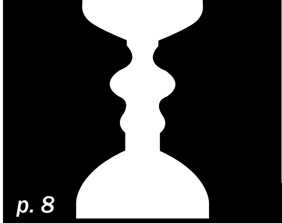
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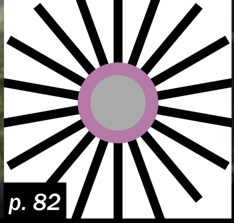
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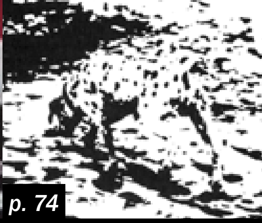
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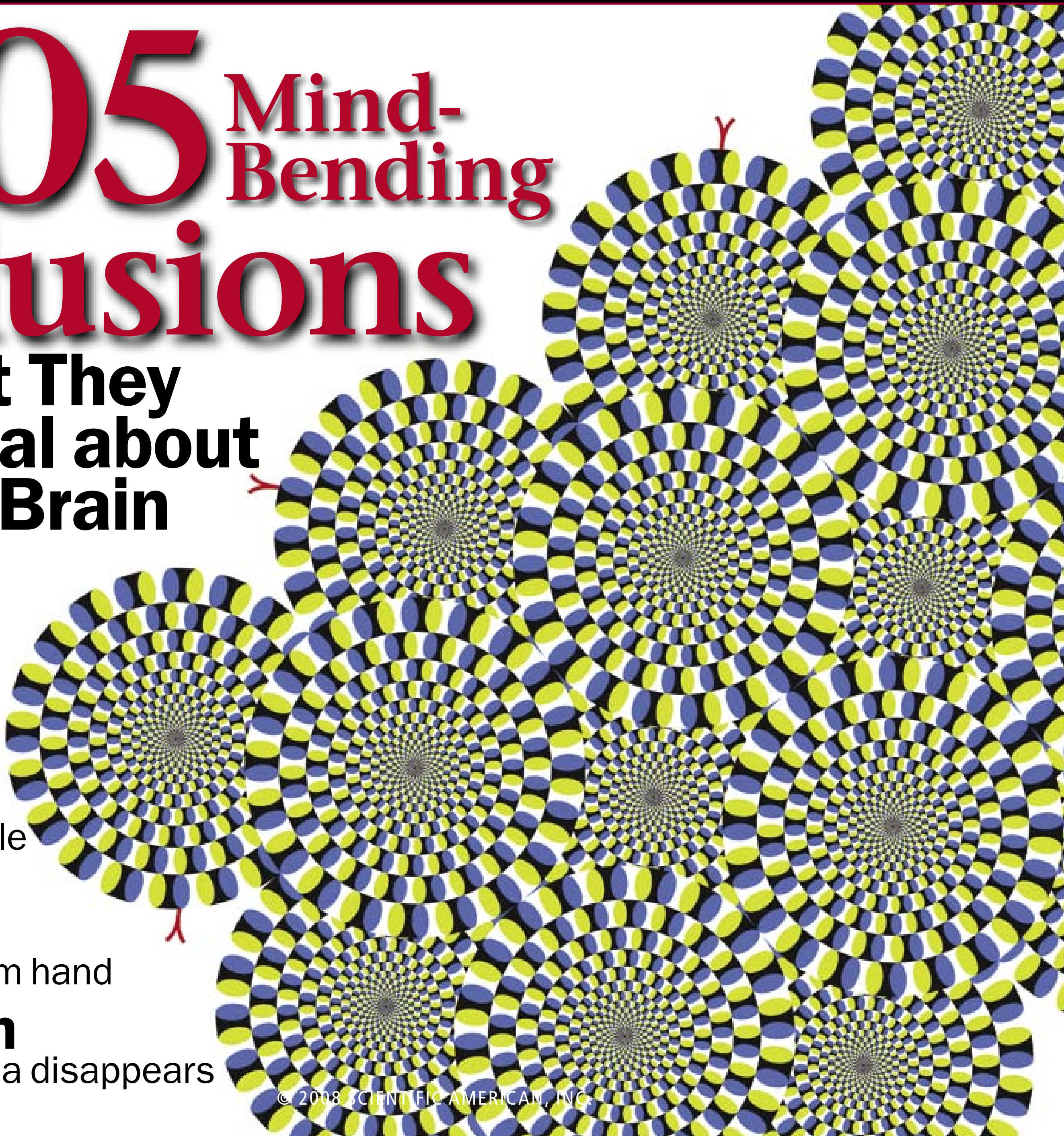
105 Mind-Bending Illusions

What They Reveal about Your Brain

See
impossible objects

Feel
a phantom hand

Watch
as a gorilla disappears



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REPORTS

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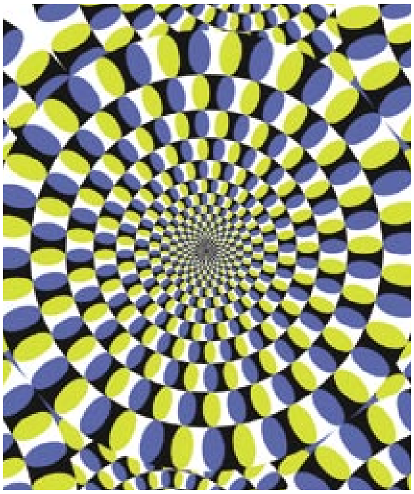

AKIYOSHI KITAOKA 2003

The "Real" World

"The camera does not lie," the saying goes. And we tend to think of our eyes and our other sensory organs as video equipment, faithfully recording all the details of our busy lives. As you will learn from the articles on illusions collected in this special issue, however, we see with our *brains*, not with our eyes. And our brains make instant value judgments about the jumble of incoming sensory information, depending on what is important at that moment to us, to create a sensible narrative of the world around us.

Rather than pondering every bit of light that enters our orbs, the brain quickly jumps to conclusions, based on millions of years of evolution. Humans are intensely visual creatures, and we have developed an incredible apparatus for detecting things that are critical to our survival, such as predators, prey and mates. For instance, we can instantly mentally assemble several tiny patches of orange with stripes peeking through dense foliage: "tiger!" As we glance around a room, the image bounces on the retina (the light-receiving tissue at the back of the eye) as various areas of the scene excite different groups of cells. Yet the world appears stable to us, the view a smooth pan across our surroundings. The brain even fills in missing bits of picture in the eye's blind spot, where the optic nerve pierces the retina.

On the other hand, we do not see everything. Something that is irrelevant to a particular task will not make it to our conscious awareness. In one telling experiment, volunteers had to count how many times a basketball got passed between players. A person in a gorilla suit then strutted across the room. Concentrating on those ball passes, about half the volunteers did not see the gorilla.

Of course, the brain cannot actually tell us about what it is thinking as it processes sensory inputs, focusing on certain items and ignoring others. But our responses to illusions can be just as revealing. Scientists have long used these disarmingly simple—and fun—sensory tricks to probe the mind's inner workings. This special edition offers an amazing collection of such illusions and the lessons that they teach us about the brain. We can promise you one thing: you won't believe your eyes.

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Executive Editor
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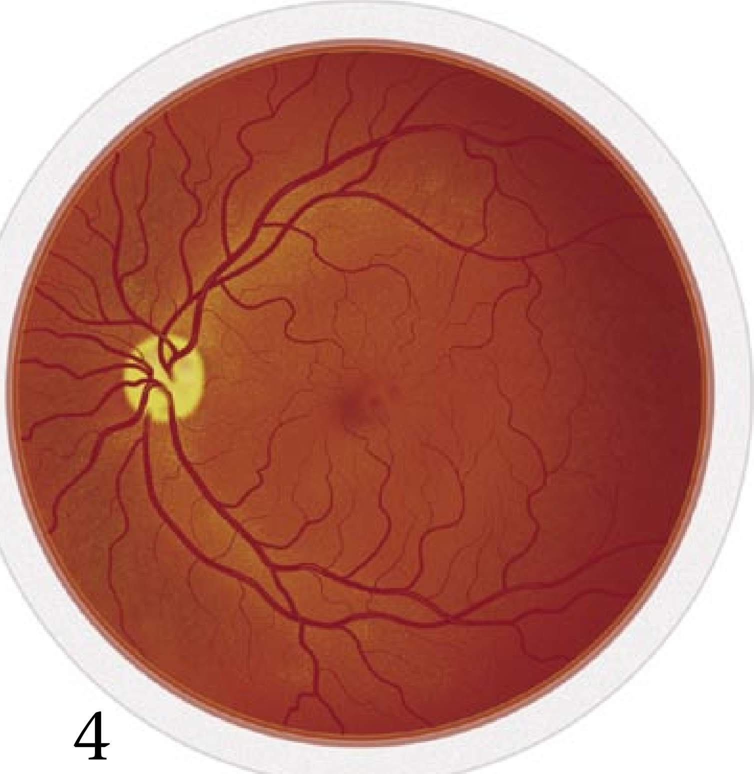

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Articles in this special edition are updated from previous issues of *Scientific American Mind* and *Scientific American.*

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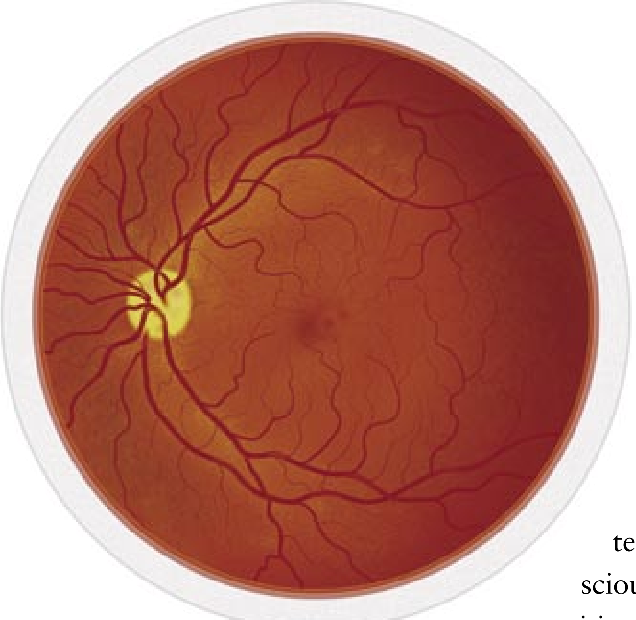
Mind the Gap

The brain, like nature, abhors a vacuum

BY VILAYANUR S. RAMACHANDRAN AND
DIANE ROGERS-RAMACHANDRAN


Your retina has a blind spot where the optic nerve exits the eyeball.

MARK MILLER *Photo Researchers, Inc.*

OUR PERCEPTION of the world depends, to a surprising degree, on intelligent guesswork by the brain. An oval-shaped white image exciting your retina could be produced by an egg, or a perfectly circular, flat tilted disk, or an infinite number of intermediate shapes, each angled to the right degree. Yet your brain "homes in" instantly on the correct interpretation of the image. It does this by using certain unconscious assumptions about the statistics of the natural world—suppositions that can be revealed by visual illusions.

The manner in which the brain deals with inexplicable gaps in the retinal image—a process called filling in—provides a striking example of this principle. You can demonstrate this using the blind spot of your eye.

Examine illustration *a*. With the right eye shut, look at the center of the lower white box. Hold the page about a foot away from your face and slowly move it toward you and away from you. At a certain distance the disk on the left vanishes. It has fallen on the blind spot of your left eye, a small patch of retina called the optic disk that is devoid of receptors (an imperfection caused by the optic nerve piercing the retina as it exits the eyeball).

