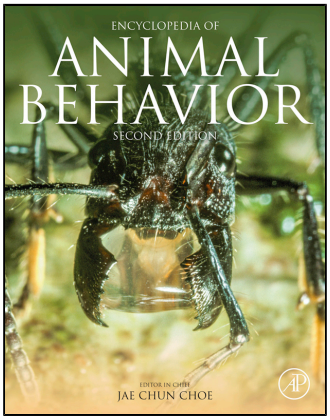

From Morehouse, N.I., Outomuro, D. (2019). Visual Signals Using Incident Light. In: Choe, J.C. (Ed.), Encyclopedia of Animal Behavior, (2nd ed.). vol. 1, pp. 500–507.
Elsevier, Academic Press.
ISBN: 9780128132517

Visual Signals Using Incident Light

Nathan I Morehouse and David Outomuro, University of Cincinnati, Cincinnati, OH, United States

Abstract

Organisms, from animals to plants to bacteria, use incident light to communicate with others. They do so using pigments and structures that reflect, refract, scatter or absorb light, thereby changing their appearance. In this article, we review the optical strategies organisms use to produce visual signals. We describe common pigments and nanostructures found in organismal tissues, highlighting how these contribute to visual signal production across the tree of life. Visual signals can also vary across space and time, so we describe how these basic elements are combined to the create complex patterns and displays often used in communication. We conclude by briefly discussing ongoing efforts to understand the evolution of visual signals.

Keywords

Biophotonics; Communication; Iridescence; Nanostructures; Optics; Pigmentary coloration; Sensory ecology; Structural coloration; Visual displays; Visual signals

Visual signals are a ubiquitous feature of life on earth. Plants, animals, fungi, even protists and bacteria use incident light to communicate with other organisms. They do so using properties of their body surfaces, including pigments and nanostructures, that alter the path of incoming light through reflection, refraction, scattering, or absorption. The result is the carnival of colors and patterns we find in a busy coral reef or an alpine meadow in full bloom. But why do so many organisms use light to communicate? The answer is two-fold. First, in many terrestrial and aquatic habitats, light provides an abundant source of information about an organism's surroundings. To capitalize on this valuable information source, animals have repeatedly evolved visual systems to see the directionality and properties of incoming light, including brightness, color, and polarization (Land and Nilsson, 2012). Thus, most animals are able to perceive visual signals. Second, light offers a number of advantages for communication. It transmits information faster than other signaling modalities such as chemical signals. In most environments, it also provides information from greater distances than modalities such as mechanoreception. This larger 'active space' allows visually guided organisms to avoid threats at greater distances, plot trajectories toward objects of interest, and communicate rapidly with each other (Cronin *et al.*, 2014).

But what are visual signals and how are they produced? The aim of this article is to describe some of the common ways in which organisms use incident light to communicate. One critical thing to keep in mind is that visual signals are shaped by the visual abilities of their audiences. These audiences are often composed of both intended receivers (e.g., prospective mates or pollinators) and unintended receivers (e.g., predators or parasites). In addition, the quality of available light and the properties of background objects can shape which visual signals work most effectively in a specific environment (Cronin *et al.*, 2014). Thus, the visual ecology of focal organisms can help to explain why organisms use some types of visual signals and not others. Animal taxa with sophisticated color vision, such as birds or butterflies, often make more extensive use of color in their communicatory displays, whereas organisms like cephalopods, which are typically colorblind but sensitive to polarization, emphasize achromatic patterns and polarization during signaling (Marshall *et al.*, 2014). Nocturnal animals tend to make more limited use of visual signals, or emphasize bright, achromatic patterns. Sometimes, organisms even use visual signals to which they themselves are blind. A trivial example is floral coloration, a visual signal to which pollinators are quite sensitive but flowering plants are obviously not. However, similar examples can also be observed in the animal kingdom. For example, nudibranch molluscs often use bright colors they cannot perceive to warn fish predators of their toxicity (Winters *et al.*, 2017).

We begin this article by describing how visuals signals are produced via interactions with light. We then discuss visual signal complexity across space and time. We conclude by highlighting key evolutionary considerations and perspectives on future work.

Interactions With Light

Animals produce visual signals via selective reflection, refraction, absorption, and/or scattering of incident light. In some unusual instances, animals may also selectively absorb and re-radiate light in a phenomenon called fluorescence, a topic which is the subject of another article in this series. The result is differences across the body surface in the amount and quality of light that travels back to the eyes of receivers. Body surfaces that reflect (or fluoresce) some wavelengths of light but not others produce signals that can be perceived as colors by observers, whereas those that reflect more evenly across the range of wavelengths visible to receivers produce achromatic signals such as whites, greys, or blacks. In both instances, these signals are produced by a combination of two mechanisms: absorption of light via pigments and reflection/scattering of light by nanostructures. Although these so-called 'pigmentary' and 'structural' mechanisms are often described as being distinct from each other, we now know that most visual signals involve contributions of both (Shawkey *et al.*, 2009; Shawkey and D'Alba, 2017). For example, pigmentary colors like the vivid yellows of American goldfinches (*Carduelis tristis*, **Fig. 1**) rely on both wavelength-selective absorption by carotenoid pigments and the light

