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Spatiotemporal Dimensions of Visual Signals in Animal Communication

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form, motion, pattern, texture, vision, visual ecology

Abstract

Much of the information in visual signals is encoded in motion, form, and texture. Current knowledge about the mechanisms underlying visual communication is spread across diverse disciplines. Contemporary perspectives on the physics, psychology, and genetics of visual signal generation and perception can be synthesized into a conceptually integrative approach. Developmental mechanisms of pattern formation suggest that small changes in gene regulation or structure can result in major shifts in signal architecture. Animals in many species have been shown to attend to variation in higher-order stimulus properties. Preferences for these properties can be innately specified or learned, and may also show large shifts or reversals. Perceptual mechanisms, particularly visual attention, associated with spatiotemporal features are likely to be a major force in shaping the design of visual signals.

INTRODUCTION

The leopard's spots, the high-contrast bands on the wings of a *Heliconius* butterfly, the intricate filigree on the face of a Picasso triggerfish—so much of what we find compelling about animal diversity has to do with complex visual signals. The information in visual signals is encoded in spatiotemporal patterns: variation in color and intensity across time and two- or three-dimensional space (**Figure 1**). These patterns pose a challenge across disciplines. To developmental biologists, spatial patterns are a compelling model for studying the ontogeny and evolution of form (Brunetti et al. 2001, Parichy 2003). To sensory ecologists, they offer the challenge of understanding how multivariate signals are transmitted in heterogeneous environments (Endler & Mielke 2005, Fleishman et al. 2006). The perception of texture, motion, and shape

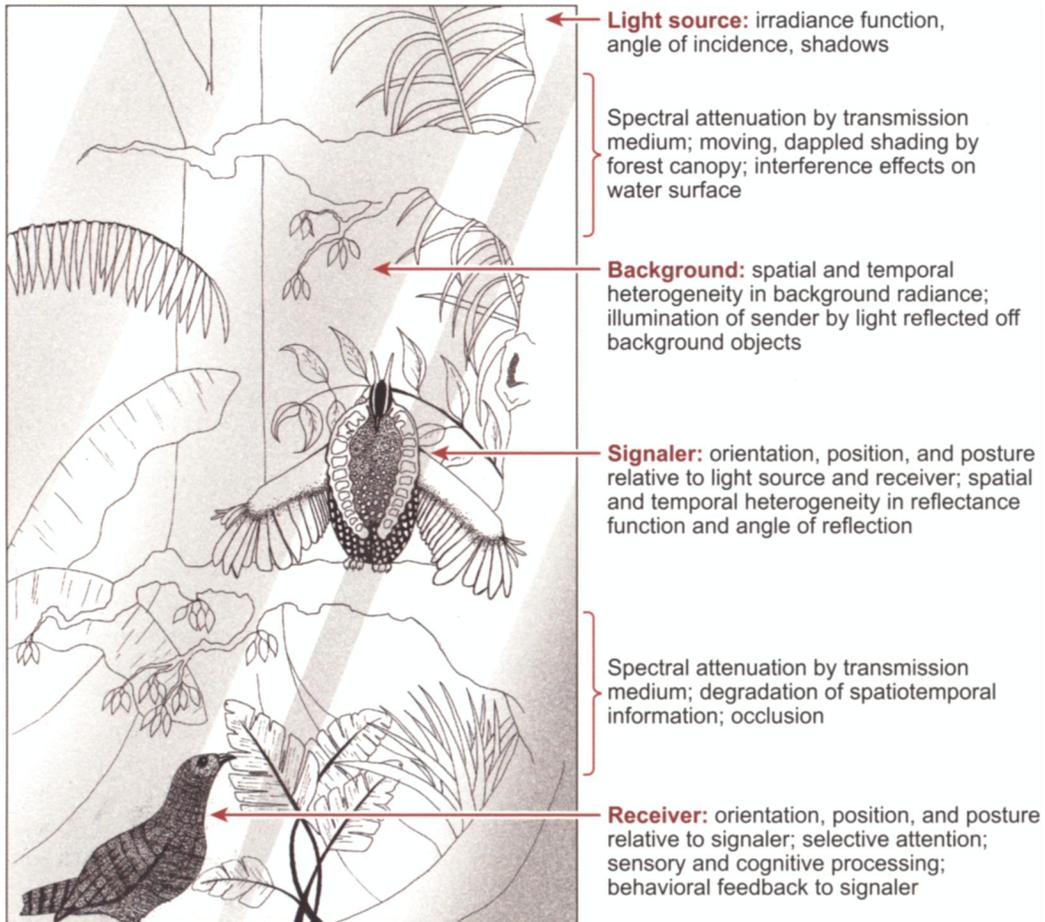


Figure 1

Schematic of the steps involved in production, transmission, and reception of visual signals. Drawing by Nick Ratterman.

encompasses some of the key problems in cognitive psychology (Kovacs & Julesz 1994, Maunsell & Treue 2006), and analysis of visual images is the domain of physicists and applied mathematicians (Billock et al. 2001, Chubb & Yellott 2000). Current knowledge of the biology of complex visual signaling is thus spread across vastly different disciplines. An encyclopedic review of the relevant literature is impossible, and this brief treatment of a massively broad topic is necessarily both superficial and incomplete. The aim of this review, nevertheless, is to encourage the synthesis of these diverse perspectives into a conceptually coherent approach to studying visual communication.

THE MAGNITUDE OF THE PROBLEM

Figure 1 illustrates the scope of understanding complex visual communication with a hypothetical male signaler courting a female with a complex visuomotor display. Photic energy is provided by sunlight, which varies in intensity, color, and angle as a function of season and time of day. Light is filtered by the atmosphere, affecting the characteristics of the photic environment in which animals find themselves communicating; dynamic patches of light and shade are further produced by motion of the forest canopy (Endler 1993) or waves on the water surface (Loew & McFarland 1990). Some of this light is reflected off other objects in the environment before striking the signaler. The male's position, orientation, and posture at any given time determine how this complex visual field illuminates his body: both the path taken by the light (e.g., direct sunlight versus sunlight filtered by leaves and reflected off the ground) and the angle of incidence determine the radiance of light reaching the body surface at any given point in space and time.