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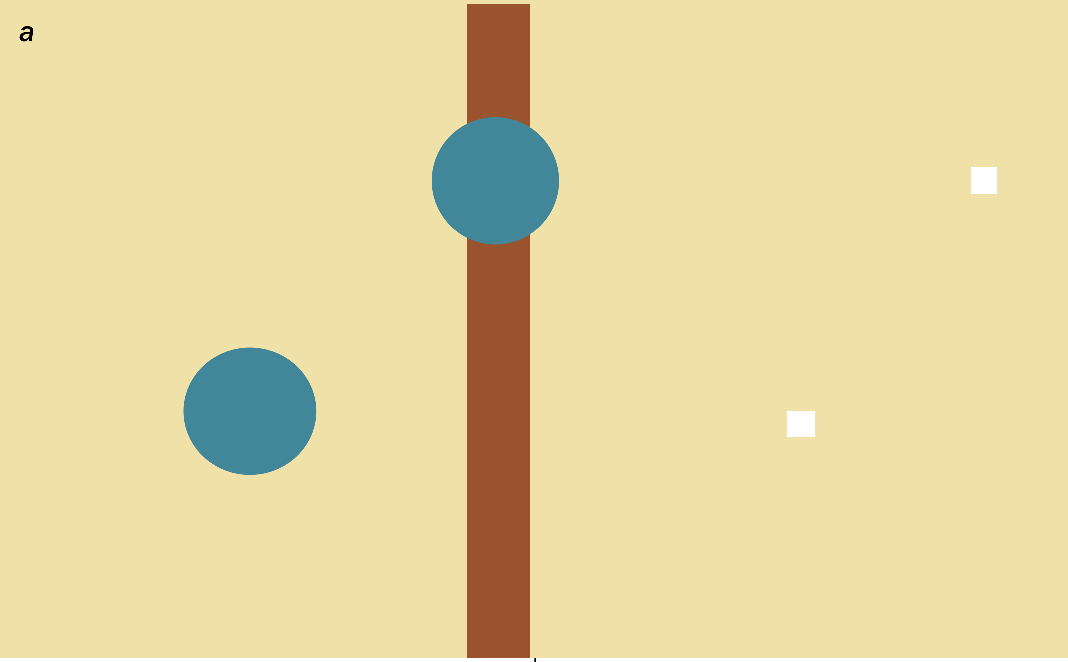

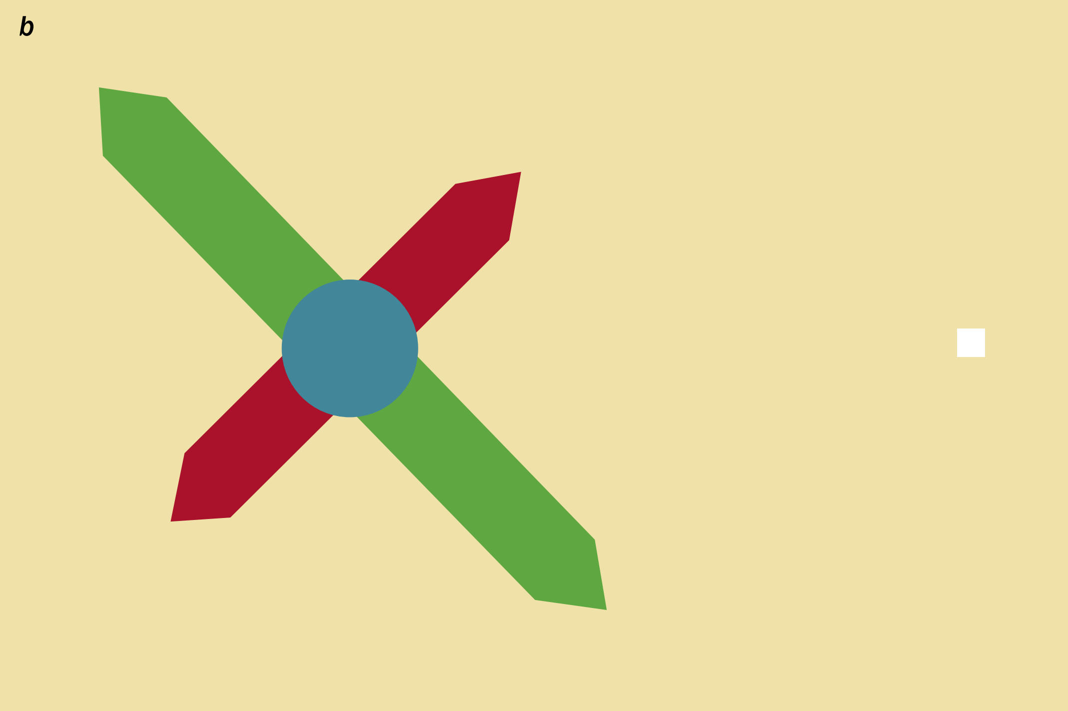

Victorian physicist Sir David Brewster was struck by how when the disk disappears, you do not experience a dark shadow or gaping hole in its place. The region corresponding to the disk is "filled in" by the background color. He attributed this process to God, the "Divine Artificer."

Even a straight line running through your blind spot is not lopped off in the middle, as you can see by doing the same exercise but this time looking at the higher white box in *a*. The missing segment of the line appears complete. It is as if the brain regards it as highly unlikely that two short lines could lie on either side of the blind spot simply by chance. So the cells in the visual centers fire just as they would if the bar had been complete, and you therefore see a continuous line. You can try coloring the two segments differently (for example, red and green) just for fun. Do you still complete the line?

The blind spot is surprisingly big, almost the size of nine full moons in the sky. Try closing your left eye and then look around the room with

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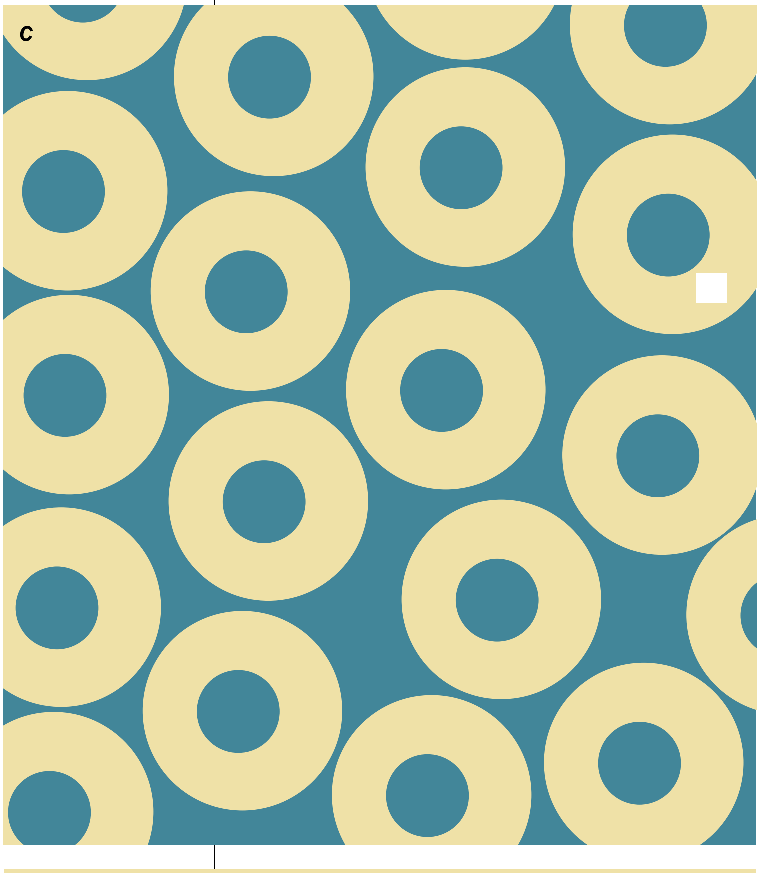

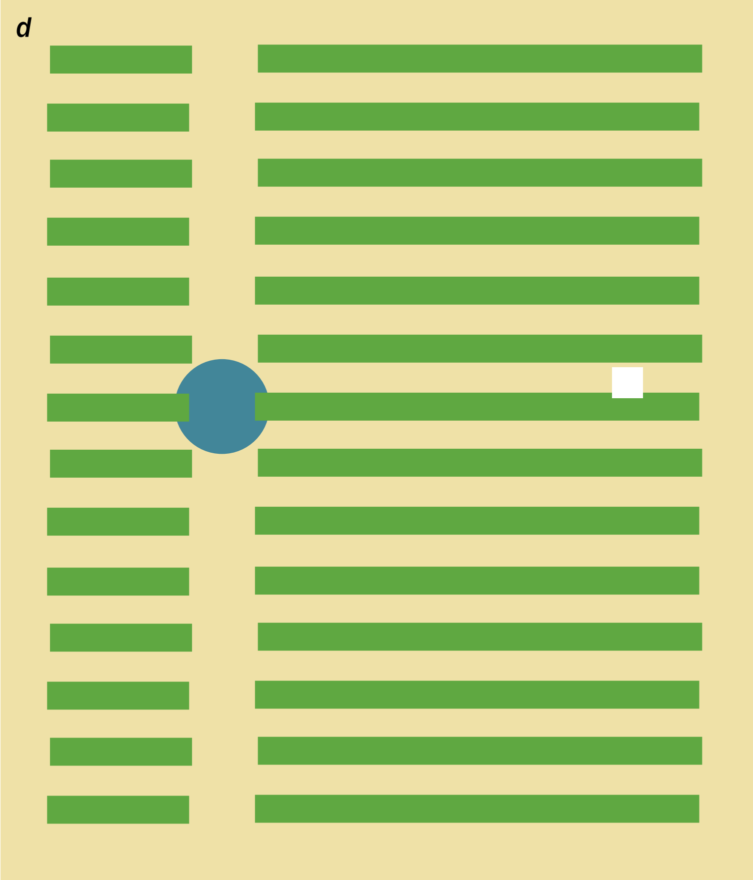

your right. With some practice, you should be able to "aim" your blind spot on any small object to make it disappear from the visual field. King Charles II of England used to aim his blind spot on a prisoner's head to "decapitate" him visually before an actual beheading. We often enjoy doing the same thing to rivals at faculty meetings.

How sophisticated is the filling-in process? If the middle of a cross falls on the blind spot, would it get filled in? What about repetitive wallpaperlike patterns? With just a few colored felt-tip markers and sheets of paper (or a computer graphics package), you can explore the limits of filling in and the "laws" that govern the process. I will describe a few examples here, but you can invent your own.

In *b,* on the preceding page, your blind spot falls on the center of an X made of a long green line crossing a short red one. If you are like most people, you will see that *only* the longer of the two lines is completed across the blind spot. (Whereas there is no difficulty filling in the missing part of the short line if it is presented on its own.) This simple exercise demonstrates that, under some conditions, filling in is based on integrating information along the whole length of the line rather than information that is spatially adjacent.

In other circumstances the brain fills in only what is *immediately* around the blind spot. If you aim your left eye's blind spot on the center of a yellow doughnut, you will see a yellow disk instead of a ring; the yellow fills in. Even more remarkable, the same thing happens in *c;* most people will see the yellow disk pop out conspicuously against a background wallpaper of yellow rings. Instead of extrapolating the repetitive ring patterns, your visual system performs a strictly local computation. It fills in just the homogeneous yellow immediately around the disk.

Yet this is not always true, as you will see from *d*. Notice the vertical illusory strip running through the parallel horizontal lines. Aim your left eye's blind spot on the blue disk to make it vanish. Now the question is, Do you fill in the missing segments of horizontal lines running through the blind spot? Or do you fill in the vertical illusory strip? The answer depends on the spacing of the lines.

Why does filling in occur? It is unlikely that the visual system evolved this ability for the sole purpose of dealing with the blind spot (after all, the other eye usually compensates). Filling in is probably a manifestation of what we call surface interpolation, an ability that has evolved to compute representations of continuous surfaces and

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(We actually "see" very little of the world and rely on **educated guesswork** to do the rest.)

"Filling in" by the brain makes these cats look whole rather than sliced up.

J. L. KLEIN AND M. L. HUBERT *Biosphoto/Peter Arnold, Inc.*

contours that occur in the natural world—even ones that are sometimes partly occluded (for example, a cat seen behind a picket fence looks like one whole cat, not like a cat sliced up). Physiologists (especially Leslie G. Ungerleider of the National Institute of Mental Health, Ricardo Gattass of the Federal University of Rio de Janeiro and Charles D. Gilbert of the Rockefeller University) have explored the neural mechanism of this process by monitoring the manner in which single neurons in the visual centers respond to objects partially covered by the blind spot or by opaque occluders.

If you get bored playing with your natural blind spot, try this. Toward the right side of your TV screen tape a tiny (half a centimeter in diameter) bit of white cardboard with a black spot in its center. Next, turn the TV to a channel that isn't broadcasting so that you see just twinkling "snow." Affix a two-centimeter-square patch of thick gray cardboard (about the same color as the TV snow) 12 centimeters or so away from the white cardboard. Stand a meter away from the TV set. If you open both eyes and stare at the small black dot steadily for 15 seconds, the large gray square will vanish completely, and the region "vacated" by it becomes filled in with the snow—you hallucinate the snow where none exists! Remarkably, if you now look away at a gray wall, you will see a square patch of dots twinkling in the region where the filling in occurred. Even a solitary red blob seen against a background of green blobs will disappear in the same manner—the green blobs fill in. The brain, it would seem, abhors a vacuum.

These experiments show how little information the brain actually takes in while you inspect the world and how much is supplied by your brain. The richness of our individual experience is largely illusory; we actually "see" very little and rely on educated guesswork to do the rest. **M**

VILAYANUR S. RAMACHANDRAN and DIANE ROGERS-RAMACHANDRAN are at the Center for Brain and Cognition at the University of California, San Diego. They serve on *Scientific American Mind*'s board of advisers.

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Stability of the Visual World

When your eyes scan a room, why doesn't the world appear to bounce like the real image on your retina?

BY VILAYANUR S. RAMACHANDRAN AND
DIANE ROGERS-RAMACHANDRAN

WHY IS THE STUDY of perception so appealing? One reason is that you can gain deep insights into the inner workings of your own brain by doing relatively simple experiments that any schoolchild could have done 100 years ago. More on those in a moment.

Hermann von Helmholtz

CORBIS

Your sensory experience of the world does not involve faithfully transmitting the retinal image to a screen in the brain so that it can be "seen" by some inner eye. One piece of evidence for this fact is that your perception of an object (in *a,* do you see two faces or a goblet?) can change radically even if the image on the retina is held constant, which implies that even the simplest act of observation involves judgment by the brain.

Less obvious, but equally important, is the converse. Your perception of the world—or an object in it—can also remain stable if the image is changing rapidly on the retina. One example is how you take in a scene when you move your eyes around. Every time you glance around a room, the image dances around the retina at warp speed, hundreds of feet per second. Yet all appears rock steady. Why?

