



INVITED PAPER

Von Uexküll Revisited: Addressing Human Biases in the Study of Animal Perception

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Synopsis More than 100 years ago, the biologist Jakob von Uexküll suggested that, because sensory systems are diverse, animals likely inhabit different sensory worlds (umwelten) than we do. Since von Uexküll, work across sensory modalities has confirmed that animals sometimes perceive sensory information that humans cannot, and it is now well-established that one must account for this fact when studying an animal's behavior. We are less adept, however, at recognizing cases in which non-human animals may not detect or perceive stimuli the same way we do, which is our focus here. In particular, we discuss three ways in which our own perception can result in misinformed hypotheses about the function of various stimuli. In particular, we may (1) make untested assumptions about how sensory information is perceived, based on how we perceive or measure it, (2) attribute undue significance to stimuli that we perceive as complex or striking, and (3) assume that animals divide the sensory world in the same way that we as scientists do. We discuss each of these biases and provide examples of cases where animals cannot perceive or are not attending to stimuli in the same way that we do, and how this may lead us to mistaken assumptions. Because what an animal perceives affects its behavior, we argue that these biases are especially important for researchers in sensory ecology, cognition, and animal behavior and communication to consider. We suggest that studying animal umwelten requires integrative approaches that combine knowledge of sensory physiology with behavioral assays.

Introduction

In the early 20th century, the Baltic German biologist Jakob von Uexküll used the term *umwelt* (often translated as “environment” or “self-centered world”) to describe an organism's perceptual experience (von Uexküll 1920, 1934). Based on experiments with echinoids, medusae, arachnids, and other taxa, von Uexküll concluded that animals (by which we mean non-human animals throughout this article) could live in different umwelten even while occupying the same environment, as a result of differences in the sensory information they could perceive. Von Uexküll argued that an animal's perceptual world is primarily dictated by the characteristics of its sensory physiology and neural processing, stating, “The real thing is that there is no real world but as many worlds as species” (von Uexküll 1920, 92–93).

Since von Uexküll's time, physiological and behavioral work has confirmed that certain animals can detect sensory stimuli that we cannot, for example

magnetic and electric fields, infrared and ultraviolet wavelengths of electromagnetic radiation, and ultra- and infra-sound. Biologists now take it as a given that an animal may be capable of obtaining sensory information to which we humans are insensitive. We are, however, less adept at recognizing that some things that humans can perceive are not necessarily perceived in the same way by animals. Such perceptual differences may arise as a result of physiological or cognitive differences, or simply due to the fact that sensory and perceptual systems often filter out information that is irrelevant to an animal. As Rüdiger Wehner put it, animals (and in some cases humans as well) do not solve problems by “resorting to abstract computations performed within three-dimensional Newtonian space, but by adopting approximations, shortcuts, and simple tricks” (Wehner 1987, 512).

For those sensory channels that we do share with animals, the assumption that animals perceive the world the same way we do can in turn influence

experimental design and our hypotheses about the function of stimuli. These biases fall into three categories:

- (1) We make untested assumptions about how sensory information is perceived, based on how we perceive or measure it;
- (2) We may attribute undue significance to things that we ourselves perceive as complex or striking;
- (3) We may assume animals are doing the math, that is, that they perceptually divide sensory stimuli the same way that we do as scientists when quantifying stimuli (e.g., separating color into hue, saturation, and brightness)

Here, we discuss each of these biases in turn, and argue that because most animal behaviors are strongly influenced by what an animal perceives, these biases are particularly relevant for researchers who study sensory ecology, animal behavior, communication, and cognition. Because vision and audition are so central to how humans experience the world, these are the modalities in which the biases we discuss tend to be most common. As a result, the majority of examples we discuss here are visual or auditory, but we attempt to reference other modalities where relevant.

Bias 1: we assume animals perceive sensory information the same way we do

One way that our own perception may bias our hypotheses and predictions is that we often assume that if we can perceive something, an animal perceives it in the same way that we do. There are many factors, however, including aspects of how sensory and perceptual systems have evolved, that can change or limit which attributes of a stimulus are perceptible.

Sensory physiology

A sensory system is characterized by a number of factors, two of which are its sensitivity (the tuning of sensory cells to different stimuli) and its acuity (the fineness with which a sensory system can parse information). When animal and human sensory systems differ in either, animals may not perceive stimuli the way that humans perceive them.

An acoustic example comes from the mating calls of the closely-related toads *Anaxyrus americanus* and *A. woodhousii* (formerly in the genus *Bufo*). When males of these two species occur in sympatry, they sometimes call in the same pond simultaneously to attract mates. Although these calls sound nearly

identical to our ears and look nearly identical under spectrographic analysis, they differ in the time domain, being amplitude modulated at different rates, a feature of the sounds that we attend to less. By recording from neurons in the midbrain, [Rose and Capranica \(1984\)](#) showed that the auditory systems of females of the two species are tuned to different rates of amplitude modulation. Specifically, neurons in the midbrain act as matched temporal filters, meaning that females of each species filter the calls in a way that matches the species-specific differences in amplitude modulation rates. Thus, not only do the two frog species in question perceive the calls differently than we do, but they also perceive different aspects of the calls from one another. In this case, we and toads can both hear male toad calls, but the toads are processing those stimuli differently from how we do.

