


Review

Backgrounds and the evolution of visual signals

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Color signals which mediate behavioral interactions across taxa and contexts are often thought of as color 'patches' – parts of an animal that appear colorful compared to other parts of that animal. Color patches, however, cannot be considered in isolation because how a color is perceived depends on its visual background. This is of special relevance to the function and evolution of signals because backgrounds give rise to a fundamental tradeoff between color signal detectability and discriminability: as its contrast with the background increases, a color patch becomes more detectable, but discriminating variation in that color becomes more difficult. Thus, the signal function of color patches can only be fully understood by considering patch and background together as an integrated whole.

Signals, color, and sensory perception

Sensory systems garner information that may subsequently influence the behavior of an organism. A primary way in which organisms gather information about other individuals is via **signals** (see [Glossary](#)) – defined as acts or structures that have evolved to modify the behavior of receivers [1,2], and from which receivers can reliably obtain information that, on average, benefits both senders and receivers [3]. Signals mediate behavior in many contexts, including species recognition, mate choice, aggression, and mutualistic interactions. Many visual signals involve color, which presents a particular challenge for effective perception and assessment by signal receivers. This is because how color is perceived by an organism depends on a variety of factors ranging from the visual and cognitive system of the viewer to environmental illumination.

One important factor influencing color signal perception is the visual background against which a color patch is displayed. Patches can contrast with their backgrounds in either brightness (referred to as **achromatic contrast**) or in spectral properties such as hue and saturation (referred to as **chromatic contrast**). It is well established by studies of visual physiology that contrast with the background – both chromatic and achromatic – strongly impacts color signal perception. The majority of signaling structures, such as color patches, differ from their background in both brightness and color, and thus have both achromatic and chromatic contrast with the background. Despite this, the effects that backgrounds have on the perception of color signals have not been widely incorporated into our understanding of signal function, structure, and evolution.

The detectability–discriminability tradeoff

Signals must be detectable to function. All else being equal, visual signals are predicted to maximize color and/or brightness contrast with the background to improve either the probability of detection [4] or the distance at which they can be detected in attenuating media such as water or fog [5]. In non-human animals, the background against which a stimulus is viewed impacts how detectable it is (e.g., [4,6–8]). Generally, high color contrast between a patch and its background increases its **detectability** (e.g., a yellow patch on a blue background). For example, birds are more able to detect fruits that have greater chromatic contrast with their backgrounds [9]. Likewise, in a range of taxa, high brightness contrast between a stimulus and its background – for example, a black patch on a white background – makes the stimulus more detectable (e.g., [10,11]).

Highlights

Color signals often comprise a colorful patch viewed against a background that is another part of the same animal or part of the environment; backgrounds can be achromatic, ranging in brightness from black to white, or colorful, varying in hue, saturation, and brightness.

The background against which a color patch is displayed fundamentally affects how that color is perceived.

Backgrounds engender a tradeoff between signal detectability and signal discriminability, with implications for signal function and evolution.

Similar detectability–discriminability tradeoffs may exist in modalities outside of vision, such as chemical and auditory signals.

Signal and background should be considered together as a 'multicomponent' signal, in that signal components within a modality can interact and serve as a perceptual whole.

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Many color patches that serve as animal signals have evolved to contrast strongly with their background. For example, conspicuous color signals (those that have high color and/or brightness contrast with the background) can serve to attract mates or repel rivals [12,13], attract mutualistic partners [14], or signal aspects of the signaler such as toxicity or unpalatability [15].

However, detection is only part of what must be considered. For many types of signal function, receivers also must be able to discriminate variation in the signal. For example, variation in signal color or brightness among individuals may be reliably correlated with aspects of signalers that are meaningful to receivers, such as parasite resistance [16,17], nutritional status [18,19], unpalatability [20], immune function [21], and contest success [22]. Because of this correlation, receivers potentially benefit from discriminating color or brightness among signal variants displayed by different senders, or by the same sender at different points in time.

In humans, the **discriminability** of targets that differ in brightness is greatest when the brightness of the background is more similar (i.e., has lower brightness contrast) to the target stimuli being discriminated [23]. This effect, called **crispening**, although long appreciated by artists [24], was first described scientifically by Takasaki [25] and continues to be an active area of study in human psychophysics (e.g., [26–28]). Crispening describes the effect by which the perceived difference between two targets of similar brightness appears to be enhanced when the brightness of the background is intermediate between the two stimuli being compared (Figure 1A). The effect is similar when the contrast is chromatic (Figure 1B): humans more easily discriminate between target stimulus colors that have low hue contrast with the background (Figure 1B) [29].

