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# Hering's opponent-colors theory fails a key test in a non-Western culture

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## Abstract

Opponent Colors Theory advances that four colors have special status and are yoked in opponent fashion (yellow-versus-blue, and red-versus-green). Classic hue cancelation studies provide evidence for this theory: people readily pick out colors that are neither red nor green, usually yellow. Here we conducted a version of a hue-cancelation experiment with the Tsimane' people, a non-industrialized culture in the Amazon. Tsimane' speakers readily identified reddish and greenish color chips, but they showed idiosyncratic choices when asked to identify a color that is neither reddish nor greenish, unlike English speakers who consistently select focal yellow. The Tsimane' participants who also spoke Spanish and had a consistent label for English "yellow" ("amarillo"), performed similarly to the Tsimane' monolinguals, suggesting that simply having a label for "yellow" is not sufficient to explain the consistency of English speakers. The results add to a growing body of evidence that does not support Opponent Colors Theory.

**Keywords:** color perception; cross-cultural differences; Opponent Colors Theory

## Introduction

How does the brain compute color appearance? The first stage of color depends on the activation of three classes of cone cells (termed L, M, and S, for the location of the peaks in their spectral sensitivity functions to long, middle, and short wavelengths of the visible spectrum) (Conway, 2009). But how the photoreceptor signals are combined to give rise to color appearance remains unknown. The most prominent theory, which was formalized by Ewald Hering in 1905 (Hering, 1964) but can be traced in Western culture to ideas held by DaVinci (DaVinci, 1877), maintains that color appearance depends on four elementary colors (red, green, blue, yellow). Hering argued that these colors are yoked as two opponent mechanisms (red-versus-green; blue-versus-yellow) that are hard-wired in the physiology of the visual system (Lindsey et al, 2020). Hering had advanced opponent-colors theory to account for a troubling failure of trichromacy: if color were constructed from the activation of combinations of retinal primaries, we should be able to perceive continuous mixtures of the primaries, which we cannot (e.g., we do not see reddish greens). The set of four elementary colors have been called the "Unique Hues" because, according to Hering, they are the complete, elementary set of irreducible colors. Dogma is that these hues are sufficient to describe all colors (so "orange" is reddish-yellow); and they themselves cannot be described by any more elemental terms. The theory remains a pillar of contemporary accounts of color appearance in psychology textbooks (Goldstein, 2017) and underpins the influential ideas regarding the evolution of color terms by Berlin and Kay (1991).

Despite its intuitive appeal, Opponent Colors Theory has failed to gain convincing empirical support (Mollon and Jordan, 1997; Valberg, 2001; Broackes, 2011). The primary evidence mustered by supporters of the theory is the influential hue-cancellation experiments of Hurvich and Jameson, which were conducted in English speakers (Hurvich and Jameson, 1957). One set of tests in these experiments involved asking participants to add red or green light of enough intensity to render a spectral test light neither reddish nor greenish. For example, an observer might be shown a monochromatic light that appears orange. They would then add enough green light to it, to cancel the reddish quality. The resulting light that appears neither reddish nor greenish appears uniquely yellow. Moreover, the amount of green required to yield unique yellow is remarkably similar among people, and the task is easy and intuitive (Dimmick and Hubbard, 1939; Jameson and Hurvich, 1955; Werner and Wooten, 1979). These two observations—the ease of the task and the fact that people end up with the same color that appears neither reddish nor greenish—have been considered evidence that the Unique hues correspond to hard-wired color-encoding mechanisms that are not dependent on cultural factors.

Setting aside the hue-cancelation experiments, the special status of the Unique Hues has been called into question by other behavioral data, beginning with the observation of substantial individual differences in unique hue settings, especially for blue and green (Webster et al., 2000). In addition, Unique Hues are not selected with lower variability than intermediate hues (Bosten and Lawrance-Owen, 2014; Wool et al., 2015), color categories assessed in infants do not align with the Unique Hues and include a non-unique category (purple) (Skelton et al., 2017; Mylonas and Griffin, 2020), and perceptual discrimination thresholds of colors defined by cone-opponent mechanisms do not consistently align with unique hue categories (Hansen and Gegenfurtner, 2006; Witzel and Gegenfurtner, 2018).

