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The Evolution of Simplifying Heuristics in Visual Cognition: Categorization, Specialization, and Visual Illusions

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Abstract

Animals live in visually complex environments. As a result, visual systems have evolved mechanisms that simplify visual processing and allow animals to focus on the information that is most relevant to adaptive decision making. This review explores two key mechanisms that animals use to efficiently process visual information: categorization and specialization. Categorization occurs when an animal's perceptual system sorts continuously varying stimuli into a set of discrete categories. Specialization occurs when particular classes of stimuli are processed using distinct cognitive operations that are not used for other classes of stimuli. We also describe a nonadaptive consequence of simplifying heuristics: visual illusions, where visual perception consistently misleads the viewer about the state of the external world or objects within it. We take an explicitly comparative approach by exploring similarities and differences in visual cognition across human and nonhuman taxa. Considering areas of convergence and divergence across taxa provides insight into the evolution and function of visual systems and associated perceptual strategies.

INTRODUCTION

A major visual challenge faced by all animals is the complexity of the visual world. An animal's visual environment often contains far more information than is needed to inform adaptive behavior. Some visual information is essential to an individual's survival (e.g., the location and/or behavior of predators, prey, or conspecifics), while other information is largely extraneous. Animals must therefore contend with a huge amount of visual information and extract only that which is most essential for success. As a result, animals use sensory and/or cognitive heuristics that adaptively reduce the visual complexity of their environment.

This review focuses on two key mechanisms by which animals manage visual information: categorization and specialization. Categorization occurs when an animal's perceptual system sorts continuously varying stimuli into a set of discrete categories (Bornstein 1987). Visual specialization occurs when particular classes of stimuli are processed using cognitive operations distinct from those applied to other stimuli (Maurer et al. 2002, Shettleworth 2009). We review current research suggesting that categorization and specialization are adaptive mechanisms that, on average, allow animals to make faster, more accurate decisions about relevant stimuli. We also review a nonadaptive consequence of the sensory and cognitive heuristics that reduce visual complexity: visual illusions. Visual illusions are produced when perceptual heuristics lead to misestimations of the state of the world and/or objects within it based on a particular stimulus or set of stimuli (the visual illusion).

We provide an explicitly comparative perspective on visual cognition by reviewing commonalities and differences in visual categorization and specialization across species, and we ask what a comparative lens might tell us about both unique histories and shared constraints in the evolution of visual perception. Animal visual systems are incredibly diverse, varying in characteristics including eye number, eye placement, type of photoreceptor cells, spectral sensitivity, and visual acuity (Nilsson 2021). Many species can also perceive visual information that humans cannot. For example, although absent in primates, UV vision is found in a wide range of vertebrates and invertebrates. On the other hand, many species perceive a narrower range of stimuli than do humans; for example, the majority of species have lower visual acuity (ability to perceive detail) than do humans (Caves et al. 2018a). Likewise, and sometimes related to differences in visual function, there is diversity across species in visual cognitive abilities. For example, some species of *Polistes* wasps are able to recognize individual conspecifics based on differences in facial patterning (Tibbetts 2002), whereas other species within the same genus are incapable of facial recognition (Tibbetts et al. 2019a). Understanding similarities and differences between taxa provides important insight into the evolution and function of visual perception.

CATEGORIZATION: A PERCEPTUAL DOWNSAMPLING MECHANISM

To gather and process information efficiently and accurately, perceptual systems often need to extract, enhance, or simplify only that visual information that is relevant to adaptive decision making (Wehner 1987). Examples of such downsampling mechanisms include generalization and categorization. Generalization occurs when animals treat distinct stimuli as similar despite their differences being physiologically discriminable (see Jones et al. 2001). Categorization is a form of generalization wherein stimuli are lumped into classes such that stimuli within a class are treated similarly while, at the same time, stimulus classes remain discriminated from each other. Stimuli may be categorized despite an animal being perceptually capable of discriminating between them. Categories are typically defined around exemplars, i.e., prototypical versions or examples of a category; for example, normally sighted native speakers of American English generally agree on exemplars of color categories (Berlin & Kay 1969, Shepard & Cooper 1992). Generally, the further a stimulus is from an exemplar on a physical continuum (such as a color hue), the less likely it is to be included in the same category. Recent comparative work across species is beginning to reveal convergence in some aspects of stimulus categorization, generalization, and discrimination, while other aspects seem to be adapted to the perception of important stimuli in a given species.

Color perception serves as a valuable case for the comparative study of perceptual processing because color stimuli play important roles in foraging, mate choice, aggression, and other behavioral contexts across a broad array of taxa. Hue forms a continuum, but, given that it can be advantageous to categorize important stimuli into different groups based on hue or other color properties, selection may have acted on perceptual systems to divide the hue continuum into categories. Humans categorize color, identifying colors by name and grouping visible wavelengths into hue sets (e.g., blue, green, or yellow) with definitive boundaries (Berlin & Kay 1969). Animals across an array of taxa, including macaques (Sandell et al. 1979), pigeons (Wright & Cumming 1971), bees (von Frisch 1964), and poultry chicks (Jones et al. 2001), also generalize colors into categories. Across species, there are also similarities in the limits of color categorization. For example, both poultry chicks and humans can interpolate between certain color pairs, such as red and yellow or red and blue, but not between others, such as blue and yellow (Jones et al. 2001). Similarly, just as the human visible spectrum forms a color wheel that curls back on itself at the point where long-wavelength (red) spectral stimuli join with short-wavelength (blue) spectral stimuli via nonspectral purples, the pecking pattern of pigeons trained to identify color categories indicates that their visible spectrum also fits a circular pattern (Blough 1961, Wright & Cumming 1971).