Backgrounds also affect discrimination between color variants in non-human animals, although the effects of background on discrimination between colors are much less well studied than the effects of backgrounds on detectability. In zebra finches (*Taeniopygia guttata*) the threshold above which two color variants were discriminable from one another was a function of both the color and brightness contrast of the target with its background [30]. Specifically, for two colors

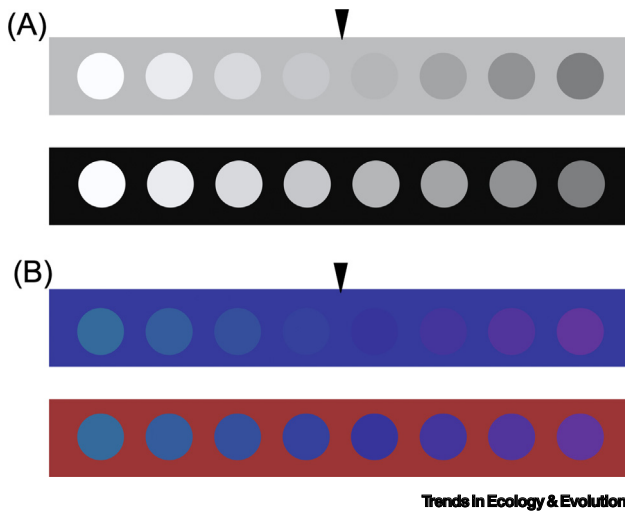


Figure 1. The crispening effect and the detection–discrimination tradeoff. (A) For achromatic stimuli (circles) that vary in brightness against an achromatic background, discrimination is easiest when the background brightness is intermediate between the brightness of the stimuli being compared (crispening effect). The black arrows represent where on the achromatic continuum the background brightness falls between the circles on either side of the arrow. Discriminating between the circles on either side of the black arrow is easier when the background brightness is more similar to the stimulus brightness (upper bar) than when the background brightness is very different (lower bar). (B) The crispening effect also occurs when the stimuli vary in hue; in

this case, the stimuli and backgrounds are all of the same brightness, but differ in hue. Again, discriminating between the circles on either side of the black arrow is easier when the background hue is more similar to the stimulus hue (blue bar) than when the background hue is very different (red bar). Within each panel (A) and (B), the stimulus circles are identical in the upper and lower bars. Note that in both examples of crispening, the stimuli being compared (any neighboring pair of circles) are less detectable (lower contrast) on the background where it is easier to tell them apart.

Glossary

Achromatic contrast: the luminance (or intensity) ratio between two surfaces (e.g., a patch and its background), which is perceived as a difference in brightness (luminance as determined by the luminosity function of the relevant viewing species, often taken to be the wavelength sensitivity of the middle-wavelength-sensitive cone).

Chromatic contrast: the distance between two stimuli in the color space of a viewer.

Detectability: how easily a signal is perceived as distinct from the visual background. Sometimes referred to as 'conspicuousness'.

Discriminability: how easily a signal is identified as distinct from similar signals or similar versions of the same signal. Importantly, we use the term discriminability to refer to discrimination between different variants of a particular type of signal, and not to the discriminability of a signal against its background.

Signal: any morphological, physiological, or behavioral trait which has evolved to convey information that, on average, benefits both the signal sender and the signal receiver.

to be discriminable from one another when the chromatic contrast with the background was high, the value of ΔS , a measure of chromatic distance between those two colors, had to be fivefold higher than the value of ΔS required to discriminate those same colors when contrast with the background was low. Similarly, high achromatic contrast with the background can affect the ability of zebra finches to discriminate between color pairs. Davis *et al.* [31] trained zebra finches to discriminate between pairs of colored targets, and then varied the achromatic contrast between target and background, and measured the percentage of trials in which finches could still discriminate between the colored targets. They showed that a 20% increase in achromatic contrast between target and background resulted in the rate at which zebra finches could discriminate between a given color pair dropping from ~40% to ~20%.