Now, at first you might think the world does not appear to lurch because all motion is relative. The clouds glide in the twilight sky, but we assume they are stable and attribute the motion to the smaller object, the moon.

A simple experiment demolishes this idea. Close one eye—let us say the left. Then, keeping the right eye open, use the right index finger to displace the right eyeball, rocking it side to side slightly in its socket. (Gently!) You will see the world jump as if in an earthquake, even though there is no relative motion on the retina.

Why do we see a stable world when we swivel our eyes naturally but not when we jiggle an orb manually? The answer came from the great 19th-century physician, physicist and ophthalmologist Hermann von Helmholtz. He suggested that when the command to move the eyes is sent from the frontal lobes to the muscles of the eyeballs, a faithful copy of the command (like a

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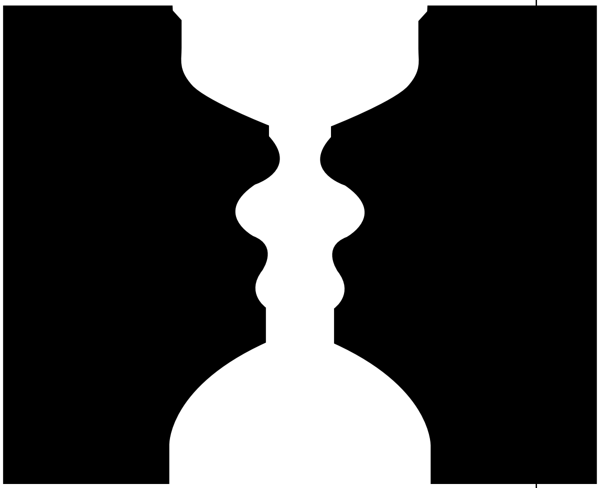


a

"CC" for an e-mail) also goes to visual motion–detecting centers in the back of the brain. As a result, they are tipped off ahead of time: "You are going to get some motion signals, but they are not caused by real movement of the world, so ignore them."

We can speak of two independent systems in the brain, either of which can signal a sensation of motion. Neuropsychologist Richard L. Gregory of the University of Bristol in England calls these the image/retina system (caused by image movement on the retina) and the eye/head system (generated by sensing the movement of the eyes). Ordinarily, the brain subtracts one signal from the other. When you move your eyes around, these two motion signals cancel each other out and the world remains stable.

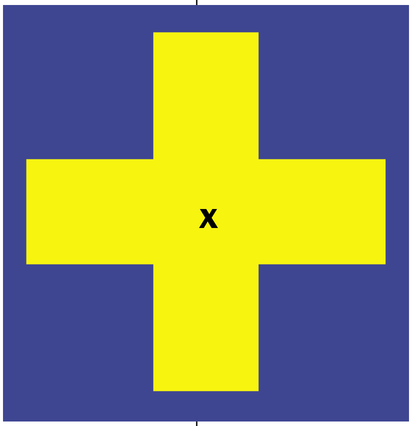
We know that the image/retina system exists because of the experiment in which you jiggled your eye with your finger. But how do we know the eye/head system can independently evoke a motion sensation? Think about what happens when your eyes track a glowing cigarette tip moving across a completely dark room. You correctly see it moving several feet, even though the cigarette image does not move much at all on your retina. Instead your eyes are making a big excursion. So the brain "concludes" that the cigarette must have moved an amount equivalent to the eye movement. Again, we can speak of the final movement perceived as resulting from the subtraction of image/retina signals (close to zero because you are tracking it) from eye/head signals (large, because the eyes move a large distance to keep the cigarette's image on the fovea, the area of the retina responsible for acute vision). The net result is that you see the glowing orange spot moving several feet.

You can produce a more striking version of this effect by having a friend take a photograph of you while you look directly at the flash. The result is a persistent afterimage of the bulb caused by continued activity of the receptors long after the light burst is gone. This flash image is "glued" to your retina; it cannot move even a tiny bit. Yet if you go to a dark room and move your eyes around, you see the afterimage moving vividly with the eyes. The eye/head system is signaling a large value, but the image/retina signal is zero—so as a result of the subtraction, you see the afterimage moving even though it is fixed and stationary on the retina.

You can create a similar fixed afterimage without a flash by staring for 30 seconds at the central X in the image in *b;* you will see the afterimage when you shift your gaze to a blank sheet of paper. (Blink your eyes to refresh the image if necessary.)

Forward and Back

Next question: What is the source of signals generated by the eye/head system? One possibility, called feedforward, is that a copy of the command from eye-movement centers is delivered to the sensory motion–detecting centers so that they will expect—and thus cancel—spurious image/retina signals. A second option, called the feedback theory, is that receptors in the eye muscles themselves sense the degree of eye movement and send the "cancellation" information to the sensory motion–detecting centers. Which is correct?



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To find out, Helmholtz performed a heroic experiment. He paralyzed his eye muscles using a local anesthetic instilled around the eyeballs. Every time he then tried to move his eyes (unsuccessfully, of course), the world appeared to move in the opposite direction—even though neither the image nor the eyes were moving. He concluded that the feedforward model was correct. His brain could not have relied on feedback, because his eye muscles were paralyzed. It is as if a copy of the intention to move the eyes is sent (feedforward) to the motion-sensing areas to be subtracted from the expected image/retina movement. But be-

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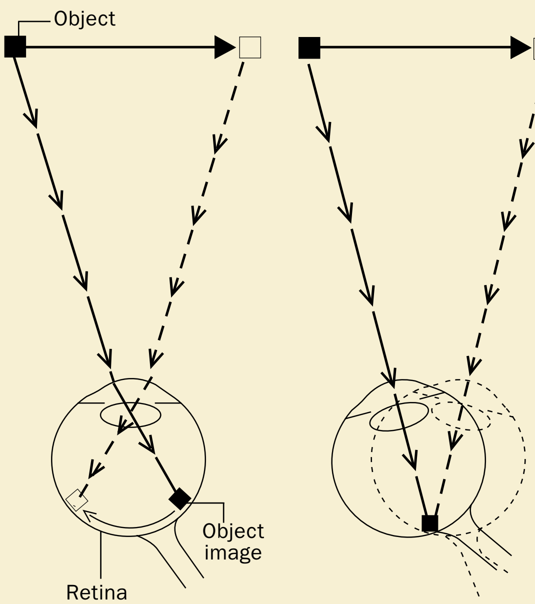
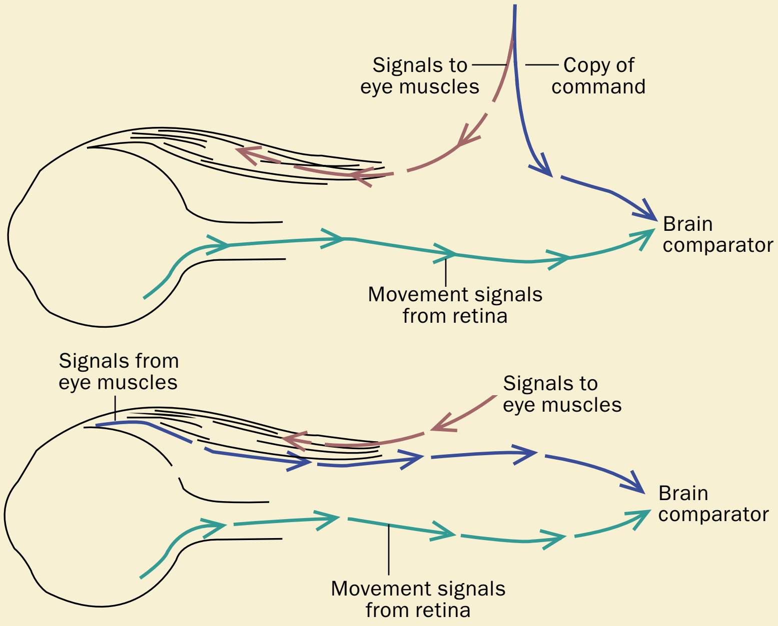
Movement Detectors



In the image/retina system (*left*), an object produces sequential firing of receptors as it moves along the retina while the eye is still.

In contrast, in the eye/head system (*right*), the moving eye keeps an object stationary on the retina, but a person perceives movement because the brain monitors its own commands signaling the eyes to move.



To judge whether an object is moving, the brain subtracts signals from the image/retina and eye/head systems in one of two ways. The feedforward theory (*top*) posits that a copy of the command from eye-movement centers is delivered to the sensory motion–detecting centers, so they will expect—and thus cancel—spurious signals. The feedback theory (*bottom*), shown to be incorrect, holds that receptors in the eye muscles themselves sense the degree of eye movement and send the “cancellation” information.

RICHARD L. GREGORY *University of Bristol*

cause there is nothing to subtract, the net result is motion perceived in the opposite direction.

Another bit of evidence. Create an afterimage on one retina using a flash (keep the other eye closed). What happens if in a dark room you now jiggle the eyeball with your finger? The answer is … absolutely nothing. You do not see the afterimage jiggling. The reason is that in the dark when you jiggle the eyeball the afterimage remains perfectly still on the retina. So there are neither image/retina signals nor any command signals from the eye-movement motor centers. Subtract zero from zero, and you get zero. The experiment is also indirect evidence for the feedforward theory and against the feedback theory (because when you push your eyeball around, stretch receptors in the eye muscles are activated—albeit not in a coordinated manner).

Now consider an extreme example. Create an afterimage of a flash in one eye. Now imagine (do not actually try it!) that you pluck the eye from its socket, keeping the optic nerve undamaged. Holding the eye in your hand, turn it so it is looking behind your shoulder. Where do you think you would see the afterimage? You would still see it in front even though the eye is pointing backward because there is no way the visual centers could know that the eye is pointing backward.

The Joint Is Jumping

Let us imagine another scenario. You walk into a discotheque lit by a strobe light. Given the right strobe rate, if you just move your eyes around, the entire world—including people and furniture—will appear to be jumping. When you move your eyes, the commands from the eye/head system go to the motion-sensing areas. Usually these messages would be canceled by image/retina motion signals. But your eyes in effect take static snapshots with each strobe, sampling the image. These samples behave effectively like afterimages. The ensuing failure to subtract retinal signals from commands results in a net perceived movement of the world.

Better still, have a friend hold a tiny lumi-

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(If you now strobe the room, every time you move your eyes, your friend will appear to **jump around**.)

nous spot—like a lit cigarette or tiny-wattage penlight—motionless. Move your eyes, and it will, of course, look stationary. If you now strobe the room, every time you move your eyes, your friend will appear to jump around, but the glowing point will remain exactly where it is. This is because the light, being self-luminous and continuously visible, generates image/retina motion signals that are canceled by eye/head commands. Yet the rest of the room and your friend, being "sampled" with the strobe, do not generate retinal motion and therefore appear to jump with the eye. The astonishing paradoxical perception you see is the penlight flying away from the person.

Our former mentor Fergus W. Campbell, who was a physiologist at the University of Cambridge, found an ingenious practical application for this effect in a London nightclub. He had the cabaret women wear skimpy luminous bikinis as they danced in a strobe-lit room. When patrons moved their eyes around, they would see the luminous bikinis flying off tantalizingly, yet they revealed nothing. The illusion was a hit and was perfectly legal because there was no real nudity. We sometimes wonder whether science itself is the same way; each time you think you are unveiling the truth, all you get is a teasing glimpse of what turns out to be yet another veil.

The intelligent reader who has followed our reasoning so far will inevitably ask the following question: When I move my eyes intentionally, the "volition" signals get sent to the sensory motion areas to cancel out the spuriously produced image-on-retina motion. But why can't the same type of cancellation or subtraction occur when you voluntarily use your finger to jiggle the eyeball? Why can't you send "finger movement" signals to the visual-image motion centers? After all, you *know* you are moving your eyeball.

The answer tells us something very important about perception. Even though it appears "intelligent" at times and can benefit hugely from high-level stored knowledge, it is by and large on autopilot, because it has evolved to do things quickly and efficiently. Even though you know you are pressing on your eyeball, no cancellation occurs because—unlike the eye-movement command centers—the finger-movement centers in the brain simply do not send the CC message to the motion-sensing areas. Our forebears apparently developed connections between eye-movement command centers and sensory-visual areas because we often do move our eyes. But our ancestors did not, we can be sure, walk around tapping their eyeballs with their fingers. Hence, there was never any evolutionary selection pressure to evolve such connections. **M**

In a disco lit by strobes, your eye takes "snapshots" that make it look as though the whole world is moving.

BOJAN BRECELJ *Corbis*

VILAYANUR S. RAMACHANDRAN and DIANE ROGERS-RAMACHANDRAN are at the Center for Brain and Cognition at the University of California, San Diego. They serve on *Scientific American Mind*'s board of advisers.