The male's body surface then reflects light in a variety of ways, resulting in the richly textured spatial pattern that we see. For example, the pigment in some feathers selectively absorbs high-energy photons, producing a bright red, whereas air spaces in some feathers scatter all wavelengths in all directions, producing a bright, diffuse white light (Finger 1995). Eyes, shiny scales, and some exoskeletons, however, act like mirrors, producing specular highlights (Blake & Buelthoff 1990, Zeil & Hofmann 2001). This spatial variation is complemented by temporal variation in the male's posture and orientation in the course of a courtship display. En route to the female, water or humid air changes the spectral quality of the light reflected off the male (Lythgoe 1979); particles in the transmission medium and occluding objects degrade spatial and temporal information (Kenward et al. 2004). All of these factors combine to affect particular components of the visual signal, and the efficacy of that signal, before it ever reaches the eyes of the female.

How the female perceives the signal depends on how her two eyes are placed relative to the male and the light source—if he is backlit by sunlight, he appears as a black silhouette; if they are facing each other straight on (Dantzker et al. 1999), the reticulate pattern on his chest appears to be regularly spaced and the iridescence on his throat shines a brilliant blue (Rutowski et al. 2007). The movement of the female's head, eye, and body supply her with information about the three-dimensional structure of the scene. Her gaze is drawn to his plumage ornaments, and the patterns

these project onto her foveas are parsed by spatial-frequency, temporal-frequency, color, and orientation filters in her retina and brain (Kandel & Wurtz 2000). This information is ultimately integrated into a behavioral response that in turn influences subsequent actions by the male (Patricelli et al. 2002).

Perhaps because of the immensity of the problem, the study of the visual communication process has been somewhat atomized. The production of spatiotemporal patterns is almost exclusively the domain of developmental biologists, while their perception is largely studied by cognitive psychologists. Integrative studies—focusing on signal production, transmission, and perception—have mostly fallen into two categories: evaluating behavioral responses to qualitative variation in stimulus characteristics, and quantitative studies involving color. As **Figure 2** illustrates, however, it is impossible to interpret color data without taking spatial information into account. For example, Barry & Hawryshyn (1999) found that colors reflected by Hawaiian coral reef fish on average matched the background irradiance (**Figure 2d**). Clearly, however, some pattern elements (like the yellow tail of the queen angelfish in **Figure 2a**) present a sharp contrast with both the background and other elements

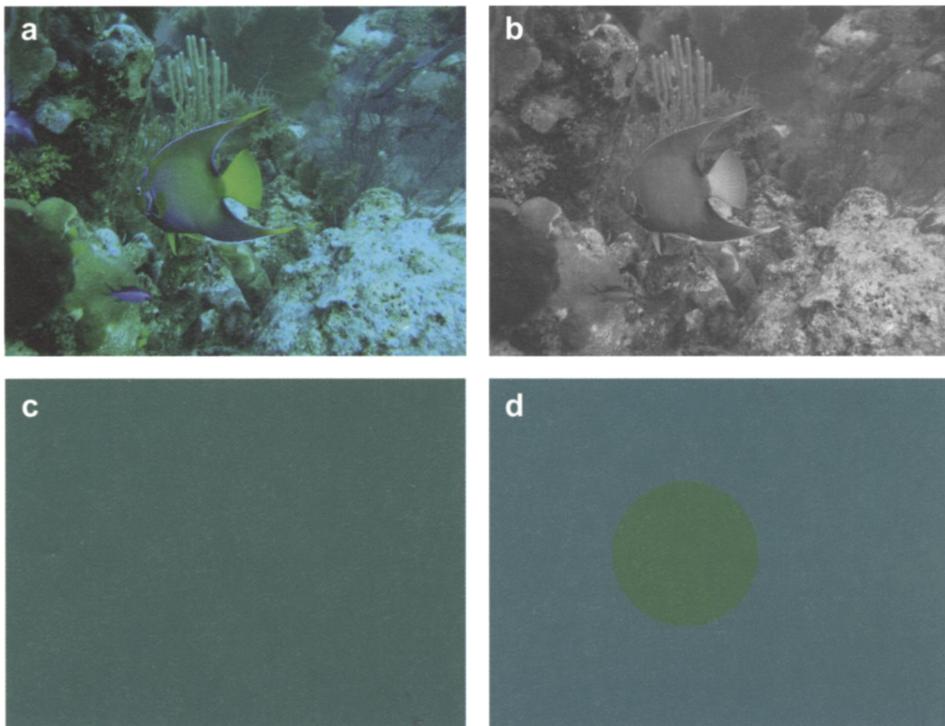


Figure 2

Queen angelfish (*Holacanthus ciliaris*) against a complex coral reef background (Glover's Reef, Belize). (a) Unmanipulated digital color image; (b) chromatic information removed; (c) spatial information removed; (d) spatial information removed separately from angelfish and background.

on the animal's skin. Marshall (2000) suggested this allows many reef fish to remain camouflaged from a distance yet conspicuous at close range, via smearing of high-spatial-frequency, high-contrast color patterns like blue and yellow. Microhabitat selection may further modify contrast relationships.

I begin by reviewing mechanisms of signal production and perception, and then discuss how knowledge of perception can help us quantify complex visual signals. I then review the burgeoning literature on the integrative biology of complex visual communication.

TYPES OF SPATIOTEMPORAL SIGNALS

An encyclopedic work by Cott (1940) remains the most exhaustive treatment of the diversity of complex visual signals. Spatiotemporal signals can either be cryptic, whereby they are designed to minimize detection or recognition by receivers, or conspicuous, where they serve to maximize information transfer. The spatial component can involve variation in the pigment or structural composition of the skin, exoskeleton, hair, feather, or scales; as well as modified appendages, horns, and other morphological structures. Many signals have repeating components, known as textures.

The temporal component, which is often absent in crypsis, typically involves muscle-mediated changes in orientation, posture, and position relative to the receiver, and often raising and lowering of hair, feathers, or appendages. In birds and mammals, modulation of blood flow can effect limited color change in the skin (Bradbury & Vehrencamp 1998). In ectothermic vertebrates, neurally-mediated control of chromatophore cells (Bagnara & Hadley 1973) allows for temporal variation in pattern over a range of time scales, both within the course of a signaling display and over longer periods of time (Rosenthal & Lobel 2006). Male haplochromine cichlids *Astatotilapia burtoni*, for example, express a drab, female-like pattern when socially subordinate and a high-contrast sexually dimorphic pattern when dominant and reproductive; although this pattern is maintained for the duration of the male's social status, it is reversible and can change rapidly (Fernald 1990). Similarly, in birds, plumage badges serve as indicators of dominance status, and are modified during seasonal molts (e.g., Qvarnstrom 1997) or hidden and revealed through postural changes (Hansen & Rohwer 1986).