The study by Davis and colleagues [31] supports the prediction that signal colors with lower contrast relative to the background are more discriminable from one another. The colored targets that they used ranged from orange to red, reflecting the natural range of male zebra finch beak colors which vary with male quality and are an important signal assessed by females during mate choice

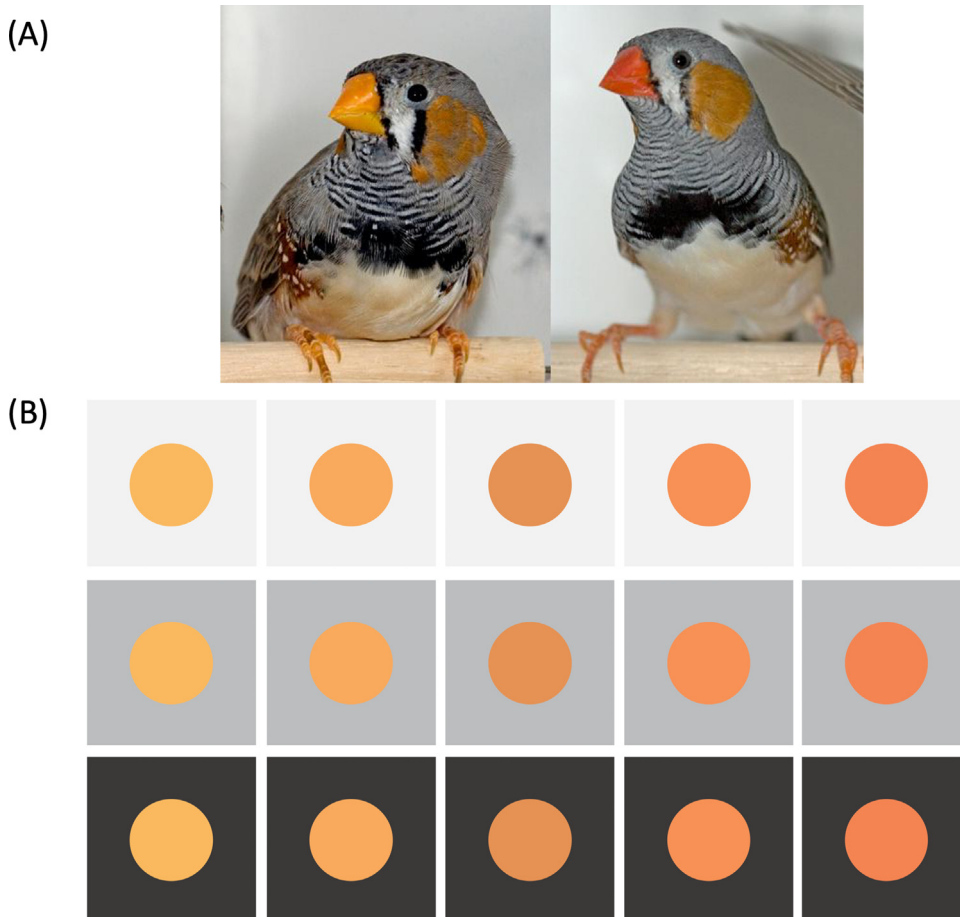
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Figure 2. Perception of a color signal by zebra finches (*Taeniopygia guttata*) depends on the contrast with the background. (A) The color of male zebra finch beaks ranges from light orange to red, and is assessed by females during mate choice. (B) One study [31] showed that female zebra finches were most able to discriminate between colored targets that parallel the natural range of male beak colors on a low-contrast, gray background that was similar to male zebra finch facial feathers (middle) than on high-contrast white (top) or black (bottom) backgrounds. Panel (A) photo credit: Stuart Dennis.

(Figure 2; details in [32]). In addition, the three backgrounds tested in this study were black, white, and gray, where the gray background roughly approximated the gray feathers that provide part of the visual background for the beak signal (Figure 2). Their results showed that orange-red beak colors were most discriminable against the gray background; this was not only the background with the lowest contrast relative to the signal colors but also the most naturally relevant background tested.

Although not explicitly testing color discrimination in a signaling context, further evidence for how backgrounds affect color discrimination comes from chickens (*Gallus gallus*), where highly contrasting backgrounds make color discrimination more difficult and decrease the certainty of discrimination decisions [33]. Discrimination thresholds were nearly twice as high for chickens discriminating green stimuli on an orange background (1.11 just-noticeable differences, JNDs) than green stimuli on a green background (0.67 JNDs). Similarly, goldfish (*Cassius auratus*) are better at discriminating between the saturation of two different stimuli when a spectrally neutral background is illuminated with light that more closely matches the stimulus color [34]. However, the effect of contrast between a color patch and its background on the discriminability of variation in the patch is opposite to that of its effect on detectability [23].

