Response to Comment on "Floral Iridescence, Produced by Diffractive Optics, Acts As a Cue for Animal Pollinators"

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Morehouse and Rutowski make interesting comments on the difficulties of untangling complex optical phenomena. However, our use of a four-colored transfer test in our original study, along with spectrophotometric analysis of the nonoverlapping colors produced by our target disks, allows us to conclude that bees can learn to use iridescence as a foraging cue.

We thank Morehouse and Rutowski (*1*) for the opportunity to expand on our findings on the effect of floral iridescence on bee visual response (*2*), although we find that their concerns are unwarranted. Target detectability depends in part on the amount of contrast that is presented to a visual system over time (*3*); iridescing objects will therefore increase detectability. For a forager searching for suitable targets, an iridescent object will produce more visual change per unit time than one that is homogeneously pigmented. We did not claim that we had measured such an increase in detectability, but we find that noniridescent disks of the sort used in our original study require search times around 30% greater (statistically significant) than those required for the iridescent disks. This increased detectability could have substantial effects on the behavioral ecology of pollinators. However, increased detectability arising from iridescence might come with a serious cost that has rarely been considered formally in the literature on biological iridescence. The complication is that iridescence corrupts object identity. Color generated by flowers enables pollinators to identify and recognize flowers, and facilitates species-specific pollen transfer (*4*). If an iridescing floral target changes color while the pollinator is approaching, the pollinator might abort its approach, "thinking" that it is approaching the wrong flower.

We agree with Morehouse and Rutowski (*1*) that it is important to clarify whether bees can identify flowers not just despite their iridescence, but use the iridescence to identify the flowers. It has already been shown that bees can identify a target that changes rapidly between blue and green from a steady mixture of the two, or from any one of the individual colors (*5*). However, it would be even more convincing to show that bees can learn to pick iridescent targets, no matter what range of colors is spanned by the iridescence. Human observers, for example, can classify mother-of-pearl and compact discs as displaying the same optical phenomenon—not because they might both have a component of, for example, yellow when viewed from a certain angle but because both have the phenomenon of changeability of hue, that is, iridescence.

To test for this possibility in bees, we exploited the cognitive ability of bees to learn rules. Honeybees, for example, can learn a rule that says "Choose the asymmetric patterns." After being rewarded with eight different asymmetric patterns, and then faced with novel patterns never seen before, they will always choose the asymmetric ones, even if these are otherwise wholly dissimilar from the patterns seen previously (*6*). It has been argued that learning rules is an adaptive way to deal with small memory capacity, circumventing having to memorize multiple individual patterns, but instead learning the rule that identifies them all (*7*). In the same vein, we asked whether we could train bumblebees to "Choose the iridescent ones." We trained bees not to one but to three differently pigmented iridescent targets, and they had to learn to avoid three identically pigmented, but noniridescent, ones. Moreover, we subsequently faced bees with a transfer test in which they were confronted with two completely novel types of flowers with a previously unfamiliar pigmentation, one iridescent and one noniridescent. The bees picked out the iridescent ones with high certainty, even though they had never been rewarded on this particular target type before and had not previously encountered this range of colors. Thus, one interpretation is that bees had indeed learned to identify iridescence. As in other experiments of rule learning, however, Morehouse and Rutowski are correct in pointing out that there might be another cue that is common to all the members of the category. If, for example, all four iridescent targets produce the same shade of blue when viewed from one particular direction, bees might learn the difficult task of approaching each flower from that vantage point.

Analysis of our colored targets suggests that this is extremely unlikely. For bees to be able to use a single static color produced by the grating, that color would have to be present on all the iridescent disks. None of the bees used only a single color disk in the first half of the experiment. As shown in our original study (*2*), both overlying structure and underlying pigment contribute to the flower color that a bee would observe. Spectrophotometry reveals that this is also the case for the iridescent disks used in our experiments; there is no one color cue present on all the iridescent disks. Instead, the iridescent disks are spatially separated from one another in bee color space. In the absence of any single static cue that unites the disks with diffraction gratings, we conclude that it is their changeability, that is, their iridescence, that bees are learning and applying in the later transfer test.

Morehouse and Rutowski suggest that there could be an "average hue" generated by the diffraction grating used in these experiments. However, it is the nature of grating interference that all color contributions average to that of incident light when integrated over all angles. The average wavelength distribution of a disk with a grating is therefore identical to one without a grating. For the same reasons, it is not possible for an animal's vision to average the colors of the iridescent disks in our original experiment and find them different from noniridescent disks. We therefore conclude that the bees can indeed see iridescence and that it enhances target detectability.

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References

1. N. I. Morehouse, R. L. Rutowski, *Science* **325**, 1072 (2009); www.sciencemag.org/cgi/content/full/325/5944/1072-d.
2. H. M. Whitney *et al.*, *Science* **323**, 130 (2009).
3. M. Giurfa, M. Lehrer, in *Cognitive Ecology of Pollination*, L. Chittka, J. D. Thomson, Eds. (Cambridge Univ. Press, Cambridge, 2001), pp. 61–82.
4. L. Chittka, N. E. Raine, *Curr. Opin. Plant Biol.* **9**, 428 (2006).
5. M. Lehrer, M. Wunderli, M. V. Srinivasan, *J. Comp. Physiol. [A]* **172**, 1 (1993).
6. M. Giurfa, B. Eichmann, R. Menzel, *Nature* **382**, 458 (1996).
7. M. V. Srinivasan, *Curr. Biol.* **16**, R58 (2006).

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