Invited Commentary

Exploring the perceptual canvas of signal evolution

Darrell J. Kemp and Thomas E. White

Department of Biological Sciences, Macquarie University, North Ryde, New South Wales, 2109, Australia

Albert Einstein once famously remarked that "reality is merely an illusion, albeit a very persistent one." In the hallmark of Einstein, this simple phrase encapsulates worlds of conceptual complexity across physics, biology, psychology, and philosophy. From a biological perspective, the essence of this idea is that an individual's perceptual reality presents a mere caricature of its objectively verifiable existence. This can be readily appreciated through situations where individual perception obviously departs from objective reality, as in the case of many popular human visual (optical) illusions. Such images intrigue us because our perception of them so starkly contrasts with our cognitive understanding of what is actually true. That is, they reveal how our brains can err in making sense of the world around us.

In their review, Kelley and Kelley (2014) consider the potential role of visual illusions in the biological world. That the human perceptual system builds verifiably imperfect caricatures of reality suggests the same for other organisms, which presents intriguing possibilities for visual communication. Could the appearance of prey be adaptively shaped to elicit illusionary perception in predators? Could mating signals have evolved to push the envelope of sexual advertisement through illusion? Could deceptive signals such as prey lures take advantage of such perceptual tricks? The overwhelming message from Kelley and Kelley's review is that—for most systems—current knowledge is too sparse to convincingly tell. There is, nevertheless, value in posing such issues to behavioral ecologists, not in the least because they force explicit consideration of perception as the ultimate canvas for signal evolution (see, e.g., Endler et al. 2010). Behaviorists have increasingly accounted for the visual capabilities of relevant viewers (e.g., Stoddard and Prum 2011), thereby more accurately characterizing signal reception, but true perception only occurs once the eye's neurally encoded outputs arrive in the brain.

Empirically, the key issue is how to appraise perceptual illusions in the broader world. Humans identify such phenomena as mismatches between perception and cognitive expectation. The challenge with nonhuman animals is that we have an extremely limited basis for predicting when and how such mismatches might actually occur. One approach is to assess whether other species are tricked similarly to humans when presented with known illusionary phenomena (e.g., Murayama et al. 2012). However, as Kelley and Kelley (2014) point out, there is great variation among species in this regard. Not only do some human-perceived illusions not apply to other species but also some even work in the opposite direction (e.g., Watanabe et al. 2013). Such findings demonstrate that the rules of image perception vary greatly across different animals, which implies that the potential

"illusionary toolkit" should be correspondingly large. Rather than expecting common iterations of a limited range of illusions, we might therefore expect many, often species-specific, examples. Intriguingly, it follows that the true opportunity for illusion in the natural world will greatly transcend our perception of it; that is, there are likely countless potential routes to illusion that humans cannot even begin to imagine. This deepens the empirical challenge because we neither know where to look nor what to look for in the first place.

By the same token, the presence of interspecific variation in the nature of perceptual illusions also implies great potential for signal adaptation. Intraspecific signaling systems may evolve in ways that elicit illusions in conspecific but not heterospecific viewers, or vice versa. Otherwise highly conspicuous sexual ornaments may, for example, be tuned to distort the perception of dominant predators. Kelley and Kelley (2014) also explore how ornaments may also be displayed in ways that selectively activate illusions, such as the displays of fiddler crabs (Callander et al. 2013) and guppies (Gasparini et al. 2013). These examples, however, lead us back to the broader issue of empirical estimation. Although each could signify the operation of an Ebbinghaus illusion (whereby a focal object appears deceptively larger in comparison with smaller adjacent objects), they are also consistent with explanations based around comparative decision making and social signaling. Heuristically, this underscores the need to convincingly demonstrate that perceptual illusion is actually at play. This may be accomplished through detailed knowledge of visual and spatial processing or through linking vision and behavior in highly specific contexts. Putative motion-related illusions, for example, such as the role of snake bands in reversing their apparent direction of travel (Jackson et al. 1976), may be informed by knowledge of refresh rates in the eyes of relevant viewers. If we knew how fast such a snake need ideally travel to distort the perception of its predator(s), then this might offer a basis for testing against actual snake movement in ecologically relevant situations. Compelling evidence may also reside in signals that match predictions for perceptual distortion based on generalizable features, such as perspective (as in the well-described bower bird example; e.g. Endler et al. 2010).

Overall, Kelley and Kelley (2014) present an impressive insight into the varied potential for perceptual illusion in visual signal evolution. The crucial next step forward demands a guiding empirical framework for testing such phenomena. Given the indelible stamp of our own perception of what constitutes a visual illusion, the need for objectivity in such work will perhaps prove paramount among all the endeavors of behavioral ecology.

REFERENCES

Callander S, Hayes CL, Jennions MD, Backwell PRY. 2013. Experimental evidence that immediate neighbors affect male attractiveness. Behav Ecol. 24:730–733.

Endler JA, Endler LC, Doerr NR. 2010. Great bowerbirds create theaters with forced perspective when seen by their audience. Curr Biol. 20:1679–1684.

Gasparini C, Serena G, Pilastro A. 2013. Do unattractive friends make you look better? Context-dependent male mating preferences in the guppy. Proc Biol Sci. 280:20123072.

Jackson JF, Ingram W III, Campbell HW. 1976. The dorsal pigmentation pattern of snakes as an anti-predator strategy: a multivariate approach. Am Nat. 110:1029–1053.

Kelley LA, Kelley JL. 2014. Animal visual illusion and confusion: the importance of a sensory perspective. Behav Ecol.

Murayama T, Usui A, Takeda E, Kato K, Maejima K. 2012. Relative size discrimination and perception of the Ebbinghaus illusion in a bottlenose dolphin (Tursiops truncatus). Aquat Mamm. 38:333–342.

Stoddard MC, Prum RO. 2011. How colorful are birds? Evolution of the avian plumage color gamut. Behav Ecol. 22:1042–1052.

Watanabe S, Nakamura N, Fujita K. 2013. Bantams (Gallus gallus domesticus) also perceive a reversed Zöllner illusion. Anim Cogn. 16:109–115.