Furthermore, despite intensive search, there is no decisive neuroscientific evidence that color is encoded by the retina and the brain with mechanisms matching the Unique Hues

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(Bohon et al., 2016; Bosten and Boehm, 2014; Mylonas and Griffin, 2020; Webster et al., 2000; Witzel and Gegenfurtner, 2018; Wool et al., 2015). The best neural evidence for the privileged status of the Unique Hues is from event related potentials: the P2 peak is slightly earlier for Unique Hues (Forder et al., 2017). As Forder et al recognize, conventions about color naming could be sufficient to account for this result.

The lack of clear neurophysiological data for the primacy of the Unique Hues, together with the behavioral studies described above have not substantially undermined the status of the Unique Hues as the foundation for psychological theories of color appearance, in part because the original hue-cancelation experiments seem so compelling. Yet as Mollon and Jordan point out, the hue cancelation experiments are "only an extension of the basic determination of the unique hues." In other words, hue cancelation simply provides a method for determining which colors are Unique. The special status of the Unique Hues rests entirely on the assertion that, as Mollon and Jordan put it, "there exist four colors, the *Urfarben* of Hering, that appear phenomenologically unmixed." But an alternative reason that these colors might be considered special could be that the query is made of people from industrialized countries where we are taught from an early age that red, yellow, green, and blue are primary colors. Perhaps there is something about the behavioral demands placed on the color system that makes these colors especially useful.

Here we set out to test the claim that the Unique Hues are universal. A critical test would be provided by data collected in cultures where people are not taught from an early age to identify red, green, blue, and yellow as elementary colors (Lindsey et al., 2020). We take up such a test in the Tsimane' people of the Bolivian Amazon. Tsimane' culture differs from Western culture in many ways, for example, the Tsimane' have relatively richer ethnobotanical knowledge (Reyes-Garcia et al., 2003) and are not indoctrinated with primary colors as is typical of Western education (Conway et al., 2020; Gibson et al., 2017). The Tsimane', like other non-industrialized cultures (Abbott et al., 2016; Lindsey et al., 2015; MacDonald et al., 2018; Zaslavsky et al., 2018), can see all colors and, distributed across the population, they have rich color knowledge (Conway et al., 2020; Gibson et al., 2017). But like many other non-industrialized cultures, the Tsimane' have fewer words for colors than industrialized cultures. Whereas they have a color word that corresponds closely to English "red" ("jaines"), the English colors "green" and "blue" are represented together in one Tsimane' color term ("shandyes" in some speakers, "yushnyes" in others, sometimes called a "grue" term).

Useful for present purposes, the Tsimane' have no consistent term for English "yellow", although some speakers use the word "chames" in a broad color category around English "yellow". Superficially, one might think that not having words for the four unique hues would be evidence against the Unique Hues theory. But Opponent Colors Theory should not depend on language, since it ostensibly pertains to how color is encoded by the visual system. The words we have for colors probably reflect the things we want to label, not how we see (e.g., Lindsey et al., 2015; Gibson et al., 2017; Zaslavsky et al., 2018; Conway et al., 2020); fundamental color-encoding mechanisms are likely the same in all people with normal color-vision genetics (Heider and Oliver, 1972) and in trichromatic non-human primates (Stoughton et al, 2012; Gagin et al, 2014). Consequently, the lack of a consistent "yellow" or "blue" in many cultures is not evidence against the Unique Hues color vision theory. These cultures thus provide a potential opportunity to test Opponent Colors Theory: if the theory is correct, people should show evidence of the privileged status of all Unique Hues, including those for which they lack a consensus color term. To obtain this evidence, we deployed a version of the hue cancelation experiment.

Our experiment focused on yellow, since selections for spectral unique yellow span a narrow range providing the strongest support for the Unique Hues theory (Dimmick and Hubbard, 1939) and because the Tsimane' lack a consensus term for this purportedly Unique Hue. First, we had participants identify the best exemplars of the Tsimane' term for red, and the Tsimane' term for green, and determined that their answers are broadly similar to those provided by English speakers. Next, we presented each participant with the portion of the standard Munsell array of color chips that span the reds, oranges, yellows, and greens, and asked them to identify the color chip that was neither reddish nor greenish: least red and least green. We refer to this task as the "neither-nor" task (corresponding to neither red nor green). This task is similar to the classic hue-cancelation paradigm (Mollon and Jordan, 1997), but is more amenable for use with remote populations, who are not familiar with monitors. If Hering's opponent colors theory reflects the universal privileged status of the Unique Hues, the participants should readily and reliably select the focal unique hue situated between red and green (yellow or brown), and the selections across the population should be as consistent as they are for other populations, in our case, English speakers. Contrary to this prediction, the participants showed tremendous variability in the chips they selected. These results represent a failure of Hering's opponent colors theory and support the alternative hypothesis: that the privileged status of the Unique Hues reflects something about the use of color in Western culture, not the brain mechanisms for encoding color.