In the visual domain, the ability to perceive and discriminate colors is important in a variety of behavioral contexts. We differ from many animals in color vision capability (see [Cronin et al. 2014](#), Chapter 7), and it is now widely accepted that we must account for an animal's color vision when studying visually-guided behavior. Though some animals have color vision capability that we do not, such as ultraviolet sensitivity, current evidence suggests that many animals—including non-primate mammals ([Osorio and Vorobyev 2008](#)), crustaceans ([Marshall et al. 1999](#)), and fish ([Schweikert et al. 2018](#))—have mono- or di-chromatic vision, and thus can discriminate fewer colors than we can. As a result, in some cases, colors that appear quite obvious to us (e.g., red) may not be discriminable by a given viewer. This is important but unfortunately often overlooked, for example, in warning coloration, which may appear quite conspicuous to us and many predatory animals, but is not discriminable by many potential prey animals ([Fig. 1](#)). As a result, animals with warning coloration likely effectively advertise unpalatability to potential predators, but should simultaneously remain less conspicuous to potential prey, though this idea is largely untested (but see [Brandley et al. 2016](#)).

Human and animal sensory systems can also differ in acuity. Visual acuity, for example (defined here as the ability to resolve static visual detail), varies by at least four orders of magnitude across species with eyes, with humans and certain raptorial birds having the highest visual acuity ([Fig. 2A](#); reviewed in [Caves et al. 2018a](#)). This means that most animals likely perceive considerably less visual detail than we do ([Fig. 2B](#)). In particular, animals with compound eyes—insects, crustaceans, as well as some chelicerates, annelids, and bivalve mollusks—and those with



Fig. 1 Animals like this Texas coral snake (*Micrurus tener*) display warning coloration that to humans appears red and yellow (top). However, many potential prey of the coral snake, for example small mammals like rats, have dichromatic vision, and thus would not discriminate red from yellow the same way that we do. Image was modified by first converting it to “Lab Color” (CIELAB color space) in Photoshop CS4 (version 11.0.2; Adobe Inc.), and then setting the red–green channel to a single middle gray value. Image from Wikimedia Commons. A color version of this figure is available online.

very small camera eyes tend to have far lower acuity (Land and Nilsson 2002; Caves et al. 2018a). Therefore, we must exercise caution when developing hypotheses about the function of fine-scale pattern elements as potential signals.

As an example from our own research, cleaner shrimps are a polyphyletic group of decapod crustaceans that offer cleaning services to reef fish “clients” by removing ectoparasites and dead skin (reviewed in Losey et al. 1999; Côté 2000). Most cleaner shrimp species are also quite beautiful, displaying color patterns made up of small spots and thin stripes. They often live in pairs or groups (e.g., Fletcher et al. 1995; Bauer 2006; Chapuis and Bshary 2010; Briones-Fourzán et al. 2012; Huebner and Chadwick 2012), so one hypothesis is that their color patterns serve an intraspecific signaling function. In addition, cleaner shrimp interact with a variety of reef fish, which themselves display brilliant colors and complex patterns, leading to a second, related hypothesis that cleaner shrimp might assess client color patterns when deciding whether to engage with them. However, after quantifying the

spectral sensitivity and visual acuity of three species of cleaner shrimp (Caves et al. 2016), we found that all three species are color blind and have low-resolution vision. It is unlikely, therefore, that cleaner shrimp can perceive one another’s color patterns or fine-scale aspects of client color patterns, even at close range (Fig 3A). Overall, we found little support for two hypotheses of color pattern function that were originally based on human visual perception of cleaner shrimp and client fish. Furthermore, behavioral experiments showed that the cleaner shrimp *Ancylomenes pedersoni* will signal to and attempt to clean even simple visual stimuli displayed on a screen, including black and white rectangles, triangles, and circles (Caves et al. 2018b).

As a second example, the diverse and striking color patterns of many reef fish have long presented a puzzle to human observers, since conspicuous coloration may make an animal more visible to predators. Accounting for reef fish visual acuity and the absorption and scattering of light by seawater, however, shows that many of these color patterns are likely only conspicuous, even to predatory fish with relatively acute spatial vision, over short viewing distances (Fig. 3B). Some color combinations that are common among reef fish, such as blue and yellow, even act as camouflage, largely because the acuity of many reef fish is such that the stripes blend together to match the background from distances as short as a few meters (Marshall 2000). Thus, our assumptions about the function of animal color patterns may be biased by our own acute vision.