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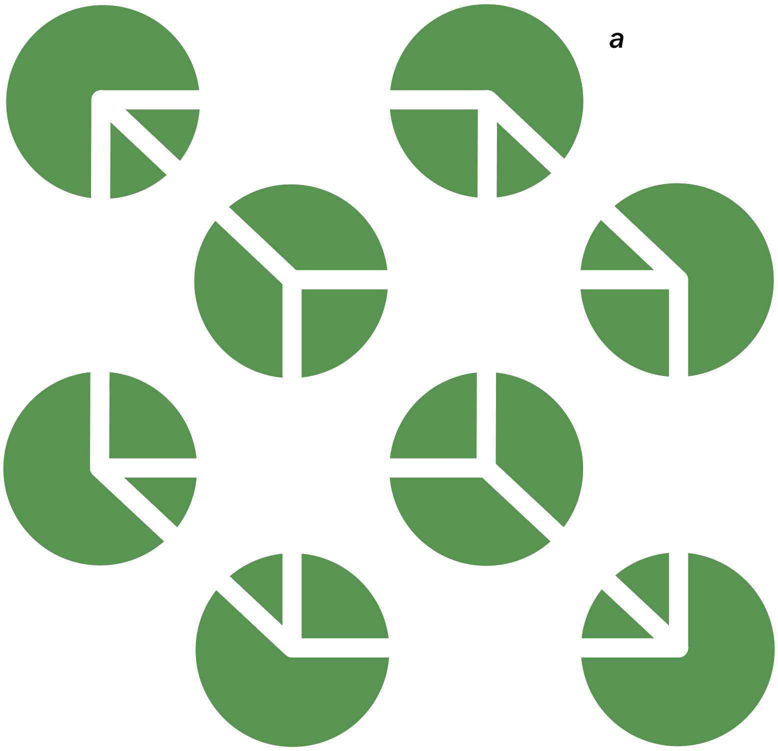

When the Two Eyes Clash

A tale of binocular rivalry

BY VILAYANUR S. RAMACHANDRAN AND
DIANE ROGERS-RAMACHANDRAN

WE LOOK AT THE WORLD from two slightly different vantage points, which correspond to the positions of our two eyes. These dual vantage points create tiny differences between the two eyes' images that are proportional to the relative depths of objects in the field of view. The brain can measure those differences, and when it does so the result is stereovision, or stereopsis.

To get an idea of this effect, extend one arm to point at a distant object. While keeping your arm extended, alternately open and close each eye. Notice how your finger shifts in relation to the object, illustrating the horizontal disparity between the eyes.

JOHNNY JOHNSON

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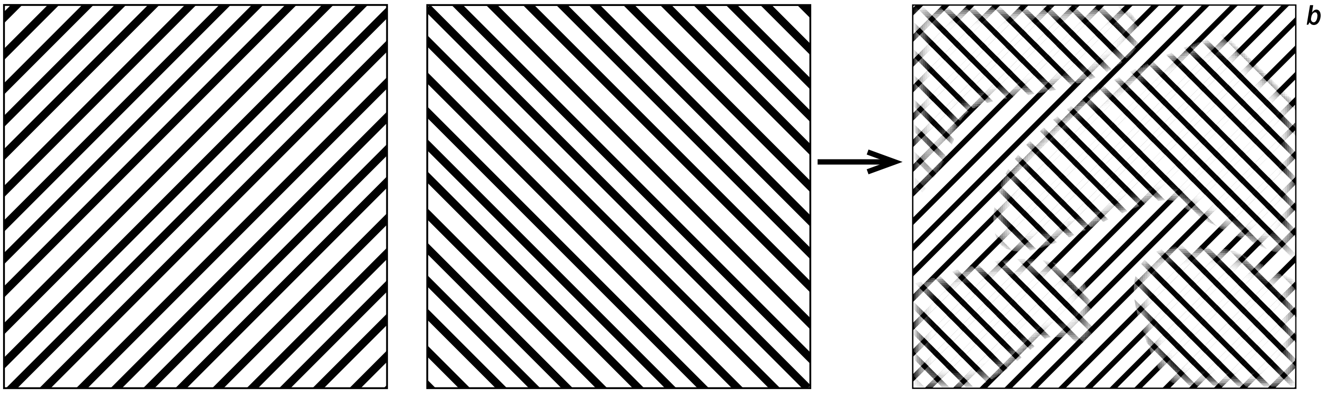


Viewing devices that took advantage of stereopsis to create illusions of depth in images of natural scenes, architectural monuments and even pornography became immensely popular in Victorian drawing rooms. View-Master and Magic Eye are their familiar descendants available today.

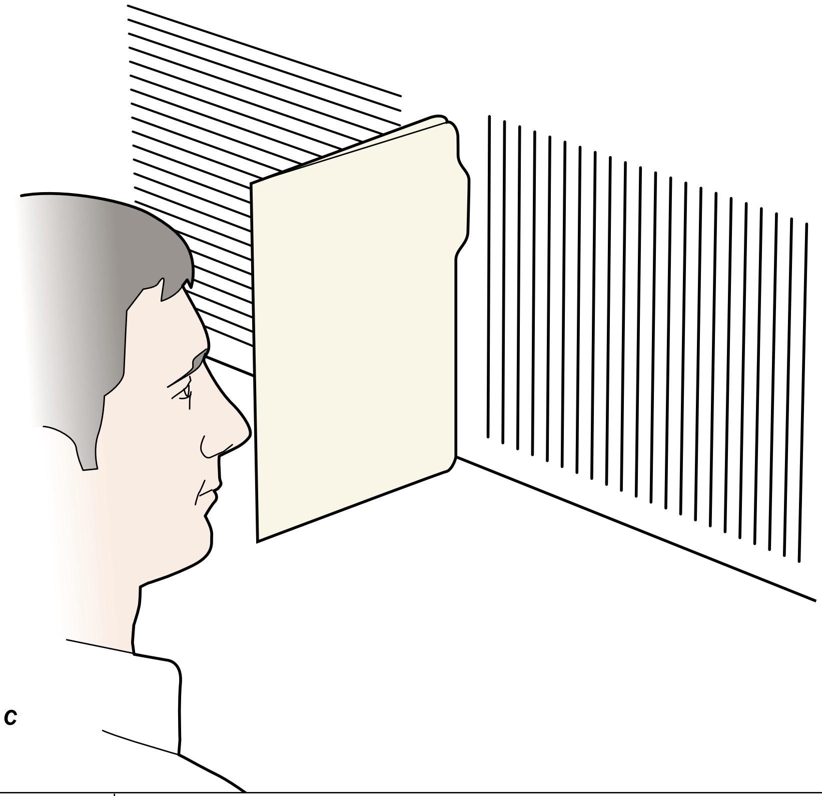
Brain Fusion

A less commonly appreciated fact about stereovision is that even though we see two images of an object—one through each eye—we perceive only one object. (In similar fashion, if you touch a single banana with your two hands, you feel one banana, not two.) Thus, the images of the two eyes must be "fused" somewhere in the brain to give rise to a unitary item of perception, or a percept. But we can ask the questions, What if the eyes look at completely dissimilar things? Would we perceive a blend?

Try the following experiment. Get low-power reading glasses, such as you can find in any drugstore. Affix two colored filters, one bright red and one bright green, to the front of each lens. Put the glasses on. If you now look at, say, a white object or surface, what do you see? If you close one eye or the other, you see red or green as expected. But what if you open both? Do the two colors harmonize and blend in your brain to produce yellow as they would if blended optically? (As any preschooler knows, red and green make brown if you mix pigments like tempera paints. But if you mix lights by projecting them onto a screen, red and green produce yellow.)

The surprising answer is that you see only one thing at a time. The object appears alternately red and then green. The eyes seem to take turns politely, as if to avoid conflict. This phenomenon is called binocular rivalry, and the effect is similar to what you see in the Necker cube (*a*). To the viewer, it may seem as though these dynamic perceptual experiences arise because the object is itself changing. Yet the stimulus is perfectly stable, and it is instead the pattern of brain activity that is changing during viewing and producing the perceptual alterations or the illusion of an unstable object.

We can use rivalry as a powerful tool to explore the more general question of how the brain resolves perceptual conflicts. Let's try another experiment. Instead of two different colors,



SCIENTIFIC AMERICAN MIND (*top*); JASON LEE (*bottom*)

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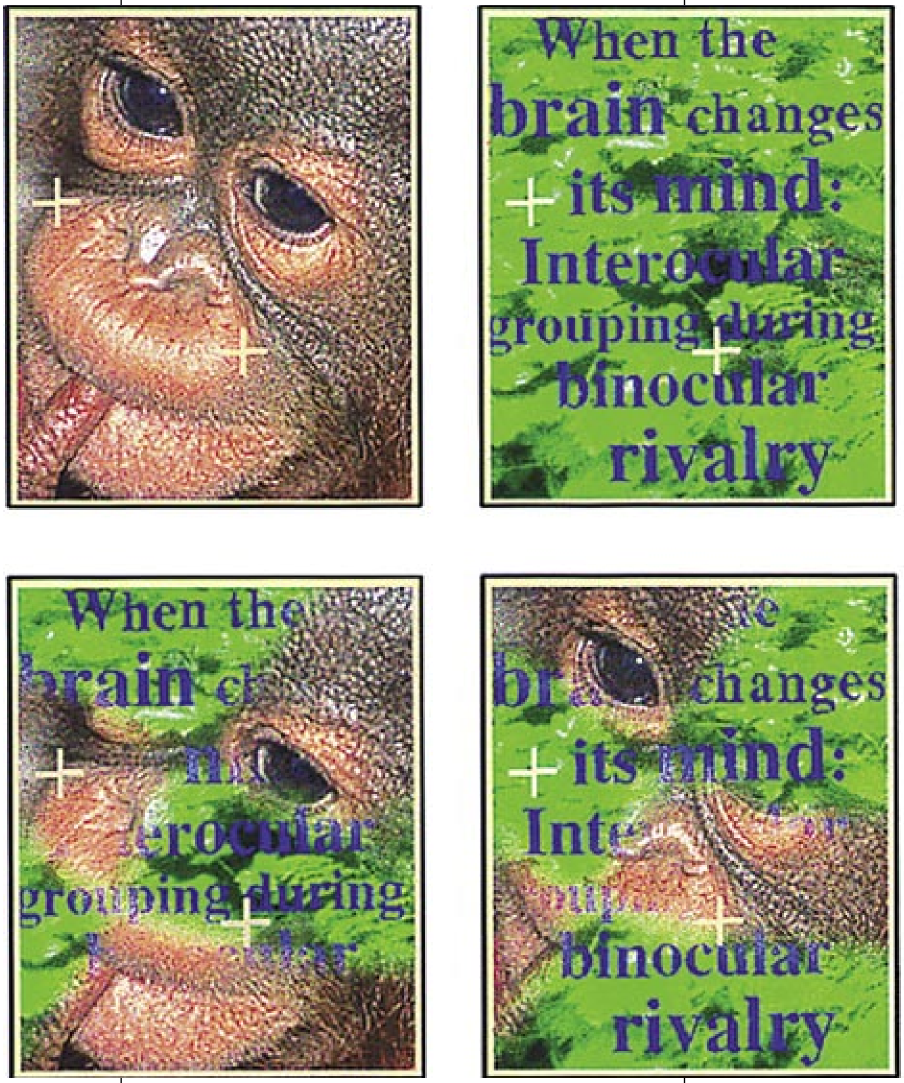

d

SOURCE: "WHEN THE BRAIN CHANGES ITS MIND: INTEROCULAR GROUPING DURING BINOCULAR RIVALRY," BY ILONA KOVÁCS, THOMAS V. PAPATHOMAS, MING YANG AND ÁKOS FEHÉR, IN *PNAS*, VOL. 93; DECEMBER 1996, ©1996 BY THE NATIONAL ACADEMY OF SCIENCES, U.S.A.

what if you give the eyes two sets of stripes that are perpendicular to each other? Would they produce a grid? Or do they clash? The answer is that sometimes you see them alternate—but equally as often you see a mosaic of patches, with sections of both eyes' images interleaved (*b, on preceding page*). No grid.

Theoretically, you could do this experiment by putting vertical stripes for the right eye and horizontal for the left in a stereo viewer. But if you do not have one, you can create what we call the poor man's version (*c, on preceding page*). Just prop up a vertical partition, like a manila folder, right at the boundary between two images corresponding to left and right eyes. Put your nose on the partition so the left eye looks exclusively at one image and the right eye at the other. You will see either the stripes alternating or a fluctuating mosaic but never a grid. With practice you can dispense with the partition and just learn to "free fuse" the two images by converging or diverging your eyes. It helps if you initially look at a pencil tip halfway between the images and your face.

Once you have learned this trick, you can try a number of new things. We know, for example, that different areas of the brain are involved in processing color and form of visual images. So we can ask, Does the rivalry occur separately for these two, or do they always happen together? What if you looked at the left eye's stripes through a red filter and the right eye's through a green one? There will now be both rivalry of color and rivalry of form. Can these two rivalries come about independently, so that the left eye's color goes with the right eye's stripes, or do they always "rival" synchronously? The short answer is that they do so together. Putting it crudely, the rivalry is between the eyes themselves rather than in processing the colors or shapes.

Complete the Picture

But that is not always true. Consider the curious display in *d*. Each eye's picture is a composite of a monkey's face and foliage. Intriguingly, if the brain fuses the images, it has a strong tendency to complete either the monkey or the foliage—even though doing so requires assembling fragments from two different eyes to complete the patterns. In this case, the brain is picking bits

(If the brain fuses the images, it has a strong tendency to complete **either the monkey or the foliage**.)

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(You can use relatively simple experiments to gain **deep insights** into visual processing.)

from each eye that make "sense" as a holistic pattern when combined correctly.

