Visual Signals

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Introduction

Visual signal studies have a history that is in part marked by the role of coloration in the design of signals. Humans have long been interested in the richness of colors in animals (e.g., butterflies, snakes, birds) and in the taxonomic differences in sensitivity to color. In this article, the focus is on the mechanisms of visual signal production and perception by the sender and the receiver, respectively, rather than on their function, which is covered in other articles. In other words, how organisms are equipped to gather, process, and react to the information presented in a visual signal is addressed. This approach can provide a framework to understand interspecific differences in visual signal production and perception.

An Informational Framework

From a sensory perspective, the costs of gathering information from a visual signal depend on the properties of the visual system, which vary between species. For instance, some species may have low visual acuity but large visual coverage (e.g., low ability to detect objects of a given size from far, but wide visual field). Thus, all else being equal, visual signals would likely be perceived best at close distances irrespective of the position of the sender relative to the eyes of the receiver. In other species with high visual acuity but low visual coverage (e.g., high ability to perceive objects of a given size from far, but narrow visual fields), receivers would be able to perceive the sender from farther away, but senders would need to display the signal in the direction of the receiver's eyesight to maximize information transfer. Therefore, differences in visual system properties could have important ecological implications, such as the positioning of senders and receivers, which could eventually affect neighbor distance, territory location, etc. Additionally, the receiver's responses to a visual signal may involve different sensory modalities: some species may respond visually, whereas others may use acoustic or chemical signals, or a combination of all of them.

Consequently, the configuration of the visual system may affect the ability to perceive and respond to signals, and the interspecific variability in the mechanisms of information gathering through the visual sensory modality may influence differences in signal shape between species.

Furthermore, we can expect that the processing of a visual signal may be associated with the existence of certain structures in the brain specialized in handling that information. The principle of proper mass specifies that the mass of neural tissue devoted to controlling a specific function will be proportional to the amount of information necessary for that function. The implication is that if the requirements of processing information increase, so would the volume of the brain regions involved.

Have You Got What It Takes to Signal Visually?

What does it take to convey information with a visual signal? The answer to this question may be more complex than simply a bright color that looks attractive or repulsive to our eyes. There are factors that can affect the design of a signal and the efficacy with which information goes from the sender to the receiver: signal properties, the relationship between visual signals and ambient light (e.g., contrast of signal in relation to background), the behavioral display of the signal by the sender, the distance to the receiver, the visual properties of the receiver, the attention level of the receiver in relation to the signal, etc. To exemplify these factors, we focus on birds because of the relatively good understanding we have of the way they produce, transmit, and detect visual signals. Examples from other taxa are also used when appropriate.

Signal Properties

There is a huge diversity in the shape and size of visual signals. The basic form is a visual stimulus set against a contrasting background. The contrasting effect can also be achieved through the *movement* of the stimulus in relation to the background. A visual stimulus could then vary from a dark patch surrounded by white plumage to a white-colored tail that is moved at a certain speed in a dim-light habitat.

One of the questions that scientists have asked is what signals are made of. In the case of bird coloration, signals can be made of chemical pigments and/or structural colors. There is a wide diversity of chemical pigments in birds (melanins, carotenoids, etc.), which lie in integumentary structures (e.g., feathers, skin, beak, etc.).

Melanin is the most common pigment in birds, responsible mostly for black, brown, rufous, and gray shades. Melanins are present for instance in the black plumage of red-winged blackbirds *Agelaius phoeniceus*, the brown dorsal feathers of Japanese quail *Coturnix japonica*, and the rufous breast plumage of Eastern bluebirds *Sialia sialis.* Melanins are produced by the animal through a process called melanogenesis. The factors affecting the costs of melanogenesis are not fully understood, but there is some evidence that the dietary availability of amino acids and minerals could influence the ability to synthesize melanins. For instance, diets supplemented with tyrosine and phenylalanine enhanced the blackness of the throat badge of house sparrows *Passer domesticus*, but did not affect the size of the badge. Steroid and nonsteroid hormones can also influence melanization; for example, house sparrows develop larger black throat badges when given testosterone. This could have effects for male signaling, as the size of the badge could be a proxy of individual quality because it indicates an individual's ability to endure the costs associated with melanization.