Perceptual processing

Sensory physiology alone does not entirely predict which stimuli are perceptible or discriminable, because there are also a number of higher-level neural processes that can modify sensory information. One such process is categorical perception, in which an animal’s perceptual system sorts continuous variation into discrete categories. Two features of categorical perception are that a viewer (1) labels a continuous range of stimuli as being the same or different, indicating that they do or do not fall within the same perceptual category, and (2) exhibits increased ability to discriminate between stimulus pairs that come from different categories compared to stimulus pairs that differ by the same magnitude but come from the same category (Harnad 1987). Categorical perception occurs when different stimuli along a continuum are potentially equally discriminable by the sensory mechanism transducing the relevant stimulus, but an animal’s behavior shows they

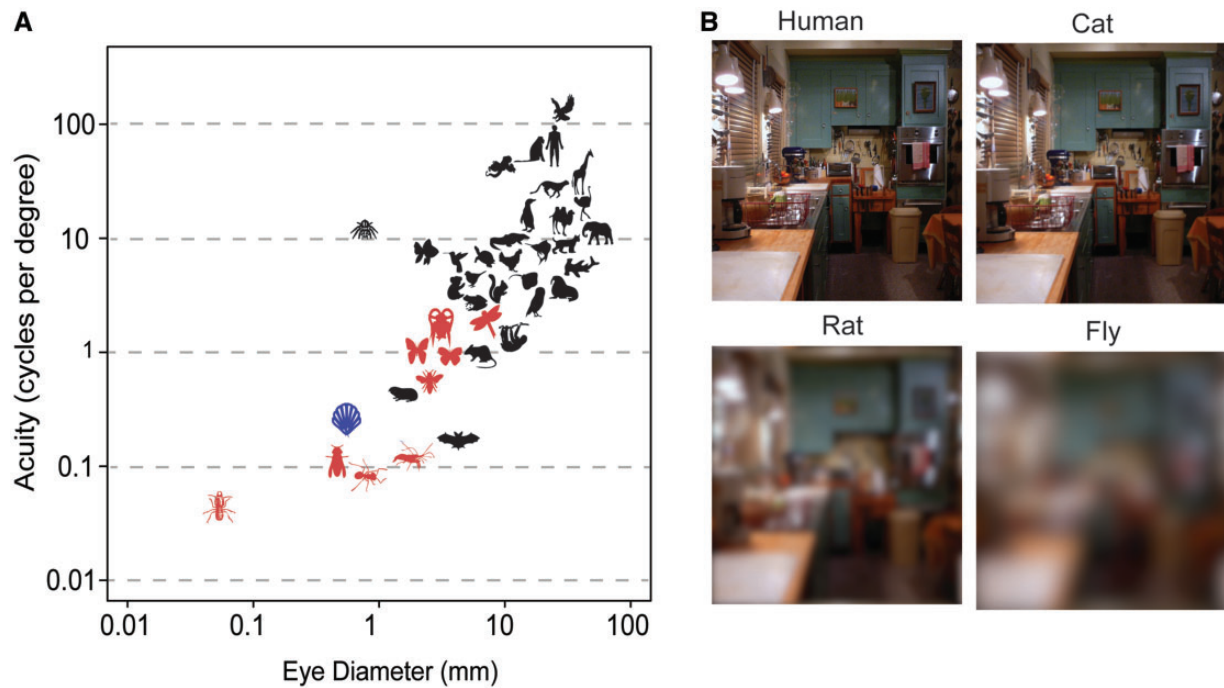


Fig. 2 (A) Acuity varies by at least four orders of magnitude across species with camera (black), compound (red), and mirror (blue) eyes. Acuity is reported in units of cycles per degree, or the number of black and white stripe pairs that can be discriminated within a single degree of visual angle. (B) Differences in acuity across species mean that many animals perceive less spatial detail than humans do, as represented by the four potential kitchen inhabitants shown here. Image credits: (A) Reproduced with permission from [Caves et al. \(2018a\)](#); (B) Wikimedia Commons. Images were modified to reflect a viewer's acuity using the AcuityView R package ([Caves and Johnsen 2017](#)), assuming that the scene of interest is viewed by the highest resolution portion of the retina. Importantly, the Acuity View tool shows what spatial information can and cannot be sampled by a given photoreceptor array, but it does not necessarily reflect what an animal actually sees. This is because a variety of factors can result in details being resolvable beyond what we would expect from the photoreceptors alone, including active sampling via eye movements such as saccades (e.g., [Juusola et al. 2017](#)), and motion (e.g., [Nakayama 1985](#)), among others. A color version of this figure is available online.

are not. Specifically, receivers exhibit an increased ability to perceive those differences when the two stimuli come from different sides of a perceptual boundary.