Temporal and spatial components of signals are typically expressed in concert. In courtship displays, conspicuous male ornaments are usually coupled with stereotyped movements that present them to the best advantage (Rosenthal et al. 1996). The reverse is true for cryptic species: a remarkable case is the reef cornetfish *Fistularia commersonii*, which expresses a disruptive banded pattern when stationary, and rapidly transitions to uniform silvery coloration when in motion (Thomson et al. 2000).

SIGNS AND RITUALS: SPATIOTEMPORAL PATTERNS THROUGH THE MID-TWENTIETH CENTURY

Because we need no special instrumentation to detect most aspects of visual signals (with the notable exceptions of polarization patterns and UV cues) it is not surprising that they have generated a long history of scholarship. The role of complex visual

signals in animal communication was well established early on (Cott 1940). Numerous experiments in a broad variety of taxa demonstrated that animals attended to nuances in color, motion, texture, and form (Eibl-Eibesfeldt 1970).

Much of mid-twentieth century ethology was concerned with systematizing rules of cause and effect in animal behavior. The finding that complex behavioral responses could be elicited by simple stimuli, called innate releasing mechanisms, had a fundamental effect on contemporary thinking about visual signals. Crude models, which resembled natural signals in only a few, key salient ways, could elicit the same responses as parents, potential mates, or competitors. Even so, spatial relationships among signal elements played a critical role. Tinbergen (1951), for example, found that male sticklebacks produced aggressive behavior only when models were presented in the proper orientation, with red coloration on the underside of the object. Furthermore, Eibl-Eibesfeldt (1970) cited a number of studies showing that though releasers seemed to play a large role in aggressive interactions, a mating response required more nuanced stimuli. Cott (1940) also remarked that mating signals were generally far more complex than aposematic signals, arguing that simpler patterns were more likely to be memorable to predators.

Visual signals were therefore classed into distinct, “simple” and “complex” categories. Lorenz (cited in Eibl-Eibesfeldt 1970) dichotomized visual signals into simple, innately specified “sign stimuli” and complex, learned “gestalten”:

Where an animal can be ‘tricked’ into responding to simple models, we have a response by an innate releasing mechanism; where it cannot be thus confused, we have an acquired recognition of a gestalt.

Lorenz’s assertion, though implicitly accepted, remains to be thoroughly explored. In some cases, behavior toward spatiotemporal patterns has a strong learned component (Engeszer et al. 2004). We know that low-level visual processing can be highly dependent on early visual experience; for example, the color of ambient light during a critical period can influence the expression of visual pigments in retinal photoreceptors (Fuller et al. 2005) and, as shown in classic studies by Hubel & Wiesel (1963), cortical cells that parse spatial frequency and orientation are also sensitive to early visual input. On the other hand, work on auditory imprinting in birds (Marler 1997) showed that individuals have an innate predisposition to learn conspecific song, which differs from that of heterospecifics in multiple acoustic dimensions.

Complex stimuli may thus be innately specified in some cases. Two bird species innately recognize the color, orientation, and shape of patterns characteristic of venomous coral snakes (Smith 1975, 1977), which differ from nonvenomous heterospecifics primarily in the spatial organization of repeated pattern elements. The intricate, species-typical color patterns of coral reef fishes are also likely to have an innate component. Most marine fishes release their gametes into the plankton, leaving no possibility for learning parental phenotypes.

A simple, innately specified set of cues may also serve as a trigger to attend to and imprint on a more complex stimulus. For example, newborn humans attend preferentially to faces, but this appears to be specified by a general bias toward up-down asymmetry in a spatial configuration; abstract patterns with more elements

in the top part of the image are more attractive than upside-down faces (Turati et al. 2002). A subset of image components, or even a cue in another modality, may thus direct learned recognition of a complex image.

DEVELOPMENTAL EVOLUTION OF SIGNALS

Despite the profusion of complex visual signals, an animal's body is not a blank canvas. Pattern expression is constrained by evolutionary history in a number of ways. Complex motor patterns are often modified, or ritualized, from nonsignaling antecedents; Hurd et al. (1995) used neural network algorithms to corroborate Darwin's (1872) principle of antithesis, showing that selection favors signal complexes that are maximally different in opposing contexts, e.g., aggressive escalation versus submission. Although signal motor patterns tend to have nonsignaling precursors, many animals have evolved specialized musculature and motor control systems dedicated to communication (e.g., Ma 1995a,b).

Spatial patterning also involves nonsignaling precursors, both in ontogeny and phylogeny. The patterning of spatial signal elements is often developmentally dictated by the location of nonsignaling structures. In salamanders and zebrafish, for example, lateral stripes are specified by the position of lateral-line precursors (Parichy 2003).

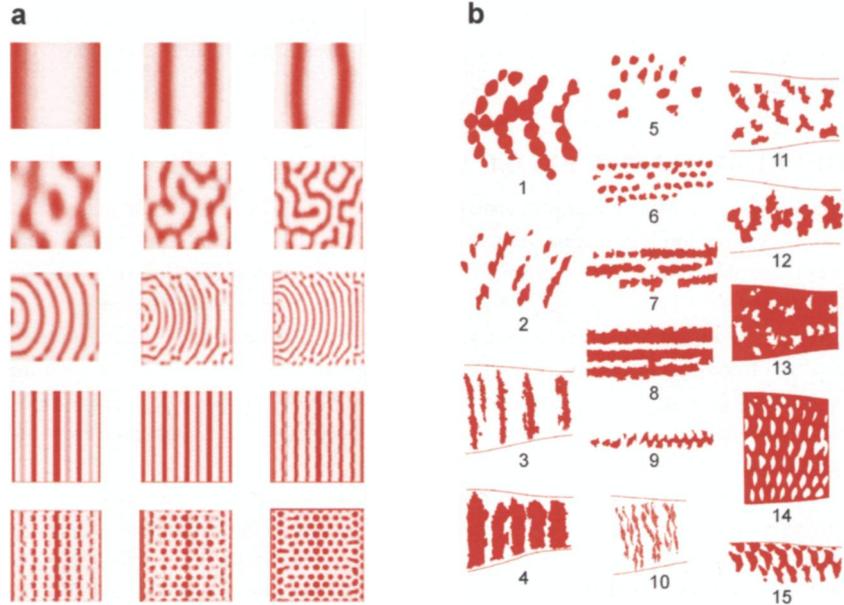
The problem of skin patterning has received some attention from developmental biologists. A diversity of repeating patterns, or textures, can be produced by subtle changes to a relatively simple molecular mechanism. Turing (1952) proposed the reaction-diffusion system, whereby spot and stripe patterns arise as a result of instabilities in the diffusion of two or more morphogenetic chemicals (morphogens), in the skin during early development. Differences in boundary and initial conditions, and in the number of morphogens and diffusion properties of each morphogen, can interact to produce an array of stripe and spot patterns (Kondo & Asai 1995, Murray 1981, Painter et al. 1999). Shoji & Iwasa (2003) further suggested that a reaction-diffusion system could act in concert with small differences in diffusion anisotropy of morphogens (caused by structures with directional conformation such as scales) to induce directionality in stripe patterns.