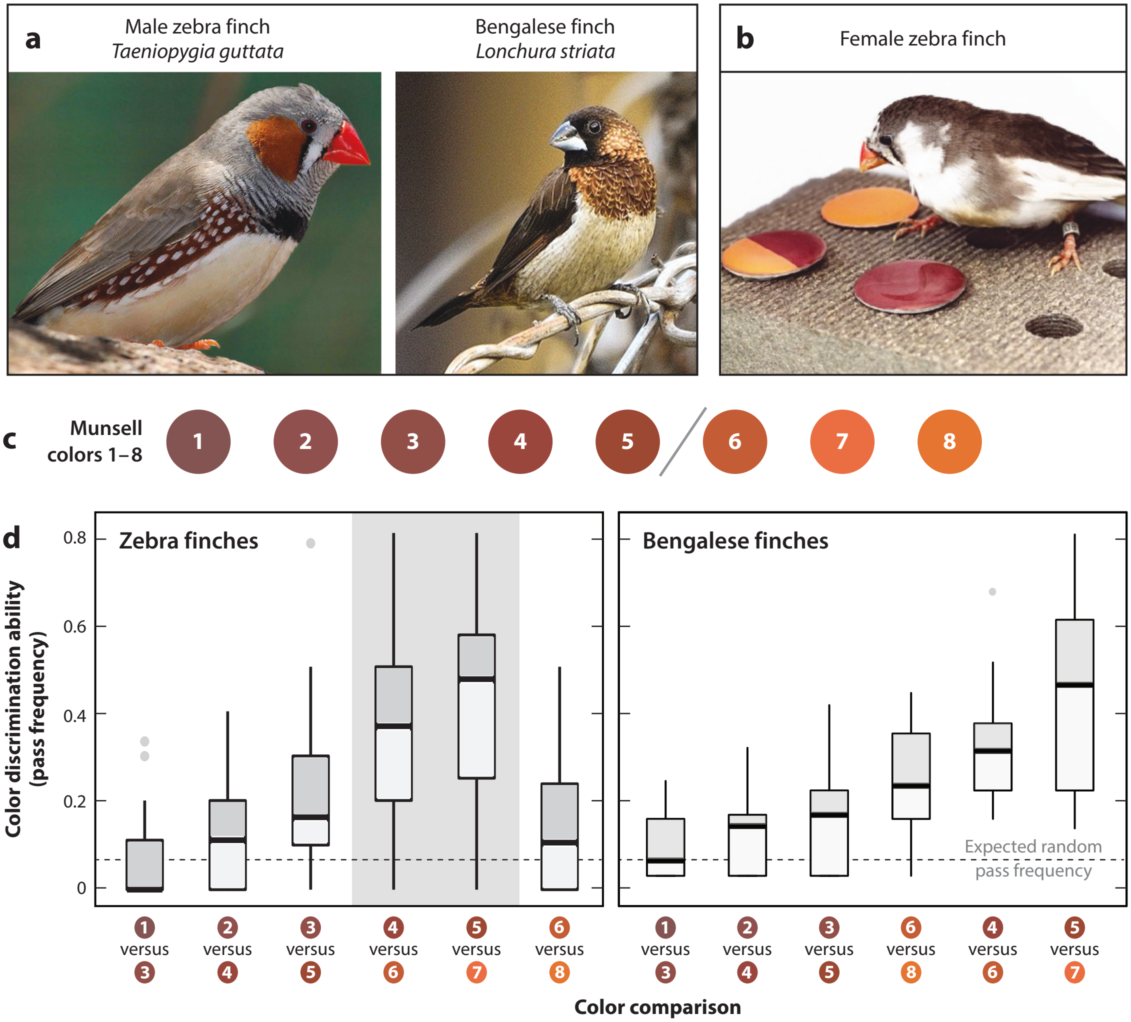
Broadly, green-blue and yellow-green hue category boundaries in humans relate closely to first- and second-stage visual mechanisms, i.e., the wavelength discrimination function of the photoreceptors and the cone-opponent channels, and macaques show partitioning of the photic spectrum into basic hue categories that is similar to that of adult humans (see Siuda-Krzywicka et al. 2019). The category boundaries in bees, pigeons, and chicks, however, differ, corresponding to their own wavelength-discrimination functions, in that regions of relatively good wavelength discrimination correspond closely with perceived hue boundaries, while regions of poor wavelength discrimination correspond with hue categories (Von Helversen 1972, Wright 1972). Thus, basic hue categorization may be a fundamental feature of color perception [as Sandell et al. (1979, p. 635) concluded in their study on macaque color vision, "to see color may be to categorize the spectrum"], but the locations of the boundaries between hue categories may vary with a species' visual physiology.

Most experiments on color categorization make use of operant conditioning paradigms that train animals to identify stimuli that may or may not be relevant to a species' ecology, but color categorization also occurs in nature, as shown by experiments with brood parasites. Brood parasitic birds lay their eggs in the nest of a host, and some species lay eggs that visually mimic those of their hosts, to trick hosts into accepting and incubating the parasitic egg (Davies 2000). Some hosts visually identify eggs as self or nonself and reject foreign eggs based on appearance, providing an ideal natural system in which to probe color categorization in nature. Hanley et al. (2017) tested the responses of two host species, blackbirds (*Turdus merula*) and American robins (*Turdus migratorius*), to foreign eggs that varied along a natural (blue-green to brown) color gradient. They found that hosts categorized eggs as self and nonself based on color, rejecting brown eggs and accepting blue-green eggs, regardless of the perceived hue dissimilarity relative to their own egg.

Categorical Perception: Deemphasizing Differences Within, and Enhancing Differences Between, Categories

Distinct from categorization is a perceptual process known as categorical perception, which was first described in the context of human speech (Liberman et al. 1957) but has been shown to operate across modalities and taxa (Green et al. 2020). Categorical perception occurs when individuals (*a*) categorize, or label, continuous variation along some dimension of a stimulus into categories and also (*b*) exhibit enhanced discrimination of stimuli from different sides of the category boundary compared with equally different stimuli from within the same category (Harnad 1987). Thus, categorical perception differs from categorization because, when a stimulus range is categorically perceived, differences between objects from the same category are perceptually deemphasized, whereas differences between objects from different categories are enhanced (Goldstone & Hendrickson 2010). Humans categorically perceive color, and it was initially assumed that categorical color perception is associated with language (Davidoff et al. 1999, Roberson et al. 2000). However, demonstrations of categorical color perception in zebra finches have recently challenged this view (Caves et al. 2018b, Zipple et al. 2019).

Zebra finches (*Taeniopygia guttata*) (**Figure 1*a***) are small passerine birds that assess color information during mate choice. Male zebra finches have beaks that range across individuals from



(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

(*a*) Male zebra finches (*Taeniopygia guttata*) (*left*) have beaks that range from light orange to dark red across individuals and that are used as a visual signal of quality during mate choice, whereas closely related Bengalese finches (*Lonchura striata*) (*right*) display piebald coloration comprising white, black, and brown. (*b*) A female zebra finch performing a food-reward color discrimination task in which she has been trained to search for food rewards (millet seeds) underneath discs that comprise two different colors. In each trial, females were presented with two bicolor discs and four solid discs; passing a trial occurred when a female flipped both bicolor discs before flipping any solid discs. (*c*) Discs in the food-reward task in panel *b* were made using Munsell paper of colors 1–8, a set of colors that was selected specifically to span the known range of beak color variation in male zebra finches, and which a model of avian color vision predicted to be equally discriminable from one another and, thus, a true color continuum to an avian viewer. (*d*) The rate with which females passed the disc-flipping task (*y* axis) for a given color combination (*x* axis; numbers refer to those in panel *c* and are in the format of color 1 versus color 2) in zebra finches (*left*) was best predicted by a category boundary between colors 5 and 6. Specifically, the ability of females to discriminate color pairs was heightened for color pairs in which colors came from opposite sides of the category boundary (*shaded gray area*), as opposed to equally different color pairs from within the same category (*white background*). By contrast, color discrimination ability in Bengalese finches (*right*) was best predicted by the Michelson contrast between two colors; in the graph on the right, color pairs are ordered by Michelson contrast. In both graphs, the dashed line represents the expected pass frequency if individuals flip discs at random. Data in the graph on the left are taken from Caves et al. (2018b); data in the graph on the right are taken from Caves et al. (2021). The images in panel *a* are (*left*) "Taenipygia guttata" by Peripitus, licensed under Creative Commons Attribution-Share Alike 3.0 Unported License, and (*right*) "Society Finch" by Anil Kumar, licensed under Creative Commons Attribution-Share Alike 4.0 International License. Both images were altered by cropping. The image in panel *b* was used with permission from Ryan Huang, Terra Communications LLC. Panel *d* (*left*) adapted with permission from Caves et al. (2018b) and (*right*) adapted with permission from Caves et al. (2021).

light orange to dark red; beak color is carotenoid based, and females prefer males with darker, redder beaks (Blount et al. 2003, Collins & Ten Cate 1996). Caves et al. (2018b) used a food-reward protocol in which female zebra finches were trained to remove colored discs to access food rewards (**Figure 1*b***). The two halves of the discs were either the same color (solid) or different colors (bicolor), using colors from an orange-red continuum that matched the color of male beaks and that were predicted to be equally discriminable from one another in a color space tailored to avian vision [derived from the receptor noise-limited model of color vision (Vorobyev & Osorio 1998)] (**Figure 1*c***). Only bicolor discs were baited with food rewards, and females were trained to search for food under discs that they perceived as comprising two different colors. By varying the colors comprising the discs and testing the ability of females to remove bicolor discs before removing any solid discs, Caves et al. (2018b) demonstrated both of the criteria that are necessary to demonstrate categorical perception. First, females labeled the colors along this orange-red color continuum as belonging to two discrete categories, as indicated by which color pairs they perceived as distinct. Additionally, female zebra finches were better able to discriminate between equally distinct colors that were from different color categories compared to those that were from the same color category: A female's ability to discriminate colors that differed from one another by a given amount was, on average, approximately 25 percentage points higher when those colors came from different categories rather than the same category (**Figure 1*d***).

