigment and the spectral sensitivities of certain cones are narrowed
by a coloured oil droplet filtering light signals (Partridge, 1989; Bowmaker et al., 1997). The
fifth, double cone type, constitutes about half of all cones. These have a different oil droplet
filter and thus broader spectral tuning (Bowmaker et al., 1997). Employing a more refined
approach, involving the sequencing of a part of the gene coding for avian retinal opsins,
Odeen and Hastad (2003) have shown that avian colour vision is more complex than had
previously been thought. Their data support that sensitivity biased toward violet short
wavelength has evolved independently at least four times. The mechanism of colour
perception in the chicken has been examined in a study (Osorio et al., 1999) showing the
degree of sophistication in processing light signals. The chicken processes colour inputs by at
least three opponent mechanisms: one comparing between the outputs of ultraviolet- and
short-wavelength-sensitive receptors, one between the outputs of medium- and long-
wavelength receptors and a third comparing outputs of short- and long- and/or medium-
wavelength receptors. Kelber, Vorobyev & Osorio (2003) more recently have discussed how
photoreceptor signals are combined and compared to allow for the discrimination of
biologically relevant stimuli.

Five retinal pigments have been found in butterflies and many more in sea organisms
such as the mantis shrimp and the sea manta, a giant ray (Cronin, Caldwell & Marshall, 2001;
Marshall, Cronin & Kleinlogel, 2007). While the human eye cannot detect all of the
electromagnetic spectrum emitted by the sun, and UV being in any case absorbed by the
human cornea, it has been found that lobsters, gold fish, trout, bees, tortoises, many bird
species, and also rodents such as rats and mice, are able to detect light in the UV region
(Cuthill et al., 2000).

Colour vision in non-primate mammals is a widely studied topic, and much of the
research in this field has insisted on the sometimes considerable differences between species,
often dependent on the nocturnal or diurnal nature of the animal. Although a lot of current
research is devoted to elucidating the capacity of colour perception in different animal
species, there remains a vast number of species for which little concrete data are available.
While some mammals, such as the shrew and certain squirrels, are considered to be
trichromatic, non-primate mammal colour vision is generally believed to be relatively limited.
Variations in colour perception may result 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 behaviour, certain mammals have rod-dominated retinas and many lack cones with a red-sensitive pigment, and therefore have only dichromatic colour vision. Some species lack cones completely, such as the guinea pig, and thus are totally colour blind. Bulls, despite the alleged importance of this colour for getting them excited in bull-fights, are insensitive to red. Similarly, the dichromate cat is incapable of perceiving red, with cones only sensitive to blue/indigo and to yellow/green, as found in the ferret (Calderone & Jacobs, 2003). 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). A different system has evolved in rats and mice which have excellent night vision, due to a higher number of rods than cones, but see poorly in colour although both are dichromatic. Both rat and mouse cones co-express two photopigments, one sensitive to wavelengths around 510nm and another sensitive to ultraviolet. Their visual systems, as for that of gerbils, exploit these differences to enable them to discriminate certain dichromatic colours, (Jacobs & Williams, 2007; Jacobs, Fenwick & Williams 2001; Jacobs, Williams & Fenwick, 2004; Jacobs and Deegan 2nd., 1994). Diurnal rodents and rodents which live in almost lightless conditions have been found to have similar colour vision (Williams, Calderone & Jacobs, 2005; Jacobs et al., 2003).

Sound data have confirmed the long held suspicion that colour vision in primates including humans, apes, and Old World monkeys, is better developed than in other mammals (Jacobs, 1993). In spite of data lacking on many species, primates are largely considered to be trichromatic, although variations exist (Jacobs, 1993; Jacobs, 1996; Jacobs & 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 predicts that all male New World monkeys are dichromatic while, depending on their opsin gene arrays, individual females can be either dichromatic or trichromatic (Jacobs & Deegan 2nd., 2003; 2005; Rowe & 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 vertebrates such as certain birds, aquatic creatures, and certain insects including butterflies and honeybees. Birds vary according to species in their capacity to perceive 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 infrared end of the spectrum with a relatively high proportion of rods and are colour-blind. Raptors are bifoviate, increasing the potential number of cones, some of which are double, a phenomenon also observed in fish, amphibians, and reptiles. Fish appear to have quite well developed visual systems, comparable in some species to those of birds. Retinas with four classes of cones involved in colour perception (tetrachromatic vision) have been reported in fish (Palacios et al. 1998). Most of the latter have photoreceptors with peak sensitivities in the ultraviolet range. 95% of all known fish species seem to perceive red, yellow/green/blue, violet and UV up to 365nm. However, since sea water selectively absorbs longer wavelengths, i.e. red light, many fish living below 10 metres see poorly in the red 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).
Poralla & Neumeyer (2006) showed in behavioural experiments that there is no direct transition between green and red, but that there is yellow in-between.