Recent molecular-genetic studies are illuminating mechanisms of pattern formation. Parichy (2003) provides a concise review of the developmental genetics of stripe formation in zebrafish (*Danio rerio*) and their close relatives. Asai et al. (1999) argued that the zebrafish *leopard* gene may be acting as a component of a reaction-diffusion system. Small changes in gene structure or regulation could thus induce qualitative changes in pattern elements (Painter et al. 1999; see **Figure 3a**), producing dramatic differences in signal structure. Such a process could account for the striking differences in pattern sometimes seen among closely related species (**Figure 3b**).

Eyespots on butterflies provide insight into the development of aperiodic signals, and suggest another set of mechanisms for generating signal diversity (Brunetti et al. 2001). The location of a focal morphogen—which will become the center of the eyespot in the adult—is specified during early development. The focus induces rings of regulatory gene expression that determine the size, color, and arrangement of concentric pattern elements. Variation in these properties can arise through several

Figure 3

(a) Diversity of patterns generated by reaction-diffusion models. Top two rows show heterochrony in a stripe-splitting sequence; third row, changes in parameter values produce stripe addition instead of splitting; bottom two rows, stripes change into spots as domain size increases. (b) Distribution of red body pigmentation of fifteen species of Cameroonian *Aphyosemion* killifish [adapted from Painter et al. 1999 (National Academy of Sciences, USA) and Amiet 1987].



channels: differences in the regulatory domains of transcription factors operating downstream of the focus, different combinations of regulatory genes recruited to specify pattern properties, and differences in the regulation of structural genes involved in scale pigmentation. As with Turing patterns, eyespot formation suggests that small genetic changes could yield substantial differences in pattern structure (Brunetti et al. 2001).

In some cases, patterns are intricate and highly specified. The aptly named Picasso triggerfish, *Rhinocanthus aculeatus*, for example, exhibits a black-and-white polka-dot pattern just anterior to the caudal fin; four white stripes running diagonally from the insertion of the anal fin to the midline of the body; brown and gray bands on the dorsum; a filigree of electric blue lines originating parallel at the eye and curving to meet on the gill cover; and a blue “mustache” above the mouth contrasting with a broad russet band that slopes down to meet the white belly. How are the locations, spatial extents, and chromatic properties of all these elements specified?

In some cases, ontogenetic changes in pattern expression continue through adult life. Plumage badges in birds, for example, intensify with age (Qvarnstrom 1997). A dramatic example is provided by sequential hermaphrodites, where female patterns are replaced by dramatically different male patterns over a period of a few days (Warner & Swearer 1991).

Pattern ontogeny of both motor patterns and spatial patterns is susceptible to environmental influences. For example, in the grasshopper *Schistocerca gregaria*, development of a conspicuous, black-and-yellow aposematic pattern requires both use of a toxic host, and high densities during larval instar stages (Sword 1999). In satin bowerbirds, juvenile males solicit courtship from older males, suggesting that there may be a learned component to these intricate dances (Collis & Borgia 1993).

SIGNAL RECEPTION

The reception of complex visual signals can be broadly divided into receiver decisions, which determine how light reflected from the signaler and background enters the visual system as a function of space and time; and receiver processing, which determines how the visual system analyzes the spatial, temporal, and chromatic distribution of light. Receiver decisions have three components (**Figure 1**). First, a general property of communication, which will not be discussed further, is that receivers provide behavioral feedback that influences the behavior of the signaler. Second, receiver behavior influences the three-dimensional structure of the scene: how is the receiver's field of view oriented and positioned relative to the light source, the background, and the signaler (Heindl & Winkler 2003; see **Figure 1**)? Third, how does the receiver attend to different components of the scene, of the signal, and of the background?

Receiver Decisions

Receiver behavior. Spatiotemporal relationships among signalers, backgrounds, receivers, and illuminant sources are crucial variables in visual communication. Receiver motion provides information about three-dimensional depth and about spatial relationships among scene elements (Wexler & van Boxtel 2005). The geometry of signal illumination, and the position and orientation of the receiver, are early determinants of how the signal will be perceived (Fleishman et al. 2006). The positioning of receivers thus has a profound influence on signal expression. Body patterning in pelagic animals, for example, is often countershaded, with a dark dorsal surface and a light ventral surface that minimize contrast with the substrate and water surface, respectively (Cott 1940). At the other extreme, many courtship displays are expressed in contexts that maximize conspicuousness to receivers: spatial patterns are expressed in concert with motor patterns that showcase them to maximal advantage. In a wide variety of species, male courtship displays involve movements at characteristic viewing distances directly in front of the female (Dantzker et al. 1999). Male orange sulphur butterflies (*Colias eurytheme*) direct their courtship so as to maximize the brightness of iridescent UV coloration (Rutowski et al. 2007).

Receiver attention. Despite a growing literature on attentional constraints and foraging ecology (Dukas 2004), attentional processes have received little explicit consideration in animal communication. Attention plays two roles that are of major importance in signaling interactions. First, some signal features are involved in initially directing attention toward or away from the signaler. Ocelli (false eyespots) on many animals have long been thought to redirect predator attention in a way that facilitates escape (Cott 1940; Stevens 2005).

In contrast, early stages of courtship and aggressive interactions often involve high temporal frequency movements in a characteristic direction, readily detectable in the visual periphery, that direct a viewer to focus on and attend to the signaler (a 'visual grasp reflex', Peters et al. 2002). Signals may also be designed to hold receiver attention. Habituation is a universal property of nervous systems, and large,

diverse song repertoires in songbirds maximize attractiveness in part by delaying the habituation of receivers (Ryan 1998). Intricate dances and patterns in courtship may play a similar role.