Encyclopedia of Animal Behavior, Second Edition, 2019, 500–507

Fig. 1 An example of the huge diversity of color signals across animal, plants and fungi. From left to right, and top to bottom: Male American goldfinch, whose bright yellow color is due to carotenoids and the structure of the feather tissues; male *Morpho* sp. butterfly, with iridescent blue scales thanks to a multi-layer thin film and melanin; Bengal tiger, showing rufous fur colored by phaeomelanin and black fur colored by eumelanin; fly agaric, whose cap red color is based on betalains; eggs of the American robin, with a blue coloration due to bile pigments; and the purple base of the petals of *Hibiscus trionum*, the result of a diffraction grating. Photo credits, in the same order: J. Benson, B. Spragg, J. Jones, D. Reber and F.D. Richards.

scattering structural properties of associated feather tissues (Shawkey and Hill, 2005). Similarly, even in classic examples of structural coloration, pigments play an important role. For example, color saturation of the 'structural' blues of *Morpho* butterflies (**Fig. 1**) is improved by the presence of melanin pigments, which absorb stray light (Giraldo and Stavenga, 2016).

Below, we survey the common pigmentary and structural mechanisms used by animals to produce visual signals. New discoveries are being made every year in the study of animal coloration, and much remains unknown. Nevertheless, this primer should offer a starting point for researchers interested in embarking on their own studies of visual signals in the living world.

Pigmentary Coloration

Pigments produce colors and patterns by absorbing incident light. Their contribution is therefore subtractive, meaning they are very rarely responsible for reflecting the light that returns to a receiver's eye (but see Morehouse *et al.*, 2007). Instead, to create colors, pigments must be embedded in tissues that scatter light such as the complex tissues of feather barbs (Hill and McGraw, 2006) or the reflective layers of amphibian skin (Grether *et al.*, 2004). Thus, pigment-based visual signals are visible to receivers thanks to the backscattering of photons that escape pigment absorption.

Pigments absorb light by shifting valence electrons from a ground state to an excited state, with the energy difference between these two states being equal to the energy of the absorbed photon. This energy difference is dictated by molecular structure, with conjugated double bonds (e.g., C=C, C=O, C=N, and N=N) playing an important role in lowering the required energy into the range offered by photons of visible light. Thus, pigments often exhibit a series of conjugated double bonds, either in rings or long chains. Longer conjugated systems require less energy for valence electron excitation, allowing them to absorb longer wavelength photons, which contain less energy. For example, lycopene, the carotenoid responsible for the color of ripe tomatoes, has eleven conjugated double bonds, and is therefore able to absorb lower energy blue and green photons, making it appear red. In contrast, the carotenoid pigment retinol (vitamin A) has a chain of five conjugated double bonds, and strongly absorbs high energy violet photons, appearing yellow in solution. Functional groups such as $-NH_2$ and –Cl can also play important roles as electron donors or acceptors. Once a photon is absorbed, its energy is either re-radiated as heat or fluoresced as another photon of lower energy (and longer wavelength), allowing the pigment's electrons to return to their ground state. Photonic energy absorbed and re-radiated as heat can have a role in thermoregulation in terrestrial animals, making darker pigments often advantageous at colder latitudes or altitudes.

Plants, animals, and other organisms use a wide variety of pigments to color their bodies. Some of these pigments are synthesized by organisms across the tree of life, including melanins, tetrapyrroles, pterines, purines, and quinones (Fox, 1976). Others are only synthesized by one type of organism, but extensively used by others. For example, carotenoids and flavonoids are synthesized

by plants and fungi, but are regularly used in the visual signals of animals that derive them from diet (Hill and McGraw, 2006; Kayser, 1985). Yet other classes of pigments are highly restricted in their synthesis and use, including psittacofulvins (restricted to parrots, Hill and McGraw, 2006) and papiliochromes (only known from papilionid butterflies, Kayser, 1985).

Here, we briefly describe some of the most common pigment types used in visual signaling. We begin with melanins, which are the most common and yet least colorful pigments in the living world. Rather than producing vivid colors, melanins absorb more evenly across all visible wavelengths. This makes them responsible for blacks, browns, and greys, particularly in the animal kingdom. There are two main types of melanins: eumelanins, which produce blacks and greys, and phaeomelanins, which produce rufous and rust browns. For example, the distinctive rufous and black striped appearance of Bengal tigers (**Fig. 1**) is the product of phaeomelanin (rufous) and eumelanin (black stripes) deposited in the tiger's fur. Melanins are synthesized from the amino acid tyrosine and deposited as long polymers in skin tissues or integumental structures such as feathers, hairs or scales. In birds and mammals, specialized epidermal cells called melanocytes are responsible for melanin synthesis, whereas in other vertebrates, melanins are often produced by melanophores in the dermis (Fox, 1976). In arthropods, including insects and spiders, melanins are typically synthesized in the dermis and deposited into developing cuticular structures (True, 2003). In addition to their role in visual signaling, melanins provide a number of other functions, including mechanical toughening of tissues, photoprotection, antioxidant protection and thermoregulation (McGraw, 2003). In arthropods, they also play a critical role in immune defense through their involvement in the encapsulation response (True, 2003).