## Material and Methods

### Participants

For the hue-cancellation task, 27 Tsimane' monolingual speakers and 31 additional native Tsimane' speakers who also spoke Spanish as a second language performed the experiment. A language questionnaire administered to 22 of the Tsimane'-Spanish speakers indicated that they were dominant in Tsimane' relative to Spanish, having acquired Spanish late in life (mean=12.4 years, SD=3.32) and using Spanish only occasionally (mean use of Tsimane' =74.2%;

mean use of Spanish=25.8% of total time). As a control group, 21 native English speakers also performed the experiment. For the color-selection task, data from an additional 43 Tsimane' monolingual participants were obtained; while for the focal task, data from an additional 40 Tsimane' monolingual speakers were obtained. The sample consisted of the maximum number of the key population of participants (Tsimane') that we could test within the time constraints of the field work, and was equal to or greater than sample sizes in comparable studies. The sample population (Tsimane') was selected because of their properties as a culture with limited exposure to Western culture and industrialization, as needed to use hue cancelation to test Hering's opponent colors theory without the confound of industrialization and Western education. All participants were screened for color-blindness (Neitz and Neitz, 2001) prior to the study, received compensation for their time, gave an informed consent as required by the MIT's Committee on the Use of Humans as Experimental Subjects (COUHES) and were paid for their participation.

## Tasks

**Color selection task.** Participants first performed a task in which they were presented with a test grid of 84 colored chips. This test grid was created by subsampling the standard Munsell array of 320 colors (Kay et al., 2011). The subsampled Munsell array consisted of 80 colored chips evenly sampling the complete Munsell array. Each chip was about ~0.5" square, and the set of chips were arranged in an 8 x 20 grid (Figure S1). We also showed participants 4 achromatic chips (white, black, dark grey, light grey). Participants were then asked to identify basic color terms in the grid in their native language. Tsimane' monolingual and bilingual speakers were asked to identify 8 terms: *tsincus* (glossed as black), *jaibes* (white), *jaines* (red), *yushnyes* (blue), *shandyes* (green), *itsijesi* (purple), *chocolateyesi* (brown), *chames* (yellow). English speakers were asked to identify 11 color terms (black, white, red, green, blue, yellow, grey, orange, pink, brown, purple). Participants were allowed to pick as many chips as they wanted for each of the color terms and were asked to inform the researcher when they had come to a stop.

**Focal color task.** Next, participants performed a task in which they were asked to identify for each color term the single color chip that served as the best example for the term.

**Hue cancellation task: the "neither-nor" task.** Last, participants completed a task in which they were asked to identify colors in a portion of the test grid that encompassed 30 chips (6 rows by 10 columns of the grid, in which half of the squares are blank; see Figure S1) spanning the reds, oranges, yellows, and greens. We refer to this task as a hue-cancellation task, drawing an explicit reference to the classic cancelation experiments of Jameson and Hurvich (1955) and Werner and Wooten (1979). As Mollon and Jordan (1997) state in reference to the hue-cancelation experiments "in these experiments the strength of, say, the green chromatic response was established by finding at each wavelength the amount of a fixed, reddish, wavelength that needed to be added to yield a light that looked neither reddish nor greenish…it is completely equivalent to ask the subject to identify directly the sets of non-spectral chromaticities that are neither reddish nor greenish" (Mollon and Jordan, 1997). The portion of the test grid was revealed through an aperture in an opaque cardboard mask put on top of the 8 by 20 grid. Participants were asked to pick the chip that was the least red and least green. The Tsimane' instructions were derived from English instructions that elicit behavior which recover the classic observation of the colors least red or least green in the set (see Figure 1). These instructions were in Tsimane' as follows:

Yacchutidye': Quin' ra' tupuj cave' mi yiris shevtacsi' paper därsi'. Chime' ra' tupuj cave' mi paper shevacsi' miqui'ves shandyes judyeya' jäijnäs. ¿Tupuj buty choco'je' mi chirijriya' yiris shevtacsi' paper miqui'ves shandyes? ¿Judyeya' quin' na, me' buty tupuj choco'je' mi yiris shevtacsi' paper miqui'ves jäijnäs? Yoshopay