Second, attentional processes play a primary role in how receivers assign importance to different aspects of a complex stimulus: What are receivers actually looking at? In satin bowerbirds, for example, young females select males based on the static attributes of their bower constructions, whereas older, more experienced females attend mainly to variation in the relatively dynamic temporal features of the male courtship display (Coleman et al. 2004). Attention is not merely a question of concentrating on a spatial dimension of the visual field; subjects can shift their attention between different features of a scene, e.g., shape, color, or velocity (Maunsell & Treue 2006). Such dynamic shifts in attention may explain how receivers weight multiple traits differently across comparisons (Kirkpatrick et al. 2006).

A recent study on humans (Rowe et al. 2007) showed that the breadth of attentional focus in a visual task (correctly identifying a central letter flanked by other letters) depends on affect; positive mood was associated with impaired performance, because individuals were attending to the flanking letters as well as the central target. “Sad” individuals focused their attention on the central target. The multifaceted suites of male traits present in most courtship signals may have evolved in order to satisfy the inconstant attention of happy females. Conversely, because arousal in a negative context is associated with a constriction in attentional focus (Easterbrook 1959), one might expect graded aggressive signals to address progressively narrower attentional demands.

Attentional constraints, which have been amply considered in the context of foraging behavior (Dukas 2004) may therefore play an important role in signal evolution. Assays like the flanker task in Rowe et al. (2007) are straightforward to apply to nonhuman animals. Gaze direction, a widely used indicator of attention in human studies, can now be studied noninvasively in animals thanks to novel tracking methodologies using neural network algorithms (Piratla & Jayasumana 2002). These approaches make it feasible to begin studying the role of attentional mechanisms in animal communication.

Receiver Processing

The sensory periphery influences two key aspects of visual perception: color sensitivity (reviewed in Yokoyama & Yokoyama 1996 [vertebrates] and Briscoe & Chittka 2001 [insects]) and spatial acuity, i.e., the spatial resolving power of the eye. Spatial acuity increases with the size of the eye (by increasing the eye’s focal length, analogous to a camera F-stop), with photoreceptor density on the retina, and with the ratio of cones to rods (because of the reduced summation of cones to downstream cells). There is thus a fundamental size constraint on spatial acuity. Moreover, there is a tradeoff between acuity and visual sensitivity, resulting in reduced acuity for animals in low-light environments. As reviewed by Bradbury & Vehrencamp (1998), acuity varies by more than three orders of magnitude across taxa. Temporal frequency resolution, or critical flicker fusion frequency, is also inversely related to sensitivity and shows substantial variation among species (Frank 2000).

Sensory constraints thus place limits on the spatial and temporal frequency of visual signals. From a signaler's point of view, this can impact both the design of spatiotemporal components and the optimal viewing distance. For example, males in some species of swordtails (genus *Xiphophorus*) exhibit conspicuous vertical bars during courtship, coupled with a back-and-forth lateral display (Ryan & Rosenthal 2001). Casual observation suggests that display speed is higher in species lacking bars, with males sometimes executing a 180° turn in 100 ms or less. The signal value of the bars would be lost if they were presented at a rate exceeding the female's critical flicker fusion frequency of about 43 Hz (Rosenthal & Evans 1998). One should also expect environmental demands on sensory systems to constrain the evolution of spatiotemporal patterns, much as has been demonstrated for color (Endler 1992). Specifically, displays in species that are active in low-light environments, and therefore have reduced spatial and temporal resolving power, should be slower and spatially simpler.

Although spatial and temporal resolution impose an upper bound on information transfer, it is unlikely that there is tight coevolution between signal structure and the spatial- and temporal-frequency tuning of receivers. The reason is that the angular size of the same signal on the retina (and therefore the angular speed as well) will vary with viewing distance. One of the challenges of visual processing is to use unstable, two-dimensional images to extract stable information from a complex, three-dimensional world. Size constancy, the ability to judge the real size of objects independent of distance, is ubiquitous in vertebrates (Douglas et al. 1988). Size constancy requires integrating at least two streams of information: the visual angle an object subtends on the retina, and spatial or spatiotemporal indicators of distance such as binocular disparity or accommodation (focus) cues. Similarly, most visual systems are likely to exhibit some degree of constancy with respect to rotation, shape, brightness, color, and texture (Dyer 2006, Kandel & Wurtz 2000).

It is nevertheless probable that there are ecological correlates of higher-order visual processing. Simple cells in the macaque primary visual cortex exhibit diverse, apparently haphazard responses to specific combinations of stimulus orientation, spatial frequency, and speed. van Hateren and van der Schaaf (1998) showed that the distribution of simple cell characteristics corresponded to that of natural image properties, leading these researchers to conclude that "the apparent randomness of simple cell properties may not be the sign of a sloppy design, nor of random variability in development, but may in fact be a deliberate attempt to match the requirements of processing natural images." Selection may thus favor distinct emphases in early visual processing. For example, most salient stimuli for large ungulates are likely to be confined to the horizontal plane, whereas small rodents, preyed upon by swooping aerial predators, should additionally attend to the vertical. Párraga et al. (2002) used natural image statistics and psychophysical data to argue that in humans, sensitivity to chromatic modulation at low spatial frequencies has evolved in the context of a specific ecological task, namely detecting ripe fruit against a complex background. Parsing of natural scenes is thus likely to reflect strong selection for performance in particular contexts.

In addition to extracting invariant features of stimuli from the environment, the other principal challenge of visual processing is image segmentation: distinguishing

between the salient stimulus (the signaler) and the background. The question of how visual processing of local scene elements is integrated into a unitary percept is one of the key foci of cognitive psychology (Kovacs 1996; Kovacs & Julesz 1994). This is far from a trivial task (**Figure 2**): Both visual backgrounds and signaler properties are heterogeneous and depend heavily on lighting, distance, and perspective, and the problem is further complicated by occluding objects between signaler and receiver. Edge detection begins with center-surround cells in the retina (Rodieck 1998) and provides early information about discontinuities in the visual scene. Balboa & Grzywacz (2000) showed that occluding objects produce sharp disjunctions between image features and can be detected in early retinal processing. As discussed below, edge-detection mechanisms are exploited by cryptic patterns in camouflage. High-contrast edges are, however, a ubiquitous feature of conspicuous displays. Because these are almost always expressed in concert with motor patterns, motion coherence (Sekuler & Blake 1994) of the patterns on the signaler should facilitate separation of the signaler from the background. Many of the high-contrast markings thought to be ‘amplifiers’ (Hasson 1989), allowing receivers to more reliably assess honest indicators, may simply provide a means for facilitating figure-ground assignment by receivers.