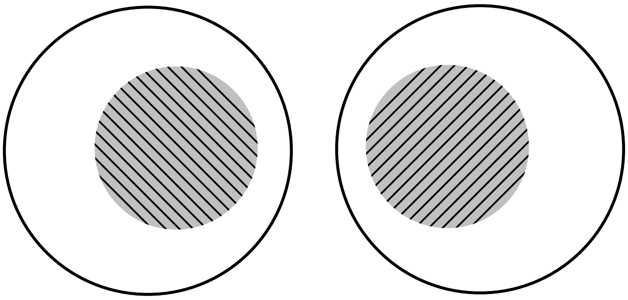
Let's return to stereopsis, the computation of relative depth from images in the two eyes that are slightly different because the eyes are separated horizontally in the skull. Here both image fusion and stereo depth occur instead of rivalry. It is quite remarkable that people wandered our planet for millennia without recognizing stereopsis (probably assuming that the benefit of two eyes is that if you lose one you have a spare). Leonardo da Vinci pointed out that this information existed 500 years ago; the fact that the brain actually uses it was discovered by Victorian physicist Charles Wheatstone. You can create an example of Wheatstone's discovery by viewing a drawing of a bucket shape as seen from the top. When you fuse the two eyes' pictures (using free fusion or the partition card), a gray disk jumps out at you—as if suspended mysteriously in thin air—from the plane of the outer circle.

But do you *need* fusion for stereopsis to occur? This may seem like a trick question, because one would think so intuitively, but that intuition is wrong. Three decades ago Anne Treisman of Princeton University, Lloyd Kaufman of New York University and one of us (Ramachandran) independently showed that, paradoxically, rivalry can coexist with stereopsis.

To understand this phenomenon, look at the stereogram shown in *e*. It has two patches of stripes shifted horizontally in opposite directions relative to the outer circles. When the brain fuses these circles, something extraordinary happens. You will see the entire patch floating out in front—yet only one patch at a time, because the stripes themselves are orthogonal. In other words, the brain extracts the stereo signal from the patches as a whole—interpreting the individual chunks as blobs—yet those patches themselves are seen to rival.

The information about the location of the patches on the retina is extracted by the brain and produces stereopsis, even though only one eye's image is visible at a time. It is as if information from an *invisible* image can nonetheless drive stereopsis.

e



Such "form rivalry" occurs in a different brain area from stereopsis, so the two can coexist in harmony. The correlation between them in normal binocular vision is coincidental, not obligatory. This discovery that certain visual information can be processed unconsciously in a parallel brain pathway reminds us of the enigmatic neurological syndrome of blindsight. A patient with damage to the visual cortex is completely blind. He cannot consciously perceive a light spot. But he can reach out and touch it using a parallel pathway that bypasses the visual cortex (which you need for conscious awareness) and projects straight to brain centers that are on a kind of autopilot to guide your hand.

A similar experiment could, in theory, be done for binocular rivalry. When one eye's image is suppressed entirely during rivalry, can you nonetheless reach out and touch a spot presented to that eye, even though that spot, for the suppressed eye, is invisible?

The phenomenon of rivalry is a striking example of how you can use relatively simple experiments to gain deep insights into visual processing. **M**

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(Further Reading)

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How Blind Are We?

We have eyes, yet we do not see

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

See anything unusual? About 50 percent don't.

PRETEND YOU ARE a member of an audience watching several people dribbling and passing a basketball among themselves. Your job is to count the number of times each player makes a pass to another person during a 60-second period. You find you need to concentrate, because the ball is flying so quickly. Then, someone dressed in a gorilla suit ambles across the floor (*left*). He walks through the players, turns to face the viewers, thumps his chest and leaves. Astonishingly, as Daniel J. Simons, now at the University of Illinois, and Christopher F. Chabris of Harvard University learned when they conducted this study, 50 percent of people fail to notice the gorilla.

We think of our eyes as video cameras that make a flawless recording of the world around us, but this demonstration shows how little information we actually take in at a glance.

The gorilla experiment is the culmination of a long line of related studies on attention and vision that were begun more than three decades ago by, among many researchers, Ulric Neisser of Cornell University, Ronald A. Rensink of the University of British Columbia, Anne Treisman of Princeton University, Harold Pashler of the University of California, San Diego, and Donald M. MacKay of Keele University in England.

Researchers refer to the gorilla effect as "inattentional blindness" or "change blindness," which in turn is part of a more general principle at work in our visual system. Our brain is constantly trying to construct meaningful narratives from what we see. Things that do not quite fit the script or that are not relevant to a particular task occupying our interest are wiped wholesale from consciousness. (Whether such deleted information is nonetheless processed unconsciously has yet to be investigated.) A simple example of how the brain's running narrative can interfere with perception is the children's game "spot the difference" (*below left*). The two images are similar enough that the brain assumes they must be identical; it takes minutes of careful inspection to locate the disparities.

Spot the differences: If two images are similar, the brain assumes they are identical.

The value of having an underlying brain "story" becomes clear when you consider how jumbled sensory inputs can be. As you survey the room around you, the image on your retina is jumping rapidly as various parts of the scene excite different bits of retina. Yet the world appears stable. Researchers once believed that the experience of having an unbroken view was entirely created by the brain sending a copy of the eye-movement command signals originating in the frontal lobes to the visual centers. The visual areas were thought to be "tipped off" ahead of time that the jumping image on the retina was caused by eyes moving and not by the world moving.

FROM "GORILLAS IN OUR MIDST: SUSTAINED INATTENTIONAL BLINDNESS FOR DYNAMIC EVENTS," BY D. J. SIMONS AND C. F. CHABRIS, IN *PERCEPTION* (PION, LONDON), VOL. 28; 1999. FIGURE PROVIDED BY DANIEL J. SIMONS (*top*); EMILY HARRISON (*bottom*)

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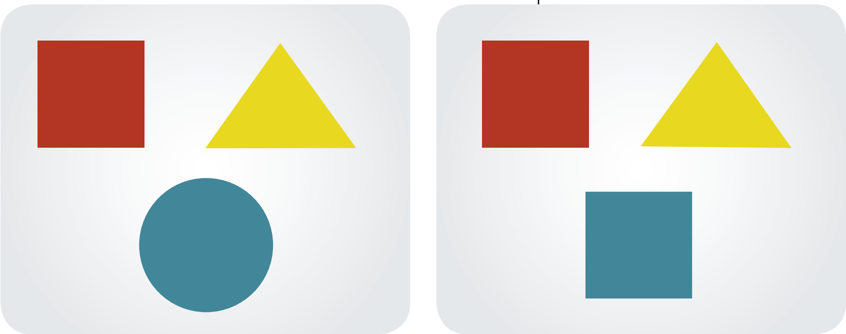
> (Have you noticed **any gorillas walking by**? How can you be sure that none did?)

But an effect you can demonstrate for yourself at home shows that this cannot be the entire reason. (Jonathan Miller, an opera director in London, and one of us [Ramachandran] independently observed the effect in the early 1990s.) Turn a television set upside down. Gently! Better yet, flip the TV's image optically with a prism. Alternatively, you can turn the TV sound off and then stand slightly to the side of the set, looking at the screen with your peripheral vision. Put the TV on any channel and watch what happens. You will see sudden, jarring changes and visual jolts. Next, gaze at the broadcast with the TV right side up, viewing it straight on and with the sound at normal volume. Now the cuts and pans of the camera flow smoothly and seamlessly into one another—in fact, you do not even notice them. Even when the scene switches, say, from one talking head to the other as they alternate in conversation, you do not see a head transforming or morphing from one to the other as your mind alternates between each of the two speakers. Instead you experience your vantage point shifting.

What is going on? The answer is that when the TV is right side up and you can hear the sound, the brain can construct a sensible narrative. The cuts, pans and other changes are simply ignored as irrelevant, however gross they might be physically. In contrast, when the scene is upside down or viewed with peripheral vision and the sound is off, it is hard for the brain to make meaningful sense out of what the visual centers perceive, so you start to notice the big changes in the physical image. This effect is not true just for visual scenes on the boob tube but also for your entire life's experiences; the unity and coherence of consciousness is mostly convenient, internally generated fiction.

The scene does not have to be complex for change blindness to occur, either. In 1992 British neurobiologist Colin Blakemore and Ramachandran conducted an experiment on attendees of a seminar we gave at the Salk Institute for Biological Studies. We first showed a movie frame containing three abstract, colored shapes: a red square, a yellow triangle and a blue circle (*left illustration, above*). We left this frame up for two seconds, then replaced it with the same three shapes, which were each shifted in position by a small degree. The audience observed that all three appeared to flicker or "glitch" slightly. The big surprise came when we then swapped one of the three shapes—the circle—with a different form: a square (*right illustration, above*). Most people simply did not notice, except in those few instances when someone accidentally happened to be focusing all his or her attention on that particular object. Even with three simple objects, we experience sensory overload and change blindness.



Most people simply will not notice if a shape in one movie frame is changed in the next.

Finally, imagine that you are staring fixedly at a little red X. Slightly off to the left we briefly show you a cross. All you have to tell us is which is longer—the cross's vertical or horizontal line. That task is something people can do effortlessly. Now we surreptitiously introduce a word directly on the cross during the second that you are judging line lengths. Arien Mack of New School University and Irvin Rock, then at Rutgers University, discovered that people will not spot the word.

Maybe you are reading this article in a busy cafe. Have you noticed any gorillas walking by? Given the Simons demonstration, how can you be so sure that none did? We suppose it depends on how interesting and attention-grabbing you have found this article to be. **M**

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- **Inattentional Blindness.** Arien Mack and Irvin Rock. MIT Press, 2000.
- Several papers and a demonstration on attention and failure to see change by Ronald A. Rensink and his co-authors are available at **www.psych.ubc.ca/~rensink/flicker/**

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Hidden in Plain Sight

Camouflage in fish and other animals provides insights into visual perception

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

ONE OF THE MAIN FUNCTIONS of visual perception is to detect objects in the environment as a prelude to identifying them as prey, predators or mates. Not surprisingly, both prey and predators go to enormous lengths to conceal their physical boundaries by blending in with the color and texture of their surroundings. Indeed, we can almost think of higher visual processing in the brain as having mainly evolved to defeat camouflage. Studying the strategies of camouflage can therefore indirectly also tell us a great deal about the mechanisms of vision.

In 1896 American painter and amateur naturalist Abbott Handerson Thayer speculated that animals developed "protective coloration." As his theory held, "animals are painted by nature darkest on those parts which tend to be most lighted by the sun's light, and vice versa." He was surely right about this effect (scientists now call it "countershading"). But then he went on, even suggesting that peacocks' tails match foliage and that flamingos are pink to allow them to blend in with the sunset (*a*)!

To modern scientists, Thayer obviously got a bit carried away. Yet as the saying goes, "fact is stranger than fiction." Some animals, such as cuttlefish, octopuses and flounder, can alter their markings and hues to suit whatever surface they happen to land on. Although chameleons are often credited with this skill, they are actually quite bad at it; most of their color changes are reserved mainly to attract mates and protect their territories and are thus unrelated to camouflage.

Biologist Francis B. Sumner, one of the founders (but not the sole flounder) of the Scripps Institution of Oceanography, showed nearly a century ago that cold-water flounder have an amazing capacity to match the "graininess" of their skin-surface markings with gravel or pebbles in their background. Sumner's work was supplemented by the experiments of S. O. Mast, who in the early 20th century showed that the matching depends on vision; blinded flounder do not change.

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JAKE WYMAN *Getty Images*

Sumner's findings made a big splash when he published them. But they were later challenged by neurobiologist William M. Saidel, now at Rutgers University at Camden. Saidel claimed that the markings on flounder changed only slightly but that they had a kind of "universal" texture that allowed them to blend in with most backgrounds. So, he argued, in a sense it was the viewer's eye that was doing the blending—not the flounder itself.

Cold-water flounder live in a rather drab, monotonous sandy environment. It occurred to us that this fact could account for the poor show put on by Saidel's flounder, which would not have had the evolutionary pressures to adapt to a greater range of backgrounds; unlike the cold-water locations, the tropical environment contains more varied surfaces. In collaboration with Christopher W. Tyler of the Smith-Kettlewell Eye Research Institute in San Francisco, Richard L. Gregory of the University of Bristol in England, and Chandramani Ramachandran, now a student at the University of California, Berkeley, we therefore decided to experiment with the tropical reef flounder *Bothus ocellatus,* commonly known as the eyed flounder.

We obtained six specimens from an aquarist. After the fish had adapted to a "neutral," beige-colored fine-gravel floor in a holding tank (*b, on next page*), we moved them into small experimental tanks that each had different patterns on their floors. We selected patterns that, though not found in nature, would clearly demonstrate the limits of the fish's ability to adapt actively, or dynamically, to their surrounding environment.

The results were remarkable. In every case, the fish were able to achieve an impressively good match when "plaiced" on various backgrounds of coarse check patterns (*c, on next page*), medium and fine checks (*d, on next page*), pebbles (*e, on page 21*) or fine gravel. Even more startling, we found that the fish transformed in just two to eight seconds—not the several minutes that Mast and Sumner had implied. We knew then that there must be a neural "reflex" at work. The reaction was too fast to be hormonal.

