# Chapter 2
# Visual Illusions: Insights from Comparative Cognition

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**Abstract** Visual illusions emerge as a byproduct of an otherwise highly functional perceptual system, leading to dissociations of the physical world and the perceptual interpretation of environmental stimuli. Insights from comparative cognition research are discussed in this chapter, including the role of species' unique evolutionary pressures, perceptual mechanisms, and the impact of experimental paradigms on the emergence of illusory phenomena, including visual illusions and perceptual completion.

**Keywords** Perception · Visual illusions · Perceptual completion · Pigeons · Primates

## Introduction

The comparative study of animal perception sheds light on the neural and cognitive mechanisms underlying perceptual experiences, as well as the role of ontogenetic and environmental influences. This endeavor—the study of how nonhuman animals (hereafter animals) interpret their physical worlds via diverse sensory systems—has a long history in psychology and related fields. The famed ethologist, von Uexküll (1934/1957), emphasized the need to evaluate an animal's unique perceptual experience as a function of the environment in which it evolved. In particular, the concept of the *Umwelt* or the animal's "self-world" emerged, in which each species' sensory system affords it a unique lens through which it perceives and subsequently interacts with its external world.

A comparative approach to the study of perception contributes to our understanding of the mechanisms underlying both the accurate interpretation of environmental stimuli and misperceptions of the external world. These misperceptions emerge as visual illusions, which are largely considered to be byproducts of an otherwise

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J. R. Anderson, H. Kuroshima (eds.), *Comparative Cognition*,
https://doi.org/10.1007/978-981-16-2028-7_2

efficient perceptual system that quickly processes vast amounts of incoming information. The manner in which animals experience visual illusions has attracted the interest of psychologists for the better part of the last century, with the earliest comparative studies emerging in the 1920s (Révész 1924; Warden and Baar 1929). A variety of illusory arrays have since been presented to diverse taxa across the animal kingdom including insects, fish, reptiles, and mammals (for recent reviews, see Agrillo et al. 2020; Feng et al. 2017; Kelley and Kelley 2014), with an increased focus on the mechanisms that underlie visual illusions. Similarities in the processing of illusory stimuli are thought to reflect commonalities in the neural mechanisms of visual processing that extend beyond a species-unique interpretation of the external world.

Kazuo Fujita and his colleagues championed the systematic study of visual illusions as perceived by pigeons and primates, conducting influential work on the Ponzo, Müller-Lyer, and Ebbinghaus illusions, as well as perceptual completion. Fujita's and others' application of the psychophysical approach to the study of illusions and perceptual processing has opened a window into the inner workings of animal minds (see Matsuno and Fujita 2009 for a review), an approach that many comparative psychologists continue to apply in their investigations of visual illusions and perceptual phenomena. Moreover, Fujita's work highlights the importance of systematically varying the parameters of illusory figures to determine the mechanisms that lead to their emergence (or not), as well as the invaluable role of directly comparing species using nearly identical methods. In this chapter, I present a review of comparative research on visual illusions with an emphasis on the illusions (and perceptual mechanisms) most heavily studied by Fujita and his colleagues.

## The Psychophysical Study of Geometric Illusions

Geometric illusions emerge when the physical dimensions of a stimulus (e.g., area, length, height, orientation) are misperceived as a function of the context in which it is presented. Geometric illusions are comprised of multiple elements, including a to-be-judged target stimulus and an illusory-inducing context (e.g., see the Ponzo illusion in Fig. 2.1a, in which a horizontal, target line placed closer to the apex of two converging lines is misperceived as longer than an identical line placed farther from the apex). Geometric illusions often are discussed in light of a species' ability to organize the elements within an illusory array, such that perceptual grouping of the elements leads to greater sensitivity to illusions, whereas an inability to or delay in grouping may disrupt their emergence. Thus, perceptual mechanisms that underlie perceptual grouping, in particular those that vary across species, have been a large focus within comparative investigations.

