PERCEPTION

ngineers often load a structure with weight until it collapses or shake it until it flies apart. Like engineers, many scientists also have a secret love for destructive testing-the more catastrophic the failure, the better. Human vision researchers avoid irreversible failures (and lawsuits) but find reversible failures fascinating and instructive-and sometimes even important, as with the devastating spatial disorientations and visual blackouts that military pilots can experience. At the U.S. Air Force Research Laboratory, the two of us explore the most catastrophic visual failures we can arrange. We create conditions in which people see images flowing like hot wax and fragmenting like a shattered mosaic. Here, we tell the story of the two most intriguing perceptual breakdowns we have studied: forbidden colors and biased geometric hallucinations.

Have you ever seen the color bluish yellow? We do not mean green. Some greens may appear bluish and others may appear yellow-tinged, but no green (or any other color) ever appears both bluish and yellowish at the same moment. And have you ever seen reddish green? We do not mean the muddy brown that might come from mixing paints, or the yellow that comes from combining red and green light, or the texture of a pointillist's field of red and green dots. We mean a single color that looks reddish and greenish at the same time, in the same place.

By arranging the right conditions, we have seen these unimaginable, or "forbidden," colors, as have our experimental subjects. And we have found ways to control, or bias, the hallucinatory patterns of concentric circles and wheel spokes that people can see in rapidly flickering light although the bias worked opposite to our expectations. Both these phenomena reveal something new about the neural basis of opponency, one of the oldest concepts in the science of perception.

Opponency is ubiquitous in physiology. For example, to bend your arm, you relax your triceps while contracting your biceps; biceps and triceps are opponent muscles, in that they act in direct

Seel

)pbidder

People can be made to see reddish green and yellowish blue—colors forbidden by theories of color perception. These and other hallucinations provide a window into the phenomenon of visual opponency BY VINCENT A. BILLOCK AND BRIAN H. TSOU

opposition to each other. In 1872 German physiologist Ewald Hering suggested that color vision was based on opponency between red and green and between yellow and blue; at each spot in the visual field, the redness and greenness muscles, so to speak, opposed each other. Perception of redness at a spot precluded perception of greenness there, and vice versa, just as you cannot simultaneously bend and straighten your arm. All the hues that people do see could be made by combining red or green with yellow or blue. Hering's theory explained why humans can perceive blue and green together in turquoise, red and yellow together in orange, and so on, but never red with green or blue with yellow in the exact same time and place.

Crazy Colors

The observation that people never see mixtures of opponent colors has been one of the most secure in cognitive science. Research has suggested, moreover, that color opponency begins in the retina and the midbrain-the first brain region involved in vision-with nerves carrying data that amount to one color signal subtracted from another. The raw color signals originate with cone cells in the retina, which detect light in three overlapping bands of wavelengths. Other cells add and subtract the outputs from the three kinds of cone cells, producing signals relating to four primary colors-red, green, yellow and blue. But it is as if the visual system is wired with two data channels for color: a red-minus-green channel (in which positive signals represent levels of redness, negative signals represent greenness and zero signal represents neither) and a similarly operating yellow-minus-blue channel. Such hardwiring enforces Hering's laws of color opponency.

In 1983, however, Hewitt D. Crane and Thomas P. Piantanida of SRI International in Menlo Park, Calif., reported a way to dodge the perceptual rules that forbid such colors as reddish green and yellowish blue. They had their subjects look at side-by-side fields of red and green or yellow and blue. Their apparatus tracked their subjects' eye positions and moved mirrors to keep the color fields stabilized—that is, frozen in place on each subject's retina despite all the continual little movements of the eye. Image stabilization can lead to many interesting effects, such as an image seeming to break into pieces that wax and wane in visibility. Of particular interest to Crane and Piantanida was the propensity for borders to fade in stabilized images.

Indeed, their experimental subjects saw the border between the two opponent colors evaporate; the colors flowed and mixed across the vanishing border. Some subjects reported seeing the forbidden reddish greens and yellowish blues. Others saw hallucinatory textures, such as blue glitter on a yellow background.

Crane and Piantanida's article should have provoked widespread interest: two highly competent investigators were reporting a major violation of the best-established psychophysical law. Instead the paper became the study that vision researchers did not talk about—the Crazy Old Aunt in the Attic of Vision.