The fish's eyes, we determined, must be getting a highly foreshortened, distorted view of the background, given their vantage point at the bottom and the distortions of its optics. The fish have turretlike eyes mounted on stalks, with which they quickly scan the surrounding floor texture. Our colleagues are often very puzzled

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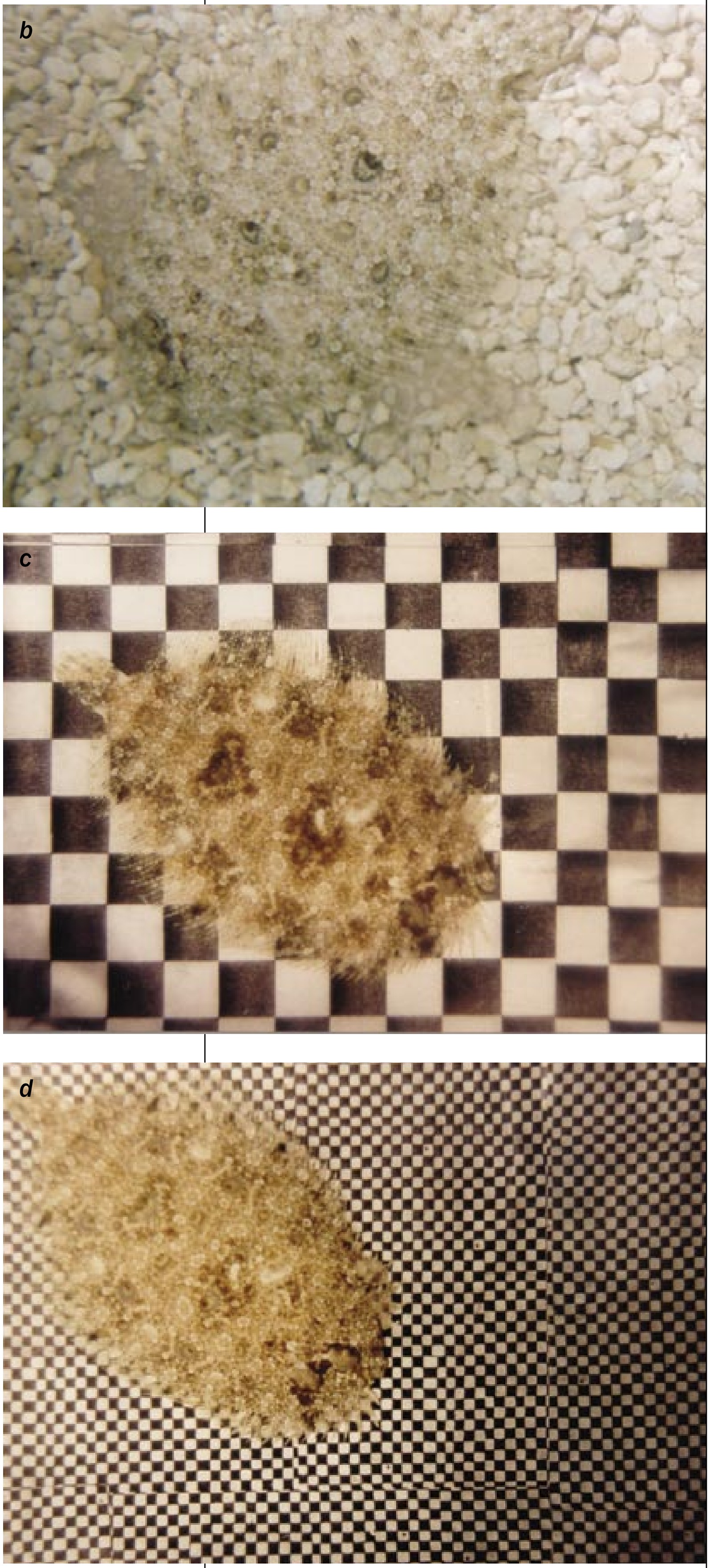

that the fidelity of matching is so precise given these distortions. But this conformity is no more unexpected to neuroscientists like ourselves than is the fact that we do not see the world upside down, even though the retinal image is. Because no actual cinema screen with a picture exists in the brain, the question of "correction" does not even arise; the brain encodes visual information in such a way that the correction for a flawed or noisy sensory input is already implied in the code itself. In much the same way, the fish's brains must make adjustments so that the camouflage pattern is produced accurately.

How do the fish achieve such dynamic camouflage? Examination through the dissecting microscope revealed that the skin has clusters of cells containing the dark pigment melanin, called melanophores. By varying the dispersal of melanin pigment granules in these cells, the fish can alter the contrast of small patches of skin. In addition, we saw what appeared to be at least four classes of clusters of different sizes and a single isolated cluster on the middle of the fish. By independently varying the contrast of these four types of clusters—a bit like dialing up the contrast knob on an old television set—the fish can vary the *ratio* of different pixel types and achieve a reasonable facsimile of the most commonly encountered textures on the ocean floor where they live. This system is analogous to the manner in which one can use just three "primary" wavelengths in various ratios to produce any conceivable color that the eye can see. By analyzing the pattern on the fish and corresponding background with a mathematical technique called principle component analysis, we were able to establish that the fish have independent visual control of each set of markings.

Just for the halibut, we tried putting the fish on a background of polka dots. Amazingly, their entire skin went pale and became homogeneous except for one small, conspicuous black dot right on the center of the body (*f*). The fish were making a valiant attempt to match the polka dots! See if you can spot the fish in the photograph.

Flounder also use other visual tricks to deceive predators. When we approached one menacingly with an aquarium net, it would move forward and stir up the sand, "pretending" to bury itself in one location while it actually retreated at lightning speed and buried itself elsewhere.

Squid, cuttlefish and octopuses (*g*) are also masters of camouflage. Yet instead of dispersing pigments, they simply open or close opaque "shutters" across skin patches. Even more intriguing, they match not only the color and tex-

V. S. RAMACHANDRAN

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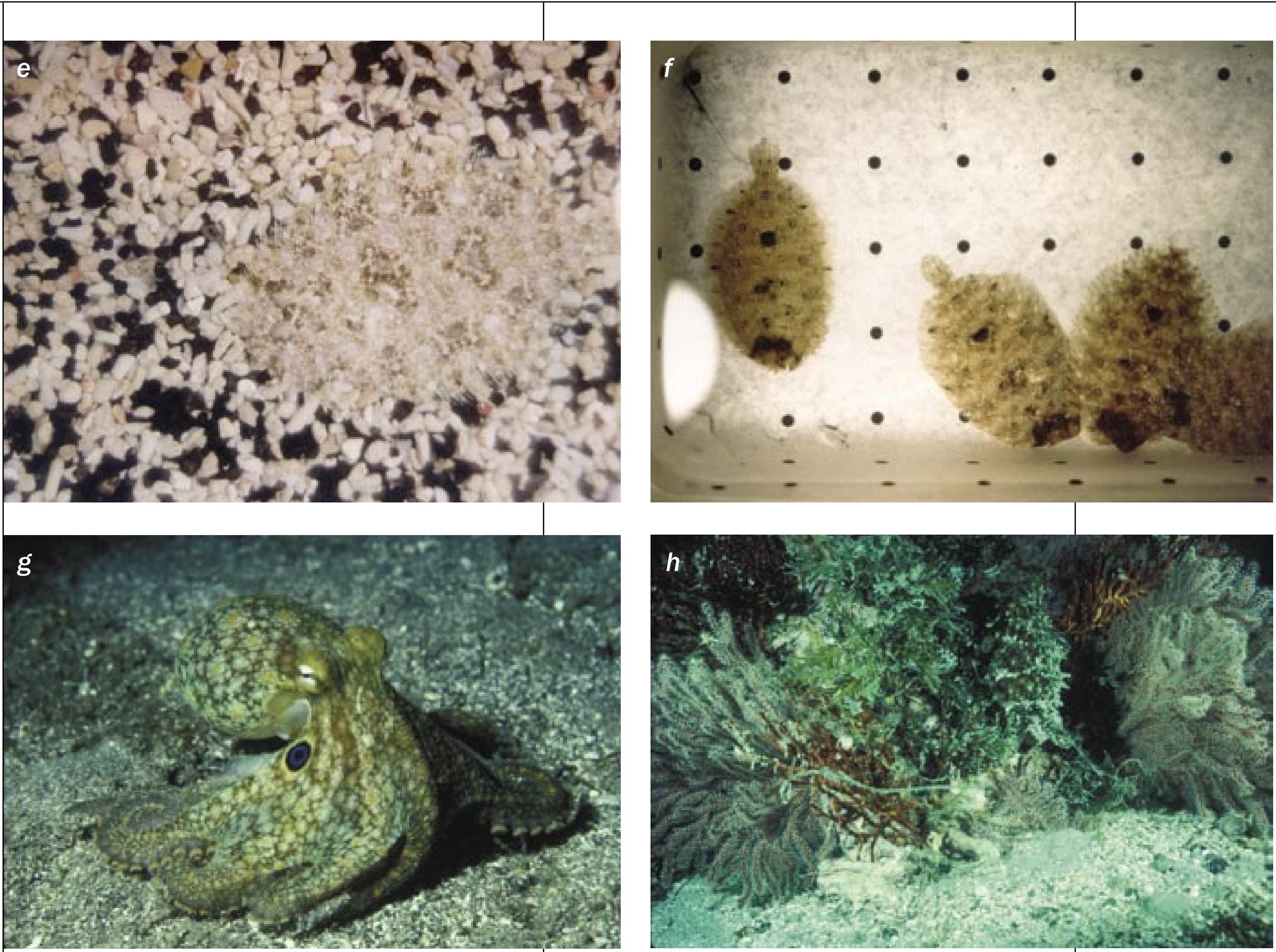
(Octopuses can **distort their forms** to mimic various poisonous sea creatures, such as snakes and lionfish.)



V. S. RAMACHANDRAN (*e* and *f*); ROGER T. HANLON *Marine Biological Laboratory* (*g* and *h*)

ture of the background but the *shapes* of objects in the vicinity as well (*h*)—as elegantly shown by Roger T. Hanlon and his colleagues at the Marine Biological Laboratory in Woods Hole, Mass. Octopuses can distort their forms to mimic various poisonous sea creatures, such as snakes and lionfish. The mechanism is not known. Nerve cells—called mirror neurons—have been identified in the brains of primates that may be involved in mimicry of the postures and actions of others. We suggest that analogous cells have evolved in the brains of cephalopods through convergent evolution—which would be astonishing given that vertebrates diverged from invertebrates more than 60 million years ago.

Figuring out the mechanisms of dynamic camouflage in flounder may have obvious military applications. Taking a lesson from the fish, the military could use a small number of changing pigmented splotches to "match" a tank to its background much better than a static paint scheme. Such experiments, far from being just a fishing expedition, can give us vital clues about the evolution of visual perception. **M**

VILAYANUR S. RAMACHANDRAN and DIANE ROGERS-RAMACHANDRAN are at the Center for Brain and Cognition at the University of California, San Diego. They serve on *Scientific American Mind*'s board of advisers.

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- Information about adaptive camouflage is available at Roger T. Hanlon's site at the Marine Biological Laboratory: **www.mbl.edu/mrc/hanlon**

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Right Side Up

Studies of perception show the importance of being upright

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

THE LENS IN YOUR EYE casts an upside-down image on your retina, but you see the world upright. Although people often believe that an upside-down image in the eyeball gets rotated somewhere in the brain to make it look right side up, that idea is a fallacy. No such rotation occurs, because there is no replica of the retinal image in the brain—only a pattern of firing of nerve impulses that encodes the image in such a way that it is perceived correctly; the brain does not rotate the nerve impulses.

Even leaving aside this common pitfall, the matter of seeing things upright is vastly more complex than you might imagine, a fact that was first pointed out clearly in the 1970s by perception researcher Irvin Rock, then at Rutgers University.

Tilted View

Let us probe those complexities with a few simple experiments. First, tilt your head 90 degrees while looking at the objects cluttering the room you are in now. Obviously, the objects (tables, chairs, people) continue to look upright—they do not suddenly appear to be at an angle.

Now imagine tipping over a table by 90 degrees, so that it lies on its side. You will see that it does indeed look rotated, as it should. We know that correct perception of the upright table is not

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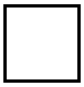
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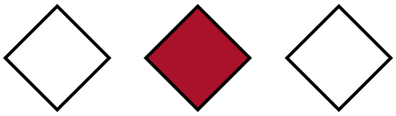
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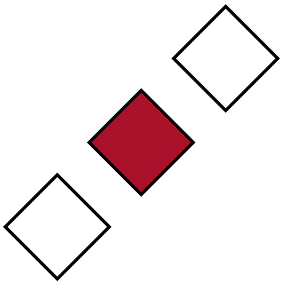

c

because of some “memory” of the habitual upright position of things such as a table; the effect works equally well for abstract sculptures in an art gallery. The surrounding context is not the answer either: if a luminous table were placed in a completely dark room and you rotated your head while looking at it, the table would still appear upright.

Instead your brain figures out which way is up by relying on feedback signals sent from the vestibular system in your ear (which signals the degree of head rotation) to visual areas; in other words, the brain *takes into account* head rotation when it interprets the table’s orientation. The phrase “takes into account” is much more accurate than saying that your brain “rotates” the tilted image of the table. There is no image in the brain to “rotate”—and even if there were, who would be the little person in the brain looking at the rotated image? In the rest of the essay, we will use “reinterpret” or “correct” instead of “rotate.” These terms are not entirely accurate, but they will serve as shorthand.