Follow-up work (Zipple et al. 2019) used the same protocol described above but with a blue-green color range that has no function during mate choice in zebra finches. As with the orange-red experiments, two color categories were identified in the blue-green range; however, zebra finch females exhibited greater ability to discriminate between colors from the same category, and thus less enhancement of cross-boundary discrimination, than in the orange-red experiment, overall indicating that categorization of blue-green colors is less pronounced. This finding parallels work on human categorical color perception, in that human ability to categorize and discriminate colors is less well defined in the blue-green than in the orange-red range (see, e.g., Purves & Lotto 2011). Thus, species as divergent as humans and zebra finches both exhibit categorical color perception, and there is further convergence in that, in both humans and zebra finches, categorical color perception varies across the spectrum.

Interestingly, however, comparative work in birds suggests that categorical color perception is not a fundamental feature of vision in all species and instead can differ even between closely related species. Bengalese finches (*Lonchura striata*) (**Figure 1*a***) are closely related to zebra finches, and, given the highly conserved spectral sensitivities of the photoreceptors in the family Estrildidae (Hart et al. 2000), they likely have very similar sensory physiology. They differ, however, in that they display no carotenoid-based (orange-red) coloration and instead have characteristic piebald (black, white, and brown) coloration. When the above experiments from zebra finches were repeated in Bengalese finches, labeling tests did not indicate a category boundary, and variation in discrimination of equally spaced color pairs was better explained by the brightness contrast between colors than by color category (Caves et al. 2021) (**Figure 1*d***).

The Evolution of Categorization and Categorical Perception

Why have categorization and categorical perception evolved at all? Sensory systems are predicted to adaptively evolve to specifically provide information about fitness-related stimuli (e.g., signals used during communication, cues used during foraging). The evolution of task- or context-related categorization may arise because categorization can serve to simplify complex tasks. In combination with a decision-making rule, categorization could allow individuals to assign a stimulus to a functional category in the face of variation. For example, the finding that zebra finch females categorically perceive both orange-red and blue-green color ranges, but that the categories are more defined in the orange-red range, aligns with the hypothesis that color perception may be the result of selection on the communicative function of orange-red coloration in the context of mate choice. Mate choice is much simplified if zebra finch females assess male beak color categorically; rather than having to compare small differences in beak color between males, they could instead label males with beaks in the red category as good enough and males with beaks in the orange category as not good enough.

Similarly, brood parasite hosts that categorize eggs by color to decide if they should be accepted or rejected do not exhibit reliable categorization of an artificial gradient of colors (green to purple) that are never found on eggs in nature. However, they do categorize natural egg color variation (Hanley et al. 2017), showing that color categorization is tuned to the important task of detecting and rejecting parasitic eggs. The hosts of brood parasites are under selection to maximize the likelihood of correctly detecting and rejecting a parasitic egg without accidentally rejecting one of their own. Hanley et al. (2017) found that the likelihood that a robin rejects a parasitic cowbird egg from its nest sharply increases as the parasitic egg color shifts along a color continuum from blue-green to brown, demonstrating that the perceptual category boundary sets a threshold for the accept–reject decision.

Beyond color, both humans and damselfish categorically perceive faces (Parker et al. 2020), which are visual stimuli that play an important role in social interactions. For example, humans categorically perceive faces that represent continuous variation across a variety of axes, including race, gender, age, and facial expression (Bülthoff & Newell 2000, Cloutier & Macrae 2007, Fiorentini & Viviani 2009, Levin & Beale 2000). Damselfish (*Pomacentrus amboinensis*) show a similarly categorical response to a continuously morphed set of fish facial patterns that run from conspecific to a heterospecific with similar facial patterning (*Pomacentrus moluccensis*) (Parker et al. 2020). Thus, within a species, selection may act to tune categorization mechanisms to certain stimulus ranges or types that are of natural relevance.

Overall, categorization may reduce the costs associated with processing and comparing signals. These may include developmental and energetic costs associated with the neural machinery necessary to perceive and process information (Sterling & Laughlin 2015) or costs that arise as a result of taking time to sample and compare stimuli, and categorization may facilitate more rapid decision making (see Green et al. 2020).

Opportunities for Future Categorization Research

One long-held view posits that the massive amount of sensory information available to sensory systems is far more than the brain is capable of processing, and perceptual mechanisms such as categorization and categorical perception have evolved to help filter out irrelevant information and enhance relevant information (e.g., Itti & Koch 2000). This hypothesis would be supported by evidence that downsampling heuristics (*a*) vary with the neural cost of downsampling, which could require greater neural complexity or occur at the periphery and thus not require greater investment in cognitive capacity, and (*b*) be positively correlated with environmental complexity or task complexity or speed. An alternative hypothesis is the ecological view of attention (EVA), which holds that limiting sensory information is adaptive regardless of brain capacity, and that perceptual mechanisms evolve to help focus an animal's attention and properly direct its behavior (Gibson 2014, Lev-Ari et al. 2022). The EVA would be supported by evidence that downsampling heuristics are widespread across species and deeply ancestral, with the precise parameters of those heuristics possibly being tuned to a given species' ecology or behavior.

As discussed above, there is evidence showing similarities or convergence in some aspects of perceptual processing across species—for example, in basic hue categorization. However, limited but growing evidence suggests that mechanisms like categorical perception may be adapted to a species' ecology and behavior. Overall, the widespread occurrence of visual categorization across taxa as diverse as primates, birds, and fish suggests that it is often advantageous, or at least not costly, to categorize variation. Moving forward, however, we have much to gain by exploring categorization and categorical perception in additional species. Honeybees (*Apis mellifera*), for example, seem able to generalize between visual stimuli (Benard et al. 2006), but categorization has not yet been demonstrated, and visual perception in invertebrates more broadly is highly understudied compared to vertebrates. By exploring categorization and categorical perception in a wider array of species, we can begin to uncover the generality of these processes, revealing the extent to which their evolution is a basic process in brain evolution or a feature under selection due to a species' ecology and behavior.

VISUAL SPECIALIZATION

Another way in which animals simplify visual information is via visual specialization. Visual specialization occurs when specific stimuli are processed using cognitive operations distinct from those used for other stimuli (Maurer et al. 2002, Shettleworth 2009). Most stimuli are processed using general-purpose (flexible) mechanisms, rather than specialized mechanisms. For example, cups and tables are identified using similar processes, rather than there being a special mechanism used only for cups and a different mechanism used only for tables (DiCarlo et al. 2012, Logothetis & Sheinberg 1996). Flexibility is important because identifying diverse stimuli is necessary for social and ecological success. As a result, there is a great deal of interest in examples of visual specialization, as well as in how and why specialization arises (Gauthier et al. 1999, Kanwisher et al. 1997, Leopold & Rhodes 2010, Parr 2011).