Carotenoids are another widespread pigment class, perhaps second in ubiquity only to melanins. Although these tetraterpenoid pigments are synthesized by plants and fungi, they are also found coloring the tissues of many animals, which must sequester them from diet. The one known exception to this phylogenetic pattern is carotenoid synthesis by pea aphids (*Acyrthosiphon pisum*), an ability these animals appear to have acquired via horizontal gene transfer from fungi (Moran and Jarvik, 2010). Over 700 carotenoids have been identified, and in plants, these pigments often play a role in red, orange, and yellow signals used to attract insect pollinators to flowers or frugivores to fruits (Willson and Whelan, 1990; Grotewold, 2006). In animals, they are likewise involved in many of the red, orange, and yellow colors that decorate feathers, scales, and skin. Binding of carotenoids to accessory proteins expands the range of associated colors to include purples and blues, and in many insects, green body colors are the product of combinations of blue bile pigments and yellow carotenoids (Kayser, 1985). Because animals cannot synthesize carotenoids, they must be transported from the digestive system to their final destination, typically by lipoproteins due to their lipophilic nature. Along the way, they are often metabolically modified and can interact with a number of other biological processes, including free-radical scavenging and immune defense, making them important modulators of animal health.

In plants and fungi, two additional pigment classes are commonly involved in visual signaling: flavonoids and betalains (Willson and Whelan, 1990; Grotewold, 2006). These pigments are responsible for color signals used by flowers, fruits, and fruiting bodies to communicate with animals, including reds, oranges, yellows, whites, and even purples and blues. Flavonoids are a diverse group of biochemicals synthesized from phenylalanine and tyrosine, and include important subgroups such as anthocyanins (from the Greek *anthos* and *kyaneos* meaning "flower" and "dark blue", responsible for blues, purples, and magentas of many flowers and fruits) and anthoxanthins (from Greek *anthos* and *xanthós* meaning "flower" and "yellow", responsible for creamy whites and yellows of many floral parts). Betalains are also synthesized from tyrosine, but are chemically distinct from flavonoids and are never expressed in the same plants. Instead, these pigments produce the deep reds of flowers and other tissues in the plant family Caryophyllales (including beets, where they were first described and from which they derive their name). In fungi, betalains are responsible for the vivid reds of mushroom fruiting bodies such as the aposematic visual signals of fly agaric caps (*Amanita muscaria*, **Fig. 1**; Stintzing and Schliemann, 2007). While synthesis of these two pigment classes is restricted to plants and fungi, diet-derived flavonoids are known to be used in insect coloration, including butterfly wing colors (Kayser, 1985). Their participation in other physiological functions is not well characterized, although both exhibit antioxidant properties, a common feature of many pigments.

Another diverse and widely distributed pigment class is the tetrapyrroles, including porphyrins (where the four pyrrole-based *N*-heterocyclic rings form a larger macrocyclic ring) and bile pigments (where the pyrrole rings form an open chain). These pigments are unusual in that they produce a range of colors not typically found in other pigment classes, including blue and green. Porphyrins often bind ions in the interior of their macrocycle, including iron in the home group of hemoglobin, and magnesium in the center of the chlorin section of chlorophyll. These pigments, including hemoglobin and chlorophyll, are often responsible for the colors of live tissues used in animal and plant signals, such as the red of a rooster's wattle (hemoglobin-based, Hill and McGraw, 2006) or the green colors of unripe fruits and some flowers (Grotewold, 2006). Unusual classes of porphyrins can also be found in bird feathers, such as the metalloporphyrins turacin (red) and turacoverdin (green) of African turacos (Hill and McGraw, 2006). Bile pigments, including bilins and biliverdin, are used in a number of blue and green animal colors, from robin's egg blue (**Fig. 1**) to the wing colors of butterflies in the genus *Graphium* (Hill and McGraw, 2006; Kayser, 1985). Connections to other physiological functions are obvious for many porphyrins (due to their role in respiration and photosynthesis), but remain poorly understood for bile pigments.

Pterins are heterocyclic compounds composed of a pyrazine ring and a pyrimidine ring. They are found in nearly all plant and animal tissues, but their use as colorants is largely restricted to insects and some vertebrates. In insects, they are widely used to color butterfly wings, from which they derive their name (from the Greek *pteron* for "wing"). In these insects, they are deposited as small pigment granules that simultaneously absorb short wavelength light and scatter long wavelength light, resulting in the vivid reds, oranges, yellows, and whites characteristic of the butterfly family Coliadinae (Morehouse *et al.*, 2007). They have also been described from the eyes of flies, including *Drosophila* (e.g., drosopterin), and the bodies of Hemiptera (Kayser, 1985). In vertebrates, they participate in the body coloration of fish, amphibians, and reptiles (Grether *et al.*, 2001, 2004) and the iris colors of many birds (Hill and McGraw, 2006). Pterins are synthesized from guanosine triphosphate (GTP) and, due to their high nitrogen content, can

be expensive to produce for nitrogen-limited herbivores. Intriguingly, pterins are known cofactors in the conversion of tyrosine to dopa during melanin synthesis, a biochemical connection which may help to explain why pterins and melanins are often found together in animal color patterns (Kayser, 1985).