Amphibians see fairly well in colour, with a maximum day vision principally in yellow and at night in green. Colour vision is also well developed in reptiles, which have tetrachromatic vision (Fleishman, Loew, and Leal 1993) with turtles able to distinguish between blue, green and orange and lizards between yellow, red, green and blue. Reptiles have genera that possess four spectral classes of cone each giving them the potential for tetrachromatic colour vision (Bowmaker, 1998).

Many insects 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 has a pentachromatic visual system, i.e., the eyes contain five different types of cones, sensitive to UV, violet, blue, green, and red wavelength peaks. The windmill butterfly 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 perceive purple but not yellow. Bees are equipped with complex compound eyes, responding to yellow/green light, blue light and ultraviolet light. An additional feature of bee vision is that they are sensitive to polarized light, but they and many other insects have evolved specializations in their photoreceptors to allow them to perceive the same colour in all directions (Wehner and Bernard, 1993).

The role of animal colours in mate choice

The choice of a sexual partner in the animal kingdom is determined in one of three distinct ways. In some species, in particular in mainly polygamous animals, the male eliminates potential rivals by chasing them away aggressively, or by active combat which can, in animals that have pronounced teeth, antlers or horns, lead to serious injuries resulting in younger males having to wait many years before having the opportunity to mate. Even certain bird species employ displays of elaborate feather patterns to aggress and chase rival males before fecundation with available females. After elimination of competitors, the female, or often a harem of females, is left with one alpha male as sexual partner by default. In addition to leaving little freedom of choice to the female of the species, the successful aggressive displays can be viewed by the female as a reflection of the most successful genes. Alternatively, a male “seduces” a potential female by parading his attributes as ornaments, which correspond to his secondary sexual characteristics. Such “nuptial” behaviour frequently leads to exaggerated display of the ornaments, which include shimmering of peacock feathers or lifting the bright blue webbed feet of the blue footed boobies of the Galapagos archipelago, well known for having inspired Darwin’s theory of evolution during his studies there in 1835. The female thus has a selective choice, based on her estimation of the “best” genes, which may be considered to reflect how impressive her potential partner’s ornaments are in terms of size and colour intensity, signalling the physical condition and immune-competence of the male. This process is frequently employed in monogamous animals and in particular in monogamous birds. The female preference to mate with males with exaggerated external ornaments may have arisen from evolutionary pressure, when a female preference for some aspect of male morphology provoked selection for males with the appropriate ornament, a possibility generally known as the sexy son hypothesis. Alternatively, genes responsible for the development of impressive ornaments or fighting ability in males may simply show off greater disease resistance, or a more efficient metabolism. This could, in terms of the good genes hypothesis, prove beneficial to their offspring. Sometimes, a reversal of roles has been observed in certain fish in mating competition, with male-male competition and intensive courtship behaviour in males switching to active courtship behaviour in females during the short breeding season (Forsgren, Amundsen, Borg & Bjelvenmark, 2004). Plasticity in sexual
mate choice behaviour has also been observed in birds during the course of the breeding season, which is accompanied by a reduced variation in the size and brilliance of ornaments. Later in the season the choice based on male ornaments is replaced by a choice based on genetic complementarity (Oh & Badyaev, 2006). Although most studies have focused exclusively on the role of female mate preferences in maintaining or promoting colour variation, a recent study (Pryke. and Griffith, 2007) highlights that both female and male components of mate choice should be taken into account. Females showed a strong preference for mates with the most elaborate sexually dimorphic traits, while males were particularly choosy, associating and pairing only with females of their own morph-type. Sometimes, even in highly coloured male and female fish, males rather than females make the choice of a sexual partner (Houde, 2001), which suggests that female ornamentation male also be sexually selected (Amundsen and Forsgren, 2001).