Carotenoids are not as abundant as melanins, but they have received more empirical attention. Carotenoids are obtained through the diet, although birds can metabolize the ingested carotenoids into other forms. Carotenoids are responsible for red, orange, and yellow hues; such as the red and yellow plumage of hairy woodpeckers *Picoides villosus*, the yellow and orange rectrix tips and red waxwing of cedar waxwing *Bombycilla cedrorum*, and the orange tarsi of mallards *Anas platyrhynchos*. Carotenoids have been involved not only as colorants but also as antioxidants, although the trade-off between these two functions is controversial. This is important because it raises the possibility that individuals may use them as indicators of individual quality. For example, house finches *Carpodacus mexicanus* that have a higher carotenoid intake tend to show a redder coloration, and this increases the degree to which females are attracted to them. In general, there seems to be stronger sexual selection on carotenoid- than on melanin-based coloration.

The role of carotenoid-based coloration in mate choice requires the high degree of specificity observed not only in the visual signal, but also in the visual sensory abilities of conspecifics. Toomey and McGraw provided evidence that the levels of carotenoids in the house finch plasma were positively correlated with carotenoid concentration in the retina of both sexes, which opens up the possibility that individuals with greater levels of carotenoids in the retinal oil droplets would be able to better distinguish subtle differences in plumage coloration.

There are other endogenously synthesized chemical pigments in birds; such as porphyrins found in the crests and wings of several Turaco species (*Tauraco* sp.); pterin found in the eyes of blackbirds, starlings, owls, etc.; and psittacofulvin found in the red, orange, and yellow plumage of parrots.

Finally, structural colors in birds are different from pigments and result from the interaction between light and the varying refractive indices of nanoscale structures in the plumage, skin, and eyes of birds. More than 150 species of birds have structural colors, the iridescent coloration of hummingbirds being a prominent example. Structural colors are responsible for the iridescent colors in a wide range of wavelengths, noniridescent blue, violet, green, UV hues, and white unpigmented feathers. However, many colored visual signals in birds are actually formed by a combination of structural mechanisms and chemical pigments. For instance, the yellow skin of the toco tucan *Ramphastos toco* is produced by a combination of collagen nanostructures and yellow carotenoids.

Visual Signals in Relation to Ambient Light

We can think of the information transmitted by a visual signal as a stream of light being reflected by some body part of the sender because of ambient light (e.g., direct or indirect sunlight that goes through clouds, vegetation, etc.). On their way to the receiver's eyes, light can be absorbed or scattered by various types of particles in the air. The light that is neither absorbed nor scattered reaches the cornea, lens, vitreous humor, and oil droplets in the photoreceptors, which filter light before hitting the visual pigments present in the cones and rods.

Two key components of visual signaling are ambient light and the visual background, which vary from habitat to habitat and in turn affect the light conditions upon which signals are transmitted and perceived. These habitat-specific differences in ambient light and background spectra can affect the design of male attraction signals (e.g., color or brightness). Ambient light and background spectra can also affect a female's ability to discriminate between signals of different quality and therefore impact the chance of mate-choice errors. This process, called sensory drive, can enhance the divergence of mating signals, and lead to reproductive isolation, and eventually speciation.

Some visual ecologists take into consideration these habitat-specific differences in ambient light not only to understand the mechanisms of signal production and perception, but also to develop models that quantify the degree of chromatic (color) and achromatic (brightness) contrast between a signal and the background. For instance, John Endler developed a model in the 1990s that has been the foundation for many studies that seek to assess the variability in signal design in relation to light conditions. Generally speaking, the model requires information on (I) irradiance, (Rb) reflectance of the background, (Rs) reflectance of the signal, (T) transmittance, and (S) sensitivity of the retinal visual pigments and oil droplets. Simplifying substantially, the model calculates two products, one for the background ($I \times Rb \times T \times S$) and one for the signal ($I \times Rs \times T \times S$), which estimate

the ability of the receiver to perceive a signal against the background. The higher the difference between the two products, the higher the contrast between the signal and the background. As a rule of thumb, more contrasting signals are those with spectral properties similar to those of the prevailing ambient light but different from those of the background. For instance, the shade under a closed forest canopy is rich in green and yellow colors as a result of light being reflected by dense vegetation. However, the shade under open woodland is rich in blue due to sunlight being less affected by vegetation. Signals in closed forests are expected to increase conspicuousness by being red or orange against the green background, whereas signals in open woodland are expected to increase conspicuousness by being blue.