Categorical perception was first described in the context of human speech ([Liberman et al. 1957, 1961, 1967](#)) and has since been demonstrated in a variety of acoustic signals across taxa (e.g., [May et al. 1989; Nelson and Marler 1989; Wytenbach et al. 1996; Fischer 1998; Baugh et al. 2008; Lachlan and Nowicki 2015](#)). One early demonstration of categorical perception of an acoustic signal came from work on Japanese macaques (*M. fuscata*). Japanese macaques produce “coo” sounds in different behavioral contexts ([Green 1975](#)). Coos produced by juveniles when they have lost visual contact with adults and those produced by adult females during courtship are acoustically quite similar, with the primary difference being when during the call a frequency inflection occurs (i.e., a change from a rising to a falling frequency modulation). On average, this inflection occurs earlier in juvenile coos than in female

coos, but individuals vary in their production of coo sounds, such that across a population there is potential overlap in the timing of juvenile and female frequency inflections. [May et al. \(1989\)](#) demonstrated, however, that macaques categorically, rather than continuously, perceive variation in the position of the frequency inflection relative to call duration. Macaques were trained to press a bar to receive a food reward upon hearing one of the coo types but not the other, and the results showed they only press the bar when the inflection occurs past a certain point in time, indicating a category boundary. In addition, macaques could better discriminate between two coo variants from different sides of the perceptual boundary than between those on the same side of the boundary.

Humans also perceive colors categorically (e.g., [Franklin et al. 2008; Webster and Kay 2012; Yang et al. 2016; Skelton et al. 2017](#)), and recently, categorical perception has been shown to operate in the visual modality in at least one animal as well. In specific, female zebra finches categorically perceive

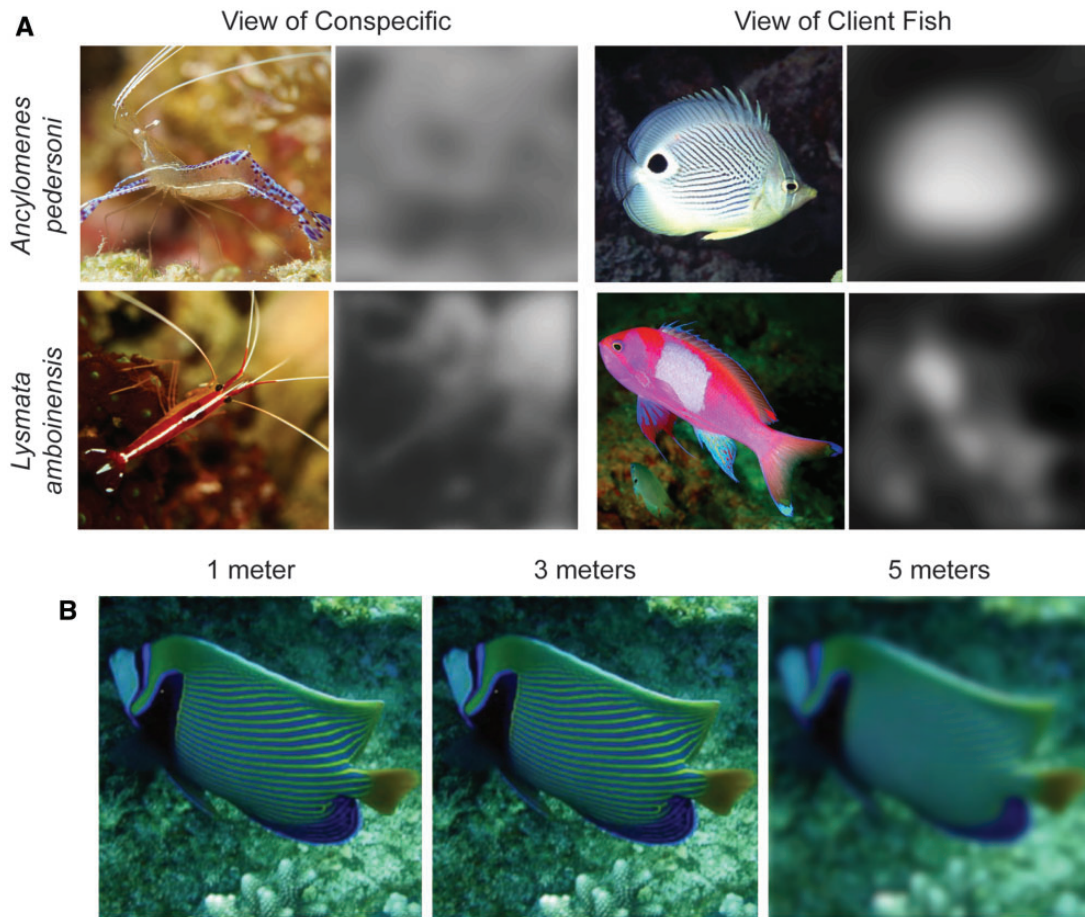


Fig. 3 (A) The cleaner shrimp *A. pedersoni* and *Lysmata amboinensis* have monochromatic vision and low acuity, and likely are not able to perceive the fine scale color patterns of conspecifics (left, viewing distance = 2 cm) or potential client fish (right, viewing distance = 10 cm). (B) The color patterns of many reef fish, like this Emperor angelfish (*Pomacanthus imperator*), appear conspicuous to human viewers, but blend together over relatively short distances when viewed by other reef fish (after Marshall (2000), acuity = 10 cycles/degree). Image credits: (A) modified with permission from Caves et al. (2016); (B) Sönke Johnsen. Images were modified to reflect a viewer's acuity using the AcuityView R package (Caves and Johnsen 2017). A color version of this figure is available online.