Animal colourations are employed for signalling presence, and are often literally flaunted, either to attract members of the same species, or to repel those of others. Both colour and ultraviolet reflectance play an important role in attempting to attract a sexual partner as well as in communicating other worthwhile information to the potential mates. This is well documented in fish (Boulcott, Walton & Braithwaite, 2005; Rick & Bakker, 2008b; Modarressie, Rick & Bakker, 2006; Sköld et al., 2008), where bioluminescence has also been shown to play a significant role (Herring, 2000). Many fish can display dramatic colour changes during courtship displays related to the degree of sexual arousal of the male. Such changes are produced in the short term by pigment redistribution within melanophores. The biological significance of structural colours was first investigated mainly in birds (for reviews see Auber, 1957; Dyck, 1976) and many more recent reports have emphasized the potential biological role of both visible colour, UV reflectance and fluorescence in avian communication (Andersson & Amundsen, 1997; Hunt et al., 1999, 2001; Örnborg et al., 2002; Siitari et al., 2002; Pearn et al., 2003; and for recent reviews see Hill and McGraw, 2006). Male individuals of various avian species exhibit conspicuous colours on their feathers evolved by sexual selection driven by mating preferences (Andersson, 1994; Darwin, 1871; Solís, et al., 2008). In Males of the cooperative breeding azure-winged magpies (Cyanopica cyanus) where only a fraction of the male population access the breeding status display conspicuous blue plumage coloration, males that became breeders had a more brilliant and saturated blue coloration and showed a more violet hue. The additional capacity of avian ornaments to reflect UV plays an important role during sexual displays (Hausmann et al., 2003; Hunt et al., 2001; Andersson and Amundsen, 1997; Bennett et al., 1997; Finger, Burkhardt & Dyck, 1992; Pearn, Bennett and Cuthill, 2003; Siitari et al., 2002; Parker, 1995; Bennett, Cuthill, Partridge & Lunau, 1997). Experimental alterations of the UV component in plumage have been shown to significantly affect sexual signals in many bird species (Maier & Bowmaker 1993; Bennett et al. 1996, 1997; Andersson & Amundsen 1997; Hunt et al. 1997, 1998, 1999).

Ultraviolet reflections have been shown to be important in determining mates not only in birds but in many other species. For instance, while male spiders possess complex iridescent markings, some of which are structural (Land et al. 2007) and reflect in the UV range, a property that is variable and changes with age and feeding patterns, females do not. While female green fluorescence is important in attracting males, UV appears to influence female choice in mating behaviour (Matthew, Lim, Li, & Daiqin, 2008). Ultraviolet reflection from structural colours has been studied in many other species such as butterflies (Ghiradella et al., 1972), spiders, and fish (Smith et al., 2002). Sometimes male coloured traits determine female choice, which may have in some species evolved in parallel with male preferences (Houde and, Endler, 1990). In particular, hormone dependent colour changes during nuptial displays are also common in fish (Sköld et al., 2008).
King Penguins (*Aptenodytes patagonicus*) display highly coloured ornaments, notably the yellow/orange breast and auricular feathers and the two orange/pink UV reflecting beak horns on each side of the beak and these have been suggested to be implicated in mate choice (Dresp et al., 2005; Dresp-Langley & Langley, 2010). It is significant that during courtship displays King Penguins flaunt their beak ornaments when encountering potential partners, which is reminiscent of the shimmering iridescent display of peacocks. This may explain why the King Penguin beak, too, looks so attractive and “sexy” (Carmichael, 2007). The fact that the horn is both ultraviolet and also orange-pink in colour increases the signal, as more than a single type of photoreceptor in the observer would be activated and its perception would also be heightened by a contrast effect since the tissue surrounding the horn is black. In addition, the multiplicity of microstructures with slightly different orientations producing the UV reflectance spreads both the wavelength and also the angle over which it is reflected, producing a more easily perceptible signal. Such UV reflecting ornaments are absent in sexually immature individuals, often called juveniles (Jouventin et al., 2005; Massaro, Lloyd & Darby, 2003; Dresp, unpublished results). Apart from the function of visually attracting potential mates, ornamental colours can also communicate information about the general fitness of individuals, in particular whether an individual is well nourished and healthy, providing additional criteria particularly for males in attracting female partners (McGraw et al., 2002). In addition to pure survival, mate selection, breeding performance, fecundity and growth, colour traits appear to be associated in various ways with immunity (Hamilton & Zuk, 1982; Svensson, Raberg, Koch, & Hasselquist, 1998; Lochmiller & Deerenberg, 2000; Nolan, Dobson, Dresp, & Jouventin, 2006).