Thus, visual backgrounds engender a fundamental perceptual tradeoff between detectability (how easy it is for a receiver to perceive a signal in the first place) and discriminability (how easy it is for a receiver to distinguish variation in a signal). Specifically, with increasing contrast between a patch of color and its background, patches become more detectable; at the same time, however, discrimination of variation in that same color becomes more difficult. Although these effects are well established in terms of responses of animals to color patches or artificial stimuli, less work has examined this tradeoff in the context of animal communication and signaling. Indeed, for some signals, selection may act to increase either detectability or discriminability; signals that function for detectability should contrast strongly with the background in color and/or brightness, whereas signals that require receivers to discriminate should be more similar to the background in hue and brightness. In other cases, both detection and discriminability may be equally important, for example in sexual signals where mates must not only be detectable but also be discriminable from other potential mates. Understanding how this tradeoff operates in natural signaling contexts is an important knowledge gap to fill.

Local versus global backgrounds

There are two types of visual backgrounds of a color patch to consider. First, a background can be local, directly surrounding the patch, and thus will also be a part of the signaling organism (e.g., an adjacent part of the integument for an animal, or petals surrounding the center of the flower on a plant). Local backgrounds can be of a color different from that of the patch of interest [35–37], or achromatic, spanning the gamut from ultra-black [38,39] to bright white [40]. For example, local color contrast between iridescent patches with different primary hues increases their conspicuousness in species such as hummingbirds, beetles, and butterflies, thus likely impacting on detectability [41]. Dark patches bordering colorful signals create high brightness contrast between the signal and local background in birds [42,43], fishes [44], lizards [45], and butterflies [46], thus increasing detectability. Because local backgrounds are part of the same organism that exhibits the color patch, the background and patch may evolve in concert. Thus, to overcome the detectability–discriminability tradeoff in the case of a local background, selection can act on the color patch itself or its local background, or both.

Second, a background can be global. The global background refers to the color and brightness properties of the larger visual context in which the patch is observed, and thus includes the environment in which a signaling individual finds itself. Some global backgrounds can be dynamic, for example due to changes in the location of the signaler or receiver, or diel or seasonal variation in the environment. Like

local backgrounds, global backgrounds also can have a significant impact on how a patch of color is perceived, notably on its detectability and thus, in an inverse fashion, on its discriminability.

In contrast to local backgrounds, global backgrounds – such as vegetation, soil, sky, and so forth – are not directly affected by natural or sexual selection acting on the signaling animal and thus cannot coevolve with color signals as can happen with local backgrounds. Animals can, however, evolve coloration that contrasts with the background. For example, several species of bowerbirds [47], *Anolis* lizards [48,49], and some species of freshwater fish [50,51] have evolved coloration that contrasts strongly with the environmental backgrounds against which they display. Animals can also evolve behaviors whereby they optimize either the detectability or discriminability of a color patch by modifying the conditions under which a color patch is observed. For example, animals may preferentially signal against particular natural backgrounds or under specific lighting conditions. Courting male muscid flies (*Lispe cana*) preferentially signal against darker backgrounds, and the magnitude of the contrast between signal and a given background predicts both the level of female attention as well as mating success [52]. Male guppies (*Poecilia reticulata*) choose display locations relative to females that result in them being viewed more often against a water background which maximizes the chromatic contrast of the male with the background compared to gravel or other streambed substrates [53]. Some species of lekking neotropical birds select specific light environments in which to place their leks and perform displays, and in particular choose light environments in which the color pattern of their plumage is most detectable against the visual background [54].

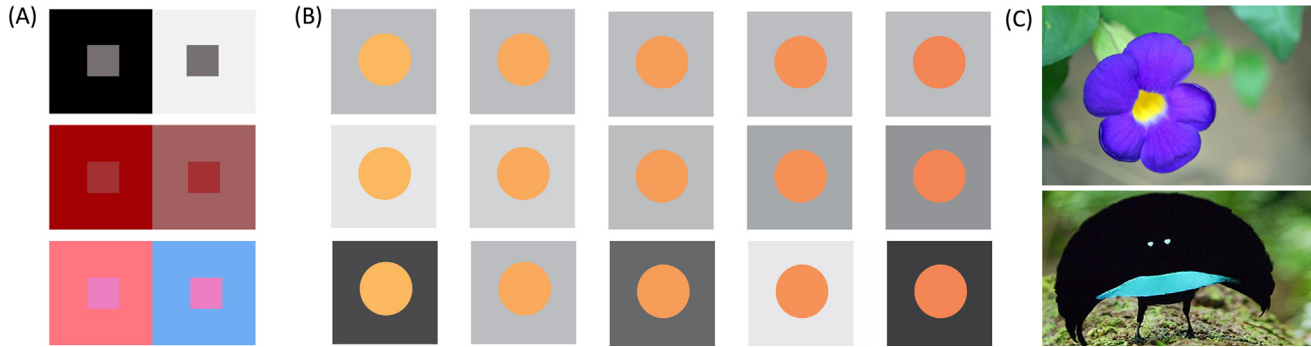
Animals also can manipulate the global background against which a color patch is observed (reviewed in [55]). For example, great bowerbirds (*Chlamydera nuchalis*) selectively choose bower ornaments that are non-random samples of the visual background to increase the color contrast of bower decorations against the background [56]. Similarly, gold-collared manakins (*Manacus vitellinus*) increase color and brightness contrast by clearing their display courts to create a darker, more homogenous background [57].