Ommochromes and their precursor 3-hydroxykynurenine are widespread animal pigments found in the body tissues of insects, spiders, crustaceans and cephalopods (Kayser, 1985; Van Den Branden and Decleir, 1976). These red, yellow, cream, or brown pigments were first described from insect compound eyes, where they are found in the facets or ommatidia, from which they derive their name. Although their primary function in this context is to tune visual sensitivities by filtering incoming light, they also alter the outward appearance of these compound eyes. Ommochromes are also found in the wing tissues of butterflies, the integumental colors of the odonates, phasmids, and lepidopteran larvae, and the chromatophores of cephalopods. Ommochromes are synthesized from tryptophan, and in insects, these pigments may serve as a convenient way of removing excess tryptophan, an amino acid that can rise to toxic concentrations during metamorphic transitions.

Several other pigment classes are worth mentioning briefly here. Purines such as uric acid and guanine, play an important role in the visual signals of fish, where they are often used to reflect or scatter light from skin or scales (Land, 1972). Anthraquinones and aphins impart, respectively, violet to green or red to purple colors in homopteran insects (e.g., aphids, for which aphins are named, Kayser, 1985). Papiliochromes are yellow to reddish-brown pigments restricted to the scales of swallowtail butterflies (Kayser, 1985). Finally, the psittacofulvins are a pigment class unique to parrots, where they produce a range of colors including red, pink, orange, and yellow (Hill and McGraw, 2006).

Structural Coloration

Structural colors are the result of interactions between light and tiny periodic structures called nano- or photonic structures. In contrast to pigmentary colors, structural colors rely on reflection rather than absorption for their spectral properties. As a result, they can be considerably brighter than pigmentary colors, and are responsible for some of the most vivid and visually arresting signals in the living world. Some structural colors exhibit a property called iridescence, which means that they change in color and brightness depending on their angle of view. Others lack iridescence, but may exhibit other unusual properties such as circular polarization. Yet others reduce light reflection from surfaces, making these surfaces more transparent.

One concept fundamental to understanding structural coloration is the refractive index (RI) of nanostructure materials. RI is a measure of how light propagates through a material, and is related to the speed of light through a given material compared to the speed of light in a vacuum (i.e., $RI=c/v$ where c is the speed of light in a vacuum, and v is the speed of light in a given material). Biological materials differ in their RI, ranging from $\sim$1.33 for water-filled elements to $>$2.0 for heavily pigmented structures. RI determines two phenomena relevant to structural coloration: the amount of light reflected from the interface between two media of differing RIs (i.e., the greater the difference in RI, the more light is reflected from the interface), and the extent to which the non-reflected light is bent via refraction. Many common biological materials exhibit RIs higher than their surrounding media (e.g., when surrounded by air or water, with RIs of $\sim$1 and 1.33 respectively), resulting in light reflection from their surfaces. For example, chitin, a common structural molecule in arthropod exoskeletons, has an RI of roughly 1.56, although this number can change depending on other compounds embedded in the chitin matrix. Keratin is a common structural molecule in many vertebrate integumentary structures such as feathers or scales, and its RI has been estimated in the range of 1.50–1.55. Pigments, when embedded in tissues, typically raise RI. For example, chitin matrices containing melanin, and pterin granules in butterfly wing scales, can exhibit RIs exceeding 2.0 (Shawkey *et al.*, 2009; Wilts *et al.*, 2016).

The optical properties of nanostructures are determined by the size and periodicity of the interfaces they present to incoming light. When these interfaces are randomly positioned but of appropriate size, light is incoherently scattered, resulting in spectrally broadband and non-iridescent reflection of light. Such incoherent scattering is found across the living world, from white feathers (incoherent scattering from the spongy layer of feather barbules) to the dusty pruinescence of dragonfly abdomens, blueberries, and mushroom caps. As the spatial arrangement of scattering surfaces becomes increasingly ordered, light can interact with nanostructured tissues "coherently", meaning that phase interactions between light reflected from different surfaces leads to constructive and destructive interference of different wavelengths. The result is structural coloration, the properties of which are determined by the RI of the nanostructure materials and the periodicity of interfaces.