Codacdyes jemonacsi': ¿Judyeya' quin' na, me' buty tupuj choco'je' mi yiris shevtacsi' paper miqui'ves mo' jam anic shandyes judyeya' mi jam anic jäijnäs?_Jam juijya' ji'jäcva' yocsi'can peyacdye': ¿yiris shevtacsi' paper miqui'ves mi jam shandyes judyeya' mi jam jäijnäs?. Yejcoisi' codacdyes peyacdye': ¿Oij na shivacsi' paper miqui'ves shandyes buty? ¿Oij na shevacsi' paper miqui'ves jäijnäs buty?

The instructions for the task in English are reproduced below:

Set up: "You are now seeing a reduced version of the grid. As you may notice, it contains some chips you have previously identified as green, and some chips you previously identified as red. Could you point towards a green chip? [Researcher verified that a green chip is picked] And now, could you point towards a red chip? [Researcher verified that a red chip is picked]. Thank you."

Critical question: "And now, could you pick the chip that is the least green and the least red? Or, in other words, that is neither green nor red?" [Researcher notes down the chip] Follow-up questions regarding the color chip that the participant picked: "Is this chip red? Is this chip green?" If the participant gave a positive response to either question, they were asked again the critical question as well as the follow-up questions.

For the initial 10 Tsimane' speakers, the follow up questions were not asked; of those, one subject was eliminated given that they chose the same chip for both the best example of green in the focal task as well as for the hue cancellation task, making it likely that they did not understand the task.

All three tasks were performed indoors and under controlled lighting conditions with the use of a light box (nine phosphor broadband D50 color-viewing system, model PDV-e, GTI Graphic Technology, Inc.).Data were analyzed with R package 'munsellinterpol v.2.6-1' (Gama et al., 2018). Statistical analyses on the hue values obtained from the munsellinterpol package were performed using bootstrapping with R package 'boot' (Canty and Ripley, 2021). The

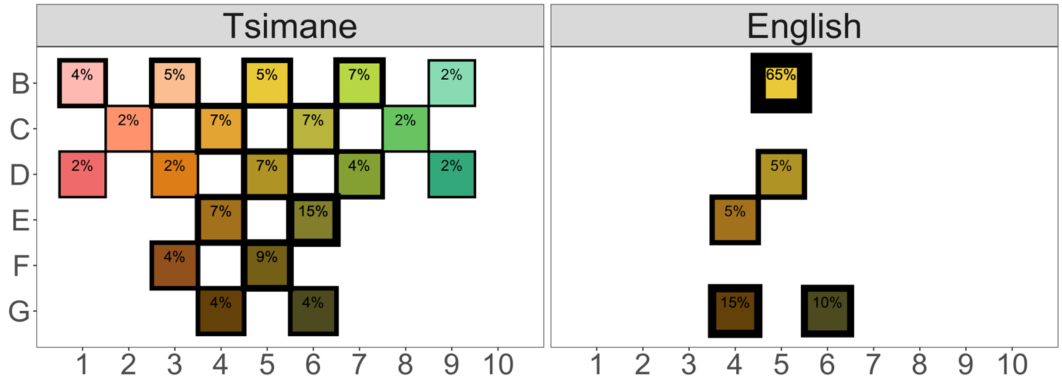

Figure 1: Proportion of responses to the hue cancellation task. Percentages have been rounded up to the nearest integer. The thickness of the border around the chip is proportional to the amount of subject who selected it in the hue cancellation task.

distribution of the chips within the grid were performed using Chi-Square tests.

## Results

When asked to identify the colored chip that is neither reddish nor greenish from an array that encompasses reds, oranges, yellows, browns, and greens, English speakers will consistently select from a limited number of chips that most speakers would describe as yellow (Figure 1, right panel). The array we used, developed initially by Albert Munsell, is the standard that has been used in most studies of color naming. This pattern of results in our neither-nor experiment is consistent with those from classic hue-cancelation experiments. Faced with the identical task, Tsimane' speakers identify chips that span a much greater range of the color array (Figure 1, left panel; Figure S2 shows the results for Tsimane' participants broken down between monolingual and bilingual groups). The pattern of results in the English and Tsimane' speakers is different (Pearson's Chi-squared test, X-squared = 46.29, df = 22, p = 0.002). Moreover, choices made by English speakers were more consistent across the population than choices made by Tsimane' speakers (Figure S3, p<0.0001 after 100,000 bootstraps of variance).