Shifts in color appearance

Visual backgrounds also can induce shifts in color appearance, meaning that colors may appear more different against one background than they do against others. Of relevance to signaling and the detectability–discriminability tradeoff, the fact that the perception of a color patch may shift depending on its background color means that two patches that are identical in their color properties (i.e., the same hue, saturation, and brightness) may appear different to an observer, and thus discriminable from one another, depending on the background color. Conversely, two patches having only similar color properties may appear to be identical, again depending on their background.

The best-described color shift is called simultaneous contrast, which refers to the way in which two patches that share an edge (such as would be the case for a patch and its background) affect the perception of each other. Simultaneous contrast can occur for brightness (resulting in two patches of equal brightness appearing differently from one another; Figure 3A, top) or color (resulting in two patches of identical spectral composition appearing differently; Figure 3A, middle and bottom). Thus, the overall effect of simultaneous contrast is to shift the perceived hue, saturation, and brightness of a patch away from that of another patch [58]. Simultaneous color and brightness contrast have been demonstrated in humans [58], as well as non-human animals, including goldfish (*Carassius auratus*) [59], guppies (*Poecilia reticulata*) [60], honeybees (*Apis mellifera*) [61], butterflies (*Papilio Xuthus*) [62], and pigeons (*Columba livia*) [63].

There are many signaling backgrounds that can potentially induce perceived color shifts through simultaneous contrast (Figure 3C), including global backgrounds such as the open ocean, sky,



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Figure 3. Backgrounds can induce shifts in color appearance. (A) Simultaneous contrast is one well-studied example of a background-induced color shift, which results in identical color patches (center squares) appearing to be different from each other depending on the properties of the background color, including when the backgrounds differ in (top) brightness, (middle) saturation, or (bottom) hue. In each panel row, the center squares are identical to each other, but appear to differ from each other depending on the visual background. (B) Background-induced shifts in color appearance may vary across individuals owing to a lack of correlation between color patch and background. For example, stimuli ranging from orange to orange-red are easily discriminable when placed on a uniform background (top) or when the background brightness is reliably correlated with the stimulus color (middle). Discrimination becomes more difficult when the background brightness is variable but does not correlate with the stimulus color (bottom), as may occur within a population of signalers with varying signal and background colors. Note that the variation in color of the circular patches from left to right is identical in all three rows. (C) Examples of natural signaling backgrounds that may induce perceived color shifts through simultaneous contrast, for example local backgrounds such as purple flower petals surrounding a yellow center (top), and the black feathers of the superb bird-of-paradise (*Lophorina superba*) surrounding the blue 'face' (bottom). Panel C (Top): 'Purple flower with 5 petals' by Mayoorezan is licensed under CC BY-SA 3.0. Panel C (Bottom): 'Cape presentation display of superb birds of paradise' by Edwin Scholes and Tim Laman is licensed under CC BY 4.0, and has been altered to show only panel B of an original two-panel image.

and large areas of sand, stone, or soil. In such cases the effect of simultaneous contrast can be to 'push' color parameters such as hue, saturation, and/or brightness in the opposite direction to the background. For example, in the case of dark, desaturated purple flower petals around a yellow center, the yellow center will appear brighter, more saturated, and more yellow than it would against a different background. Animals also can manipulate the backgrounds against which a color patch is viewed, and thereby exploit the effects of simultaneous contrast to make some patches appear brighter than they really are (reviewed in [64]). Positioning oneself in a specific environmental context could also potentially induce shifts in perceived color: both humans and triggerfish perceive a 'lightness cube' illusion in which identically colored targets appear to be of different brightness as a result of environmental cues such as the presence of shadows [65].