We think four reasons contributed to this negligence. First, the result was inconsistent: some subjects saw the hallucinatory textures instead of forbidden colors. Second, the forbidden colors were hard to describe. Crane and Piantanida tried to get around this problem by having artists describe the colors. It did not help. Third, the experiment was hard to replicate. Crane had invented their special eye tracker, and it was expensive and difficult to use. Finally, researchers had no theoretical basis for understanding the result. We are convinced this was the crucial obstacle—

KEY CONCEPTS

- Red and green are called opponent colors because people normally cannot see redness and greenness simultaneously in a single color. The same is true for yellow and blue.
- Researchers have long regarded color opponency to be hardwired in the brain, completely forbidding perception of reddish green or yellowish blue.
- Under special circumstances, though, people can see the "forbidden" colors, suggesting that color opponency in the brain has a softwired stage that can be disabled.
- In flickering light, people see a variety of geometric hallucinations with properties suggestive of a geometric opponency that pits concentric circles in opposition to fan shapes.

—The Editors

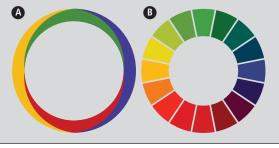
[COLOR EXPERIMENT] SEEING HUES OLD AND NEW

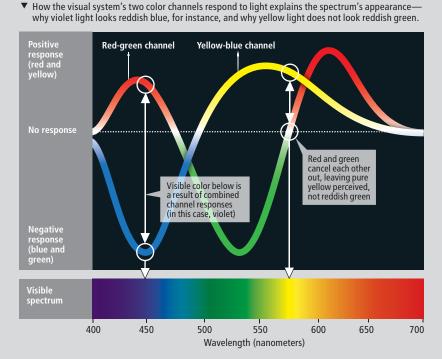
The authors showed that the cognitive phenomenon of color opponency (below) can be suspended to allow perception of colors not normally seen (opposite page).

HOW COLOR OPPONENCY WORKS

Human color vision seems to be based on two pairs of colors known as opponent colors: yellow and blue; red and green. Perception of one member of a pair (say, yellow) somewhere in the visual field usually precludes perception of the opponent color (blue) at that spot at the same time. Hence, although people routinely see colors that combine other colors—such as purple appearing to mix red and blue—we usually cannot see yellowish blue or reddish green. Our visual system seems to use two channels for color information (*right*): a yellow-minus-blue channel, which can signal yellowness or blueness but not both, and a red-minus-green channel.

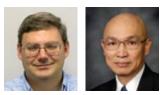
▼ Blending various amounts of yellow or blue with red or green (*a*) produces all the hues we see (*b*). This illustration is modeled after one by Ewald Hering, who proposed the theory in 1897.





things that do not fit into the existing paradigm are hard to think about. Crane and Piantanida guessed that they had bypassed the part of the visual system responsible for color opponency and activated a perceptual filling-in mechanism, but they did not develop the idea.

[THE AUTHORS]



Vincent A. Billock and Brian H. Tsou are biophysicists who bring the perspective of complexity theory to problems in human color and spatial vision. They conduct research together at Wright-Patterson Air Force Base in Ohio. Billock is a lead scientist for General Dynamics in Dayton, Ohio. Tsou is a principal scientist at the U.S. Air Force Research Laboratory. Tsou *never* sees reddish green—he is red-green colorblind, a condition that motivated him to study color vision.

Our Luminant Idea

Several years ago the two of us had an insight into a potential explanation for the varying perceptions of Crane and Piantanida's observers. We knew that, along with image stabilization, one other experimental condition leads to a similar loss of border strength: namely, when two adjacent colors have equal luminance. Luminance is similar but not identical to perceived brightness. Two colors are equiluminant to an observer if switching them very rapidly produces the least impression of flickering.

When subjects stare at two adjacent fields with equiluminant colors, they see the border between the colors weaken and disappear, allowing the colors to flow into each other—except in the case of red-green or yellow-blue pairs. We knew that this border-collapse effect is strongest when the observer minimizes eye movements. Perhaps the effects of equiluminance and stabilization would combine synergistically, leading to border collapse and color mixing powerful enough to happen consistently even with opponent colors. To test this idea, we teamed up with our Air Force Research Lab colleague Lt. Col. Gerald A. Gleason, who studied eye movements.