To date, most research on visual specialization has focused on face specialization, spurred by evidence that humans use different mechanisms to recognize face and nonface objects. Humans identify most objects using features such as color, contour, shape, and contrast. In contrast, humans identify faces using configural mechanisms that involve learning both the features of a face and the relationship between features (e.g., distance between the eyes and nose). As a result of

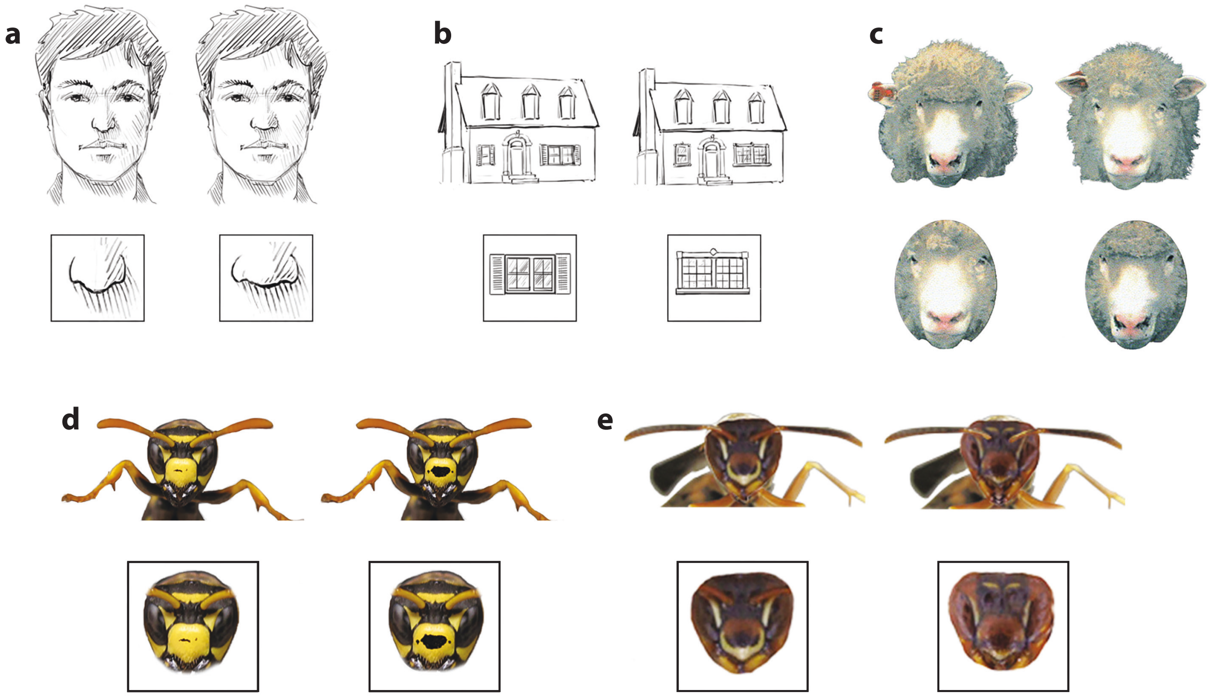


Figure 2

Example of the part–whole method used to test face specialization. (*a*) Humans, (*c*) sheep, and (*e*) *Polistes fuscatus* wasps use conspecific faces for individual recognition and are specialized for discriminating between conspecific faces. As a result, they discriminate parts of faces (e.g., noses, inner faces) less accurately than whole faces. Specialized processing only occurs for conspecific faces. (*b*,*d*) Humans and paper wasps lack specialization for nonface stimuli. (*d*) For example, *P. fuscatus* are not specialized for heterospecific faces, as demonstrated by the fact that *P. fuscatus* are equally adept at discriminating whole and inner heterospecific, *Polistes dominula* face, images. (*b*) Humans are equally adept at discriminating nonface objects, like windows, when they are presented as part of a whole house and in isolation. Panels *a*–*c* created by John Megahan, inspired by Peirce et al. (2000) and Tanaka & Farah (1993). Panels *d* and *e* adapted from Tibbetts et al. (2021).

the specialized, configural mechanisms used for face processing, face recognition and memory are disproportionately disrupted by altering the configuration of a face (Maurer et al. 2002). For example, accuracy at discriminating parts of faces (e.g., noses) is lower when part of the face is presented in isolation rather than in the context of the whole face (i.e., the part–whole effect; see **Figure 2**). In contrast, parts of nonface objects in isolation (e.g., windows in a house) are straightforward to discriminate (Tanaka & Farah 1993) (**Figure 2**). Similarly, recognition and memory for faces are disproportionately impaired when faces are inverted (inversion effect; see Yin 1969). Inversion reduces recognition of nonface stimuli by only 10%, while recognition of faces is reduced by approximately 25% (Carey & Diamond 1977). Specialization for nonface stimuli also occurs, particularly following extensive experience with stimuli that have a predictable configuration (Avargues-Weber et al. 2010, Boggan et al. 2012, Gauthier et al. 2000, Truppa et al. 2010, Vogelsang et al. 2017). Specialization for nonface stimuli is discussed further below.

The neural basis of face recognition has attracted substantial attention (Gauthier et al. 1999, Kanwisher 2000), but we know relatively little about neural specialization in nonhumans. As a result, we focus in this section on behavioral evidence for face specialization, rather than neural mechanisms. Face specialization is the best-studied example of visual specialization in both humans and nonhumans, so it provides a good model for exploring broader questions about selective pressures that may shape the evolution of visual specialization and how specialization develops.

Evolution of Visual Specialization

Much of the early research on visual specialization focused on human faces, leading to questions about whether there is something special about discriminating human faces that requires visual specialization. Subsequent work has shown that human face discrimination does not strictly require visual specialization. A wide range of taxa, including nonhuman primates, honeybees, and crows, can learn to discriminate between human faces without any visual specialization for face discrimination (Brecht et al. 2017, Dyer et al. 2005, Parr 2011). Individuals of these taxa do not naturally pay attention to human faces or identify humans based on facial features, but they can be trained to discriminate between human faces during controlled experiments. When individuals of these taxa are trained to discriminate human faces, they use general object mechanisms for discrimination, rather than using specialized, configural mechanisms. While specialization is not strictly required for face discrimination, current research suggests that face specialization has evolved as an adaptation to facilitate fast, accurate social recognition in taxa where face recognition is essential for social success (Behrmann & Avidan 2022).

Comparative analysis of face recognition and visual specialization across multiple taxa indicates that face recognition has likely shaped the evolution of face specialization. During face recognition, individuals use differences in conspecific faces to identity who is who (Behrmann & Avidan 2022). To date, the data show that both face recognition and face specialization are evolutionarily flexible, rather than strongly conserved across taxa (Burke & Sulikowski 2013, Leopold & Rhodes 2010). Furthermore, the pattern of evolutionary gains and losses of visual specialization indicates that face recognition and face specialization are linked (Behrmann & Avidan 2022). Many taxa that naturally use conspecific faces for social recognition also use specialized mechanisms for assessing conspecific faces; these taxa including humans, some nonhuman primates, a cichlid fish, dogs, sheep, and a paper wasp (Kendrick et al. 2001, Parr 2011, Racca et al. 2010, Tibbetts et al. 2021, Wang & Takeuchi 2017). The distribution of face recognition and face specialization across long-diverged taxa (e.g., primates, dogs, fish, wasps; see Kawasaka et al. 2019, Parr 2011, Tibbetts et al. 2021) indicates that multiple taxa have independently evolved both traits, and that social recognition of faces drives the evolution of visual face specialization. Although current data are compelling, future large-scale phylogenetic comparative analyses across additional taxa will be important to provide a more detailed analysis of the evolutionary history of specialization.