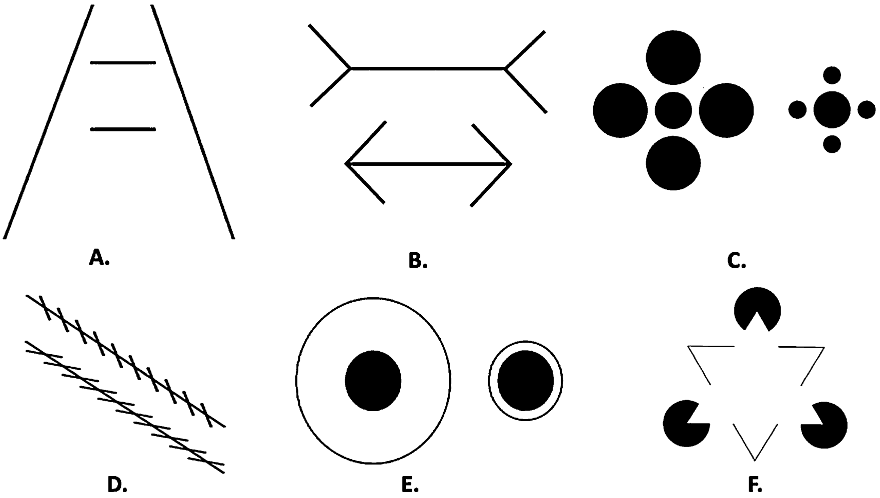

**Fig. 2.1** Visual illusions including the (**a**) Ponzo illusion, (**b**) Müller-Lyer illusion, (**c**) Ebbinghaus illusion, (**d**) Zöllner illusion, (**e**) Delboeuf illusion, and (**f**) Kanizsa triangle (perceptual completion)

## *The Ponzo Illusion*

In one of their most well-known extensions of the psychophysical approach to illusory phenomena, Fujita and colleagues investigated perception of the Ponzo illusion by pigeons (*Columba livia*), rhesus macaques (*Macaca mulatta*), and chimpanzees (*Pan troglodytes*) as compared to humans (*Homo sapiens*) in a series of studies (Fig. 2.1a; see Fujita et al. 2012 for a review). As aforementioned, in the Ponzo illusion, human subjects typically perceive a horizontal line as longer when positioned closer to the apex of two converging lines forming an inverted V-shape than when it is positioned farther from the apex. In their first investigation of the Ponzo illusion, Fujita et al. (1991) simultaneously presented pigeons with two lines of differing lengths. In this relative discrimination task, pigeons judged lines placed closer to the apex of the converging lines as longer than lines placed farther from the apex. Thus, the context created by the converging lines created an illusory effect for judging line length as compared to a control condition when the surrounding lines were parallel for the pigeons.

As an extension of this finding, an absolute classification task was presented to pigeons (Fujita et al. 1991) and primates (rhesus monkeys and chimpanzees; Fujita 1997). Subjects first were trained to classify a series of horizontal lines of various lengths as “short” or “long” relative to a pre-determined length. After training on this initial discrimination was completed, converging lines were placed at a standard location (middle context) and, in test trials, horizontal lines were positioned closer to the apex (low context) or farther from the apex (high context). If subjects perceived the Ponzo illusion, the prediction was that they would be more likely to classify the horizontal line as "long" in the low context and "short" in the high context. All species perceived the illusion in a human-like direction, with greater "long" responses for horizontal lines positioned closer to the apex of the converging lines.

An important species-difference emerged from this work; pigeons demonstrated a higher sensitivity to the low context condition (line near apex) versus the high context condition (line farther from apex) relative to primates. The authors attributed this to differential sensitivity to contrast and assimilation effects, which are responsible for the emergence of the Ponzo illusion and other size illusions (Fujita et al. 1991; Fujita 1997). The assimilation-contrast theory posits that contrast effects lead to greater perceived differences in stimuli that are positioned farther apart. Assimilation effects lead to perceptual integration of nearby stimuli and subsequent underestimation of perceived differences (see Goto et al. 2007; Robinson 1998). In this case, pigeons readily assimilated the horizontal line with the nearby converging lines, leading to overestimates in line length, subsequently strengthening the effect of the illusion (Fujita et al. 1991; Fujita 1997; Pressey 1971).