an orange-to-red color continuum that parallels color variation in male zebra finch beaks (Caves et al. 2018c), a signal that females assess when choosing mates (Collins and ten Cate 1996; Blount et al. 2003). Female zebra finch color discrimination does improve as colors become more different from one another. However, a large increase in discrimination occurs at a single point along the orange–red color continuum, and finches exhibit increased discrimination between colors from opposite sides of this point as compared with equally different colors from within a category, indicating a boundary between the categories “orange” and “red.” Importantly, each of the colors tested was predicted to be equally discriminable based on the physiology of zebra finch photoreceptors, but behavioral experiments showed that some color pairs were much more

discriminable than others in a pattern consistent with the predictions of categorical perception (Caves et al. 2018c). No studies have yet compared human and animal categorical perception of the same color range.

The phenomenon of categorical perception again illustrates that variation in a trait may not be perceived and acted on by a receiver in a way we might assume based on our own perception of that trait. An implicit assumption in many studies of animal signaling, for example, is that receivers perceive continuous variation in a stimulus continuously. Increasing evidence suggests, however, that many signals may be perceived in a categorical fashion. This in turn may impact how we think about the selection pressure that receivers can place on senders in a variety of contexts from mate choice to aggression.

Bias 2: we may attribute significance to things that we perceive as complex or striking

A second source of bias based on our own perception is that we may attribute significance to stimuli because they appear striking to us. In particular, we sometimes assume that complexity implies conspicuousness, or we assume that stimuli that appear complex or striking to us must serve a communicative function. Just because we think of something as striking or complex, however, does not mean an animal will perceive it as such or attend to it.

As an example, we often think of complex traits as being conspicuous, and thus potentially attracting the attention of a predator. Indeed, Darwin first hypothesized that predation pressure should select for the simplification of traits (Darwin 1871), and in fact predation pressure has been shown to be a key force acting against trait elaboration mediated by sexual selection (Andersson 1994). In several cases, however, signals that we perceive as complex, and thus may assume are conspicuous, are in fact adaptations for making an animal less conspicuous or even camouflaged. Thus, complexity may in some cases exploit aspects of the receiver's sensory systems to make complex traits not perceptible by some viewers.

Neotropical weakly electric fish (order Gymnotiformes) provide a case in point. The ancestral waveform of electric organ discharge in the Gymnotiformes was a monophasic pulse, but three extant families of electric fish have evolved more complex, biphasic pulsed waveforms. Stoddard (1999) found that these biphasic electric organ discharges are less detectable by electroreceptive catfish predators than are the simple monophasic discharges, illustrating that greater complexity does not always make signals more detectable. Similarly, in the visual domain, color patterns that serve as camouflage can often appear remarkably complex to a human viewer, but accounting for predator vision (e.g., Stevens 2007) or cognition (Skelhorn and Rowe 2016) reveals that this additional complexity can actually make an animal more difficult to detect.

As discussed earlier, in some cases, animals may not actually be able to perceive stimuli that we view as complex; in other cases, animals may not attend to the attributes of a stimulus that appear to us particularly striking. An example of this involves the courtship display of male peafowl (*Pavo cristatus* L.). Peacocks are highly ornamented, from their famous train of iridescent tail feathers topped with

eyesspots to the bright coloration on their head, neck, and body to the crest of feathers on their head. In the presence of females, males perform a courtship display, shaking their tail feather train and producing a rattling sound, and changing position relative to the female. Females assess these displays and choose a mate from among several contenders (Petrie et al. 1992). Numerous display components, including the number of eyespots and the length of certain feathers (Manning 1987) as well as various behaviors (Petrie and Halliday 1994; Yasmin and Yahya 1996; Takahashi et al. 2008; Dakin and Montgomerie 2011), all relate to male mating success.

Yorzinski et al. (2013), however, used gazetrackers that closely tracked the area centralis, an area of high retinal ganglion cell density akin to the human fovea to show that peahens selectively attend to only a few components of courtship displays. In particular, female gaze was most focused on the lower train of tail feathers, and surprisingly, peahens only rarely directed the center of their gaze toward other display elements that appear to us to be highly conspicuous, including the head, crest, and upper region of the tail feather train (Fig. 4). Certain display components, including train rattling and wing shaking, seemed to function in directing female gaze and attention. Follow up work showed that peacocks, when assessing rivals, exhibit similar gaze patterns as peahens, but spend more time than peahens looking at the upper eyespots of the tail feathers, suggesting that different display components could have different functions depending on the context of the display and the sex of the receiver (Yorzinski et al. 2017).