The simplest form of a colored nanostructure is a single thin film suspended in a medium of lower refractive index (e.g., air or water), the biological equivalent of a soap bubble. For such structures, some proportion of the incident light is reflected at the structure's surface, with the remainder being transmitted into the structure where it is bent by refraction. The latter transmitted light then encounters the film's lower surface where a proportion of its photons are again reflected. The photons reflected from these two surfaces (upper and lower) interact as they leave the structure, engaging in constructive or destructive interference depending on their phase. Light reflected from the upper surface undergoes a 180° phase shift because this interface is from a lower RI to a higher RI, whereas light reflected from the lower surface does not experience a phase shift because this lower interface represents a transition from a higher RI to a lower RI. For constructive interference to take place between these two sources of reflected light upon leaving the nanostructure, the photons must be in phase with each other. Thus, the photons that transmit through the upper surface and reflect from the lower interface must travel the optical distance of half a wavelength during their complete transit of the film in order to be in phase with those reflected from the upper surface. These conditions are met when the film itself presents an optical distance of one quarter wavelength between the two surfaces, leading to these structures being called "quarter-wavelength" thin films. The resulting colors of such thin films are determined by which wavelengths emerge in phase with each other, and are therefore

constructively interfered, and which wavelengths are out of phase, and are therefore destructively interfered. Single, quarter-wavelength thin films are common, and contribute to the structural coloration of, for example, butterfly wing scales, which often have chitinous basal lamina of the appropriate thickness to act as simple thin films.

A common variation on this single thin film system is thin films underlain by a layer of higher refractive index (e.g., melanized chitin). Such thin films are similar to quarter-wavelength thin films with one important distinction: light reflected from the lower surface experiences a 180° phase shift as well, as a result of that surface also being a transition from low to high RI. Thus, for light reflected from upper and lower surfaces to emerge in phase, the transmitted light must travel a full wavelength before re-emerging. This requires that these thin films be twice as thick, offering transmitted light a half-wavelength optical distance between upper and lower surfaces. These "half-wavelength" thin films are also quite common, and are found contributing to the colors of everything from bird feathers to beetle elytra (Shawkey *et al.*, 2009; Seago *et al.*, 2009).

Simple thin films are constrained in their brightness by the amount of light reflected at each of their two surfaces (typically on the order of 10% when combined). However, increases in the brightness of such thin film systems can be accomplished simply by adding more films. The result is "multi-layer" thin film systems, and these can produce nearly 100% light reflection of constructively-interfered wavelengths with as little as 8–10 films (Land, 1972). Not surprisingly, many structural colors based on multi-layer thin films use roughly this number of films and no more, suggesting that once maximal reflectance is achieved, selection against the weight and material cost of additional films prevents further elaboration. Multi-layer thin films extremely common, being found in everything from the vivid blues of *Morpho* butterflies (**Fig. 1**) to the gorgets of hummingbirds (Shawkey *et al.*, 2009; Vukusic *et al.*, 1999).

Thin film systems are periodic in only one dimension, and this leads them to be highly iridescent. The conditions for constructive interference of a given wavelength are only met for a specific geometry of incident light and view. As the angle between incident light and viewer changes, the distance that photons travel through the structure changes, leading to a wavelength shift in the color of constructively interfered light. The result is colors that change dramatically with shifts in the position of the structure. Eventually, the angle becomes too great for the thin film system to reflect visible light, and the colors disappear entirely. Thus, many thin film colors appear to flash on and off when displayed by moving animals (Vukusic *et al.*, 2001). While this "flashiness" may sometimes be part of the desired optical effect of the visual signal (e.g., Rutowski *et al.*, 2007), in other instances, such iridescence may be undesirable due to the limitations it imposes on where in space a signal is visible. Reductions in iridescence can be achieved by increasing the number of dimensions in which a nanostructure is periodic. Thin films can thus be replaced by 2-dimensional arrays of rods or even 3-dimensionally periodic photonic crystals. Although such nanostructures operate on the same principles described above, they can consistently reflect a certain wavelength range with reduced or no influence of the direction of incident light or viewer. The result is equally vivid but non-iridescent structural colors such as those found in the dermal collagen arrays of bird skin (Prum and Torres, 2003) or the gyroid photonic crystals in some butterfly wing scales (Michielsen and Stavenga, 2008).

In addition to such coherently scattering nanostructures, some organisms use diffraction gratings to create colors. Diffraction gratings are formed by a series of nanoscale parallel ridges which act to spread incident light into its component wavelengths much like a prism. The result is a rainbow of colors visible to observers depending on angle of view. Colors produced by diffraction gratings have been described from beetles and flowers (**Fig. 1**; Glover and Whitney, 2010; Parker and Martini, 2014; Seago *et al.*, 2009), although their use as visual signals remains the subject of investigation and debate (Whitney *et al.*, 2009; Morehouse and Rutowski, 2009; van der Kooi *et al.*, 2015).

An unusual case of a structural phenomenon that does not lead to color is the use of nanostructures to reduce light reflection and thereby increase transparency. Such anti-reflection structures are found on the surfaces of insect wings and eyes (e.g., Stavenga *et al.*, 2006; Sun *et al.*, 2011), both of which benefit from increasing light transmission and reducing light reflection. This is accomplished by the production of small "nipples" or tapered chitin projections from the underlying integument. These nanostructures, typically much smaller in dimension than the wavelengths of visible light, create a gradient of refractive index for incoming light, thereby eliminating the RI interface between air and the underlying chitin. The result is a reduction in the number of photons reflected at the surface, photons which transmit into the underlying material instead.