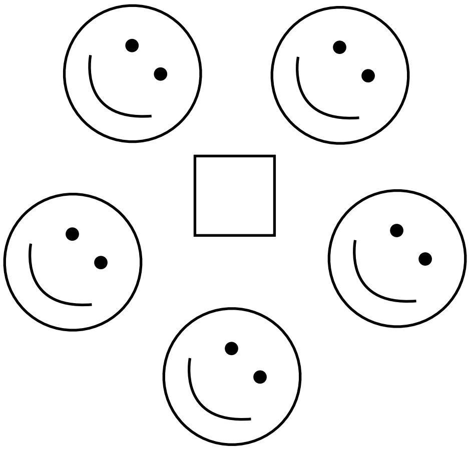
There are clear limits to vestibular correction. Upside-down print, for instance, is extremely hard to read. Just turn this magazine upside down to find out. Now, holding the magazine right side up again, try bending down and looking at it through your legs—so your head is upside down. The page continues to be difficult to read, even though vestibular information is clearly signaling to you that the page and corresponding text are still upright in the world compared with your head’s orientation. The letters are too perceptually complex and fine-grained to be aided by the vestibular correction, even though the overall orientation of the page is corrected to look upright.

Let us examine these phenomena more closely. Look at the square in *a*. Rotate it physically 45 degrees, and you see a diamond. But if you rotate your *head* 45 degrees, the square continues to look like a square—even though it is a diamond on the retina (the tissue at the back of the eye that receives visual inputs); vestibular correction is at work again.

The Big Picture

Now consider the two central red diamonds in *b* and *c*. The diamond in *b* looks like a diamond and the one in *c* looks like a square, even though your head remains upright and there is obviously no vestibular correction. This simple demonstration shows the powerful effects of the overall axis of the “big” figure comprising the small squares (or diamonds). It would be misleading to call this effect “context” because in *d*—a square surrounded by faces tilted at 45 degrees—the square continues to look like a square

(The brain takes into account **head rotation** when it interprets an item’s orientation.)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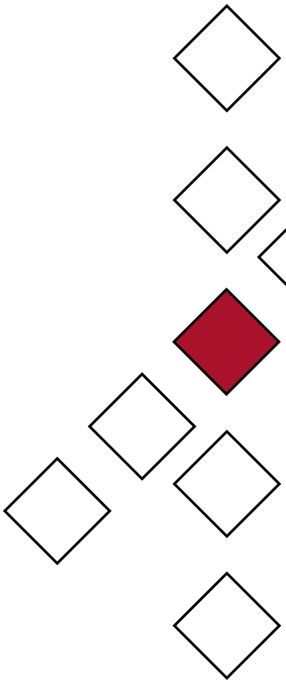


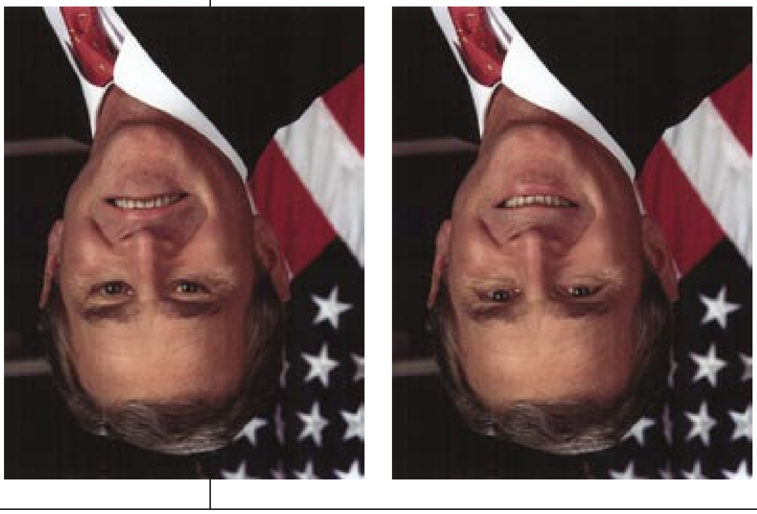
e

(though perhaps less so than when isolated).

You can also test the effects of visual attention. The figure in *e* is a composite. In this case, the central red shape is ambiguous. If you attend to the vertical column, it resembles a diamond; if you view it as a member of the group forming the oblique line of shapes, it seems to be a square.

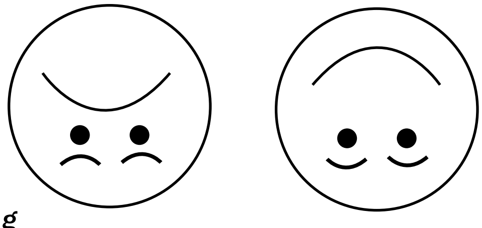
Even more compelling is the George W. Bush illusion, a variant of the Margaret Thatcher illusion, which was originally developed by psychologist Peter Thompson of the University of York in England. If you look at the upside-down images of Bush's face on this page (*f*), you see nothing odd. But turn the same images right side up, and you see how grotesque he really looks. Why does this effect happen?

f



The reason is that despite the seamless unity of perception, the analysis of the image by the brain proceeds piecemeal. In this case, the perception of a face depends largely on the relative positions of the features (eyes, nose, mouth). So Bush's face is perceived as a face (albeit one that is upside down) just as an upside-down chair is readily identified as a chair. In contrast, the expression conveyed by the *features* depends exclusively on their orientation (downturned corners of the mouth, distortion of eyebrows), independent of the perceived overall orientation of the head—the "context."

Your brain cannot perform the correction for the features; they do not get reinterpreted correctly as the overall image of a face does. The recognition of certain features (downturned mouth corners, eyebrows, and so on) is evolutionarily primitive; perhaps the computational skill required for reinterpretation simply has not evolved for this capability. For the overall recognition of the face simply as a face, on the other hand, the system might be more "tolerant" of the extra computational time required. This theory would explain why the second upside-down face appears normal rather than grotesque; the features dominate until you invert the face.



g

This same effect is illustrated very simply in the cartoon faces (*g*). Upside down, it is hard to see their expressions even though you still see them as faces. (You can logically deduce which is smiling and which is frowning, but that is not the result of perception.) Turn them right side up, and the expressions are clearly recognized as if by magic.

Finally, if you bend over and look between your legs at *f*, the expressions will become strikingly clear, but the faces themselves continue to look upside down. This effect is because the vestibular correction is applied selectively to the face but does not affect perception of the features (which are now right side up on the retina). It is the shape of the features on the retina that counts—independent of vestibular correction—and the "world-centered" coordinates that such corrections allow your brain to compute.

SCIENTIFIC AMERICAN MIND (*e* and *g*); TANIA LOMBROZO (*f*)

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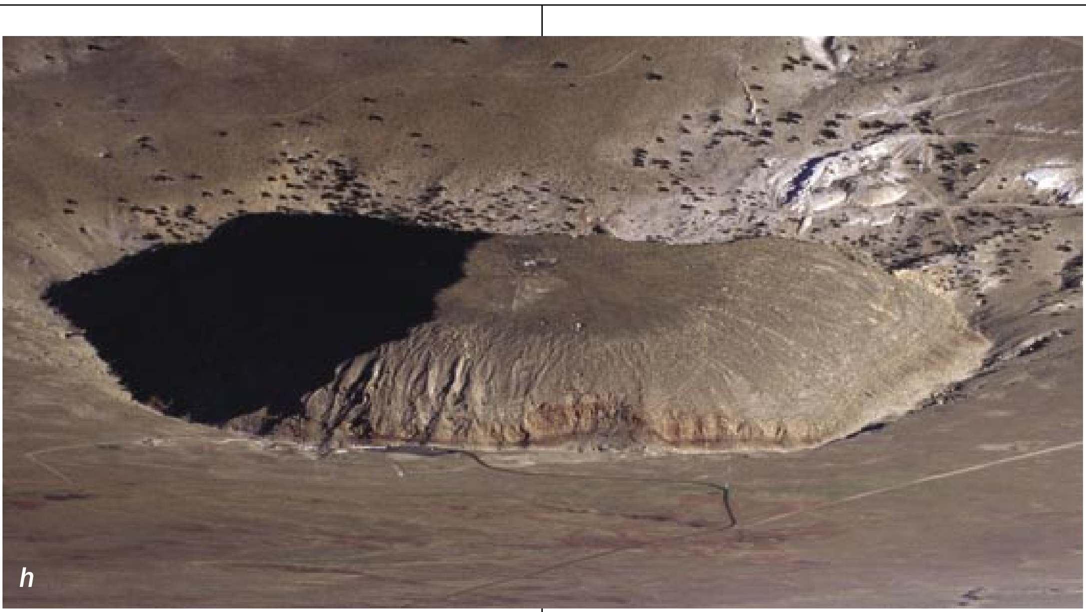
(Suddenly you will see people's heads and shoulders **bobbing up and down** as they walk.)



CHARLES O'REAR *Corbis*

Depth Cues

Vestibular correction also fails to occur when we perceive shape (and depth) from clues provided by shading. In *h,* you see what appears to be a 550-foot-tall mound in the desert. The brain centers involved in computing shading make the reasonable assumption that the sun usually shines from above, so hills would be light on top and concave areas would be light on the bottom. If you rotate the page, you will see that this is actually a photograph of Arizona's Meteor Crater.

You can verify this effect by repeating the experiment of looking between your legs while the page is right side up in relation to gravity. Once again, the mound and crater switch places. Even though the world as a whole looks normal and upright (from vestibular correction), the modules in the brain that extract shapes from assumptions about shading cannot use the vestibular correction; they are simply not hooked up to it. This phenomenon makes evolutionary sense because you do not normally walk around the world with your head upside down, so you can afford to avoid the extra computational burden of correcting for head tilt every time you interpret shaded images. The result of evolution is not to fine-tune your perceptual machinery to perfection but only to make it statistically reliable, often enough and rapidly enough, to allow you to produce offspring, even if the adoption of such heuristics or "shortcuts" makes the system occasionally error-prone. Perception is reliable but not infallible; it is a bag of tricks.

Bobbing Heads

One last point: Next time you are lying on the grass, look at people walking around you. They look like they are upright and walking normally, of course. But now look at them while you are upside down. If you can manage yoga, you might want to try your downward dog or another inversion. Or just lie sideways with one ear on the ground. The people will still look upright as expected, but suddenly you will see them bobbing up and down as they walk. This motion instantly becomes clear because after years of viewing people with your head held straight, you have learned to ignore the up-down bobbing of their heads and shoulders. Once again, vestibular feedback cannot correct for the head bobbing, even though it provides enough correction to enable seeing the people as upright. You might be bending over backward to understand all this, but we think it is worth the effort. **M**

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Seeing Is Believing

2-D or not 2-D, that is the question: test yourself to learn what shapes formed by shading reveal about the brain

BY VILAYANUR S. RAMACHANDRAN AND
DIANE ROGERS-RAMACHANDRAN

A dark back and light belly help this caterpillar avoid detection.

EMIL VON MALTITZ *Getty Images*

THE VISUAL IMAGE is inherently ambiguous: an image of a person on the retina would be the same size for a dwarf seen from up close or a giant viewed from a distance. Perception is partly a matter of using certain assumptions about the world to resolve such ambiguities. We can use illusions to uncover what the brain's hidden rules and assumptions are. In this column, we consider illusions of shading.