The specific type of social recognition most strongly linked with face specialization is individual recognition. During individual recognition, receivers discriminate a signaler from others based on the signaler's unique characteristics and associate the unique characteristics with individual-specific information about the signaler (Tibbetts & Dale 2007). For example, humans exhibit individual recognition in that they learn each other's unique facial features and respond in a unique way to each individual. Humans, chimpanzees, sheep, fish, and wasps all use conspecific faces for individual recognition and are specialized for identifying conspecific faces (Kendrick et al. 2001, Parr et al. 2000, Tibbetts et al. 2021, Wang & Takeuchi 2017). In some taxa with face specialization, we lack the specific experiments needed to demonstrate true individual recognition. For example, although dogs learn each other's unique faces, they do not exhibit individual recognition because they discriminate only between familiar and unfamiliar dog faces, rather than between individual dogs (Racca et al. 2010). Individual recognition requires that individuals learn to discriminate between different familiar individuals, rather than only identifying whether an individual is familiar or unfamiliar. Future work that tests whether dogs respond in a unique way to specific familiar faces is needed to assess whether dogs use faces only to identify familiar versus unfamiliar conspecifics or for true individual recognition.

Individual recognition may be a key selective pressure favoring the evolution of visual specialization because individual recognition requires fast, accurate discrimination of subtle differences in appearance. Visual specialization is thought to facilitate discrimination of subtle differences between stimuli and may allow faster recognition, better face memory, or more accurate recognition across different viewpoints and contexts than does recognition involving nonspecialized mechanisms (Calder et al. 2000; but see Konar et al. 2010, Pardo-Sanchez & Tibbetts 2022). For all of the taxa in which individual recognition has been demonstrated, social success depends on the ability to rapidly and effectively discriminate between individuals (Sheehan & Tibbetts 2009). The benefits of fast, accurate recognition could select for receivers with cognitive specialization for recognizing and discriminating between faces.

Polistes paper wasps provide a good example of the evolutionary flexibility of face specialization because they are one of the few taxa where specialized face learning has been tested among multiple closely related species with differences in social recognition. *Polistes fuscatus* have variable facial patterns used for individual recognition (Tibbetts 2002) and are specialized for face recognition. *P. fuscatus* excel at recognizing whole faces but are unable to discriminate faces when only part of the face is available (Sheehan & Tibbetts 2011, Tibbetts et al. 2021) (**Figure 2**). In contrast to *P. fuscatus*, two related species, *Polistes dominula* and *Polistes metricus*, lack both individual face recognition and face specialization. *P. dominula* and *P. metricus* learn to discriminate faces based on specific features, rather than specialized, configural processes (Sheehan & Tibbetts 2011, Tibbetts et al. 2021). The pattern of face specialization and social recognition in *Poliste*s paper wasps indicates that face specialization is evolutionarily flexible, and individual face recognition may be a key factor influencing the evolution of face specialization.

Although current data indicate that face recognition plays an important role in the evolution of visual specialization, other types of visual discrimination may also select for specialization. Specialization is particularly likely when (*a*) receivers must discriminate fine differences between predictable stimuli, and (*b*) the stimuli have high social or ecological importance such that accurate discrimination grants a strong selective benefit to receivers. There are interesting hints that sophisticated global visual processing mechanisms exist in a range of taxa that may reflect visual specialization that evolved in nonface contexts (Truppa et al. 2010). For example, pollinators are specialized for assessing flowers (Howard et al. 2021a), and honeybees process complex, nonface patterns in a holistic way (Avargues-Weber et al. 2010). Future work examining global processing mechanisms in diverse taxa presents an exciting opportunity to expand our understanding of the evolution of visual specialization for socially and ecologically relevant nonface stimuli.

Overall, future research on visual specialization may benefit from an explicitly evolutionary approach that considers the natural behavior and selective pressures experienced by each species. To date, research suggests that visual specialization is evolutionarily flexible and more strongly influenced by a species' behavior than by a shared evolutionary history (Behrmann & Avidan 2022, Tibbetts et al. 2021). As a result, species that rely on individual face recognition are likely to be more useful models for studying face specialization than species that lack individual face recognition (Rossion & Taubert 2019). In addition, while face specialization is important in humans and some nonhuman animals, specialization for nonface stimuli is likely to be more widespread than is currently appreciated. Future studies focusing on nonface stimuli that are essential for an animal's social and ecological success are likely to identify additional examples of visual specialization (e.g., pollinator specialization for assessing flowers).

Development of Visual Specialization

There has been considerable debate about the role of experience in the development of visual specialization (Kanwisher 2000, McKone et al. 2007). In the case of face specialization, some argue that the apparently special aspects of face processing arise during development because of extensive experience with faces, rather than because selection has favored the evolution of face specialization (Diamond & Carey 1986, Gauthier et al. 2000). However, answering the question of whether experience is required for specialization does not allow us to draw any conclusions about whether specialization is an adaptation to facilitate recognition. Developmental and evolutionary perspectives provide separate, nonconflicting ways of addressing a biological question. Tinbergen (1963) famously described four complementary categories of explanations for behavior, including adaptive function, development, phylogenetic history, and physiological mechanisms. Explanations in different categories are complementary. As a result, selection could favor the evolution of face specialization to facilitate fast, accurate face recognition regardless of the developmental mechanisms that influence how specialization arises during an animal's lifetime.

Specialization influenced by experience. Both innate differences and experience can influence the development of specialization (Gauthier et al. 2000, McKone et al. 2007). In taxa with visual specialization, current data indicate that there are early differences in the response to specialized versus nonspecialized stimuli. For example, newborn humans and rhesus macaque monkeys show spontaneous preference for face-like stimuli over nonface objects (de Haan et al. 2002, Sugita 2008). The inherent attraction to faces transitions to visual specialization as individuals age and gain social experience. For example, human use of specialized holistic processing mechanisms continues to improve over childhood and adolescence (Pascalis et al. 2005, Richler & Gauthier 2014). Experimental work in *P. fuscatus* wasps illustrates that social experience, rather than aging, is key to the development of specialized face processing (Pardo-Sanchez & Tibbetts 2022). Two-week-old wasps with normal social experience discriminate between conspecific faces using specialized, holistic processing mechanisms. Two-week-old wasps with limited social experience use nonspecialized, featural mechanisms for face recognition. One-week-old wasps with normal social experience are just beginning to develop specialized face recognition. Wasps that lack social experience are unable to discriminate between conspecific faces using either featural or holistic mechanisms (Tibbetts et al. 2019b). It is notable that only 2 weeks of experience is sufficient for face specialization in wasps, while face specialization in humans involves years of experience. The difference in required experience may be influenced, in part, by the different lifespans of wasps (a maximum of 1 year) and humans. In future work, it will be interesting to test if the type and amount of experience needed for specialized processing varies across taxa that have different lifespans and social interactions.

Given that normally developing animals gain experience with conspecifics as they mature, it is not surprising that experience is involved in the development of face specialization. What is perhaps more surprising is that the same amount of experience leads to specialization in some situations but not others. For example, experience allows *P. fuscatus* to develop specialization for the faces of conspecifics and one heterospecific that is closely related to *P. fuscatus* (*P. metricus*) but not another heterospecific that is more distantly related to *P. fuscatus* (*P. dominula*) (Tibbetts et al. 2019a). Two factors seem to influence whether experience leads to specialization: the inherited cognitive architecture of the receiver and the characteristics of the stimuli.

Specialization influenced by inherited cognitive architecture. One important reason that the capacity for visual specialization differs among species is that the inherited cognitive architecture of the receiver also differs. Some species have inherited mechanistic architecture encoded in the genome that facilitates the development of specialization. While comparative work indicates that the capacity for specialization is inherited, more research is needed to assess the precise genetic underpinnings of specialization. The genetic capacity for specialized cognitive skills likely evolves in response to specific ecological or social demands, such as social benefits associated with accurate individual face recognition (Behrmann & Avidan 2022, Leopold & Rhodes 2010, Parr 2011). For example, taxa including humans, nonhuman primates, and *P. fuscatus* wasps are inherently attuned to faces and rapidly develop specialization with normal experience (Leopold & Rhodes 2010, Pardo-Sanchez & Tibbetts 2022, Parr 2011). Cognitive architecture for specialization may also occur without direct selective benefits in taxa with a shared evolutionary history. Traits that provide no selective benefit can persist for many reasons, for example, if they are low cost or if they are plastic traits that are not expressed as phenotypic differences in the current environment (Lahti et al. 2009). Plastic traits are traits whose expression differs based on the environment (West-Eberhard 2003). Unexpressed plastic traits may not be subject to direct selection except for costs associated with maintaining plasticity, so they are often more persistent than other traits. Current work indicates that visual specialization is plastic and arises through experience (Howard et al. 2021a, Pardo-Sanchez & Tibbetts 2022, Pascalis et al. 2005). As a result, the genetic capacity for visual specialization may persist as an unexpressed trait in lineages where specialization is not beneficial.