Fujita and colleagues also assessed the perspective theory according to which subjects perceive apparent depth within two-dimensional figures (Gregory 1963). For the Ponzo illusion, perspective cues would lead subjects to perceive the line nearest the apex as more distant and thus longer to maintain size constancy. To test this possibility, pigeons and primates were presented with two conditions that varied in terms of the orientation of the illusory-inducing lines (converging versus parallel). All species perceived the Ponzo illusion in the predicted direction but to similar degrees across conditions (perceptive and non-perspective, Fujita et al. 1991; Fujita 1997), suggesting that perspective cues did not readily impact illusion emergence. Similarly, additional illusory-inducing lines surrounding the horizontal target line (predicted to increase the strength of the illusion by adding perspective cues) failed to enhance the illusion in pigeons (Fujita et al. 1991, 1993).

In a separate assessment of the perspective hypothesis, Fujita (1996) added a real image of a highway scene behind the Ponzo array, which was positioned upright (predicted to increase the strength of the illusion via depth cues) or inverted. The strength of the illusion was amplified among human subjects in the presence of the upright highway scene (even when the converging lines of the Ponzo array were removed). However, this effect was reversed among rhesus monkeys who were more sensitive to the illusion when presented with the traditional line-drawn array versus the real highway scene. Fujita (1997) further isolated features of the illusory-inducing context for the Ponzo, presenting a horizontal line with small dots on either end or short lines rather than the longer converging lines in the traditional illusion. Interestingly, results varied across primates: humans demonstrated a stronger illusion with these truncated formats versus the traditional lines, whereas the strength of the illusion was equivalent for chimpanzees across formats and no illusion emerged for rhesus monkeys using the dot and shortened line elements. Thus, although all species tested perceived the Ponzo illusion in a similar direction, the mechanisms underlying its emergence may not be ubiquitous.

The Ponzo illusion and the related corridor illusion, in which objects are depicted on a corridor background with seemingly more distant objects appearing as larger, have been documented in various species including chimpanzees (Imura et al. 2008), baboons (*Papio papio*: Barbet and Fagot 2002), and horses (*Equus ferus caballus*: Timney and Keil 1996), suggesting continuity in mammalian sensitivity to pictorial depth cues. Size constancy is important in estimating the true size of objects presented both close by and at a distance via depth cues. In a recent study by Hataji et al. (2020), pigeons were shown to be sensitive to the corridor illusion (overestimating target size for objects located higher or presumably farther away), and pigeons prioritized pictorial cues over motion parallax depth cues for size constancy similar to humans. These results, along with other studies on avian object perception (e.g., Cavoto and Cook 2006; Cook and Katz 1999; Reid and Spetch 1998), suggest that size constancy manifests similarly across vertebrate species tested to date including humans, despite variance in visual processing systems.

## *The Müller-Lyer, Ebbinghaus, and Zöllner Illusions*

To further explore the differential perception of geometric illusions among primates and pigeons, Fujita and colleagues investigated the well-known Müller-Lyer illusion, in which the length of a horizontal line is misperceived as a function of brackets in the shape of arrowheads attached to either end of the line (see Fig. 2.1b). When the brackets are outward-facing in the typical shape of an arrow, the horizontal line is underestimated in length relative to when the arrows are inverted, which leads to overestimation of line length. Using an absolute classification task similar to the Ponzo procedure, Nakamura et al. (2006, 2009) conducted several studies of the Müller-Lyer illusion with pigeon and human subjects. Ultimately, both species were biased to classify horizontal lines with inverted brackets as “long” as compared to lines with outward-facing brackets; however, the species differed in the extent to which they perceived the illusion. Specifically, pigeons did not perceive the reversed illusion when the distance between the horizontal line and the brackets was increased. This reversal is common in humans, emerging as a byproduct of contrast effects between the line and the surrounding context (Nakamura et al. 2006, 2009). Consistent with pigeons’ perception of the Ponzo illusion, these results suggest that pigeons are differentially sensitive to assimilation and contrast effects relative to primates.