Background-induced shifts in color appearance may not be the same for all individuals within a population or species if the perceived brightness of the background and the patch color and brightness do not correlate with each another across individuals. In essence, this lack of correlation may mean that, for some individuals, their color patches appear to be brighter or more saturated than they really are. This could arise, for example, because color patches themselves may vary over relatively short timescales as a result of factors such as dietary carotenoid intake (e.g., [17]), whereas the coloration of the local background may depend on the developmental history of an individual, and thus vary less over the lifetime of the individual, as can be the case for at least some structural colors (e.g., [66]). A similar lack of correlation between the perception of a color patch and its background could also occur if a single signaler is viewed by the same receiver against different global backgrounds. Thus, the shift in color patch appearance induced by the background would vary across the population or for a single individual across time, introducing a source of error in receiver assessment and decision making (Figure 3B). Furthermore, there is increasing recognition that human activities can affect both colors and backgrounds, and may potentially have adverse effects on biological signaling in nature (Box 1).

To mitigate errors due to background-induced shifts, receivers may assess the color of both the signal and local background as a pair. It is also possible that individual signalers, specifically those

Box 1. Anthropogenic effects on signal backgrounds

Each of the signal components we discuss here – a color patch, its local background, and its global background – is at risk of experiencing rapid shifts as a result of anthropogenic activity. For example, heavy metal exposure can affect carotenoid- and melanin-based feather coloration (e.g., [67]), which in turn may influence the properties of color patches or their local backgrounds, or both. The same is true for persistent organic pollutants and both fuel and oil pollution (e.g., [68,69]). As an example of anthropogenic effects on global backgrounds, coral-bleaching events – which in the past 30 years have increased in frequency and geographic range [70] – at first turn corals white and then green as more time passes and unhealthy corals become algae-covered [71]. These changes in coral background color are associated with increased predation of reef fish because prey fish are more conspicuous against these backgrounds [72], suggesting that these changes are likely large enough to also impact on color-based signals. Other impacts on global background color in aquatic environments include 'brownification' of freshwater lakes and coastal waters, whereby agricultural run-off results in waters turning more brown, and agricultural and septic run-off leads to increasing eutrophication and turns waters more green [73,74]. Human-induced changes to visual global backgrounds can also occur in terrestrial environments; for example, even relatively subtle changes in forest composition can impact on the availability of the backgrounds and light environments that are preferred by some signalers (e.g., [54]).

Ultimately, anthropogenic effects on signal backgrounds may affect the evolution of signals if selection acts to compensate for changes in local backgrounds and/or the behavior of animals, who may alter their display behavior to overcome changes to their global backgrounds. Given the pace of change, however, anthropogenic changes to backgrounds may have disruptive effects on many communication systems, thus providing some urgency to studies that increase our understanding of potential detectability–discriminability tradeoffs in signaling interactions.

of varying quality, will have different equilibria when balancing the detection and perceived saturation of a color. For example, higher-quality individuals may be able to afford a reduction in perceived saturation associated with high-contrast backgrounds. By producing a highly saturated signal with a high-contrast background, higher-quality individuals could maximize the detectability of their signal while maintaining its perceived saturation.

Mate choice as a case study

The detectability–discriminability tradeoff may be particularly important to consider in the context of color-based reliable (i.e., 'honest') signaling, where receivers are predicted to discriminate among different signalers based on variation in some signal attribute, as often occurs in mate choice [3]. Many mate choice signals are patches of color that may contrast highly with both their local and global backgrounds, and thus be highly detectable. Several species of bowerbirds, for example, have evolved display plumage that, when accounting for the visual capabilities of the bowerbird viewers themselves, is non-overlapping in color with the visual, global, background [47]. Similarly, *Anolis* lizards exhibit higher color contrast against common global backgrounds in their native habitats than do closely related species from different habitats [48,49]. Further evidence of signals evolving for detection against a particular background comes from bluefin killifish (*Lucania goodei*) and three-spine sticklebacks (*Gasterosteus aculeatus*) where the relative abundance of specific fin coloration patterns depends on the water color. In both species, the dominant color morph exhibits higher color contrast with the background water during display bouts [50,51].