This analytical approach to signal production and perception has made important contributions to our understanding of the fitness consequences of the use of signals as well as the evolution of signal design. For instance, blue tit (*Parus caeruleus*) males have a UV crown patch that they display during courtship. This crown patch shows high contrast in relation to green vegetation and brown leaf litter. Besides having colorful patches, animals can modify the visual background behaviorally to enhance plumage contrast. Golden-collared manakin (*Manacus vitellinus*) males clear vegetation from the ground to set up courts that form the visual background for their displays as females observe them from perches. Male golden plumage patches used in courtship displays have greater chromatic and brightness contrast against the cleared ground than surrounding vegetation. Increasing visual contrast is important because mating success is higher in golden-collared manakin males with brighter plumage.

A greater contrast between signal and background can also be achieved by using different heights in forested habitats, as light spectra change vertically. For instance, four species of sympatric lekking manakins living in the Amazonian forests place their leks for displays at different strata, enhancing the chromatic and achromatic contrast of their plumages against the background or color patches against their plumage. Gomez and Théry studied 40 bird species living in the canopy (green background with rich UV and blue ambient light) and understory (green/brown background with low UV light) in the French Guiana rainforest. Visual signals in these two light microhabitats seem associated with a trade-off between enhancing contrast to facilitate visual signal transmission to conspecifics and reducing contrast to decrease conspicuousness to predators or prey. For instance, rainforest birds tend to have contrasting plumage patches in different parts of the body, depending on the light conditions: patches contrasting at long wavelengths are found in chest, head, and tail in the understory, and patches contrasting at short wavelengths are found in wing and tail in the canopy. The position of these patches is related to the areas with the highest visibility toward conspecifics on a given stratum. At the same time, birds tend to have countershaded patterns, match their dorsal coloration to the background, and concentrate colorful areas on small patches in the plumage to increase crypsis.

Behavioral Display of the Signal by Sender

How can a patch of UV coloration surrounded by red plumage become more easily detected by the receiver? The answer is, by displaying the signal through movement at a frequency and at an angle in relation to ambient light that enhances detectability. For instance, painted redstarts (*Myioborus pictus*) are flush pursuers that spread their conspicuous tails and wings, move their body, and have a high-contrasting black and white plumage to trigger insect flushing behavior in the direction opposite to that of the stimulus, facilitating prey capture. Courtship displays of male peacocks (*Pavo cristatus*) appear to take advantage of light conditions. Males position themselves at a 45° to the right of the sun azimuth with the female located in front, which may enhance the iridescent coloration of the eyespots used in mate choice. Males also rattle their upper-tail feathers generating an audible sound, suggesting that this quintessential visual signal may be a multimodal signal.

Methods used to increase the visibility of a signal are also found in other vertebrates. Anole lizards (*Anolis* spp.) maintain territories by displaying head-bobs (upside-down head movements) and dewlaps (expansion of the throat fans). Males increase the rate at which they display head-bobs and dewlaps as the visual background noise from windblown vegetation increases, likely enhancing signal visibility. However, a high rate of visual displays could add costs to the sender on top of the costs of producing the signal itself (e.g., carotenoid intake, melanization, etc.). This raises the possibility of a potential trade-off between the performance (degree of movement of a visual signal) and the conspicuousness of a signal (degree of contrast between signal and background). For example, Galván found a negative association between the degree of display complexity and the proportion of unmelanized plumage in two displays used in threats and mate attraction in the black-and-white plumage of pelecaniforms (cormorants, pelicans, frigate birds, etc.). This suggests that the evolution of specialized visual signals has been affected by the costs of using different sources of signal information (degree of signal movement, signal coloration, signal shape, signal size).

Visual Acuity and Distance to the Receiver

Structurally, the difference in the size of the different components of the visual stimulus and the background has to be above the threshold of the receiver's spatial

resolving power or visual acuity. Visual acuity is the ability of a visual system to perceive fine detail, such as black stripes against a white plumage. If the visual system cannot perceive the stripes as separate at a certain distance (e.g., they are perceived as a single black area in the plumage), the efficacy of the signal drops substantially. All else being equal, the farther the signal from the receiver, the lower the chances that it will be perceived (under far distance conditions, the overall plumage color may matter more). Therefore, intra- or interspecific differences in visual acuity can have implications for patterns of spacing behavior between sender and receiver when signals are displayed. For instance, a male may wait to display until the female or a male competitor is within the threshold distance for their visual system. This could potentially affect the territory size. A butterfly with an aposematic signal may delay flashing its wings at a certain frequency until the predator is close enough to resolve the visual stimulus, which could also influence the patterns of escape behavior depending on the reaction of the predator (e.g., the butterfly may decide to flush immediately if the predator keeps approaching instead of slowing down after detecting the signal).