Polistes wasps provide an interesting example of how the same environment can lead to differences in specialization, likely based on differences in inherited cognitive architecture. Both *P. metricus* and *P. dominula* naturally lack individual face recognition and face specialization for conspecific and heterospecific faces (Sheehan & Tibbetts 2011, Tibbetts et al. 2021). When reared with *P. fuscatus*, *P. metricus* begin to develop some specialization for *P. fuscatus* faces, as evidenced by the fact that they discriminate whole *P. fuscatus* faces better than experimentally altered *P. fuscatus* faces (Tibbetts et al. 2019a). In contrast, *P. dominula* reared with *P. fuscatus* do not develop visual specialization for discriminating heterospecific faces (Tibbetts et al. 2019a). One reason for the difference may be that *P. metricus* is closely related to *P. fuscatus*, so *P. metricus* may share unexpressed mechanistic architecture for face specialization. *P. dominula* is more distantly related to *P. fuscatus*, so it may lack the inherited capacity for specialization. Future developmental experiments in additional taxa will be useful to learn more about nonexpressed capacity for specialization across taxa.

Specialization influenced by stimulus characteristics. Stimulus characteristics also influence the development of visual specialization. Stimuli are more likely to be processed using specialized, configural mechanisms when features are predictably arranged with variation in specific areas (Avargues-Weber et al. 2010). For example, human faces have a predictable arrangement (eyes above nose above mouth). Face variation occurs in the size and shape of features, as well as their spacing (**Figure 2**). In paper wasps with visual specialization for conspecific faces, wasp faces vary in brown, black, and yellow coloration in four consistent facial areas (clypeus, frons, inner eye, and outer eye; see **Figure 2**). Similarly, many bee-pollinated flowers have centrally symmetric, star-like configurations that may facilitate specialized learning of flowers (Howard et al. 2021b, Lehrner et al. 1995).

Predictable configuration can also allow specialization for novel stimuli. For example, humans develop specialization for artificial stimuli called greebles with sufficient experience (Gauthier et al. 1999, Kanwisher 2000). Greebles are symmetrical cylinders with four protruding parts that differ in both shape and configuration. At first, there were questions about whether humans are truly specialized for faces if face-selective mechanisms can be used for nonface stimuli like greebles (Gauthier et al. 1999). Subsequent work suggests that experience can lead to specialization for novel stimuli when the stimuli possess a sufficiently face-like configuration to trigger face-selective visual processes (Gauthier et al. 1999, Kanwisher 2000). The predictable organization facilitates categorization and visual search because it is straightforward for receivers to focus on the most informative visual features (Avargues-Weber et al. 2010). Therefore, certain novel stimuli can be processed using specialized mechanisms when the stimuli have configurations that coopt preexisting processes.

Paper wasps provide another example of how stimulus characteristics influence the development of visual specialization (Tibbetts et al. 2019a). *P. fuscatus* wasps naturally have both individual face recognition and face specialization for conspecific faces but not for the faces of heterospecific *P. metricus* and *P. dominula* wasps. Notably, experiences with two different species from the same genus have very different effects on face specialization. *P. fuscatus* reared with *P. metricus* show some evidence of early specialization for *P. metricus*, as they discriminate whole *P. metricus* faces more accurately than experimentally altered *P. metricus* faces. However, *P. fuscatus* reared with *P. dominula* do not become specialized for *P. dominula* faces. One reason may be that *P. metricus* and *P. fuscatus* have a relatively similar appearance, while *P. dominula* look quite distinct. Therefore, experiences with two different, related species have very different effects on face specialization, inducing specialization for one type of conspecific face but not the other (Tibbetts et al. 2019a). To date, it is clear that stimuli configuration influences specialization, but it is difficult to predict a priori whether stimuli will trigger the mechanistic architecture for specialization. Using development experiments where receivers are given experience with multiple different types of stimuli is one way to test how receiver mechanistic architecture interacts with stimuli characteristics to influence specialization.

Specialization and Phenotypic Plasticity

The literature on phenotypic plasticity provides a useful framework for thinking about the development of visual specialization. Phenotypic plasticity is the ability of a given genotype to produce a range of different phenotypes under different conditions (Pigliucci 2005, West-Eberhard 2003). The capacity for plasticity evolves in response to selection such that the type and amount of plasticity varies across taxa. For example, some taxa are highly plastic such that variation in nutrition strongly influences their phenotype, while other taxa are less plastic such that variation in nutrition has less effect (West-Eberhard 2003). In addition, the developmental environment influences the pattern of plastic changes. For example, some nutritional changes have stronger and more consistent effects than do other nutritional changes. Consistent with our understanding of phenotypic plasticity, experience influences the extent of visual specialization (Gauthier et al. 2000, McKone et al. 2007, Pardo-Sanchez & Tibbetts 2022), indicating that visual specialization is likely a plastic trait. The capacity for plasticity varies across taxa such that the same amount of experience can lead to different patterns of visual specialization in different species (Gauthier & Bukach 2007, Tibbetts et al. 2019a). Furthermore, different taxa require different types and amounts of experience to develop specialization (Tibbetts et al. 2019a). Although research on visual specialization is rarely framed in terms of phenotypic plasticity, the literature on phenotypic plasticity may provide a valuable way to extend and conceptualize research on the development of visual specialization.

VISUAL ILLUSIONS

One clear theme emerging from the sections above is that visual cognition often evolves to simplify the interpretation of incoming stimuli to enable adaptive actions. Simplifying heuristics can be selected for if they are beneficial most of the time while occasionally generating perceptual errors (so long as such errors do not have dire fitness consequences). Thus, the evolution of visual cognition can sometimes lead to misrepresentations of the world, a situation brought into sharp relief by visual illusions. Researchers have often employed experimentally generated visual illusions to explore the mechanisms underlying visual cognition (and the limits of such mechanisms). However, visual illusions themselves may also evolve in the natural world to exploit loopholes in visual perception. Such illusions may benefit signalers, even at a cost to receivers, so long as these costs do not outweigh the benefits of retaining the visual heuristic in other contexts. This phenomenon, in which a signaler benefits by inducing a behavior on the part of a receiver that benefits the signaler but not the receiver, is called sensory exploitation. These types of sensory exploits are now known to be widespread in the animal kingdom, from courtship signals that resemble preferred food items (Rodd et al. 2002) to feints that provoke escape responses in prey that are actually useful to predators (Jablonski 1999).