In the context of mate choice, however, different variants of the signal displayed by different signalers must also be discriminable from one another. A canonical example comes from work on house finches (*Haemorrhous mexicanus*). Males exhibit carotenoid-based coloration in their head and breast feathers that ranges from yellow to bright red [75], where feather coloration correlates reliably with resistance to parasites [17]. Females mate preferentially with redder males [76], and thus their ability to discriminate among males based on color differences matters at least as much as, if not more than, their ability to detect the signal in the first place. To our knowledge, the potential for a tradeoff between detectability and discriminability has not been examined in house finches. A comparative study across 50 species of manakins, however, found evidence consistent with the idea that selection for 'efficacy' (i.e., 'detectability'), and selection for 'function' (related to our use of 'discriminability'), of color patches can sometimes be opposing, leading to a tradeoff between the two [42].

The difficulty of discriminating among multiple potential mates is also exacerbated by the fact that, in many mate-choice systems, signalers are likely to be viewed successively rather than simultaneously [77]. Furthermore, signalers are mobile and may be observed against different backgrounds. In such situations, receivers face the challenge of needing to remember the colors of previous signalers, and may also need to take into account the background against which a color patch is observed. The extent to which a background may enhance the discriminability of a color patch (at the cost of reduced detectability) may lessen the cognitive demands of such serial comparisons.

There are several possible resolutions to the detectability–discriminability tradeoff. First, selection may act on signalers to exhibit a greater range of variation in color signals if these signals contrast highly with a local or global background. This increase in variation among signalers would better allow receivers to discriminate among signals from different individuals. Supporting this idea, Delhey *et al.* [78] found in a study of 55 bird species that species that display colors that are more conspicuous against natural backgrounds also have higher levels of intraspecific color variation. Importantly, for this type of correlated evolution of patch and background to occur, both sender and receiver must benefit on average from the signal [79]. Second, in cases where a color patch serving as a signal contrasts highly with the background, receivers may use a threshold response to signal variation (reviewed in [80]), and respond to signal variants below a particular threshold in one way, and those above the threshold in another. A threshold response circumvents the need for finer-scale discrimination because receivers can ignore some of the uncertainty caused by background-induced shifts in color perception or other sources of error. Third, signalers may partition detection and discrimination into separate components or modalities where each evolves optimal effectiveness for its function. For example, highly detectable color patches may be used solely to draw receiver attention to a signaler, and discrimination between signalers then occurs via a different patch (as may occur in sulfur butterflies, *Colias eurytheme*, where males have orange wings that are likely highly detectable, but female choice is predominantly based on an ultraviolet signal, e.g., [81]) or even a different signaling modality [82]. Although

Box 2. Beyond vision: detectability and discriminability in other signaling modalities

A similar contrast-dependent tradeoff between detectability and discriminability may exist in other modalities as well, for example in the olfactory signals that mediate pheromone-based mate choice [83] and plant–pollinator interactions [84]. Chemical stimuli can be mixtures of components that are present at different concentrations and relative proportions, and chemical backgrounds are themselves complex bouquets of volatile organic compounds (VOCs) [83,85]. As with visual signals, chemical signals must be detectable against these backgrounds. Evidence suggests that chemical signal detectability depends on both the complexity of the odor background and how distinct a scent is from the background (reviewed in [83]). For example, the ability of hawkmoth pollinators to detect and localize a scent can be influenced by the odor background [86], and the detectability of female-produced sex pheromones can depend upon the background odor environment in which they are emitted [87]. Similarly to visual signals, in which the background can shift the perceptual experience of a color patch, an olfactory background can alter olfactory perception [83,86]. Although studies have examined how detectable chemical signals are and how the background can alter signal detectability, little is known regarding how olfactory backgrounds can affect the ability of a receiver to discriminate between signal variants. Understanding this tradeoff for olfactory signals is important given clear evidence that, in some olfactory signaling contexts, receivers discriminate among receivers based on signal variation across individuals, which can be an honest indicator of the quality of an individual [84].

Local or global backgrounds may also affect tradeoffs between detectability and discriminability in other modalities. Considerable work has examined how acoustic signals evolve to be more detectable in noisy environments, for example by shifting frequency ranges and temporal patterns [88]. It is less clear whether increasing detectability against a global background may inherently diminish the discriminability of an acoustic signal (see Outstanding questions). In human music, for example, composers use harmony, counterpoint, rhythm, and other features of sound to make particular melodies stand out for the listener. Whether a similar phenomenon occurs in natural acoustic signals remains unexplored to our knowledge, but the possibility exists that the detectability and discriminability of an acoustic ‘patch’ – the aspect of an animal sound that stands out – may be affected by a local background that is part of the same acoustic signal. Similar questions might be posed for gestural, seismic, or electric signaling systems. Extending these questions to other modalities is timely given that anthropogenic impacts (Box 1) such as noise and chemical pollution are resulting in changes to the signaling landscape and driving changes in the signals themselves (reviewed in [89]).

we have focused here on visual signals, similar considerations may also apply to other signaling modalities (Box 2).