Visual acuity increases with eye size due to an increase in the size of the image projected onto the retina. Other factors influencing visual acuity are spacing (density) of photoreceptors, diffraction, aberration, illumination, contrast, etc. More research is necessary to assess species differences in the way these factors influence the distance at which visual displays between sender and receiver take place, and the way habitat structure reduces visibility. For instance, in open habitats, the chances that predators detect prey have been shown to increase with the predator's perch height and the spatial proximity of the perch to the prey on the horizontal plane: prey visibility declines to about 5% when a predator perches at 0.8 m high with a 20 m separation from its prey, but increases up to 40% when a predator perches at 8 m with a 120 m separation from its prey.

Properties of the Receiver's Visual System

Birds have visual systems that are quite different from that of humans, and this provides a unique opportunity to study the evolution of signal design in relation to visual properties. When a bird is head-up on the ground with its head stationary, the amount of information obtained around its head depends upon the extent of its visual field (composed of a binocular and two lateral areas), which determines its visual coverage. Importantly, visual coverage varies substantially between species (e.g., starlings tend to have narrower visual fields than ducks, **Figure 1**).

Many bird species also have at the rear of the head a blind area whose size is inversely related to visual coverage when the head is stationary. How do species with blind areas solve the problem of extending visual coverage to
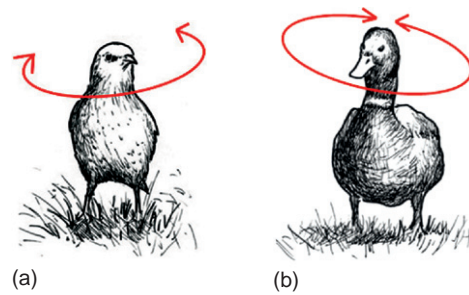
Figure 1 Schematic representation of the extend of visual coverage in (a) starlings and (b) ducks. Drawn by Gabriela Sincich.

detect a visual signal at the back of their heads? There are at least two possible strategies. First, they can move their head sideways to scan for a visual target with either lateral area. Second, in some species, they can move their eyes to enhance coverage. However, the degree of eye movement seems to be a species-specific trait that is related to the presence of contractile proteins in the extra-ocular muscles. Although the study of avian eye movement in an ecological context can be challenging because of the difficulties of recording responses in natural scenarios to meaningful visual signals, new technologies in the form of eye trackers can facilitate this task. There are other studies of head movements, that indicate that different bird species increase the speed with which they move their heads sideways when presented with a visual stimulus of interest: an unfamiliar conspecific, a predator, prey items, etc. The variability in the mechanisms of information gathering (eye movements, head movements, etc.) is an open area for future research.

In a bird that has its head steady in a head-up posture, there is a difference in visual acuity within the visual field that is influenced by optics and the density of photoreceptors and retinal ganglion cells. Areas of the retina with higher concentration of photoreceptors or retinal ganglion cells project into areas of the visual field that have higher acuity. A high-acuity area in the retina is called a fovea or area centralis (depending on whether there is a pit in the retina or not, respectively). Different species have different numbers and shapes of these high cell density areas. In some species, the lateral visual fields are subtended by areas in the retina with higher density of photoreceptors/retinal ganglion cells than the binocular visual field. The implication is that birds can have higher spatial resolution of a visual signal by placing their lateral fovea on the target of visual attention, in much the same way as humans place the center of their eyes toward a visual target. However, in birds, the placement of the fovea means that they have to move their head sideways (because their eyes are laterally placed) to get the highest visual acuity. Even raptors, which are known for their binocular vision, use their lateral areas to approach prey,

but instead of moving their heads while flying (which generates drag), they change the orientation of their flying pathways to keep either of their lateral areas focused on the prey item when raptors are about to grab the prey they switch to the binocular area.

