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Invited Commentary

Perspectives regarding future experiments on categorical perception: a comment on Green et al.

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In their review of categorical perception in animal communication and decision making, Green et al. (2020) provide an excellent overview of the field and propose a series of reasonable hypotheses to motivate future studies. We particularly appreciate the focus on the animal's umwelt and the importance of understanding variation in perceptual systems across animals. We also enjoyed reading about the history of this field where an animal-general view arose for a trait first thought to be human-specific, next tested on animals using human stimuli, and finally recognized as a trait that could be an important component of an animal's cognitive toolbox. Here, we outline four questions we believe will help stimulate important research on this topic.

First, how simple can a neural system be and still produce categorical perception? What does a perceptual system that gives categorical responses look like, and how does it compare to one providing graded responses to the environment? Our intuition suggests that a very simple nervous system could provide categorical responses (e.g., multiple sensitivity peaks in cricket auditory receptor fibers; Imaizumi and Pollack 1999), and modeling work suggests that many neural networks can give rise to categorical perception (Damper and Harnard 2000). For example, Mysore and Knudsen (2012) used first principles to show that reciprocal inhibition of feedforward lateral inhibition is a simple network that can generate flexible categorization, and this is supported by measures of neural responses in the midbrain of owls. Future work on animals with small and well-studied nervous systems (e.g., *Caenorhabditis elegans*) and neural modeling that address categorical perception per se, not just categorization, would be useful in illuminating the minimum requirements of neural circuits needed for categorical perception.

Second, can categorical perception in one modality facilitate such perception in another, and is categorical perception domain specific or domain general? For instance, categorical perception exists in human sign language (Emmorey et al. 2003), and it is unclear whether this is directly related to categorical perception in human speech. In addition, many animal communication displays contain multimodal elements, and if perception is categorical within these distinct signals, the boundaries are likely to be mismatched at least some of the time. How do animals' cognitive systems handle these types of complex information?

Third, how can we rigorously test hypotheses about the evolutionary emergence of categorical perception? We appreciate that Green et al. (2020) proposed reasonable and intuitive explanations for when and why categorical perception might emerge in animal communication and decision-making systems, but to prove or falsify these proposed factors we need experimental and/or comparative paradigms that can explain why groups of animals do or do not have categorical perception in some contexts. However, we also know from the earliest studies on chinchillas and macaques that categorical perception can exist in situations without a clear "reason" and can emerge rapidly following category training. Might categorical perception sometimes exist by default, and the explanations for its emergence provided by Green et al. (2020) instead serve to align the categorical boundary to a particular location in a stimuli's distribution? In theory, this could be tested by comparing groups in which individuals have randomly distributed boundary lines to groups in which individuals converge on a similar boundary. The logistics of such an experiment, however, seem daunting.

Finally, can there be sensory exploitation of categorical perception? While we generally think of sensory categories being shaped by or learned from the environment, it is also possible that pre-existing sensory categories shape subsequent signal production. For example, category boundaries developed for behaviors like foraging could be coopted for communication purposes. Future work on guppy coloration could be a system to detect such exploitation (Rodd et al. 2002).

Overall, Green et al. (2020) provide an excellent foundation for this key topic in understanding how animals' perception of the world shapes their communication and decision making. We also agree that their proposals to study categorical perception in egg-rejection, wasp face recognition and other modalities like odor will lead to fruitful avenues of research. We hope the ideas and proposals we present here will also spur new areas of study.

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