

The many dimensions of categorical perception: a response to comments on Green et al.

Patrick A. Green,^{a,b,✉} Nicholas C. Brandley,^c and Stephen Nowicki^{b,d,✉}

^aCentre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Stella Turk Building Treliever Road, Penryn, Cornwall TR10 9FE, UK, ^bBiology Department, Duke University, Box 90338, Durham, NC 27708, USA, ^cDepartment of Biology, College of Wooster, Ruth W. Williams Hall, 931 College Mall, Wooster, OH 44691, USA, and ^dDepartment of Neurobiology, Duke University Medical School, 311 Research Drive, Box 3209, Durham, NC 27710, USA

We appreciate the constructive commentaries on our review of categorical perception (Green et al. 2020). As we detail below, these commentaries suggest several useful pathways toward understanding the physiological, ecological, and evolutionary mechanisms underlying categorical perception's role in animal communication and decision-making.

Mason (2020) correctly states that categorical perception is not necessarily a unitary phenomenon—that is, its expression in diverse taxa (e.g., crickets, frogs, and sparrows) is unlikely to reflect a single underlying process. James and Ryan (2020) reinforce this idea by noting that neural network models have been shown to achieve categorical perception in a variety of ways. The expression of categorical perception itself may vary in the extent to which within-category discrimination is diminished or between-category discrimination is enhanced. When initially described for human speech perception, there was some debate as to whether categorical perception allowed for any within-category discrimination. It quickly became apparent, however, that humans are able to discriminate exemplars within a phonemic category, albeit far less accurately than between-category discriminations (Studdert-Kennedy et al. 1970). Categorical perception of bat calls versus conspecific calls by crickets is more absolute in the sense that there appears to be no within-category discrimination (Wyttenbach et al. 1996), and this may be attributed to the simple neural mechanism involved as Mason (2020) suggests. But a big brain may draw absolute boundaries as well, as appears to be the case for the categorical perception of note types by swamp sparrows (Prather et al. 2009). For all these reasons, we fully agree that categorical perception should not be viewed as an adaptation on its own but rather as a phenomenon that may arise in many ways depending on how evolution acts on decision-making and communication systems.

Another dimension of variation in the expression of categorical perception is whether category boundaries are fixed or flexible. Tanner and Tumulty (2020) suggest that the stimulus properties being perceived could determine the plasticity of category boundaries. We agree this is an important issue to consider further. It is already clear that category boundaries for even simple stimuli, such as the length of song note types in swamp sparrows, vary geographically (Prather et al. 2009), presumably as the result of cultural drift, just as in the case for phonemic boundaries in human speech. Additionally, in the discrimination of both words in speech (Bloch 1941) and syllables in birdsong (Lachlan and Nowicki 2015), the location of a category boundary depends on where in a vocalization the sound being discriminated occurs. As such, Tanner and

Tumulty's (2020) suggestion that plasticity is likely to be found for category boundaries involved in individual recognition, whether of human faces or wasp faces, is particularly intriguing.

As Luro and Hauber (2020) emphasize, more tests are needed of categorical perception in the wild. These studies can reveal the fitness costs and benefits of categorical perception, helping researchers understand when and how evolution acts on sensory tasks that may be facilitated by the expression of this phenomenon. Future studies of categorical perception would proceed best by combining field and lab approaches. A field study might identify the relevant stimulus variation receivers must parse, followed by lab assays under controlled conditions to test for categorical perception and delineate any category boundaries that may exist. Finally, returning to the field and testing under relevant ecological conditions can establish the fitness consequences of the way in which a stimulus is perceived. Social recognition tasks, such as neighbor-stranger recognition as suggested by Tanner and Tumulty (2020) or mate and offspring recognition as suggested by Luro and Hauber (2020) provide fertile ground for this kind of work. These studies, combined with the comparative studies proposed by James and Ryan (2020), are needed to situate categorical perception in a stronger evolutionary framework.

James and Ryan (2020) detail an additional fascinating twist to the evolutionary implications of categorical perception: category boundaries might be exploited in a fashion similar to the sensory exploitation of other kinds of receiver responses. If such proves to be the case (as seems plausible), then the strength and location of category boundaries could represent trade-offs between competing demands for how an organism parses its sensory world into useful categories.

Address correspondence to P. A. Green. E-mail: p.a.green@exeter.ac.uk

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REFERENCES

- Bloch, B. (1941). Phonemic overlapping. *Am Speech*. 16(4): 278–284.
- Green PA, Brandley NC, and Nowicki S. Forthcoming 2020. Categorical perception in animal communication and decision-making. *Behav Ecol*. 31: 859–867.
- James LS and Ryan MJ. Forthcoming 2020. Perspectives regarding future experiments on categorical perception: a comment on Green et al. *Behav Ecol*. 31: 868.
- Lachlan RF, Nowicki S. 2015. Context-dependent categorical perception in a songbird. *Proc Natl Acad Sci USA*. 112:1892–1897.
- Luro AB and Hauber ME. Forthcoming 2020. The ecological context and fitness impact of categorical perception: a comment on Green et al. *Behav Ecol*. 31: 869–870.
- Mason, A. C. Forthcoming 2020. Perception, decision, and selection: a comment on Green et al. *Behav Ecol*. 31: 869.
- Prather JF, Nowicki S, Anderson RC, Peters S, Mooney R. 2009. Neural correlates of categorical perception in learned vocal communication. *Nat Neurosci*. 12:221–228.
- Studdert-Kennedy M, Liberman AM, Harris KS, Cooper FS. 1970. Theoretical notes. Motor theory of speech perception: a reply to Lane's critical review. *Psychol Rev*. 77:234–249.
- Tanner JC and Tumulty JP. Forthcoming 2020. The signals and category boundaries that enable categorical perception: a comment on Green et al. *Behav Ecol*. 31: 871.
- Wyttenbach RA, May ML, Hoy RR. 1996. Categorical perception of sound frequency by crickets. *Science*. 273:1542–1544.