In this section, we provide a cursory review of past work on the perception of visual illusions in nonhuman animals. Much of the work on visual illusions in animals has tested illusions already known to work for human visual perception (for a comprehensive review, see Kelley & Kelley 2014). While the results have provided striking evidence that nonhuman taxa share some visual heuristics with humans, we argue that this approach of starting with human-based visual illusions foregoes a richer opportunity, namely, predicting visual illusions that might occur for animals but for which there is no precedent in human vision. We argue that extending visual illusion research beyond human-based illusions has two main benefits. First, by working from first principles to predict nonhuman illusions, we can extend the utility of work on visual illusions to aspects of animal visual cognition that have no exact counterparts in our own. For example, do *Polistes* wasps experience illusory faces (i.e., wasp-specific pareidolia) based on their unique form of face specialization? Second, by understanding novel ways in which animals might experience illusions, we open up the opportunity to identify extant visual signals that might have evolved for their illusory benefits to signalers. For example, do nonrewarding (i.e., parasitic) flowers sometimes attract pollinators based on visual illusions unique to pollinator visual processing? The latter may offer exciting new inroads into explaining the diversity of visual signals and the novel functions that they might provide.

Several visual illusions originate from heuristics that simplify size estimations through the use of contextual visual cues. For example, Ebbinghaus and Delboeuf illusions reveal how the size and position of surrounding objects can lead to misestimations of the size of a focal stimulus. In the Ebbinghaus illusion (**Figure 3*a***), a central dot is perceived by humans as being smaller if it is surrounded by larger dots, in contrast to when the same dot is surrounded by smaller dots. Empirical work has shown that the Ebbinghaus illusion is perceived in this way by domestic chicks (Rosa Salva et al. 2013), bottlenose dolphins (Murayama 2012), and guppies (Santacà et al. 2022) but has the inverse effect in pigeons (Nakamura et al. 2008) and dogs (Byosiere et al. 2017) and seemingly no effect in baboons (Parron & Fagot 2007). This variation in illusory perception is thought to be a result of species-specific differences in the use of either contrast heuristics (whereby differences between objects are overemphasized) or assimilation heuristics (whereby similarities between objects are overemphasized). Researchers have extended these findings to argue that context-based size illusions may be exploited by signalers to their benefit. For example, Gasparini et al. (2013) demonstrated that, when male guppies court females, they preferentially choose to surround themselves with males with smaller ornaments, a choice that may induce an Ebbinghaus-like effect on female assessment of the focal male's ornament size. Similarly, Callander et al. (2013) demonstrated that male fiddler crabs are perceived by females as more attractive when they are surrounded by smaller males. Whether other uses of Ebbinghaus illusions (or inverted Ebbinghaus illusions) have evolved in the animal kingdom remains an exciting area of inquiry.

Illusory contours, i.e., the perception of edges in the absence of visual contrasts that would directly define an edge stimulus, make up another common class of visual illusions that occur in

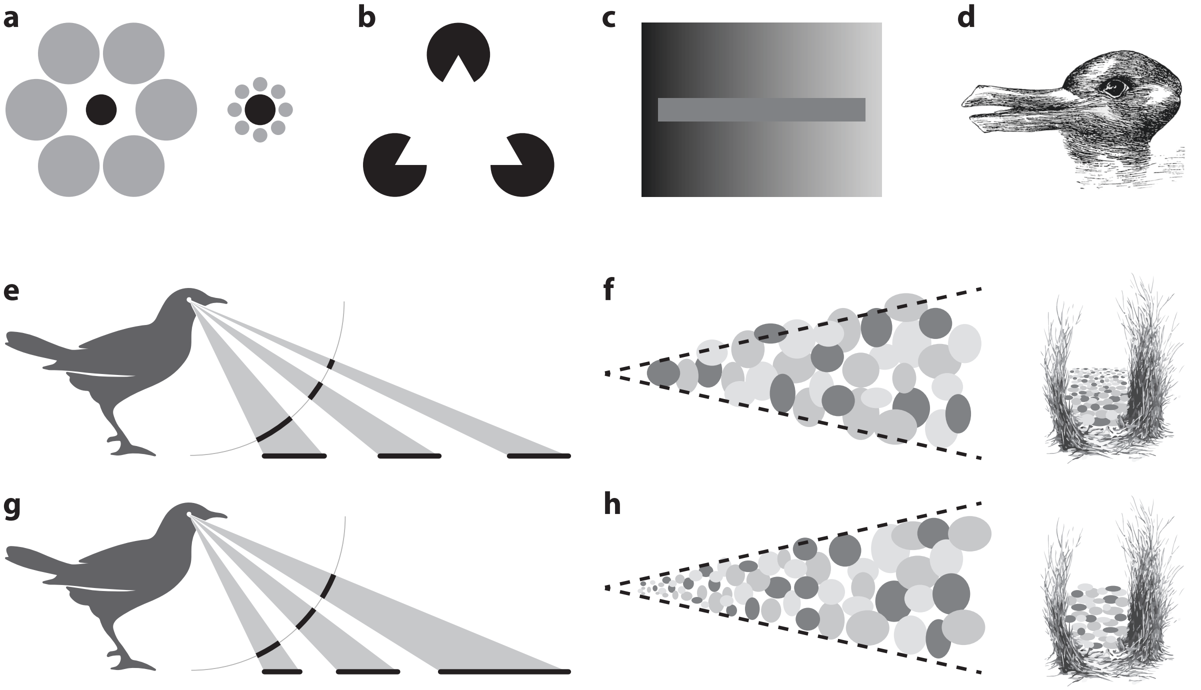


Figure 3

(*a–d*) Examples of visual illusions based on human visual cognition, including (*a*) the Ebbinghaus illusion, where the central dot appears smaller when it is surrounded by larger dots compared to when it is surrounded by smaller dots; (*b*) the Kanizsa triangle, which creates the illusion of a bright triangle in the center via inducing illusory contours; (*c*) the simultaneous brightness contrast illusion, where the central, uniformly bright rectangle appears to change in brightness based on the brightness of the surrounding visual field; (*d*) and the rabbit-duck illusion, an example of a bistable stimulus illusion. (*e–h*) An explanation of a forced perspective illusion produced by male great bowerbirds (*Ptilonorhynchus nuchalis*). Male great bowerbirds arrange uncolored objects in the court of their bower in a size gradient with smaller objects closer to the female viewer than larger objects. This changes the typical viewing experience, (*e*) where same-sized objects appear smaller the farther away they are from the female, (*f*) which would make for a perceived size gradient across the bower court, replacing it instead with (*g*) a forced perspective illusion where (*h*) the perceived size of objects does not change across the female's visual field. Panels *e* and *f* adapted from Endler et al. (2010) and Kelley & Endler (2012a), respectively.

humans. These illusions are thought to arise from perceptual heuristics related to object detection and boundary completion. For example, Kanizsa triangles (**Figure 3*b***) produce the illusion of a bright triangle via the use of fragmented Pac-man-like stimuli, none of which fully outline the perceived shape. Research in nonhuman animals has revealed that illusory contours such as Kanizsa figures are perceived by cats (Smith et al. 2021), mice (Okuyama-Uchimura & Komai 2016), goldfish (Wyzisk & Neumeyer 2007), cuttlefish (Zylinski et al. 2012), and bees (Horridge et al. 2022) but not rats (Minini & Jeffery 2006). This taxonomic diversity suggests a general benefit of heuristics that support shape detection and boundary completion during object perception, perhaps especially in spatially complex environments where shape-diagnostic edges may be interrupted by visual obstructions (Peterhans & Von Der Heydt 1991). Researchers have yet to truly explore whether animal signals have evolved that induce perception of illusory contours. However, disruptive coloration is a common form of camouflage thought to impede perception of body shape through high-contrast patterns that obscure body contours and/or create false edges (Troscianko et al. 2009). Understanding how disruptive coloration might interact with the heuristics responsible for illusory contour perception could produce novel insights into the evolution of this common antipredator strategy (for work in this area using human observers, see, e.g., Adams et al. 2019).