Several other animal species have been presented with the traditional Müller-Lyer stimuli, and most perceive the illusion in a human-like direction, including capuchin monkeys (*Sapajus apella*: Suganuma et al. 2007), rhesus monkeys (Tudusciuc and Nieder 2010), horses (Cappellato et al. 2020), an African grey parrot (*Psittacus erithacus*: Pepperberg et al. 2008), ring doves (*Turtur risorius*: Warden and Baar 1929), redtail splitfin fish (*Xenotoca eiseni:* Sovrano et al. 2016), guppies (*Poecilia reticulata*: Santacà and Agrillo 2020), and garden ants (*Lasius niger*: Sakiyama and Gunji 2013), suggesting that the mechanisms underlying size illusions are phylogenetically widespread. However, some discrepancies across species have emerged, with bamboo sharks (*Chiloscyllium griseum*: Fuss et al. 2014) and goldfish

(*Carassius auratus*: Wyzisk and Neumeyer 2007) failing to perceive the Müller-Lyer illusion. In a recent study that used a relative discrimination task, domestic dogs (*Canis familiaris*) were found to perceive the Müller-Lyer illusion in a human-like direction (Keep et al. 2018). However, follow-up experiments revealed that dogs were using overall array size instead of responding on the basis of the target line alone, underscoring the need for careful control conditions in illusion studies.

The role of assimilation and contrast mechanisms in the emergence of geometric illusions was studied further using the well-known Ebbinghaus illusion (see Fig. 2.1c; Nakamura et al. 2008, 2014). This illusion emerges when a central target dot is misperceived as a function of surrounding inducer dots, such that a central dot encircled by larger dots appears smaller (contrast effects) than when surrounded by smaller dots (assimilation effects). Employing an absolute classification test, Nakamura et al. (2008, 2014) trained pigeons and chickens (*Gallus gallus domesticus*) to classify a black circle (the central target dot) as large or small. Inducer circles of a constant size were gradually faded in from light to dark to habituate subjects to their presence. Illusion test trials with large or small inducer dots revealed that both pigeons and chickens perceived the Ebbinghaus illusion in the reversed direction from human subjects: they overestimated central dots surrounded by large inducers and underestimated central dots surrounded by small inducers. Nakamura et al. (2008, 2014) ruled out the possibility that subjects erroneously responded on the basis of total surface area (target dot and inducers combined) by introducing targets both with and without inducers. Furthermore, it did not appear that the birds were responding on the basis of inducer size alone, as the percentage of "large" responses varied as a function of central dot size within each condition. Thus, for pigeons and bantams, a reversed Ebbinghaus illusion may emerge due, at least in part, to an increased susceptibility to assimilation mechanisms that would lead to the integration of the target dot with both small and large inducers.

Similarly, pigeons and bantams perceived a reversed Zöllner illusion (see Fig. 2.1d; Watanabe et al. 2011, 2013), in which, for humans, two parallel lines appear to converge when oblique crosshatches are superimposed on the lines. In control trials, the birds were trained to peck towards one end of a pair of converging lines that appeared narrower (or wider—counterbalanced across subjects). In critical illusion trials, birds of both species perceived the illusory lines as nonparallel, but in the opposite direction from what is observed in humans (i.e., selection of the end that appears to deviate for humans as "narrower"). These avian results stand in contrast with outcomes of primate work, in which baboons (Benhar and Samuel 1982) and rhesus monkeys perceived the Zöllner illusion in a human-like direction (Agrillo et al. 2014). The mechanisms underlying this illusion relate to its global perception (Parlangeli and Roncato 1995) and the misperception of acute angles that are formed when the crosshatches intersect with the main lines; these angles are perceptually enlarged leading one to misperceive the lines as converging (White 1972). The species' differences observed in the Zöllner likely may again reflect differential sensitivity to contrast and assimilation mechanisms across primates and avian species (see Beran et al. 2020 for a review). Assimilation would lead pigeons and chickens to underestimate the acute angles between the main lines and the cross-hatches giving rise to the reversed effect, whereas primates are likely sensitive to both contrast and assimilation, necessary for the emergence of the Zöllner effect.