Once an image is segmented into “figure” and “ground,” how is complex spatiotemporal information integrated into recognition of a potential mate or a likely rival? Some units in higher-level visual processing are highly specific. For example, some neurons in the macaque inferotemporal cortex are maximally tuned to average, identity-ambiguous faces of other macaques (Leopold et al. 2006). Biederman and colleagues (Hayworth & Biederman 2006) have suggested that object recognition relies on parsing a visual stimulus into geons—simple geometric shapes that are robust to changes in rotation, scale, and noise, like cylinders and cones. Remarkably, Chen et al. (2003) showed that honeybees (*Apis mellifera*) learned to generalize patterns based on topological invariance, i.e., the number of holes contained, independent of local stimulus cues. Topology is often robust to many aspects of rotation, scale, and translation, and therefore provides reliable information about global properties.

There are therefore multiple higher-order attributes of visual stimuli that animals may use in assessing signals. Many of these share the property of categorical attribution, e.g., one hole versus none, face versus nonface, cylinder versus cube. Just as small changes in gene expression can produce discontinuities in signal expression, it may be that similarly small alterations can effect qualitative changes in both the perceptual salience and the valence of stimuli.

CHARACTERIZING SPATIOTEMPORAL SIGNALS

In order to study how complex visual stimuli and receiver properties might be coevolving, we need to be able to describe signals quantitatively, in the currency used by receivers. Fourier analysis has accomplished this, with great success, for acoustic communication. Any complex, periodic signal can be decomposed into an infinite series of pure sine waves, and the vertebrate ear acts as a frequency analyzer itself. There is thus a unified, mathematically elegant way to describe the production, transmission, and perception of sound.

Similarly, Fourier analysis is integral to studies of visual perception (e.g., Párraga et al. 2002, Shapley & Lennie 1985), and models of visual processing assume that cortical neurons act as Fourier filters (Shapley & Lennie 1985). A difficulty arises, however, when attempting to characterize the visual scenes and signals that are being processed. Although an acoustic signal impinging on an eardrum can be approximated as three-dimensional (frequency \times amplitude \times time), a projection of a moving scene onto a single retina has five dimensions (wavelength \times intensity \times vertical \times horizontal \times time). Perhaps largely because of this added complexity, there is no unified approach to analyzing visual signals, and analyses of spatial, temporal, and spectral components of visual scenes have generally been conducted separately.

Temporal Components

Pioneering studies by Fleishman (1988, 1992) used one-dimensional Fourier analysis of the vertical component of the head-bob display in *Anolis* lizards to quantify conspicuousness relative to background motion. High-frequency components of vertical motion (the jerkiness of the head-bob display) enabled the lizard to stand out from the movement of background vegetation. Peters et al. (2002) obtained a similar result for the complex display of the agamid lizard *Amphibolurus muricatus*, using the spatial distribution of velocity vectors, or optic flow fields, in successive images of a movie to calculate ellipses describing the distribution of direction and speed of movement in both lizard displays and background vegetation (**Figure 4**).

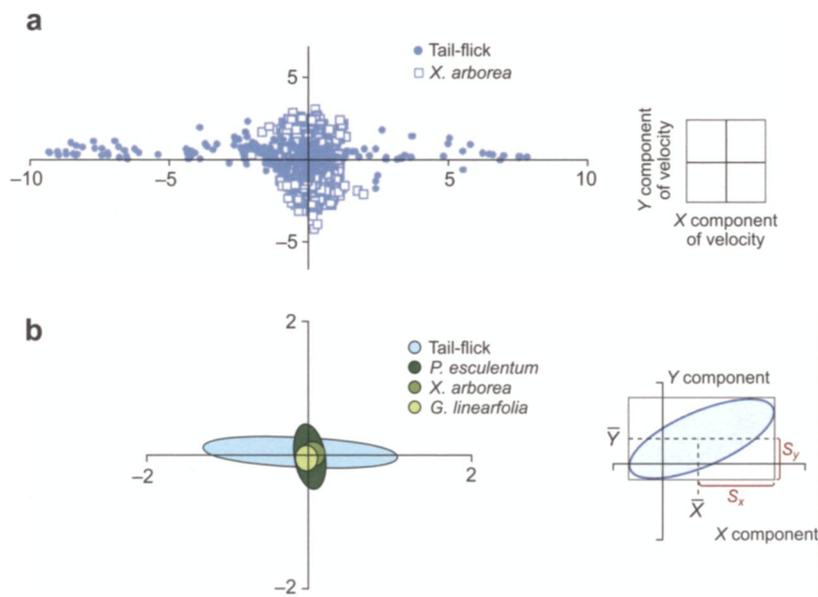


Figure 4

(a) Velocity signature of a Jacky dragon (*Amphibolurus muricatus*) tail-flick overlaid on a representative sequence of vegetation. (b) The standard ellipse for the tail-flick and each of the vegetation sequences at low wind speed. The center of each ellipse is given by the vector of x and y means, while the standard deviations and correlation coefficient define the shape and orientation of the ellipse in the X/Y plane (modified from Peters et al. 2002).

Spectral Components

Quantitative studies of vision have overwhelmingly focused on color (Grether et al. 2004). Spectroradiometry is used to measure the spectral characteristics of the visual environment (e.g., downwelling and sidewelling irradiance), and reflectance spectroradiometry to measure reflectance, commonly at point samples along the body surface. Leal & Fleishman (2004) and Fleishman et al. (2006) have pointed out the importance of illuminance geometry and orientation to this process. The principal advantage is that we can estimate the distribution of photons impinging on the retina; we are measuring directly in the currency of the visual system.

Spatial Components

Analysis of two-dimensional static images has proven far more challenging than that of temporal and spectral components of visual signals. Approaches to analyzing spatial pattern variation can be divided into signal-based analyses and scene-based analyses.