The interpretation of our experiments as relevant to the Hering opponent color theory requires that the participants understand the concepts of red and green used in the task. To assess comprehension of these concepts we analyzed data from the color selection and focal color tasks, using data from all participants in each language group for which we obtained data in these tasks (Figure 2; see Figure S4 for the same graph with Tsimane' participants broken down between monolingual and bilingual groups). We performed three different checks to ensure that both populations had a clear conception of "red" and "green", as follows.

First, we asked whether in the color selection task both Tsimane' and English speakers attribute different hues to green (Tsimane' shandyes) and red (Tsimane' jaines). Consequently, (Freeman and Dale, 2013; Maechler, 2013) we tested whether the mean of the hue values of chips chosen for green and red by each group fell between the range for green and red established by the ISCC-NBS System (Gama et al., 2018). According to this notation system, the hue for green ranges from 35 (green-yellow) to 55 (blue-green), and the hue for red in this section of the grid ranges between 0 (red) and 15 (yellow-red) (note that purples were not included; see Figure S1). In the Tsimane' group, the mean hue value was 40.7 (SD=8.2) for chips chosen as green and 9.28 (SD=5.07) for chips chosen as red, both of which fell in the established ranges for the respective colors. In the English group, the mean hue value was 40.5 (SD=6.63) for chips chosen as green and 7.82 (SD=2.50) for chips chosen as red during the color selection task, both of which also fall within the ranges established above. These results support the idea that both populations' conception of "red" and "green" fall within parameters established by the ISCC-NBS System.

Second, we compared the choices for green (Tsimane' "shandyes") and red (Tsimane' "jaines") in the color selection and comprehension tasks between Tsimane' and English speakers. The range of chips selected as green/shandyes by Tsimane' and English speakers were comparable (X-squared = 20.825, df = 27, p-value = 0.7944); and the chip selected most often as the best exemplar for green/shandyes was the same in the two groups (E8 was chosen as the best shandyes 42% of the time by Tsimane' speakers and 90% of the time by English speakers for green). But the ranges of chips selected as red/jaines by the two language groups differed (X-squared = 79.5, df = 16, p < .001). Despite this difference, the chip chosen most frequently for red/jaines was identical in in the two groups: F1 was chosen as the best jaines 96% of the time by Tsimane' and 71% of the time by English speakers for red. The distribution of the chips chosen to be the best example of a color word were different for red/jaines (X-squared = 9.992, df = 3, p-value = 0.02) and marginally different for green/shandyes (X-squared = 19.3, df = 11, p-value = 0.06). And for both pairs of color terms, the range of chips identified as the focal chip was larger for Tsimane' than for English (for red/jaines, p=0.02; for green/shandyes, p<0.001; tested by bootstrapping 100,000 samples with replacement).

Taken together, these results support the idea that the two populations have similar conceptions of "red" and "green,",

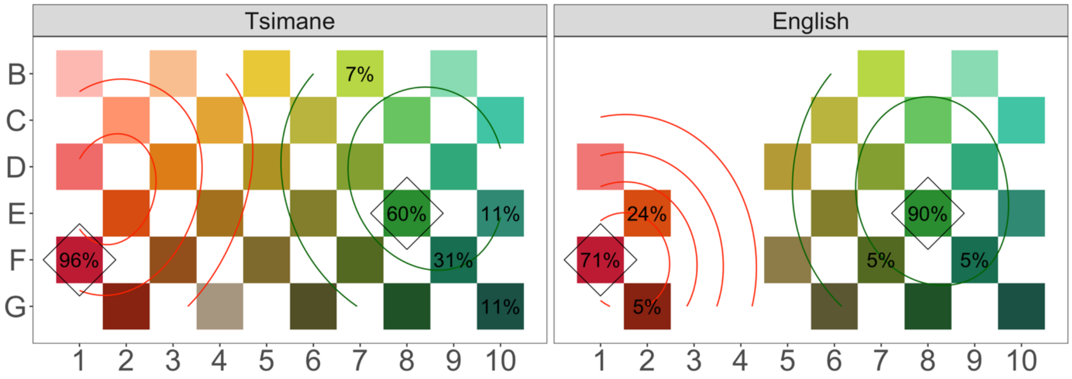

Figure 2: Color selection data across English and Tsimane' speakers. Any chip that is colored in the graph is a chip that was chosen during the color selection task, contours enclose 5%, 25%, 50% and 100% of the data. Text is the percentage of times the chip was chosen to be the best example of red and green (percentages were rounded to closest integer and only those equal or above 5 are represented in the grid). The most chosen (modal) chip is indicated by the diamond shape.

with a wider range of what counts as "jaines" (red) and "shandyes" (green) in Tsimane'.