One additional thing to note about structural colors is that their reflections often have distinct polarization signatures. Many thin films systems, for example, reflect plane polarized light, whereas some beetles and crustaceans can reflect circularly polarized light (Chiou *et al.*, 2008; Seago *et al.*, 2009). Because many animals are sensitive to polarized light (Marshall *et al.*, 2014), such optical effects may have functional significance in animal communication (e.g., Sweeney *et al.*, 2003). Investigations into this feature of structural coloration are ongoing (Cronin *et al.*, 2003; Calabrese *et al.*, 2014; Marshall *et al.*, 2014).

Interactions With Space

Visual signals do not occur in isolation, but rather are positioned in specific areas of an organism's body, often surrounded by other signals, and displayed against a dynamic background that varies through space and time. Thus, the visual context of these signals is critical to consider. First, the position of the signal on the body is important for an effective perception by the intended receiver. Second, the conspicuousness of the signal can be enhanced by increasing the contrast against the background, or against paired colors that together generate high visual contrast (**Fig. 2**; Endler, 1990; Doucet and Meadows, 2009). For example, male fiddler crabs have one enlarged claw bearing several distinct visual signals. Males wave their enlarged claws to attract females. The claw areas exposed during waving are more conspicuous against the sky, whereas the areas exposed during rest are more conspicuous against

Fig. 2 Three stages of the courtship display of a male peacock jumping spider *Maratus speciosus*. Note the conspicuous complex colored patterns displayed on the dorsal side of the abdomen, and only exposed during certain stages of the courtship. Photo credit: J. Otto.

the substrate (Cummings *et al.*, 2008). This example illustrates how signals evolve based on where they are located on the organism, and against which background are displayed.

Visual signals are often combined into patterns, which represent a complex visual signal that functions as a whole (e.g., **Fig. 2**), providing information on not only color, but also luminance, size, shape, and the pattern itself (Endler, 1978, 2012). Such patterns play a fundamental role in the evolution of aposematism, mimicry, and crypsis.

Finally, perception of visual signal patterns is influenced by the visual acuity and viewing distance of receivers, because the receiver's visual system will combine colors whose pattern falls below the resolution limit of the eye (Barnett *et al.*, 2017). This implies that a pattern can be extremely conspicuous from a close distance (e.g., the alternate black and yellow stripes of a wasp), but may be perceived as a uniform color from long distance. As a consequence, organisms can exploit this property of the visual systems by evolving colors or patterns with dual functions: warning signals at close viewing distances and cryptic signals when viewed at greater distances.

Interactions With Time

Visual signals can vary over time with respect to content (e.g., color) and persistence (e.g., intermittent signals such as iridescent colors). Regarding content, there can be physiological or morphological color changes. Physiological color changes are reversible and short-term. A common example involving pigmentary coloration is the quick color change of cuttlefish, partially caused by active rearrangement of the pigments contained in chromatophores (**Fig. 3**). In addition, changes in the spacing between the nanostructures of structural colors can lead to changes in appearance. For instance, chameleons have a superficial layer of dermal iridophores that contain guanine nanocrystals. They can actively tune the lattice of guanine nanocrystals, leading to changes in the wavelengths that are reflected (Teyssier *et al.*, 2015).

Morphological color changes, on the other hand, are long-term and often not reversible. They occur in response to internal (e.g., hormonal titers) and external factors (e.g., temperature, humidity, social context, background color) (Vukusic and Chittka, 2013). Some examples include ontogenetic color changes in animals or changes in fruit color during ripening. Migratory locusts can

Fig. 3 A female cuttlefish (left) is courted by a male (right). Note that only the left half of the male (the side visible to the female) shows a male-like pattern, while the right half is mimicking a female-like pattern. Males can use this strategy to reduce competition from other males while courting a female. Photo credit: Culum Brown.

develop, for instance, different body coloration over their lifespan by responding hierarchically to the level of crowding, the environmental humidity and temperature, and the color of the background (a phenomenon known as homochromy, Pener and Simpson, 2009). When they are raised at low population densities, the body coloration is green if the humidity is high, but they show homochromy if the humidity is low, developing yellow, brown or grey body coloration to match the likely colors of background foliage during drought. As a consequence, the coloration of the solitary locusts is cryptic. However, when they are raised under high population densities, they develop a dirty orange color with black patterns that decrease with temperature. This coloration signals to potential predators the presence of toxic compounds in the locust gut.

A visual signal can also change in persistency in time, for example due to active behaviors or postures of the organism that maximize the conspicuousness of the signal. Some visual signals may be displayed only under certain circumstances, such as sexual displays (e.g., **Figs. 2 and 3**). Animals with iridescent body structures can display flashes of color by these structurally colored traits, thereby changing their conspicuousness based on the angles of incident light and observer (Rutowski *et al.*, 2007; Doucet and Meadows, 2009). These color "flashes" can be the basis for mating displays to potential mates or warning signals to predators. For instance, male giant helicopter damselflies have two wing patches, one white and one UV-blue iridescent (Schultz and Fincke, 2009). When the males fly, the white patch remains bright across the wing beat cycle, while the UV-blue patch is periodically extinguished. The iridescent patch thus produces a flashing signal during each wing stroke. The white patch functions as a mating signal during inter- and intrasexual interactions, while the iridescent patch may function as a beacon for potential mates across forest light gaps.