Let us add another level of complexity to the retinal level. Avian retinas have in general four types of single cones, one type of double cone, and one type of rod. Each kind of single cone has a different type of photoreceptor (and associated oil droplet) with sensitivity to long, medium, short, or violet/ultraviolet wavelengths. The spectral sensitivity of these photoreceptors combined with the filtering properties of their associated oil droplets defines the overall spectral sensitivity of the retina. Interestingly, in birds the distribution of different types of photoreceptors varies considerably across the retina between species; species with similar cone distributions tend to share similar ecologies. For instance, double cones (generally associated with motion detection) are more abundant in the ventral sector of the retina in birds that forage on the ground, on top of water or canopies, whereas double cone abundance increases in the dorsal portion of the retina in birds that inhabit the mid-canopy. This has been interpreted as a result of the direction of predator attacks: motion detectors in the ventral portion of the retina project upwards in the visual field of species living in open habitats, whereas motion detectors in the dorsal portion of the retina project downwards in species living in closed habitats. However, further behavioral evidence is necessary to determine whether other factors (detection of conspecifics or food items) may be involved in this photoreceptor distributional pattern.

Between species, visual signals seem to be tuned to the sensory capabilities of receivers. Begging displays in altricial species include offspring showing gape and body skin colors to the parents to increase detectability among siblings. Recent research shows that gape coloration enhances visual contrasts with skin coloration in dark nest environments. Signals and receptors have evolved to increase chromatic contrast. In general, bird orders that have been shown to perceive in the UV are more likely to have UV-reflecting plumage. This is important because it opens up the possibility of sensory privacy; in other words, some species may signal in a wavelength range that is not perceived by competitors or predators. For instance, the badges of some songbird species are more conspicuous to songbirds with ultraviolet visual pigments than to raptors, which have violet visual pigments. Theoretically, this would allow for the transmission of signals involved in mate choice, while minimizing the costs related to conspicuousness to predators.

Within species, there are patterns of laterality in the visual sensory system that can affect different behaviors. For example, European starlings have a higher density of medium- and long-wavelength single cones in the left retina and double cones (associated with motion detection) in the right retina, suggesting that color discrimination would be better with the left eye, whereas motion detection with the right eye. This was later supported by a behavioral test, in which starlings showed higher performance scores and quicker learning rates with the left eyes when exposed to a visual discrimination task.

The overall implication is that the sender's sensitivity to the spectral properties of a given visual signal will vary depending on which sector the retina the receiver is using to gather the information, the spectral acuity of that retinal sector, and how it projects to the visual field. This would probably translate into changes in head and body posture that could increase the sensitivity to certain wavelengths, but decrease the sensitivity to others, which may be handy depending on the reflectance spectrum of the signal. Further studies are necessary to integrate all these visual dimensions into mechanisms of visual communication.

Processing of Visual Signals in the Receiver's Brain

This is probably one of the areas with the least amount of research attention because recording visual processing has been challenging. However, recent advances in new electrophysiological (neuronal) recordings, imaging (MRI), and immunohistochemical (early gene expression) tools have opened new windows into the brain.

In birds, there are three main visual pathways from the retina to the brain: tectofugal pathway (involving the optic tectum, nucleus rotundus of the thalamus, and ending in the endopallium in the telencephalon), thalamofugal pathway (involving the optic nucleus of the thalamus, and ending in the visual Wulst), and the accessory optic system and pretectum pathway involved in optokinetic responses (ending in the cerebellum and other preoculomotor/premotor structures). These visual pathways are relatively conserved in different vertebrate species. As outlined earlier, visual signals are expected to have an important motion component given by (1) the body and head movements of the sender, (2) the specific movement of the visual signal (e.g., visual display), and (3) the movement of the receiver in space while the sender signals, which requires the discrimination of the signal against the receiver's optic flow (a pattern of apparent motion of the surrounding elements caused by the relative motion of the receiver). Numerous studies have shown the complexity of the organization of these visual pathways whose components are involved in the detection of different aspects of motion, color, shape, luminance, looming, etc. The different brain areas involved have complex regulatory (e.g., hierarchical) mechanisms of activation and inhibition with neurons that have different degrees of spatial sensitivity, from covering a few degrees within the visual field to the entire field of view. Some of these

components, such as the optokinetic nuclei, are very sensitive to the exposure duration and novelty of visual signals in pigeons. Interestingly, visual information can trigger sensitivity in other sensory modalities: visual signals in a mate-choice context can affect the auditory parts of the brain in a song bird, which underscores that certain signals have multisensory nature.