Given the greater range in chips accepted as focal jaines (red) and focal shandyes (green) among the Tsimane' speakers compared to the English speakers, we performed a more conservative analysis of the results of the neither-nor task. Specifically, we asked whether participants selected a chip that they had previously not labeled as either green/shandyes or red/jaines in the color-selection task, as would be predicted if the participants clearly understood the neither-nor task instructions. For each participant for whom we had data in both the neither-nor task and the color-selection task (n=43 Tsimane', n=21 English), we asked whether the chips they identified as green/shandyes and red/jaines in the color-selection task corresponded to the chip they selected in the neither-nor task. Most participants across both language groups chose a color that they had not previously labeled as green/shandyes or red/jaines (see Table 1 and Figure S5). Note that no participant (for which we had focal data) chose a chip that they had labeled as the best representation of 'green' or 'red (Figure S5).

Table 1: Distribution of the chip picked in the hue cancellation task as either 'green', 'red', or 'other' based on each individual's answers in the color selection task.

| Language | Green | Red | Other | Total Subjects |
|---|---|---|---|---|
| English | 0 | 0 | 21 | 21 |
| Tsimane' | 6 | 3 | 31 | 40 |

Despite the support at the population-level that both Tsimane' and English speakers understood the neither-nor task, nine Tsimane' participants identified a chip as neither jaines (red) nor shandyes (green) that they had previously labeled as jaines or shandyes (Table 1). We therefore compared the data from the remaining participants: the distribution of the chips chosen in the neither-nor task remained significantly different between Tsimane' and English speakers (X-squared = 29.612, df = 15, p-value = 0.0134). These results show that Tsimane' participants, in contrast to English participants, don't generally select unique yellow in the neither-nor task, which violates the universality of the unique hues.

Finally, our data set allows us to assess whether having a clear label for English yellow might be partially responsible for choosing focal yellow as least red and green. In particular, Tsimane' monolinguals do not have a clear label for English yellow, but Tsimane' bilingual speakers do, because they speak Spanish ("amarillo" = English yellow; see Figure S6). But these populations behave the same on the neither-nor task (X-squared = 20.37, df = 21, p-value = 0.49; see Figure S2). This suggests that color use, not lexical knowledge, may be driving the effects in industrialized cultures, such that people may need to have early education in the primary colors to behave as English speakers do.

Supplementary information with further analyses and the original data can be accessed here https://osf.io/fu6eh/

## Discussion

This study provides a test of Hering's theory of Unique Hues, which is a central pillar of many contemporary theories of color appearance. The test involved a behavioral experiment in which participants were asked to identify colors that are neither reddish nor greenish, which recovers the key result of the classic hue-cancelation experiments in English speakers. Tsimane' speakers readily identified reddish and greenish color chips, but they showed idiosyncratic color choices when asked to identify a color that is neither reddish nor greenish, unlike English participants who consistently identified the same yellow (or brown) chip. These results are at odds with Hering's theory, which predicts that all people with normal color vision, regardless of culture or language, should show behavior that privileges the Unique Hues (Lindsey and Brown, 2006; Regier et al., 2005). The results provide evidence against the notion that the Hering Unique Hues reflect how color is encoded by the eye and brain, as well as evidence against the idea that a clear label for the color 'yellow' drives the results in hue cancellation tasks. Instead, our data promote alternative accounts of the Unique Hues, for example, that they reflect adaptive behavior to environmental selective pressures.

Hue cancelation experiments pioneered by Hurvich and Jameson are the bedrock of current formulations of Hering's theory (Wandell, 1995). The experiments confirm that color-encoding mechanisms are opponent. But despite the initial interpretation, the experiments do not prove Hering's theory because the task design begs the question: red, green, blue, and yellow are defined as the colors into which all colors should be decomposed. The experiments do not rule out the possibility that the color-opponent mechanisms are characterized by other sets of complementary colors, and perhaps by more than two axes. Indeed, Bosten and Boehm (Bosten and Boehm, 2014) showed that participants can rate proportions of teal, purple, orange, and lime in test colors with the same reliability that they can rate proportions of the Unique Hues, using an experimental approach developed by Boynton and Gordon (Boynton and Gordon, 1965) and popularized by Gordon and Abramov (Abramov and Gordon, 1994).

