Confusion and illusion: understanding visual traits and behavior. A comment on Kelley and Kelley

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Most of us have been fooled by visual illusions. Thousands exist to fool human perception, creating the impression of objects that do not exist, are distorted in size, shape, or color, or suggest movement where none exists. Whether animals have specifically evolved illusionary traits to exploit others is not a new suggestion, but Kelley and Kelley’s (2013) paper is probably the first to systematically discuss such a concept and to present a clear review of where illusions may exist in nature and how they might work. Their paper brings to the forefront this exciting and significantly understudied area of biology. Here, I focus mostly on visual illusions and communication.

Gregory (1998) discusses illusions in depth and describes them as occurring when perception departs from the reality of the external world. Akin to Gregory, Kelley and Kelley define illusions as traits that “…act to distort the perception of the viewer such as the size, shape, coloration or movement…” of individuals or parts of individuals. How we define illusions is a fundamental factor in how future work may proceed and how we may interpret many animal traits.

Most of the potential examples of illusions that Kelley and Kelley (2013) present, I am in agreement with. For example, they discuss potential cases involving the perceived size or color of signals and individuals, including where well known illusions exist (e.g., Ebbinghaus illusion). Likewise, illusions of perspective, such as in recent bowerbird courtship studies (Endler et al. 2010), or contour completion in animals, seem well explained as illusions. Kelley and Kelley also discuss motion dazzle, whereby the presence of stripes or zigzag markings found on fish, snakes, and some other animals could distort the observer’s ability to judge the speed and direction of object movement (e.g., Stevens et al. 2008). Along with deterring biting flies, motion dazzle is a leading contender to explain the illusion function of zebra stripes, and recent modeling of motion vision shows that zebra stripes may interfere with motion assessment (How and Zanker 2013).

Despite Kelley and Kelley’s (2013) valuable attempts to define and conceptualize illusions and relate them to animal traits and behavior, conceptual refinement is still needed in terms of what animal traits we consider as illusions. This is no bad thing because it can lead to future discussion and study. For example, Kelley and Kelley suggest that disruptive coloration, which works by destroying the outline of a body or body parts, could be viewed as an illusion of shape. Although I can see how this may be a possibility were disruptive coloration to work by preventing recognition, it is normally regarded as a type of crypts that prevents detection (Stevens and Merilaita 2009). If nothing has been detected because the visual system fails to differentiate object versus background, then presumably there is no perception of the shape of the object, because the viewer is unaware of that object’s existence. A further example is disruptive camouflage. Kelley and Kelley outline work testing whether disruptive markings draw the viewer’s eye to high-contrast nonmarginal markings, thus preventing the observer from detecting the body outline. However, as normally described, this does not seem to constitute an illusion because it refocuses gaze or attention toward one object feature at the expense of another by manipulating attention, although Kelley and Kelley’s work may challenge us to think more carefully about how distinctive features may work.

It is also not clear whether traits that manipulate receiver behavior or overstimulate/inactivate receiver responses should be examples of illusions. Clearly, there is likely to be a continuum and so pigeon-holing can be artificial, but it is important to be clear in order to carefully guide future work. For example, if the circular eyespots found on many animals that Kelley and Kelley discuss do mimic eyes (although supporting evidence is currently lacking; Stevens and Ruxton 2014), should they and other types of mimicry be considered as illusions? I argue that mimicry would usually not constitute an illusion because it involves a direct resemblance to another object, and this is not the same as distorting perspective or creating the impression of something that is not really there.

The above debates matter because if we are to understand communication and signals we need to comprehend the mechanisms by which they work. The issue of what is an illusion is not simple because perception is something quite specific to the sensory systems and brains of each animal. At the moment, more behavioral experiments are needed to demonstrate that other species really do perceive illusions, especially of more naturalistic stimuli. Kelley and Kelley’s (2013) definition seems sensible and a good start in determining which traits are illusions.

Finally, as Kelley and Kelley (2013) point out, arrangements of color and brightness can affect the perception of color patches adjacent to one another. We need to pay more attention to the composite arrangement of animal and plant markings, rather than focusing on individual elements in isolation. Studies of communication and signaling commonly analyze the color of a single patch and correlate this with some aspect of behavior and then infer what information the receiver may have extracted. Yet, if signal color patches operate synergistically, then this approach could misinterpret the information available and underestimate the efficacy of the signal. In short, we need to consider the 2D and 3D properties of animal signals, and studies of the strategic aspects of signaling need to more commonly consider issues of signal efficacy and multicomponent communication. In conspicuous signals, for example, we would expect adjacent color patches that stimulate different opponent color channels or sets of receptors (such as ultraviolet-blue patches found next to fluorescent yellow patches on some parrots; Pearn et al. 2001). In short, understanding the colors
present in signals requires considering the coloration of the animal as a whole (and the background). Clearly, there is much left to do to understand visual traits.

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**REFERENCES**


