Invited Commentary

The ecological context and fitness impact of categorical perception: a comment on Green et al.

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CONTEXT-DEPENDENT CATEGORICAL PERCEPTION

In their timely and detailed perspective piece, Green et al. (2020) propose diverse decision-making contexts where extensive overlap between continuous stimuli, limited timeframe of perception-to-decision latency, and high fitness costs of not responding or committing recognition errors, all may favor the evolution and development of categorical perception. We agree with the predictions made by Green et al. (2020) and emphasize the need for careful selection of the experimental contexts in which categorical perception is to be tested. Notably, however, amongst the many examples cited as evidence of categorical perception across animals in Green et al. (2020), only two examples involved studying animals outside the lab in the wild (swamp sparrows *Melospiza georgiana*) or in seminatural habitats (Japanese macuaques *Macaca fuscata*). Therefore, first and foremost, when feasible, future experiments should be conducted in the natural habitat of the species and individual(s) of interest (or, at least, closely resemble the natural contexts that the subjects experience) and during time periods when swift decision-making, guided by categorical perception, may be advantageous for survival and/or reproductive success.

For example, a useful paradigm for field-based experiments highlighted by Green et al. (2020) is egg rejection by hosts of avian brood parasites, where parasitized individuals must recognize and remove (the often mimetic) brood parasitic eggs laid in their nest to avoid the measurable fitness costs associated with raising unrelated offspring (e.g., Hauber 2003). Categorical perception in these systems can be readily tested by placing foreign eggs that vary along a continuous color or spotting pattern gradient into host nests and monitoring egg rejection responses (e.g., Hanley et al. 2017). Additionally, categorical perception may facilitate mate recognition and choice in species that search for suitable mates amongst signals produced by both conspecifics and heterospecifics during a limited time period. For example, co-occurring light-signaling *Photinus* firefly species must locate conspecific mates while avoiding signals produced by both incompatible congenerics and predators capable of mimicking flash signals (Lewis and Cratsley 2008).

Moreover, the design and presentation of experimental stimuli and the behavioral responses measured, along with the socioecological context tested, are critical when testing for categorical perception. Stimuli should be designed with continuous variation along an axis that is both representative of natural variation for which subjects are exposed in the wild and in perceivable units to the species of interest (i.e., "just-noticeable differences"; e.g., Hanley et al. 2017) because sensory systems often process differences between stimuli on a proportional rather than absolute scale (Akre and Johnsen 2016). Finally, measured behavioral responses should be indicative of discrimination or choice while also accounting for focal animal responsiveness and random response outcomes.

Linking fitness costs to (lack of) categorical perception

For categorical perception to be an even more valuable concept in behavioral ecology, it must have a measurable connection to or effect on fitness. Specifically, there could be 1) significant fitness outcomes (i.e., costs or benefits) associated with the perception of, assessment of, and the decision-making based upon continuously scaled stimuli and 2) measurable avoidance or mitigation of fitness costs through categorization of the stimuli when making decisions. Determining the type and extent of fitness costs associated with a lack of categorical perception should be a fundamental goal, albeit a challenging one. Social recognition tasks may be exceptionally useful for determining both the presence of and fitness costs associated with categorical perception because of their well-documented consequences for reproductive decisions and subsequent fitness. Consequently, recognition errors are often made when recognizing offspring, kin, and/or compatible mates (Hepper 1991; Rosenthal 2017), resulting in the rejection of one's own offspring (Davies et al. 1996) or mating with a relative or heterospecific (Rosenthal 2017). For instance, categorical perception may be more likely to facilitate mate preferences in sympatric rather than allopatric populations with heterospecifics and underlie the evolution of conspicuous reproductive character

displacement that reduces receiver mate recognition errors (and categorization errors) and subsequent introgression and hybridization (Akre and Johnsen 2016). Mate recognition experiments with heterospecific individuals from both sympatric and allopatric populations could test the prediction that sympatric individuals, but not allopatric individuals, should have a stringent categorical perception of continuous signals used for assessing potential mates.

CONCLUSIONS

Categorical perception is a timely topic worth exploring for behavioral ecologists and Green et al. (2020) provide a current perspective of its history, recent developments, and valuable future directions. We emphasize the necessity of testing for categorical perception in study systems where its effects on fitness can be measured or estimated. Categorical perception may prove to be widespread among animals, and behavioral ecologists have a unique opportunity to test categorical perception in diverse ecological and evolutionary contexts.

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