Concluding Remarks

Visual signals are tremendously diverse across and within species, and the evolutionary diversification of these traits remains a fertile area of ongoing research. These signals are very important for both intra- and interspecific behavioral contexts, where a plethora of intended and unintended receivers participate. Some of these relationships are extremely important for understanding ecosystem function: predator-prey interactions, parasite-host interactions, pollinator-flower interactions, and frugivore-fruit interactions.

We are just starting to understand the complex interactions between the evolution of visual systems and signals. Our current knowledge has established a strong and promising starting point, and has emphasized how important understanding a visual system is in order to comprehend how visual signals are perceived and how they evolve. Future efforts to understand visual signal evolution are likely to produce the greatest insights when they integrate morphological, physiological, behavioral, ecological, genetic and evolutionary approaches.

See also: **Communication:** Bioluminescent signals. **Foraging:** Aposematism as a defence against predation. **Methodology:** The Use of Playbacks in Behavioral Experiments. **Neurons and Senses:** Crabs and Their Visual World; Invertebrate Vision; Vision: Vertebrates.

References

Barnett, J.B., Cuthill, I.C., Scott-Samuel, N.E., 2017. Distance-dependent pattern blending can camouflage salient aposematic signals. Proceedings of the Royal Society of London B 284, 20170128.

Calabrese, G.M., Brady, P.C., Gruev, V., Cummings, M.E., 2014. Polarization signaling in swordtails alters female mate preference. Proceedings of the National Academy of Sciences 111, 13397–13402.

Chiou, T.H., Kleinlogel, S., Cronin, T., et al., 2008. Circular polarization vision in a stomatopod crustacean. Current Biology 18, 429–434.

Cronin, T.W., Johnsen, S., Marshall, J., Warrant, E.J., 2014. Visual Ecology. Princeton University Press, Princeton.

Cronin, T.W., Shashar, N., Caldwell, R.L., et al., 2003. Polarization vision and its role in biological signaling. Integrative and Comparative Biology 43, 549–558.

Cummings, M.E., Jordao, J.M., Cronin, T.W., Oliveira, R.F., 2008. Visual ecology of the fiddler crab, *Uca tangeri*: Effects of sex, viewer and background on conspicuousness. Animal Behaviour 75, 175–188.

Doucet, S.M., Meadows, M.G., 2009. Iridescence: A functional perspective. Journal of the Royal Society Interface 6, S115–S132.

Endler, J.A., 1978. A predator's view of animal color patterns. In: Hecht, M.K., Steere, W.C., Wallace, B. (Eds.), Evolutionary Biology. Springer, Boston.

Endler, J.A., 1990. On the measurement and classification of colour in studies of animal colour patterns. Biological Journal of the Linnean Society 41, 315–352.

Endler, J.A., 2012. A framework for analyzing colour pattern geometry: Adjacent colours. Biological Journal of the Linnean Society 107, 233–253.

Fox, D.L., 1976. Animal biochromes and structural colours. University of California Press, Berkeley.

Giraldo, M.A., Stavenga, D.G., 2016. Brilliant iridescence of *Morpho* butterfly wing scales is due to both a thin film lower lamina and a multilayered upper lamina. Journal of Comparative Physiology A 202, 381–388.

Glover, B.J., Whitney, H.M., 2010. Structural colour and iridescence in plants: The poorly studied relations of pigment colour. Annals of Botany 105, 505–511.

Grether, G.F., Hudon, J., Endler, J.A., 2001. Carotenoid scarcity, synthetic pteridine pigments and the evolution of sexual coloration in guppies (*Poecilia reticulata*). Proceedings of the Royal Society of London B 268, 1245–1253.

Grether, G.F., Kolluru, G.R., Nersissian, K., 2004. Individual colour patches as multicomponent signals. Biological Reviews 79, 583–610.

Grotewold, E., 2006. The genetics and biochemistry of floral pigments. Annual Review of Plant Biology 57, 761–780.

Hill, G.E., McGraw, K.J., 2006. Bird Coloration – Mechanisms and Measurements. Harvard University Press, London.

Kayser, H., 1985. Pigments. In: Kerkut, G.A., Gilbert, L.I. (Eds.), Comprehensive Insect Physiology, Biochemistry and Pharmacology, vol. 10. Pergamon, New York.

Land, M.F., 1972. The physics and biology of animal reflectors. Progress in Biophysics and Molecular Biology 24, 75–106.

Land, M.F., Nilsson, D.-E., 2012. Animal Eyes. Oxford University Press, Oxford.