Concluding remarks

Visual backgrounds give rise to a fundamental tradeoff between the detectability and discriminability of color patches. They can also induce shifts in color appearance, for example through simultaneous contrast, meaning that two patches of identical color may be discriminable from one another depending on the background color. Thus, backgrounds may play a significant role in signaling interactions and signal evolution, at least for visual signals. Despite this, there are significant gaps in our understanding of the role that visual backgrounds play in signal perception (see Outstanding questions).

Although we have focused here on signals, which must be detectable to function, visual backgrounds also potentially represent a mechanism by which a color patch can be made less detectable. For example, signal detectability evolves under tradeoffs between being conspicuous to intended receivers, such as mates, and inconspicuous to unintended receivers, for example predators, although the extent to which animal signals make use of the detectability–discriminability tradeoff to be inconspicuous (e.g., camouflaged) rather than conspicuous is underexplored (see Outstanding questions).

Incorporating backgrounds into studies of color signaling is particularly timely for several reasons. First, a key set of tools in the study of visual signaling are models (primarily the receptor noise-limited (RNL) model [90], reviewed in [91]) which can help to predict whether two stimuli are discriminable by a given animal viewer. Generally, these models work by estimating differences in quantum catches (the stimulation of different photoreceptor types) relative to the amount of noise in each channel. However, behavioral output often differs from predictions based on the RNL model (e.g., [7,32,92]). Much of this mismatch likely arises from the fact that the RNL model considers only retina-level processes, specifically photoreceptor stimulation and noise, and not mechanisms for efficient coding of natural images (e.g., [93]) or higher-order processes such as categorization (e.g., [32]) which can affect visual perception. However, the RNL model is being increasingly applied across a variety of fields (e.g., [91] and replies) to understand the function and evolution of colorful stimuli, even though it does not explicitly account for the effect of photoreceptor adaptation to the visual background (although the von Kries adaptation can be applied, e.g., [94,95]). Thus, a better understanding of how backgrounds affect perception, via mechanisms arising at a variety of levels, and thus modulate visual signaling may help us to lend realism to models of color vision. The fact that color patches are often arranged in a pattern with a specific geometry, as opposed to existing only as color patches in isolation, is receiving increased attention (e.g., [37]), and tools have been developed to help to quantify color patterns (e.g., [96,97]), although these still do not account for perceptual processes such as crispening.

Although crispening itself remains to be demonstrated in non-human animals, the mechanisms underlying crispening appear to be related to chromatic adaptation, which has been shown in many species (e.g., [98]). In addition, recent work has repeatedly demonstrated that perceptual mechanisms once thought to be unique to humans also operate in animals. For example, categorical color perception has recently been demonstrated in zebra finches [32], and triggerfish (*Rhinocanthus aculeatus*) have been shown to perceive lightness-based color illusions [65]. Some of this work suggests that aspects of color perception may be dependent upon the behavioral context (e.g., [99]), and may be under selection because of the signal function of specific colors (e.g., [92,100]). This suggests that it is important that we study color perception – even well-documented psychophysical processes – in signaling contexts in particular.

Outstanding questions

How does contrast with the visual background affect the ability of signal receivers to discriminate among senders, for example those of different quality, in signaling interactions in nature?

Does the crispening effect manifest in non-human animals, and, if so, is it under selection for the perception of specific important (signaling) colors?

Are color patches and local background colors, or their perception, correlated within populations?

Do color patches and local backgrounds coevolve in signaling systems?

How does global background variability across a species' range affect the evolution of color signals?

How do signaling behaviors, or behaviors to hide signals (i.e., camouflage), evolve in relation to global backgrounds, and how do changes to global backgrounds as a result of anthropogenic impacts affect signal function and evolution?

Do tradeoffs between the detectability of a signal relative to its background and discriminability among signal variants exist in non-visual signaling modalities?

Future work on color signals should consider measuring the color and brightness of both local and global backgrounds because, as we have argued here, the potential signal function of a color patch can only be fully understood by considering both the patch and its background taken together as an integrated whole.

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Declaration of interests

The authors declare no conflicts of interest.

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