**Colour in modern visual art**

Poorly saturated colors, since they are closer to a pure grey than intense hues, appear less “colorful” than strongly saturated colors, yet, they still contain hue information. In the visual arts, color saturation is widely exploited as a measure for balancing opponent or conflicting sensations and moods. In the 19th century, at the dawn of abstract expressionism, painters such as Turner (especially in his later works) effectively used color to suggest what should be nearer or further away to the observer in the painting, relying on chromatic brightness and saturation to express and balance figure and ground, moods, and other qualia (Fig 4). The earlier Renaissance painters had preferentially resorted to chiaroscuro and geometric cues to aerial perspective using a limited chromatic range to create landscape depth and figure-ground effects. Later in the evolution of visual art, modern architects and designers like Vasarely effectively manipulated color saturation in combination with planar shape geometry to play with foreground and background effects in a complex and abstract manner (Fig 4), illustrating how chromatic luminance, saturation, and shape can be combined to elicit powerful visual sensations suggesting three-dimensional structure. While contemporary visual artists tend to share the strong belief that saturation is a key medium for creating perceptual structure, perceptual science has not yet clarified the functional contribution of color saturation to perceptual organization. Imagine the simplest possible two-dimensional image with no more than two adjacent surface regions. When there is a difference in brightness between the two adjacent regions, they can constitute a figure-ground reversible pattern, where the region seen as figure is perceived in front of the region seen as ground. This difference in perceived depth between the two regions increases as their difference in brightness increases. The observation originally stems from an experiment by Egusa (1977), who presented two different achromatic surfaces, viewed through a small aperture, on a black screen. The surface on the right was of one of three different shades of grey, and the one on the left was either white or black. Observers made judgments regarding the apparent depth of these surfaces in terms of which of the two appeared nearer. The results of this study
were the first to reveal a systematic relation between perceived relative depth and brightness differences between adjacent surface regions, in that increasing the brightness difference increased the perceived depth separation in every observer. Whether the brighter or the darker of the two test surfaces appeared nearer differed from observer to observer. Subsequently, Egusa (1983) examined the effects of brightness, hue, and saturation on the perceived depth between two adjacent regions. Again, the stimuli consisted of two hemifields, either both achromatic, one achromatic the other chromatic, or of two different colors. Subjects were asked to state which hemifield appeared nearer, and to put a number on the perceived depth between (depth magnitude estimation). When both hemifields were achromatic, the perceived depth was found to increase with increasing brightness difference. Again, some subjects tended to judge the brighter side nearer, others the darker side. With the achromatic-chromatic combination, there were no differences in perceived depth among three hue conditions, whilst with the chromatic-chromatic combination the perceived depth depended on the hue combination. In terms of decreasing frequency of 'nearer' judgments, the hue order was red, green, and blue. When two chromatic hemifields differed in saturation only, the perceived depth increased with increasing difference in saturation, and whether the more saturated or the less saturated side was judged nearer depended on hue. Thus, the figure-ground differentiation between two adjacent chromatic regions in the visual field is jointly determined by brightness, hue and saturation, affecting the perceived distance of a given region from the observer (e.g. Dresp, Lorenceau, and Bonnet, 1990; Dresp and Bonnet, 1991; Dresp, 1992, Dresp, 1993; Dresp and Bonnet, 1993; Dresp and Bonnet, 1995; Dresp, Salvano-Pardieu, and Bonnet (1996); Dresp, 1997; Dresp, 1998; Wehrhahn and Dresp, 1998; Dresp, 1999). Since Leonardo da Vinci’s *Trattato della Pittura* (1651) mentioning luminance contrast as a cue to pictorial depth, perceptual science has confirmed that it directly determines what will be seen as nearer or further away in two-dimensional visual configurations and images (Mount et al 1956; Farnè, 1977; Rohaly and Wilson, 1993; O’Shea, Blackburn and Ono, 1994; Dresp and Grossberg, 1997, 1999; Dresp and Fischer, 2001; Dresp and Langley, 2005; Dresp, Durand and Grossberg, 2002; Guibal and Dresp, 2004; Dresp and Durup, 2009; Dresp-Langley & Reeves, 2012, 2014; Dresp-Langley, 2015, Dresp-Langley and Grossberg, 2016). These observations, however, do not cover possible interactions between hue, luminance contrast, and saturation on the figure-ground organization of color adjacent to, or surrounded by, achromatic fields or grey tones of varying luminance intensity. Reasons why such effects were not actively searched for may relate to the fact that chromatic and achromatic pathways in the visual brain are widely believed to be independent (e.g. Page & Crognale, 2005), presuming no functional interaction between chromatic and achromatic signals in the human perceptual system.
Figures

Figure 1
Figure 2
Figure 3
Figure and Table Legends

Figure 1: Male and female ducks, illustrating both size and colour sexual dimorphism. The larger male’s highly coloured feather patterns, partly due to structural colour, contrast with the plain melanin pigmentary colours of the females.

Figure 2: Coleman's shrimp camouflaged its natural environment. Colourful biological patternings of this kind have inspired many visual artists.

Figure 3: King Penguins in the Baie du Marin of the Crozet archipelago in the sub-Antarctic, illustrating the pronounced carotenoid based colourful auricular and breast patches and the structural colour based beak horns. Note the variations in hue and intensity of the beak horn between individuals. One adolescent penguin (extreme right) has breast and head carotenoid colourations, but is devoid of the beak horn ornament, which is only present in sexually mature males and females.

Figure 4: The Hungarian architect and visual artist Victor Vasarely successfully exploited colour and shape in his work, as shown in this example here, which he entitled "VEGA".
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