Marshall, J., Roberts, N., Cronin, T., 2014. Polarisation signals. In: Horváth, G. (Ed.), Polarized Light and Polarization Vision in Animal Sciences. Springer, Heidelberg.
McGraw, K.J., 2003. Melanins, metals, and mate quality. Oikos 102, 402–406.
Michielsen, K., Stavenga, D.G., 2008. Gyroid cuticular structures in butterfly wing scales: Biological photonic crystals. Journal of the Royal Society Interface 5, 85–94.
Moran, N.A., Jarvik, T., 2010. Lateral transfer of genes from fungi underlies carotenoid production in aphids. Science 328, 624–627.
Morehouse, N.I., Rutowski, R.L., 2009. Comment on "Floral iridescence, produced by diffractive optics, acts as a cue for animal pollinators". Science 325, 1072.
Morehouse, N.I., Vukusic, P., Rutowski, R.L., 2007. Pterin pigment granules are responsible for both broadband light scattering and wavelength selective absorption in the wing scales of pierid butterflies. Proceedings of the Royal Society of London B 274, 359–366.
Parker, A.R., Martini, N., 2014. Diffraction gratings in caligoid (Crustacea: Copepoda) ecto-parasites of large fishes. Materials Today 1, 138–144.
Pener, M.P., Simpson, S.J., 2009. Locust phase polyphenism: An update. Advances in Insect Physiology 36, 1–272.
Prum, R.O., Torres, R., 2003. Structural colouration of avian skin: Convergent evolution of coherently scattering dermal collagen arrays. Journal of Experimental Biology 206, 2409–2429.
Rutowski, R.L., Macedonia, J.M., Merry, J.W., et al., 2007. Iridescent ultraviolet signal in the orange sulphur butterfly (*Colias eurytheme*): Spatial, temporal and spectral properties. Biological Journal of the Linnean Society 90, 349–364.
Schultz, T.D., Fincke, O.M., 2009. Structural colours create a flashing cue for sexual recognition and male quality in a Neotropical giant damselfly. Functional Ecology 23, 724–732.
Seago, A.E., Brady, P., Vigneron, J.-P., Schultz, T.D., 2009. Gold bugs and beyond: A review of iridescence and structural colour mechanisms in beetles (Coleoptera). Journal of the Royal Society Interface 5, S165–S184.
Shawkey, M.D., D'Alba, L., 2017. Interactions between colour-producing mechanisms and their effects on the integumentary colour palette. Philosophical Transactions of the Royal Society of London B 372, 20160536.
Shawkey, M.D., Hill, G.E., 2005. Carotenoids need structural colors to shine. Biology Letters 1, 121–124.
Shawkey, M.D., Morehouse, N.I., Vukusic, P., 2009. A protean palette: Color materials and mixing in birds and butterflies. Journal of the Royal Society Interface 6, S221–S231.
Stavenga, D.G., Foletti, S., Palasantzas, G., Arikawa, K., 2006. Light on the moth-eye corneal nipple array of butterflies. Journal of the Royal Society of London B 273, 661–667.
Stintzing, F., Schliemann, W., 2007. Pigments of fly agaric (*Amanita muscaria*). Zeitschrift für Naturforschung C 62, 779–785.
Sun, M., Liang, A., Zheng, Y., Watson, G.S., Watson, J.A., 2011. A study of the anti-reflection efficiency of natural nano-arrays of varying sizes. Bioinspiration & Biomimetics 6, 026003.
Sweeney, A., Jiggins, C., Johnsen, S., 2003. Insect communication: Polarized light as a butterfly mating signal. Nature 423, 31–32.
Teyssier, J., Saenko, S.V., van der Marel, D., Milinkovitch, M.C., 2015. Photonic crystals cause active colour change in chameleons. Nature Communications 6, 6368.
True, J.R., 2003. Insect melanism: The molecules matter. Trends in Ecology & Evolution 18, 640–647.
Van Den Branden, C., Decleir, W., 1976. A study of the chromatophore pigments in the skin of the cephalopod *Sepia officinalis*. Biologisch Jaarboek (Dodonaea) 44, 345–352.
van der Kooi, C.J., Dyer, A.G., Stavenga, D.G., 2015. Is floral iridescence a biologically relevant cue in plant-pollinator signaling? New Phytologist 205, 18–20.
Vukusic, P., Chittka, L., 2013. Visual signals: Color and light production. In: Chapman, R.F., Simpson, S.J., Douglas, A.E. (Eds.), The Insects: Structure and Function, fifth ed. Cambridge University Press, Cambridge.
Vukusic, P., Sambles, J.R., Lawrence, C.R., Wootton, R.J., 1999. Quantified interference and diffraction in single *Morpho* butterfly scales. Proceedings of the Royal Society of London B 266, 1403–1411.
Vukusic, P., Sambles, J.R., Lawrence, C.R., Wootton, R.J., 2001. Structural colour – Now you see it now you don't. Nature 410, 36.
Whitney, H.M., Kolle, M., Andrew, P., et al., 2009. Floral iridescence, produced by diffractive optics, acts as a cue for animal pollinators. Science 323, 130–133.
Willson, M.F., Whelan, C.J., 1990. The evolution of fruit color in fleshy-fruited plants. The American Naturalist 136, 790–809.
Wilts, B.D., Wijnen, B., Leertouwer, H.L., Steiner, U., Stavenga, D.G., 2016. Extreme refractive index wing scale beads containing dense pterin pigments cause the bright colors of pierid butterflies. Advanced Optical Materials 5, 1600879.
Winters, A.E., Green, N.F., Wilson, N.G., et al., 2017. Stabilizing selection on individual pattern elements of aposematic signals. Proceedings of the Royal Society of London B 284, 20170926.