## Perceptual Organization and Visual Illusions

Differential sensitivity to contrast and assimilation mechanisms is directly tied to a concept that has been touched upon only briefly in this chapter thus far. Specifically, perceptual organization describes the process by which the perceptual system groups individual elements within an array into cohesive units, reflecting objects and figures within a visual scene. The readiness with which perceptual systems organize stimuli in their environment varies across species, such that some species display a global-to-local precedence (i.e., the global figure is perceived prior to the local elements) or a local-to-global precedence (i.e., the individual elements are perceived prior to the global figure). It is established that humans display a global precedence when presented with hierarchical stimuli in which the global figure is comprised of the same or different local elements (e.g., Navon 1977; a letter H comprised of small Hs or Ss). Varying the stimulus design can shift humans towards a local precedence when the individual elements of an array are visually emphasized (see Kimchi 1992, for a review).

Much of the comparative work surrounding perceptual organization has demonstrated that pigeons demonstrate a robust local precedence (e.g., Cavoto and Cook 2001), while primates show mixed results, with chimpanzees sometimes demonstrating a human-like global precedence (e.g., Fujita and Matsuzawa 1990; Hopkins and Washburn 2002) and monkeys displaying a local precedence or none at all (e.g., baboons: Deruelle and Fagot 1998; Fagot and Deruelle 1997; rhesus macaques: Hopkins and Washburn 2002; capuchin monkeys: De Lillo et al. 2005; Spinozzi et al. 2006, tamarins: *Saguinus oedipus*, Neiworth et al. 2006). However, it is important to note that, as with humans, methodological design can impact processing mode in nonhuman primates, particularly if the inter-stimulus distance and overall array size are decreased, which favors perceptual grouping and global processing (e.g., Matsuno and Tomonaga 2007; Neiworth et al. 2006; Tanaka and Fujita 2000). As discussed by Matsuno and Fujita (2009), nonhuman primates do not appear to lack the ability for perceptual organization despite these performance differences across monkeys, apes, and humans, but rather the difference lies within the degree to which primates perceptually group the individual elements within a visual array and attend to larger spatial areas.

Critical to this discussion, perceptual grouping supports the emergence of illusions (e.g., Roberts et al. 2005). For example, perception of the Ebbinghaus illusion (Fig. 2.1c) is dependent upon perceiving the central dot as a component of the larger set of inducer circles. A cross-cultural study underscored this link by demonstrating that Himba tribesman, a locally oriented human population, perceived a weakened Ebbinghaus illusion (de Fockert et al. 2007). Additionally, a weakened Ebbinghaus illusion has been documented among individuals diagnosed with autism spectrum disorder, who also adopt a more locally oriented processing style (e.g., Dakin and Frith 2005; Happé 1996). Comparative results further support this link between perceptual organization and illusory perception of the Ebbinghaus array, as one example. Species with a global precedence perceive the Ebbinghaus in a human-like direction (e.g., redtail splitfin fish (Sovrano et al. 2015) and dolphins, *Tursiops truncatus* (Murayama et al. 2012)). However, a reversed or weakened Ebbinghaus has been documented among species characterized by a local precedence (e.g., bamboo sharks (Fuss and Schluessel 2017), baboons (Parron and Fagot 2007), bantams and pigeons (Nakamura et al. 2008, 2014)).

It is important to note that processing mode is not solely predictive of illusory perception; rather, methodology plays a critical role in this relationship. Experimental methods supporting perceptual grouping of the target stimulus and illusory context can favor global processing and, in turn, illusory perception. For example, human perception of the Ebbinghaus illusion is weakened by disrupting perceptual grouping via isolating the central target dot and the inducers (e.g., increasing the inter-stimulus distance or brightness/shape of the stimuli, erasing the outer edges of the inducer circles (e.g., Choplin and Medin 1999; Coren and Enns 1993; Roberts et al. 2005)). Similarly, comparative studies often employ training procedures that visually isolate the target stimulus and illusory context, a necessary component in training non-verbal species on the discrimination rule. However, these procedures may inadvertently weaken perceptual grouping and subsequent illusory emergence, particularly among locally oriented species (e.g., gradually fading in inducer circles (Nakamura et al. 2008, 2014); differently colored inducer and target dots (Parron and Fagot 2007)).