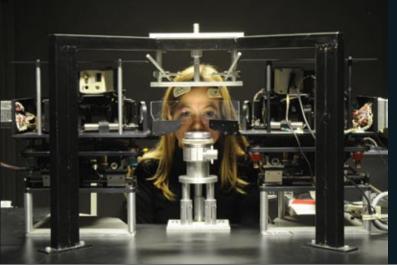
We anchored our subjects to Gleason's eye tracker using chinrests or bite bars to minimize head movement. We decided not to use artists and other laypeople as subjects. For this experiment we wanted vision researchers raised on color theory, skeptical about colors undreamt of in Hering's philosophy, and able to describe their observations in a rich shorthand of "visionese" important when you are mumbling your observations through clenched teeth. And we wanted credible subjects who could testify to our incredulous colleagues. Thus, we recruited seven vision researchers (including Billock and Gleason) with normal color vision.

Because people vary in their perceptions of the luminance of different colors, we first measured our subjects' responses to red, green, yellow and blue. Then we showed each subject side-by-side fields of red and green or yellow and blue, with the colors customized to appear either equiluminant or strongly nonequiluminant.

HOW TO SEE FORBIDDEN COLORS

The authors found unusual conditions that reliably overcame the prohibition against perceiving yellowish blue and reddish green. This result implies that color opponency in the brain is not as hardwired as is commonly thought. Apparently the opponency mechanism can be disabled.

 In forbidden color experiments an eye tracker monitors subjects' eye movements to keep the presented color stimuli in a fixed position on the retina.



When subjects stared at side-by-side fields of opponent colors (here, blue and yellow) and the image was motionless on their retinas, the boundary between the fields seemed to vanish, allowing the colors to run together (a). When one field was distinctly brighter than the other, the mixtures formed textures and patterns, such as blue dots on a yellow background. But for hues of matched luminance, most subjects saw novel colors (vellowish blues) that are usually impossible to perceiveor to depict accurately (b).

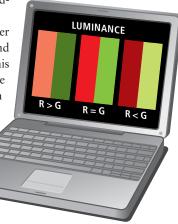
The combination of equiluminance and image stabilization was remarkably effective. For the equiluminant images, six out of our seven observers saw forbidden colors (the seventh observer's vision grayed out immediately every time). The border between the two colors would vanish, and the colors would flow across the border and mix. Sometimes the result looked like a gradient that ran from, say, red on the left to green on the right, with every possible shade of greenish red and reddish green in between. Other times we saw red and green fields in the same place but at different depths, as if seeing one hue through the other without any discoloration of either of them. Often we saw a nice, uniform reddish green or bluish yellow fill the whole field.

Intriguingly, two subjects reported that, after the exercise, they could see reddish green and bluish yellow in their imaginations, although this ability did not persist. We can thus answer the question philosopher David Hume posed in 1739: Is it possible to perceive a new color? It *is*—but the striking new colors that we saw were compounds of familiar colors.

Our observations led us to develop a model of how color opponency could arise in the brain

LUMINANCE

To see forbidden hues, it helps if you perceive the two displayed color fields to have equal luminance, which is similar to brightness. Two colors are equiluminant when swapping them very rapidly gives you the least sense of flickering. Depicting luminance on the printed page is difficult because people differ in their luminance perceptions, and printing introduces changes in the saturation of colors, along with the changes in brightness.



without relying on hardwired subtraction. In our model, populations of neurons compete for the right to fire, just as two animal species compete for the same ecological niche—but with the losing neurons going silent, not extinct. A computer simulation of this competition reproduces classical color opponency well—at each wavelength, the "red" or "green" neurons may win, but not both (and similarly for yellow and blue). Yet if the competition is turned off by, say, inhibiting connections between the neural populations, the previously warring hues can coexist.

B

A

Tiger Stripes on the Brain

In our experiment, when the red-green or yellowblue fields differed significantly in luminance we and our other subjects did not see forbidden colors. Instead we saw textures, such as green glitter on a red field or blue streaks on a yellow field, just as Crane and Piantanida reported for some of their subjects. They may have used colored images that were equiluminant for some subjects but markedly nonequiluminant for others.

These illusory speckled and striped patterns that we saw were intriguing. The study of these kinds of patterns in other contexts has a rich history. Such patterns arise in certain mixtures of

[GEOMETRY EXPERIMENT] **Controlled Hallucinations**

f you have ridden with your eyes closed in a car driven along a tree-lined street, you may have experienced "flicker," a rapid oscillation of light and dark. Flicker in a blank visual field (such as the backs of your eyelids) often induces fleeting hallucinations of geometric patterns, including concentric circles, spirals and fan shapes like spokes of a wheel. Study of brain processes uncovered by these illusions would be aided if researchers could stabilize the hallucinations and control which pattern a subject sees.