Almost all behavioral work testing the relative importance of the Unique Hues has been conducted with participants from industrialized cultures. Color-naming books for infants and toddlers, and play with coloring crayons, is ubiquitous in industrialized cultures. These activities teach us that red, green, blue, and yellow are fundamental building blocks of color ("primary colors"), which raises the possibility of a confound, that the social environment brings about the privileged status of Unique Hues and not the other way around (that the brain makes the Unique Hues, which prompts us to write books about them). When identifying colors that were neither red nor green, English speakers were strongly biased to select yellow over brown, even though both yellow and brown satisfy the instructions according to Hering's theory, and brown is encountered much more frequently in the natural world. A bias for yellow over brown is predicted if task performance is influenced by the way English-speaking children are typically taught about colors, where yellow is considered a primary color but brown is not. These considerations underscore the importance of tests in participants who are nonindustrialized cultures (Lindsey et al., 2020).

In an earlier project related to the one reported here, Lindsey et al. asked English speakers and Somali speakers to identify color samples constrained by Hering's opponent colors in various ways. Of particular relevance to our study, the participants were asked to identify yellow samples that contain no red or green, similar to our neither-nor task. Unlike the Tsimane' participants, the Somali participants in Lindsey et al.'s study behaved similarly to English speakers, consistent with the predictions of Hering's theory. But Lindsey et al.'s task is critically different from our task, in that they asked participants to choose color samples that were "yellow" ("jaale" in Somali), in addition to being neither red nor green. Asking participants to find "yellow" ("jaale") color chips begs the critical question that our neither-nor task is designed to ask. So we can't infer anything about Hering's theory from the Somali data in Lindsey et al.'s neither-nor task.[1]

Historically, when presented with behavioral evidence that Hering's theory is wrong, appeals are sometimes made to neurophysiological data, and the idea that the importance of the Unique Hues is evident in how the brain encodes and responds to color. Yet close analysis of the neurophysiological data fails to buttress Hering's theory. The first post-receptoral stage of color processing, carried out by bipolar cells and evident in the responses of midget retinal ganglion cells, shows cone opponency, but the color tuning of the opponent responses does not correspond to the Unique Hues (Webster et al., 2000; Wuerger et al., 2005). There is also no evidence that neurons in primary (striate) visual cortex encode the Unique Hues; instead, these cells show hallmarks of the cone-opponent mechanisms used by the retina to extract chromatic information from the retinal image (Conway, 2001; Horwitz, 2020; Tailby et al., 2008). Color signals are further processed by extrastriate visual cortex, including subcompartments of the V4 Complex (Conway et al., 2007). The population of neurons in these subcompartments transforms the color representation of the post-receptoral stage of color encoding (Stoughton and Conway, 2008), but despite the initial interpretation of the data, the population does not reflect the Unique Hues (Bohon et al., 2016). Instead, the cells show nonlinear color tuning, and as a population, they show relatively uniform representation of color space with a slight biased for warm colors. Regions of cerebral cortex even further along the putative visual-processing hierarchy, within inferior temporal cortex, similarly provide no evidence of a privileged status of Unique Hues, but instead appear to reflect the color statistics of the parts of scenes that hold behavioral relevance as reflected by object naming (Rosenthal et al., 2018). As far as we are aware, the only neural evidence for the privileged status of the Unique Hues is from event related potentials: the P2 peak of event related potentials (ERPs) is slightly earlier for Unique Hues (Forder et al., 2017). The effect, obtained in English speakers, is subtle and there are plausible explanations besides requiring that the Unique Hues are hard wired features of how color is encoded. For example, the results could reflect activity in frontal cortex related to how color representations are decoded, which would reflect cultural factors.

Taken together, the weight of behavioral and neurophysiological evidence shows consistent violations of Hering's theory, which suggests that Hering's Unique Hues do not reflect fundamental processes of color encoding.

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[1] Lindsey et al also asked participants to name the Unique Hue elements for random colors across the array. Somali and English participants performed differently, which could reflect differences in meanings associated with the corresponding labels: the Somali "jaale" is likely different from English "yellow". So this task is not directly relevant to testing the Opponent Colors theory.

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