The necessity of isolating the illusory target as the discriminative stimulus without disrupting perceptual grouping or habituating subjects to the illusory context has proven challenging in comparative studies. For example, in Parrish et al. (2015), rhesus macaques and capuchin monkeys initially perceived a reversed Delboeuf illusion in a relative discrimination task (Fig. 2.1e), in which a target dot typically appears to be larger when encircled by a small ring (assimilation effect) and smaller when encircled by a large ring (contrast effect). However, an absolute classification task revealed that rhesus and capuchin monkeys were, in fact, sensitive to the Delboeuf illusion consistent with human subjects, classifying the central dot as increasingly larger as ring size decreased. Critically, in the relative discrimination task, the monkeys also responded to the inducer rings rather than discriminating based solely on the target dots, a confound that was more easily isolated using the absolute discrimination task. In a recent study by Qadri and Cook (2019), starlings presented with the Ebbinghaus illusion demonstrated a similar response, appearing to perceive a reversed illusion before follow-up experiments revealed that they were inadvertently incorporating the inducer circles into the size discrimination, an important confound to control for when assessing sensitivity to the illusion (see also Keep et al. (2018) for a similar finding in dogs with the Müller-Lyer illusion).

Beyond stimulus design, the angle from which visual arrays are viewed can impact perceptual grouping and subsequent emergence of visual illusions in humans (e.g., Oyama 1960; Weintraub 1979). Subsequently, the manner in which animals interact with visual stimuli may lead to closer or more distant perspectives, the latter of which promotes perceptual grouping. For example, although domestic chickens have shown evidence of a reversed Ebbinghaus illusion when a pecking response is required, which necessitates a closer perspective (Nakamura et al. 2014), positive evidence of the illusion was documented in 4-day-old chicks of the same species required to approach the Ebbinghaus array from a farther distance to recover food rewards (Rosa Salva et al. 2013). It is proposed that the more distant viewing angle in the chick study, along with a decrease in the distance between inducer and target circles, facilitated perceptual grouping and subsequent illusory perception. The authors also discussed the role of the pecking response as linked to the central visual field, which is associated with localized rather than global or holistic processing (see Rosa Salva et al. 2013; Goodale 1983; Lamb and Robertson 1988). Future studies are needed to parse out the role of development in the emergence of the Ebbinghaus and other visual illusions, as a critical variable between these studies was age (4-day-old chicks vs. 6-month-old chickens). These contrasting findings illustrate how the methodologies by which we assess visual illusions interact directly with perceptual processing mode as well as contrast and assimilation mechanisms and subsequent illusory perceptions.

## Perceptual Completion

Organisms routinely are faced with incomplete visual information from the environment, in which an object is partially occluded behind another object (e.g., a predator partially hidden behind a tree). However, these objects are figurally completed via subjective (illusory) contours and thus perceived as whole instead of fragmented (e.g., the predator is perceived as a complete organism; Kanizsa 1979; Michotte et al. 1991; Nieder 2002). Perceptual completion represents a disconnect between one's perceptual experience and the physical stimuli under scrutiny akin to the visual illusions explored above. Specifically, modal completion occurs when one perceives object borders that are otherwise absent and amodal completion occurs when one visually completes an occluded stimulus. For example, in the famous Kanizsa triangle (Fig. 2.1f), human participants mentally complete and perceive a white triangle despite there being no connective contours. The ability to integrate multiple features of a visual scene as a unified object despite incomplete information underlies form perception, and this ability has been studied systematically by Fujita and colleagues, including research with both primates and pigeons (see Fujita 2001a, 2004, 2012 for reviews).

Several nonhuman species demonstrate human-like perception of illusory contours when presented with amodal completion tasks, including but not limited to chimpanzees (e.g., Fagot and Tomonaga 2001; Sato et al. 1997), baboons (e.g., Fagot et al. 2006), macaque monkeys (e.g., De Weerd et al. 1996; Fujita 2001b; Sugita 1999), capuchin monkeys (e.g., Fujita and Giersch 2005), squirrel monkeys