Together, these studies illustrate that our own assumptions about which components of a display are important do not always turn out to be what the animal itself is focused on. The fact that animals exhibit selective attention when perceiving a display or evaluating a signal is perhaps not surprising. In the visual modality, some work suggests that attention can only be paid to one focal object at a time, and as a result animals must “decide” where to focus their attention since multiple objects in the visual field compete for visual attention (Desimone and Duncan 1995). More generally, directing sensory attention toward only one stimulus or area might be beneficial, because it may allow animals to respond more rapidly or gather more detailed information than they would if attention was more broadly directed (reviewed in Knudsen 2007; and see Hoke et al. 2017).

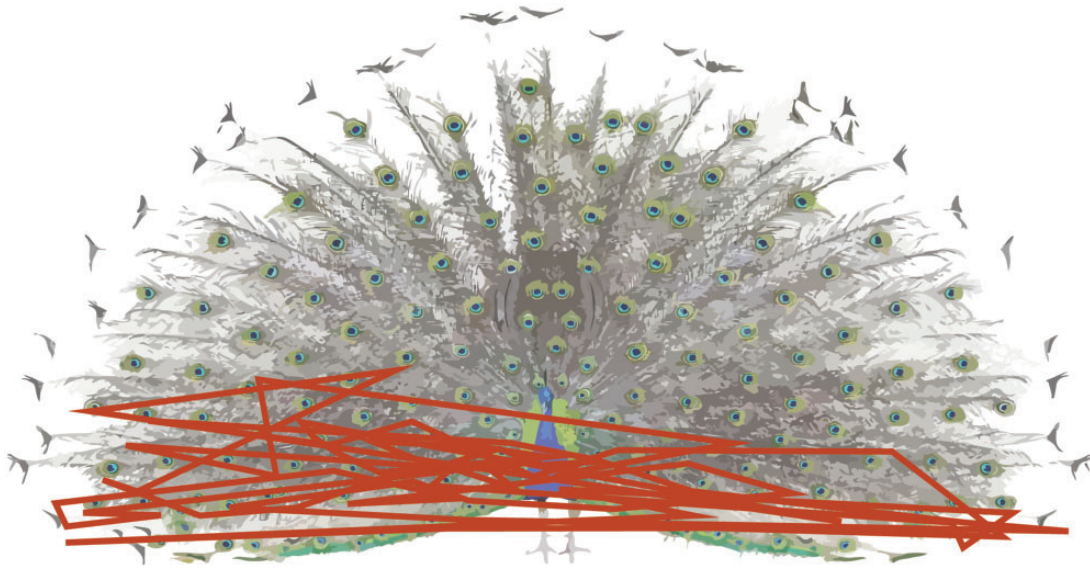


Fig. 4 Example eye tracking path of a peahen during a male display. Redrawn with permission from Yorzinski et al. (2013).

Bias 3: we assume animals are doing the math

A third source of bias in our understanding of animal perception arises from the tools and methods that we use to measure and analyze sensory stimuli. Specifically, we often separately quantify multiple aspects of a single stimulus even if the evidence suggests those aspects are integrated by the animal. Often, however, animals use “matched filters” that filter information at the receptor or sensory organ level. This limits the information that the brain receives from the outside world, but minimizes the need for the brain to perform complex computations (Wehner 1987).

Two examples of this bias occur in studies of color vision and polarization vision. First, we typically describe colors using three parameters: hue, saturation, and brightness. Hue is often what we mean when we say “color,” referring to red, blue, green, and so forth, and it is a function of the shape of the spectrum of the light reflected from it. Saturation is a measure of a color’s “purity”—crudely measured as the range of the spectral values. Pink, for example, is a less saturated version of red, because pink has a higher reflectance in the blue and green portions of the spectrum. Brightness represents the perceived intensity of the stimulus. It has commonly been assumed that many animals employ separate visual pathways for chromatic (i.e., hue and saturation) and achromatic (i.e., brightness) perception (reviewed in Osorio and Vorobyev 2005). As a consequence of this assumption, brightness is often factored out of color studies. Indeed, many color spaces

that are commonly used to describe color discriminability (e.g., Maxwell triangles and tetrahedral color spaces) remove the achromatic dimension entirely (e.g., Kelber et al. 2003; Cuthill 2006). In addition, many researchers quantify hue separately from brightness in studies of animal coloration (as described in Endler 1990). Thus, in selecting experimental stimuli for experiments of color perception, hue and brightness are often dealt with separately, or brightness is held constant.