The relationship between visual displays of ecological relevance (e.g., mating, avoidance of brightly colored prey, etc.) and the visual pathways in the brain needs more multidisciplinary attention. The principle of proper mass provides a framework to assess the volume of areas in the brain in relation to the information processing needs within and between species. For instance, we can expect that females may have larger brain areas involved in visual processing to discriminate male visual displays. Nevertheless, the main problem with this potentially fruitful area of research is that we still know little about which specific areas involved in the three visual pathways are associated with the different types of ecologically significant visual signals. Identifying these areas seems a good starting point, as overall brain size may not be a good indicator of visual signal processing in some contexts. For instance, waterfowl show sexual dimorphism in various morphological characters as a result of sexual selection; however, sexes do not differ in overall brain size.

Visual information processing in the brain has been proposed to have an important role in the social brain hypothesis, by which the large brain size of primates is explained as a result of the information loads that need to be processed while living in large and socially complex societies, primarily when it comes to establishing relationships between pairs of individuals. Some authors suggested that the extra-information load is the result of specialized mechanisms of visual information gathering (e.g., facial expression, gaze direction, etc.), which would lead to enlarged visual processing centers in the brain. Actually, the volume of and the number of neurons in the parvocellular layer of the lateral geniculate nucleus (involved in the analysis of fine visual detail and color) was found to be associated with group size in 14 primate species in a phylogenetically controlled analysis.

The evidence supporting the social brain hypothesis in birds (e.g., relationship between group size and brain size) is controversial. Nevertheless, birds have been shown to have specialized mechanisms of social visual information gathering, such as gaze direction. Furthermore, differences in the early gene expression of some areas in the brain (extended medial amygdala, ventrolateral septum, anterior hypothalamus, and lateral subdivision of the ventromedial hypothalamus) associated with social stress, arousal, avoidance, and dominance have been used to explain differences between territorial and social species. Social bird species have also been found to have whiter plumage than nonsocial species, supporting the idea that visual signals may be important to maintain group cohesion in social birds. Yet, no studies have assessed in a comparative framework the association between specialized visual areas in the brain and measures of (1) sociality (group size, neighbor distance), (2) social cohesion (speed of information transfer in groups), and (3) mechanisms to gather visual social information (gaze direction, response to different types of social cues).

Information Coded in a Signal

The variability in signal design can influence its efficacy and content. Signal efficacy is related to its conspicuousness, whereas signal content is associated with its information content (e.g., how well a signal represents the physical condition of an individual). These two elements of a signal are expected to be balanced to optimize signal transmission under a given set of ambient light and visual background conditions. A recent study by Doucet and collaborators tackled this trade-off from a comparative perspective by assessing reflectance patterns of manakin plumage in relation to forest-shade illumination and the vegetation background in 50 tropical species. The diverse plumage of male manikins exhibited higher levels of chromatic and achromatic contrast against the background in relation to the olive green plumage of females. This suggests that sexual selection may be the mechanism behind the evolution of multiple male plumage patches to increase signal efficacy during mate choice contexts. Male coloration in manakins is produced by a combination of chemical and structural colors whose degree of contrast would vary depending on the dominant wavelength they reflect and the ability of the male to display a particular colored patch. Different types of colors are then likely to result in different information contents for the receiver. Doucet and collaborators found that carotenoid coloration showed the highest level of chromatic contrast and moderate levels of achromatic contrast, which makes these signals excellent for transmitting content to the receiver (e.g., potential mates) at short distances because birds have a lower visual spatial resolution for chromatic (color) than achromatic (brightness) signals. However, black and white plumage patterns in manakins showed the highest values of achromatic contrast, resulting in greater conspicuousness at larger distances, particularly when coupled with behavioral displays. The main conclusion is that different plumage patches may optimize efficacy or content, depending on the distance between the sender and the receiver.

Concluding Remarks

Studying visual signals as a process in which information flows from the sender to the receiver allows us to assess signal transmission, gathering, and processing from a

mechanistic perspective. However, the interspecific variability found in these mechanisms can then be placed in a comparative framework to understand some of the evolutionary pathways that have led to the high degree of visual signal diversity. Combining these two approaches in the study of visual signals would allow us to better understand the function of many of these signals by better designing experiments that manipulate key factors and by choosing key parameters that will consider the visual sensitivity of the receiver.

See also: Alarm Calls in Birds and Mammals; Evolution and Phylogeny of Communication; Food Signals; Information Content and Signals; Mating Signals; Multimodal Signaling; Parent–Offspring Signaling; Vision: Vertebrates.

Further Reading

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