(*Saimiri*: Nagasaka and Osada 2000), dogs (Byosiere et al. 2019), cats (*Felis catus*: Bravo et al. 1988), rodents (Kanizsa et al. 1993), owls (*Tyto alba*: Nieder and Wagner 1999), chickens (e.g., Forkman and Vallortigara 1999; Lea et al. 1996; Regolin and Vallortigara 1995; Regolin et al. 2004), cuttlefish (*Sepia spp*: Lin and Chiao 2017; Zylinski et al. 2012), bamboo sharks (Fuss et al. 2014), redtail splitfin fish (Sovrano and Bisazza 2009), and goldfish (Wyzisk and Neumeyer 2007). This work also has been extended to more naturalistic stimuli (e.g., partially occluded predators or conspecifics), underscoring the adaptive value of perceptual completion (e.g., Darmaillacq et al. 2011; Okanoya and Takahashi 1999; Tvardíková and Fuchs 2010).

Notably, there appears to be a discrepancy in pigeons' ability to perceptually complete fragmented visual input (see Fujita 2004 for a review). For example, when presented with a target bar overlapped by a larger rectangle, pigeons did not overestimate the length of the bar touching the rectangle as did rhesus monkeys, which indicated that monkeys but not pigeons perceived the bar as continuing behind the rectangle (Fujita 2001b). For similar negative results for amodal completion by pigeons, reference the following (e.g., Cerella 1980; Fujita and Ushitani 2005; Sekuler et al. 1996; Shimizu 1998; Ushitani et al. 2001; Watanabe and Furuya 1997). As raised by Fujita (2004), these discrepancies may reflect potential differences in the adaptation of the pigeon's visual system to environmental demands, such that as grain eaters, pigeons may have less need for perceptual completion than other species. Relatedly, this "pigeon problem" (Fujita 2004, 2012) also may reflect important differences in grouping mechanisms across locally oriented species such as pigeons (see Bruce et al. 2003). Furthermore, positive evidence of perceptual completion by pigeons following extended training (DiPietro et al. 2002), in light of prior experience (Nagasaka et al. 2007), and for moving stimuli (e.g., Nagasaka and Wasserman 2008), suggests context-specificity in this ability.

Continuity and discrepancies in amodal completion and the perception of illusory contours reveal important patterns in the evolution of visual capabilities of species with variant neural mechanisms (see Nieder (2002) for a review). Grouping abilities, depth cues, motion processing, and mechanisms for delineating the boundaries between objects and their backgrounds are critical to perceptual completion. The completion of subjective contours reveals an adaptive response of visual systems to processing environmental stimuli under poor conditions of visibility and often incomplete information. Consistency in responding to such stimuli across fish, birds, and mammals suggests amodal completion is relatively widespread among vertebrates, and perhaps a result of homologous evolutionary pressures (see Rosa Salva et al. (2014) for a review). Also important, however, are the cases in which discrepancies emerge, underscoring the need to situate visual demands in an evolutionary context with an eye towards selective pressures on perception.

## Summary

As demonstrated in the works of Fujita and his colleagues alongside the many contributors to comparative perception science, susceptibility to visual illusions reflects the relationship between the visual system, perceptual mechanisms, methodological approach, and species' unique sensory worlds. Furthermore, the performance of animals within these illusory tasks, including performance in control trials for discriminating quantity and size, also depends on concomitant cognitive skills. For instance, visual illusions typically emerge at an individual's discrimination threshold (i.e., the point at which there are just noticeable differences of size, quantity, etc.). These illusory experiences often are quite subtle, generating small subjective differences among stimuli; therefore, an animal must be able to make fine discriminations or have sufficient numerical acuity to perceive certain illusions (e.g., the Solitaire illusion: Miletto Petrazzini et al. 2018). Comparative research is particularly useful in revealing the role of these mechanisms, given the variability in neurobiology, discrimination abilities, and perceptual processing mode across visually oriented species. Furthermore, researchers have begun to explore the roots of inter- and intra-species variance in the perception of illusions to understand better the role of attention, quantitative discrimination abilities, and motivation. There also is a growing interest in the role of experience and development in the perception of visual illusions, which can be systematically modeled within a variety of animal species (e.g., Rosa Salva et al. 2013; Vallortigara 2012). Through this endeavor of investigating the perceptual world of animals, comparative psychologists continue to shed light on the *Umwelt* of both closely and distantly related species.

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