Recent evidence, however, suggests that there may be interactions between chromatic and achromatic pathways, for example, in insects (Hempel de Ibarra et al. 2001, 2002; Wardill et al. 2012; Schnaitmann et al. 2013), crustaceans (Baldwin and Johnsen 2012), fish (Mitchell et al. 2017), and birds (Jones and Osorio 2004; Lind and Kelber 2011; Mitkus et al. 2017). Indeed our own color perception is such that, at least for certain colors, the perceived hue depends strongly on the brightness (Fig. 5). Together, these studies highlight an important open question in sensory ecology, which is how do hue and brightness combine to give rise to the percept of color (see Kelber et al. 2003; Johnsen 2017)?

By separately quantifying and then separately manipulating different aspects of color, we may be coming to conclusions that do not capture the complete perceptual picture. For example, carotenoids are a class of compound that underlies yellow, orange, and red coloration in many animals. If we test how animals discriminate carotenoid-based colors while holding brightness constant, we may be asking animal questions that are irrelevant in a natural

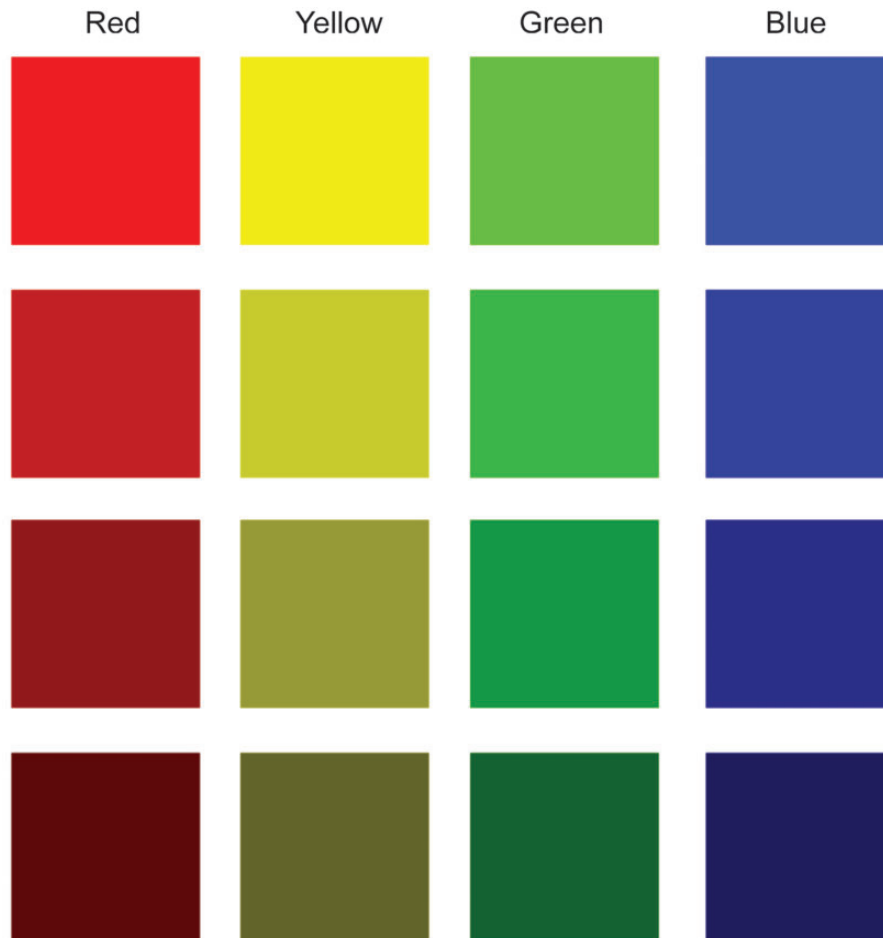


Fig. 5 Red, yellow, green, and blue hues decreasing in brightness from top to bottom. Notice that for yellow, perceived hue depends on brightness, in that bright squares in the yellow column are perceived as yellow, but dark squares appear brown.

context. Holding yellow at the same brightness as red may result in testing perception of a color that is not recognized by an animal as yellow, and is not relevant to natural carotenoid-based coloration. Therefore, when designing experiments, we should give thought to the ways in which our quantification of different aspects of stimuli may not align with how a receiver's perceptual system actually functions.

A similar issue arises in studies of polarization vision. An analogy can be drawn between polarization vision and color vision, in that we can also describe polarization using three parameters: angle of polarization, percent of polarization, and intensity (analogous to a color's hue, saturation, and brightness, respectively; Bernard and Wehner 1977; How and Marshall 2014). In studies of polarization vision, it is common to separately quantify or manipulate angle and percent polarization. For example, Shashar et al. (2004) examined how percent of polarization propagated as a function of distance from a target underwater. How percent of polarization transmits

over distance, however, additionally depends upon the angle of polarization of both the target and the background (Johnsen et al. 2016). Other studies estimate the minimum difference in the angle of polarization that can be perceived by an animal (e.g., Shashar and Cronin 1996; Hemmi et al. 2012; Temple et al. 2012). Importantly, however, the minimum angular difference to which an animal is sensitive depends upon the angles used to test an animal (analogous to how, in constructing a wavelength discrimination function, the minimum wavelength difference an animal can detect depends upon the wavelengths being tested). Using stimuli that relate to the function of the perceptual system is important for understanding how polarization vision operates in a variety of behavioral contexts (Labhart 2016); for example, the ability to discriminate differences in angle of polarization has been suggested to be important in object and predator recognition (Shashar and Cronin 1996; Pignatelli et al. 2011) as well as signaling and communication (Chiou et al. 2007).