Another class of visual illusions found in humans involves visual (mis)perceptions of brightness and hue. Many of these illusions arise because visual systems tend to emphasize perception of relative differences in brightness, chromaticity, and/or hue, rather than absolute measures of photon flux. In most adaptive contexts, information about relative differences in the color or brightness of objects or locations is more important for guiding behavior than is absolute quantification. In fact, researchers have argued that color vision itself may have arisen in part to compensate for large fluctuations in ambient light in environments, such as those found in the intertidal and epipelagic marine environments thought to be important in the Cambrian origins of vision itself (Maximov 2000). One common visual illusion that takes advantage of errors in brightness estimation as a result of localized, relative estimates of brightness is called simultaneous brightness contrast. In this illusion, gray or colored patches with equivalent luminance are perceived as being different in brightness due to the influence of local image cues (**Figure 3*c***). Evidence for simultaneous brightness contrast has been reported in butterflies (Kinoshita et al. 2012), reef fish (Simpson et al. 2016), guppies (Agrillo et al. 2016), and macaques (Huang et al. 2002), suggesting that diverse taxa respond to local differences in brightness in functionally similar ways. However, the underlying mechanisms for these illusions are not well understood even in humans (Sinha et al. 2020), and it seems unlikely that these mechanisms are shared across the range of taxa listed above. Thus, the observation of evolutionary convergence in perceptual mechanisms such as color constancy and localized brightness estimation suggests that these may represent common demands on visual systems, and therefore, that the opportunity for visual illusions related to these processes may be widespread and, perhaps, exploitable. One possible place to look for such visual illusions would be in situations where lighting varies dramatically, and animals have some capacity to select the lighting conditions that they use during communicatory displays. For example, in both fish and birds, males preferentially court in lighting environments that will most enhance their within-pattern contrast (Endler 1991, Endler & Thery 1996, Heindl & Winkler 2003). Whether courtship location choices are made to take advantage of beneficial misestimations of signals by receivers has yet to be explored.

One last class of visual illusions worth remarking on consists of bistable (or multistable) stimulus illusions. These illusions, which form when multiple visual percepts can arise from the same stimulus, are important because they highlight a perceptual challenge faced when an individual is presented with ambiguous stimuli (Eagleman 2001). Classic human-based examples of bistable illusions include the Rubin vase (in which an image can be interpreted either as a vase or as two human profiles facing each other), the Necker cube, and the rabbit-duck illusion (**Figure 3*d***). Often, these illusions play on simplifying visual heuristics that discriminate an object from its background (Rubin vase), reconstruct three-dimensionality from ambiguous two-dimensional information (Necker cube), or attempt to properly segment and classify ambiguous arrangements of recognizable features (e.g., rabbit ears versus duck bills). To our knowledge, no research has sought to explore responses to human-based bistable illusions, such as the Rubin vase or rabbit-duck illusion, in nonhuman species. However, these illusions are related to a more general phenomenon called perceptual rivalry, in which two perceptual interpretations of the world appear simultaneously (in rivalry), and the viewer must resolve the resulting ambiguity (Carter et al. 2020). Evidence from organisms ranging from insects to fish and reptiles to primates indicates that a wide variety of animals engage with and respond to perceptual rivalry (Carter et al. 2020), suggesting that these animals may also be susceptible to bistable illusions. However, even imagining what such illusions might look like for nonhuman animals (e.g., what the correlate of a rabbit-duck illusion would be for a fruit fly) is a potentially productive, if difficult, challenge.

In concluding this section, we would like to return to a point made above, now well illustrated by the overview in this section, namely, that most research on visual illusions in nonhuman animals has borrowed from visual illusions known from human visual perception. Clearly, this approach has been productive, and it offers inroads into the ways in which aspects of human vision are broadly conserved and/or converged upon in nonhuman taxa. The fact that so many animals share elements of visual cognition with humans implies a long evolutionary history in which the utility of these simplifying heuristics has outweighed the cost of the occasional misrepresentations of the world (i.e., illusions) that they produce. There are also widespread opportunities for signalers to exploit common loopholes in visual perception to their benefit (e.g., baffling predators or inducing favorable responses from prospective mates). We encourage efforts to understand these examples, which may provide exciting new interpretations of extant diversity in animal (and plant) signaling.

However, we need not expect that all visual illusions experienced by animals are shared by our own visual percepts. Instead, it seems reasonable that animals experience visual illusions based on their unique ways of visually perceiving the world. Pursuing this exciting possibility would require us to build from first principles of nonhuman visual perception, including evidence for simplifying heuristics and perceptual downsampling that might be prone to misestimations of the world. For example, how might careful selection of lighting conditions result in misestimations of male plumage brightness or chromaticity favorable to the courting male? How might perceptual ambiguities around depth cues be used by prey to avoid or frustrate predation attempts? Could animal color patterns create bistable illusions that confuse or captivate intended receivers, to the signaler's benefit? These and related questions offer the chance to open up a new world of exploration of the unique perceptual realities of nonhuman taxa.

One promising place to initiate this work is in the context of courtship displays, which are often under selection to produce perceptual experiences that garner interest and/or extend mating interactions in ways that benefit the signaler. Indeed, one of the best examples of the evolution of a visual illusion in an animal display comes from the courtship display of male great bowerbirds (*Ptilonorhynchus nuchalis*) (Endler et al. 2010; Kelley & Endler 2012a,b). In bowerbirds, males create elaborate, architecturally sophisticated bowers that serve as the stage for their dynamic courtship routines. Females visit these bowers to evaluate male mate suitability, and males have evolved several ways to capture and retain female visual attention. Among these is a forced perspective illusion (**Figure 3*e–h***) in which the male arranges uncolored objects on his bower court in a size gradient such that, when viewed by the female, the objects retain the same visual subtense in her field of view (Endler et al. 2010). This results in an elimination of the typical perspective, where objects of the same size appear smaller in the visual field the farther away they are, replacing it with an artificially flattened perspective (Endler et al. 2010). Although the cognitive impact for females of viewing this visual illusion is not entirely clear, males whose bowers include this visual illusion are preferred by females (Kelley & Endler 2012a), and experimental manipulations of the illusion influence male mate success (Kelley & Endler 2012b), suggesting that the use of this illusion has evolved based on its sexually selected utility to males. Whether similar (or distinct) visual illusions have evolved in the courtship displays of other animals remains a largely unexplored topic ripe for investigation from behavioral, perceptual, cognitive, and evolutionary perspectives.

FUTURE DIRECTIONS

1. The examples above highlight the recent progress made in nonhuman systems toward understanding visual cognition and also highlight the need for greater study to understand the diversity in sensory and neural capacities across taxa.

2. Future work would benefit from adopting an explicitly evolutionary or comparative lens, rather than an anthropocentric one, when exploring the capabilities of nonhuman animals.
3. Tests of the adaptive benefit of visual cognitive strategies remain sparse even in instances where such strategies are now well described (e.g., color categorization in zebra finches). Comparative studies that explore why closely related species differ in visual cognitive abilities are promising (e.g., color categorization across finches, face specialization across paper wasps).
4. By exploring categorization and categorical perception in a wider array of species, we can begin to uncover the generality of these processes, revealing the extent to which the evolution of categorical perception is a universal process or a feature under selection due to a species' ecology and behavior.
5. Incorporating phenotypic plasticity concepts into research on visual development may provide a useful framework for understanding the effect of experience on visual cognition, as well as how this effect varies across taxa with different behaviors and evolutionary histories.
6. The investigation of visual illusions, when approached from the viewpoint of the focal organisms, promises to reveal both adaptive aspects of visual cognition and maladaptive vulnerabilities that might be exploited by other actors during communication.
7. Alternative mechanisms for processing complex visual scenes are particularly useful in the rapidly growing sector of computer vision, which may enable everything from advances in autonomous vehicle navigation to low-disturbance, high-accuracy monitoring of threatened and endangered species.

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