Signal-based analysis. Signal-based analysis of spatial components is by far the most common approach used in studies of signal design and evolution. Given a priori reasons to believe that a particular set of traits is salient in communication, we can qualitatively or quantitatively describe phenotypes with respect to these traits. There are two main limitations to this approach. First, we may be ignoring some spatial properties that are important to the receiver; second, our characterization is unlikely to be meaningful from the point of view of visual processing. Given our human visual bias, it is often easiest to simply parse signals into discrete categories by appearance, either in terms of individual components (e.g., tail tips, vertical stripes, horizontal stripes, and spots; Ortolani 1999) or signaling complexes (Crook 1997). Although this approach has yielded powerful insights into the evolution of spatial patterns, there is an inherent subjectivity with respect to category boundaries, and variation within categories may be important; for example, the aspect ratio or relative intensity of spots may be salient to receivers. A similar approach can be used to express spatial components in quantitative terms. Numerous studies have quantitatively measured and manipulated morphological traits thought to be important in visual signaling (e.g., Andersson 1982, Sinervo & Basolo 1996, Wong & Rosenthal 2006).

An intriguing approach to signal-based analysis was taken by Mojsilović et al. (2000), who effectively asked receivers to classify patterns. They presented human subjects with all 190 possible pairwise combinations of a set of 20 color textures taken from an interior design catalog, then asked them to rate each pair as to its similarity. Using hierarchical clustering analysis, they identified a “basic vocabulary of color patterns” whose strongest determinant was pattern equivalence: if the spatial pattern between two textures was identical, they were rated as highly similar independent of color. Conditioned-response and habituation/dishabituation studies may make such an approach feasible for nonhuman animals as well.

Scene-based analysis strives to characterize the properties of images as perceived by receivers. Most scene-based analysis relies on quantitative methods, but Changizi

et al. (2006) used categorization by human observers to assess the distribution of topological configurations at contrast discontinuities in natural scenes. Much as one-dimensional Fourier analysis can be used to analyze sounds, two-dimensional Fourier analysis can be used to analyze the global properties of two-dimensional grayscale images. Godfrey et al. (1987) used this approach to evaluate the cryptic effect of zebra and tiger stripes based on analysis of images of these animals in their natural habitats; at lower spatial frequencies, both animals were moderately cryptic, but at higher frequencies only the tiger remained cryptic.

Kiltie & Laine (1992) and Kiltie et al. (1995) argued that wavelet-based methods, which perform localized analysis of frequency and orientation, approximate the response properties of visual neurons by analyzing signals across ranges of spatial scales and orientations, providing a better approximation of local analyzers in the visual system. For example, the orientation of spatial patterns, which Fourier analysis would not detect, had a major effect on the conspicuousness of zebra and tiger coat patterns analyzed by Godfrey (1987). van Hateren & van der Schaaf (1998) used a technique called independent components analysis, which is roughly analogous to wavelets, to evaluate the match between tuning of simple cells in primate visual cortex and the statistics of natural images.

Can Visual Signals Be Comprehensively Characterized?

It would clearly be desirable to simultaneously quantify the salient properties of visual signals: motion, color, and form. This poses a technical challenge and a conceptual one. First, we need to be able to collect data on the wavelength distribution of photons striking a (hypothetical) retina as a function of space and time. Hyperspectral imaging (Chiao et al. 2000a,b), which produces a spectral radiance function for each pixel of a digital image, may provide a solution. Although hyperspectral imaging is in broad use for remote-sensing applications, it has not been widely used in studies of communication (but see Zeil & Hofmann 2001).

Second, if we use expensive technology to collect massive volumes of data from even a brief visual scene (a 10-second display at a crude 100-ms temporal resolution, 300×300 -pixel resolution, and 10-nm wavelength resolution from 350–700 nm would produce over 300 million intensity values), we still need a coherent body of theory, not to mention a computational methodology, to make sense of this information. The independent-components and wavelet-based approaches discussed above are extensible to temporal and chromatic dimensions.

The key constraint is that it is impossible to take the receiver out of the picture, because the receiver's position and attention are key determinants of how the scene is going to be processed. One might begin by imaging from the receiver's point of view; this can be approximated from careful observation (Zeil & Hofmann 2001), or directly estimated through "critter cam" views or the use of camera-equipped robot receivers (Patricelli et al. 2002). Joint analysis of orientation, posture, and eye movement can be used to estimate gaze direction over the course of the signaling interaction. This provides a measure of how the receiver attends to different scene components over time, and may provide a heuristic estimate of how the receiver is segmenting the

image. Wavelets and similar methods can then be used to identify the features that distinguish the figure from the background.

COMPLEX VISUAL COMMUNICATION IN THE NATURAL ENVIRONMENT

Broadly, patterns have evolved to either maximize or minimize conspicuousness—and sometimes both, whether at different scales or to different receivers (Marshall 2000). A handful of studies have used interspecific correlations to infer function for patterns. Ortolani (1999), for example, used a phylogenetic analysis to identify correlations between ecology and carnivore color patterns, concluding that stripes and spots had evolved in the context of camouflage, whereas high-contrast tail tips might have a communicative function.

Camouflage and Crypsis: A Case Study

By far the most sophisticated studies of complex visual stimuli involve patterns that are not signals in the traditional sense, but rather have evolved to minimize the probability of detection, recognition, or attack by predators. As defined by Endler (1978) crypsis is a function of how much a pattern resembles the visual background from a predator's point of view, which depends on the properties of its visual system (including color and polarization sensitivity, and spatial and temporal resolution) as well as the viewing angle and distance with respect to the putative target. As discussed above, Kiltie et al. (1995) developed a wavelet-based method for quantifying crypsis, providing a method for quantifying pattern characteristics using spatially localized analysis of orientation and frequency components. Selection favors male guppies whose skin patterns match the grain size (i.e., the spatial frequency, and presumably the orientation as well) of background elements (Endler 1980).

Cephalopods, among others, can dynamically adjust skin patterns according to their background. The pattern they adopt depends on the relative size, contrast, and density of background elements; on a fine-grained artificial checkerboard, cuttlefish (*Sepia officinalis*) exhibit a mottled texture on the same scale as the grain. Above a size threshold, however, they cease to background-match and switch to a disruptive 'white square' pattern (Chiao & Hanlon 2001). If edges (by application of a low-pass spatial-frequency filter) and contrast (by application of a high-pass filter) in pattern elements are removed, cuttlefish no longer produce the white square (Chiao et al. 2005).