Clues to the neural basis of flicker illusions are provided by the brain's response to real examples of the patterns. Many of the patterns trigger activity along stripes of neurons in the primary visual cortex (right). When a person looks at a real fan shape, horizontal stripes activate (below, a). Concentric circles excite vertical stripes (c), and spirals excite slanted stripes (b, d). Geometric hallucinations presumably arise when flicker stimulates the primary visual cortex and the excitations self-organize into patterns of stripes.

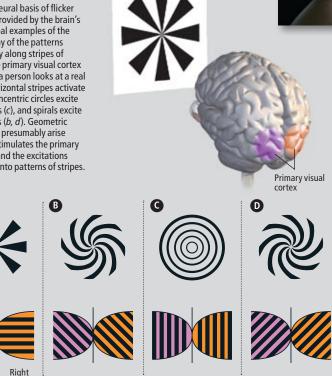
OBSERVED PATTERN

BRAIN RESPONSE

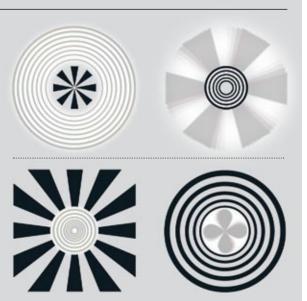
Left

cortex

cortex



To control people's flicker hallucinations, the authors showed subjects small patterns (black) and flickered the light in the surrounding blank area (top). Subjects saw hallucinations (gray) of circles around real fan shapes and rotating fan shapes around real circles. Similar effects occurred with a flickered blank area inside real patterns (bottom). These effects are analogous to a red region making an adjacent gray area seem tinted green (red's opponent color)-the circles and fan shapes act like "opponent" patterns.





reacting chemicals in which the chemicals diffuse asymmetrically or at different rates. English mathematician and computing pioneer Alan Turing introduced these reaction-diffusion systems as mathematical systems worthy of investigation, which can model the patterns seen in zebra coats, leopard skins and a variety of other biological phenomena-and in particular, hallucinations.

Visual hallucinations involving geometric patterns are generated by many triggers: drugs, migraines, epileptic seizures and-our favoritea visual stimulus called empty-field flicker. David Brewster (inventor of the kaleidoscope) investigated flicker-induced hallucinations in the 1830s, reportedly experiencing them by dashing past a high sunlit fence with his eyes closed, which produced rapid flashes of light and dark ("flicker") on the empty canvas of the backs of his eyelids. Today it is easier-and safer-to replicate the effect by closing your eyes while a passenger in a car driven along a tree-lined street or, better yet, by looking at a flickering computer monitor.

Common geometric hallucinations produced by flicker include fan shapes, concentric circles, spirals, webs and honeycombs. In 1979 Jack D. Cowan of the University of Chicago and his Ph.D. student G. Bard Ermentrout (now at the University of Pittsburgh) noticed that all these images corresponded to excitation of striped patterns of neurons in the primary visual cortex, a region of the brain at the back of the head involved in visual processing. For example, when a person looks at an actual image of concentric circles, vertical stripes of neurons in the primary visual cortex are activated. A fan-shaped pattern, such as spokes of a wheel, excites horizontal rows of neurons. Spirals excite slanted stripes.

Thus, Ermentrout and Cowan could account for many of the reported geometric hallucinations if the visual cortex could spontaneously generate striped patterns of neural activity in response to flicker. In 2001 Cowan and other coworkers extended the model to account for many more complicated patterns. These findings, however, do not offer a recipe for how to induce any particular hallucination for detailed study. Indeed, the patterns induced by flicker are both unpredictable and unstable, probably because each flash disturbs the previously elicited hallucination. Having a technique to evoke a specific stable hallucination for extended observation would be very helpful. Visual hallucinations and Turing's mathematics of pattern formation might then provide a window into the dynamics of the human visual system.

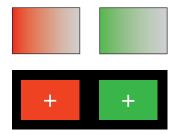
To try to stabilize the flicker-induced patterns, the two of us took inspiration from other spontaneous pattern-forming systems that can be made predictable by introducing a suitable bias. For instance, picture a shallow pan of oil, heated from below and cooled from above. If the temperature difference is great enough, the rising hot oil and falling cool oil self-organize into a pattern of horizontal cylinders, which from above look like stripes. Each cylinder rotates on its axis—fluid rising on one side and falling on the other. The pattern is stable if adjacent cylinders rotate in opposite directions, like cogwheels.