Overall, just as with color vision, polarization vision systems do not necessarily divide polarized light neatly into angle and percent of polarization in the way that researchers often do.

Together, previous studies that separately quantify hue and brightness in color vision, or angle and percent in polarization vision, have given us a foundation upon which to build. However, to truly understand how animals perceive stimuli we must consider together different stimulus attributes that might not be separated at the perceptual level.

Addressing our perceptual biases

How can we address the biases that we have discussed above? In general, methods that incorporate animal *umwelten* explicitly into the design of an experiment fall into two classes. First, there are a variety of methods that use information about the physiology of sensory receptors to make predictions about what an animal sensory system should be capable of detecting. For example, the receptor noise-limited model of vision (Vorobyev and Osorio 1998) uses information about photoreceptor spectral sensitivity, relative number of different photoreceptor types, and receptor noise to generate predictions about whether or not two colors should be discriminable by a given receiver. There are also a variety of tools that display sensory stimuli using information about sensory physiology. For example, methods exist to measure color from digital photographs and modify images based on the color vision capabilities of a given receiver (Troscianko and Stevens 2015; Johnsen 2016). If an experiment requires displaying stimuli on a computer screen, there are methods that can adjust the output of a screen to portray color-realistic imagery to animal eyes (Tedore and Johnsen 2017). Beyond color, software programs exist that can erase all spatial detail from a scene that is below the acuity of a given viewer (AcuityView; Caves and Johnsen 2017), or quantify pattern attributes in ways that roughly align with early steps in vertebrate pattern perception (NaturePatternMatch; Stoddard et al. 2014).

As a cautionary note, however, the use of tools and models based on receptor physiology must ultimately be ground-truthed by behavioral assays that directly measure how an animal behaves in response to stimuli. The results of such assays seldom align precisely with predictions based on the physiology of sensory receptors. For example, behavioral discrimination of color in triggerfish does not align precisely with the predicted discriminability based on the receptor noise-limited model of color vision

(Cheney et al. 2019), indicating that the model may be incomplete or involve incorrect assumptions (for a discussion, see Olsson et al. 2018). In studies of birdsong, we tend to use Fourier analysis because our own ears are Fourier analyzers, but behavioral work shows that birds are more sensitive to temporal fine structure than we would predict using classic methods (Dooling and Prior 2017; Prior et al. 2018). Behavioral studies in electric fish have also demonstrated temporal hyperacuity, in that fish can detect temporal differences on the order of microseconds, outperforming what can be achieved by individual receptors (Kawasaki et al. 1988).

Behavioral assays have their own limitations, of course, because they cannot distinguish what an animal perceives versus what it is motivated to respond to. Thus, it is always possible that what appear to be perceptual differences in some assays are actually due to changes in an animal's motivation or to the particular stimuli used (see, e.g., Lahti 2015 for a discussion about using artificial stimuli in behavioral research). Because of this, theory and experiment complement one another, and using an integrative approach that combines the two can yield additional insight and help us design experiments that are confounded as little as possible.

Overall, investigating the perceptual world of an animal is a complicated task. However it is also rewarding, because the *umwelt* provides a foundation for understanding why animals behave the way they do in a variety of contexts, yielding insights into the diversity and function of signals, how receivers exert selection on senders, how animals make decisions, and more. Especially as we broaden the taxonomic scope of behavioral and perceptual research, we will undoubtedly find that some animals inhabit *umwelten* that closely resemble our own, while others inhabit ones that are quite alien. Here, we have discussed cases where predictions based on our own biases have not held up when the perception of the relevant animal is considered, emphasizing instances where animals cannot perceive things that we ourselves can. Nearly 100 years ago, von Uexküll had already begun to write about these ideas, for example noting that the *umwelt* of a tick might consist of only two cues which are relevant in tick food-finding, specifically the odor of butyric acid and the temperature of mammalian blood (von Uexküll 1934). More recently, Wehner wrote that although the perceptual worlds of animals may appear incomplete to us, “to the animals they are always the full solutions to the very problems with which they must contend” (Wehner 1987, 512). Here, we revisit this idea, providing a cautionary tale rather than a set of

conclusions or predictions, and in particular urging readers to consider that animal umwelten need not necessarily be complex, nor very much like our own, to fit the needs of a given animal.

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