Such disruptive coloration, where spatial patterns serve to impair visual recognition by breaking up an animal's outline, has been the subject of two recent studies. Merilaita & Lind (2005) presented great tits (*Parus major*) with artificial stimuli that either matched average background characteristics or disrupted the stimulus. Background-matching worked only if the grain and orientation of background elements were similar to those of the stimulus, which was not always the case owing to chance variation in background structure. Disruptive coloration, however, conferred a protective advantage to the stimuli.

How does disruptive coloration actually work? Although disruptive coloration has often been described in terms of breaking up a Gestalt-like "search image" for

a stimulus, Stevens & Cuthill (2006) provided a plausible mechanism for disruptive coloration relying purely on low-level processing of edges. Using a computational model of edge detection, based partly on empirical data on avian visual physiology, they evaluated the function of disruptive coloration. By breaking up the outline of the animal, disruptive patterns on moth models were difficult to detect from background at multiple spatial scales. Furthermore, disruptive coloration often interacts with motor patterns to hinder detection and recognition (King 1993).

Conspicuousness and Beauty

By definition, something is minimally conspicuous when it is indistinguishable from a random sample of visual background. It is less clear, however, what makes a complex stimulus maximally conspicuous in multiple dimensions; and even less clear what makes one stimulus more attractive than another. Conspicuous signals minimize the signal-to-noise ratio (Ryan & Keddy-Hector 1992) for perceptual systems that are adapted to a general suite of tasks in the environment [Endler's (1992) sensory drive hypothesis]. Changizi et al. (2006) provided compelling evidence that sensory drive has framed the development of written language. The topology of symbols used in human writing matches that of contour junctions commonly found in natural scenes, even though many of these are more difficult to draw than are many configurations that are more rare in nature.

A host of studies have shown that females prefer more symmetric males in mate choice, although in most cases it is not clear that females attend to natural variation in visual asymmetry (Kirkpatrick & Rosenthal 1994). Artificial neural networks selected to recognize a particular stimulus configuration independent of translation and rotation exhibited strong responses to symmetric signals (Enquist & Arak 1994), presumably because these are more self-similar.

Kenward et al. (2004) used neural networks that mimicked retinas to address selection on repetitive elements in spatial patterns. Ubiquitous scene characteristics like translation, reflection, and occlusion all favored the evolution of repetition, as did the initial presence of a fixed, nonsignaling feature (like an eye), and the presence of edge detectors in the receiver. The evolution of repetition in response to these near-universals of visual communication may help explain the ubiquity of repeated patterns, spatial and temporal, in animal signals.

How might higher-order processing affect attractiveness? In some cases, a major determinant of attractiveness is the number of discrete components; for example, in swordtails, females prefer males expressing a greater number of vertical bars. At one extreme, this could simply be the result of a preference for increased area or perimeter of a particular color; on the other hand, it could reflect a preference based on the number of distinct objects that are perceived.

TOWARD AN INTEGRATIVE BIOLOGY OF COMPLEX VISUAL SIGNALING

“What is it like to be a bat?” Timothy Sprigge's classic question, popularized by Thomas Nagel (1974), provides a compelling metaphor for students of animal

behavior. How is the world perceived by an animal whose primary source of information—echolocation—is so alien to our everyday experience? Because we lack an intuitive understanding of the bat's Umwelt, we are forced to approach this question from the bat's perspective, by physically characterizing echolocation signatures and measuring neural and behavioral responses. This approach has served us well, and though we can never share a bat's frame of reference, we have developed a sophisticated understanding of how bats use echolocation to make sense of their environment.

So what is it like to be an eagle? We rarely ask ourselves what the visual world looks like through the eyes of another species. As humans, our nominal sense of reality is so intertwined with visual perception that it is often difficult to separate the two. We never say "You smell? There's nothing there." The previous paragraph was difficult to write without resorting to visual metaphors like "seeing the world" and "points of view." We intuitively assume that the way we process and perceive spatial and temporal relationships among parts of a visual scene gives us a veridical representation of our environment, that the contrasts and shadings and textures we attend to are the best solution to the complicated engineering problem of empirically measuring the universe. Yet differences among species in ecology, perception, and cognitive architecture dictate that there is as much variation in how animals process visual information as there is in other aspects of their biology. Paradoxically, our visual bias has made this harder to appreciate. Although we have to describe an echolocation signal in terms of decibels and Doppler shifts, we tend to describe spatiotemporal variation in terms of our phenomenological experience rather than in the sensory currency of the animals we study.

In the Future Issues, I suggest some key unresolved questions that could be fruitfully addressed by applying a quantitative perspective to the biology of spatiotemporal signals. An important implication that emerges is that there are nonlinearities in both production and perception, such that small genetic changes could result in major changes in signalers and receivers. The zebrafish *leopard* gene, a putative constituent of a reaction-diffusion system, seems a ripe candidate for comparative study.

Second, attentional mechanisms are likely to produce the most important initial filters of information. Although amply studied in human psychology, and implicitly considered in numerous studies of visual preferences, animal attention has received little scrutiny. We would like to know which components of a visual signal are salient to receivers, and how signals are designed to draw, hold, or divert receiver attention.

The intricacies of animal signals are appealing to us in part because of their exuberance. To what extent are receivers actually attending to this complexity, and how is their perception specified; how do individuals acquire preferences for complex visual stimuli?

Our appreciation of the beauty of the natural world is intertwined with the way in which our visual systems make sense of it. Mechanistic studies of communication have focused almost exclusively on detection, recognition, and discrimination; but what proximate and ultimate forces determine the valence of stimuli? Does Darwin's (1871) "taste for the beautiful" exist, a vocabulary of beauty shared across taxa? We are perhaps fortunate to find the natural world so attractive (though not, evidently,

attractive enough to preserve). The eminent naturalist Alexander Skutch (1992, p. 10) may have put it best: “Whether in the productions of nature or of art, these four—form, color, pattern, and texture—are the elements of which beauty is compounded.”

FUTURE ISSUES

1. How are biases for complex spatial patterns innately specified?
2. What are the major cognitive constraints on pattern learning, and how do they vary by taxon?
3. Do spatiotemporal patterns coevolve with sensitivity?
4. Can small genetic changes lead to qualitative jumps in pattern production and perception?
5. How do ecological constraints on spatial and temporal resolution structure signal design?
6. How does the environment structure the processing of complex visual signals?
7. Is there a relationship between pattern complexity and signal context?
8. How do attentional mechanisms shape the evolution of signals?
9. Is there a broadly shared taste for the beautiful?
10. How much of pattern complexity is meaningful to receivers?

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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