Ordinarily the orientation of the cylinders (the direction of the "stripes") is determined by chance while the pattern is forming, but if you inject an upwelling of fluid along a particular orientation, then the pattern of cylinders evolves to line up with it. Fortuitously misled by this analogy, we decided to see if presenting a pattern next to a flickering blank area would stabilize the hallucination seen by people. In experiments we displayed small circular and fan-shaped designs at a constant illumination with rapidly flashing light in the blank area around them. The physical patterns would excite stripes of a specific orientation in a person's visual cortex, and we expected the excitations induced by the flickering area would extend the pattern by adding parallel stripes. Thus, we thought our subjects would see the circular patterns and the fan shapes extended into the surrounding flickering area.

Circles and Fans

Much to our surprise, our subjects saw the opposite effect. The small physical circles were always surrounded by illusory fan shapes, which rotated at about one revolution per second. Conversely, flickering around small physical fan shapes evoked hallucinations of circular patterns, which occasionally pulsated. Similar results occurred

CAN YOU SEE IT?



Binocular vision may provide a way to see forbidden colors. Try staring intently at these pairs of rectangles, allowing your eyes to go cross-eyed so that the red and green areas overlap (in the lower case, make the crosses merge). The fused colors compete in a patchy, unstable fashion. Some people get glimpses of forbidden reddish green as the patches change color, but the method is much less reliable than using equiluminant stabilized images.



MORE TO EXPLORE

On Seeing Reddish Green and Yellowish Blue. Hewitt D. Crane and Thomas P. Piantanida in *Science*, Vol. 221, pages 1078–1080; 1983.

Perception of Forbidden Colors in Retinally Stabilized Equiluminant Images: An Indication of Softwired Cortical Color Opponency? Vincent A. Billock, Gerald A. Gleason and Brian H. Tsou in *Journal of the Optical Society of America A*, Vol. 18, pages 2398–2403; October 2001.

What Do Catastrophic Visual Binding Failures Look Like? Vincent A. Billock and Brian H. Tsou in *Trends in Neurosciences*, Vol. 27, pages 84–89; February 2004.

Neural Interactions between Flicker-Induced Self-Organized Visual Hallucinations and Physical Stimuli. Vincent A. Billock and Brian H. Tsou in *Proceedings of the National* Academy of Sciences USA, Vol. 104, pages 8490–8495; May 15, 2007. when the physical pattern surrounded a flickering empty center. In all cases, the hallucination was confined to the flickering area—it extended through the physical pattern only if we made the physical pattern flicker on and off in synchrony with the light in the empty area.

In retrospect this outcome should not have been surprising. Fifty years ago Donald M. Mac-Kay of King's College London showed that when fan shapes are viewed in flickering light, a faint pattern of concentric rings can be seen overlaying the fan, and vice versa. MacKay's result can be interpreted as arising from a kind of opponency. To understand this point, consider what happens if you see a bright flash of red light: you see a green afterimage, green being the opponent color to red. If the visual system processes fan shapes and concentric circles as opponent geometric shapes, then the faint patterns seen in MacKay's illusion can be geometric afterimages present during the dark moments between the flashes.

Our new illusion also has a color analogue: a red field can make an adjacent gray field look greenish. Under the correct dynamic conditions—our flickering setup—a geometric pattern induces the opponent geometric pattern in the empty field next to it. Stated another way, Mac-Kay's illusion involves geometric opponency separated in time (that is, the fans and circles are present at separate moments), whereas our effect is geometric opponency separated in space (the fans and circles being in adjacent regions).

Although it may be natural to regard forbidden colors and biased geometric hallucinations as parlor tricks, they illustrate important points about vision and the nature of perceptual opponencies. Forbidden colors reveal that color opponency—which has served as the model for all perceptual opponencies—is not as rigid and hardwired as psychologists thought. Softwired mechanisms such as our competition model may be needed to understand fully how the brain handles opponent colors.

Experiments that stabilize geometric hallucinations reveal that for all their exotic appearance, these hallucinations behave surprisingly like familiar visual effects involving colors. The neural nature of geometric opponencies is also very interesting. The opponent patterns involve perpendicular stripes of excited neurons in the visual cortex—could this feature be a clue to how the neural wiring produces the opponency? To answer this and other questions, researchers will have to come up with new ways to push the visual system to its breaking point and beyond.