In *a,* the disks are ambiguous; you can see either the top row as convex spheres or "eggs," lit from the left, and the bottom row as cavities—or vice versa. This observation reveals that the visual centers in the brain have a built-in supposition that a single light source illuminates the entire image, which makes sense given that we

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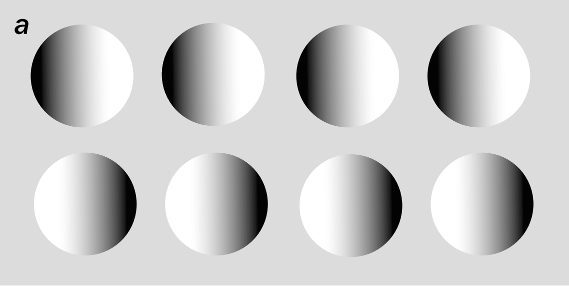
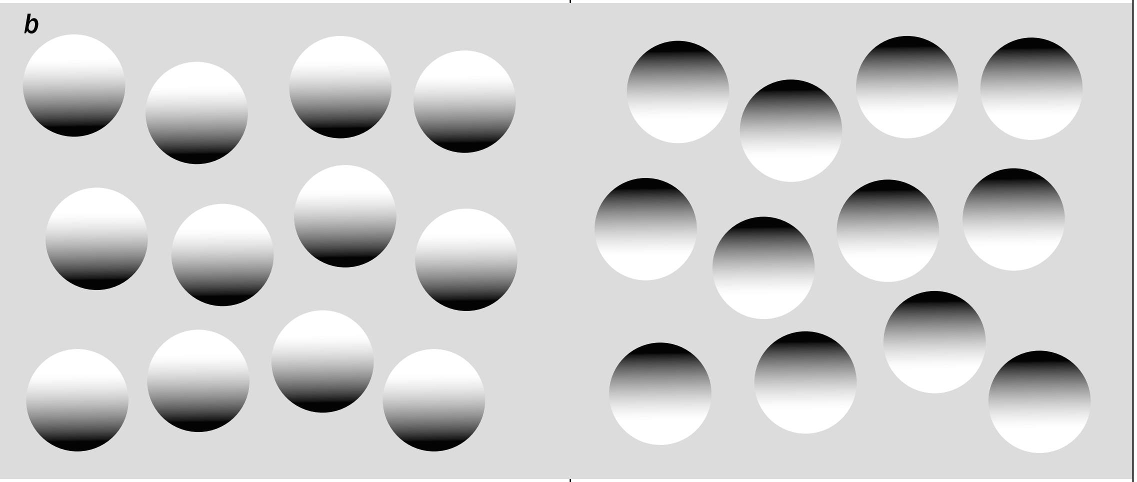
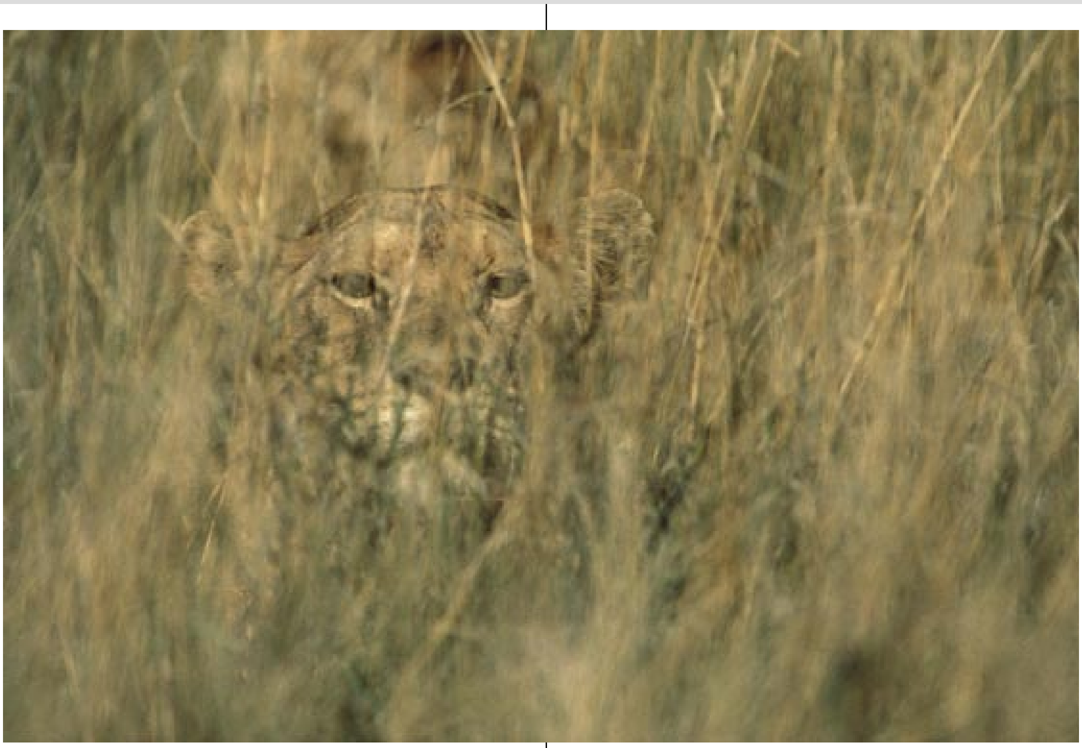
evolved on a planet with one sun. By consciously shifting the light source from left to right, you can make the eggs and cavities switch places.

In *b*, the image is even more compelling. Here the disks that are light on the top (*left*) always look like eggs, and the ones that are light on the bottom (*right*) are cavities. So we have uncovered another premise used by the visual system: it expects light to shine from above. You can verify this by turning the page upside down. All the eggs and cavities instantly switch places.

Amazingly, the brain's assumption that light shines from above the head is preserved even when you rotate your head 180 degrees. Ask a friend to hold this page right side up for you. Then bend down and look between your legs at the page behind you. You will find that, again, the switch occurs, as if the sun is stuck to your head and shining upward from the floor. Signals from your body's center of balance—the vestibular system—guided by the positions of little stones in your ears called otoliths, travel to your







The brain automatically assembles fragments of similar color, enabling you to easily spot the lion behind the foliage.

NADIA STRASSER (*illustrations*); MITSUAKI IWAGO *Minden Pictures* (*photograph*)

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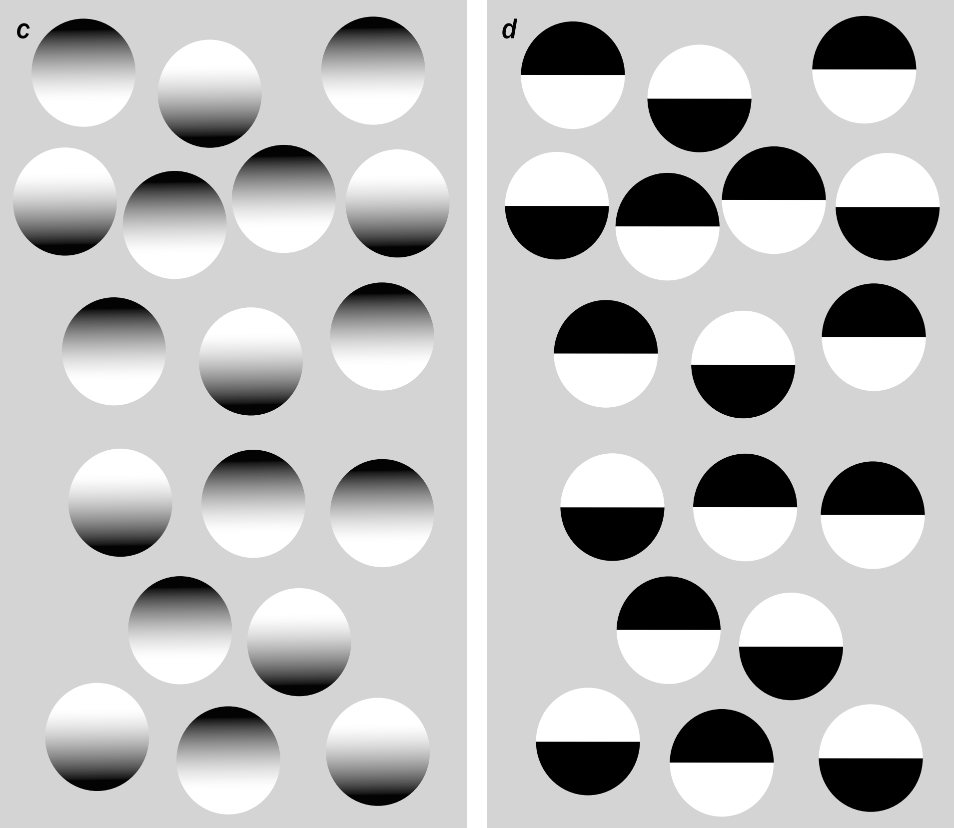

visual centers to correct your picture of the world (so that the world continues to look upright) but do not correct for the location of the sun.

From this experiment we learn that despite the impression of seamless unity, vision is actually mediated by multiple parallel information-processing modules in the brain. Some of the modules connect to the vestibular system; however, the one that handles shape from shading does not. The reason might be that correcting an image for placement in so-called world-centered coordinates would be too computationally expensive and take too much time. Our ancestors generally kept their heads upright, so the brain could get away with this shortcut (or simplifying assumption). That is, our progenitors were able to raise babies to maturity often enough that no selection pressure acted to produce vestibular correction.

If you look at *c*, you find that you can almost instantly mentally group all the eggs and segregate them from the cavities. As visual scientists discovered decades ago, only certain elementary features that are extracted early during visual processing "pop out" conspicuously and can be grouped in this manner. For example, your brain can discern a set of red dots in a background of green ones but cannot group smiles scattered among a backdrop of frowns. Color is thus a primitive feature that is extracted early, whereas a smile is not.

(It makes survival sense to be able to piece together fragments of similar color. A lion hidden behind a screen of green leaves is visible merely as gold fragments, but the visual brain assembles the pieces into a single, gold, lion-shaped form and warns: "Get out of here!" On the other hand, objects are not made up of smiles.)

The fact that you can group the eggs in *c* implies that shading information, like color, is extracted early in visual processing. This prediction was verified in recent years by recording activity in the neurons of monkeys and by conducting brain-imaging experiments in humans. Certain cells in the visual cortex fire when the observer sees eggs; others respond only to cavities. In *d*, where the circles have the same luminance polarities as in *c*, you cannot perceive the grouping; this fact suggests the importance of perceived depth as a cue that is extracted early in visual processing.

Of course, over millions of years, evolution has "discovered" and taken advantage of the principles of shading that researchers have explored only lately. Gazelles have white bellies and dark backs—countershading—that neutralize the effect of sunshine from above. The result reduces pop-out so that gazelles are not as conspicuous; they also appear skinnier and less appetizing to a predator. Caterpillars have countershading, too, so they more closely resemble the flat leaves on which they munch. One caterpillar species has "reverse" countershading—which did not make sense until scientists real-

NADIA STRASSER

> Over millions of years, **evolution has "discovered"** and taken advantage of the principles of shading that researchers have explored only lately.

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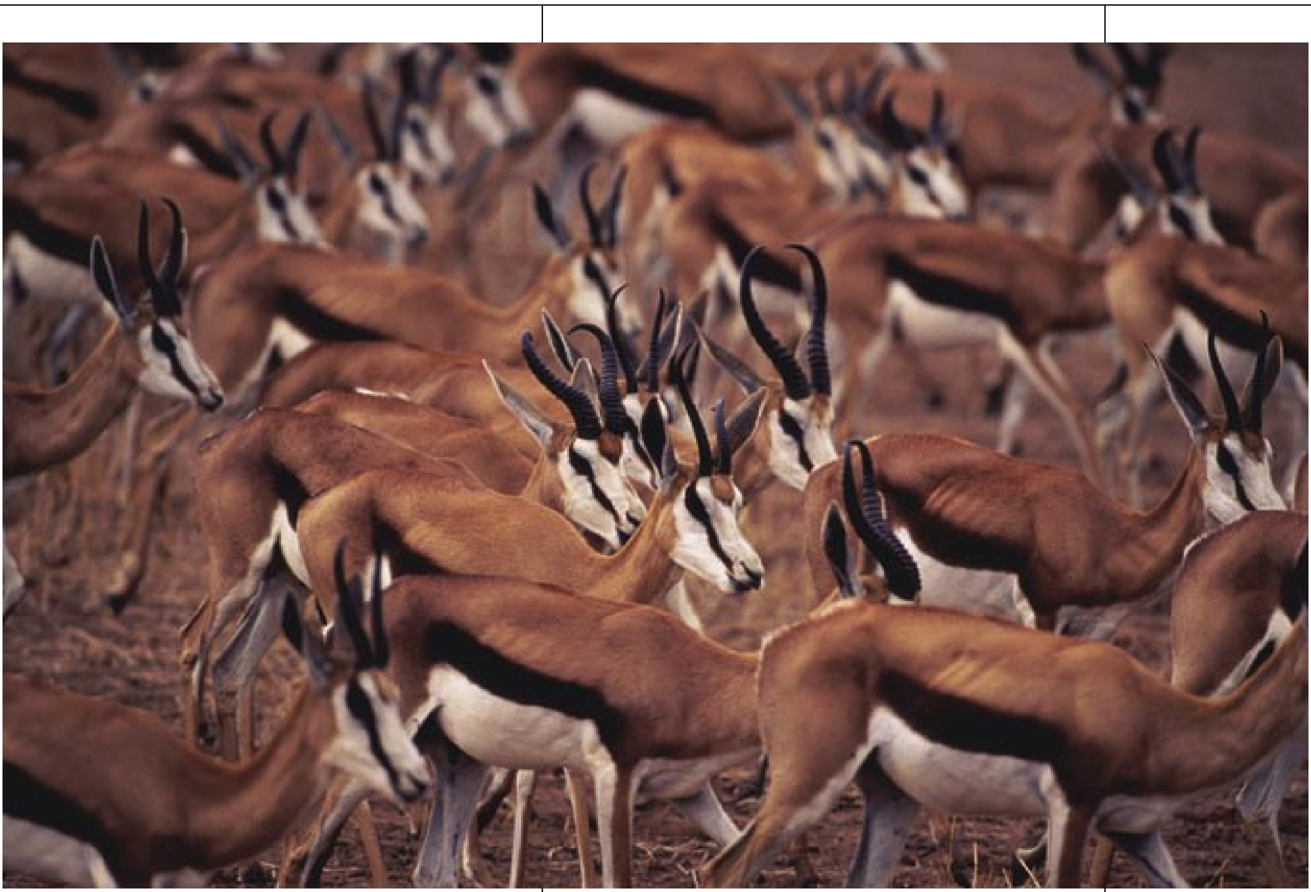
(Despite the impression of seamless unity, vision is actually mediated by **multiple modules in the brain**.)



Countershading makes gazelles look skinnier and less conspicuous.

PETE TURNER *Getty Images*

ized that the insect habitually hangs upside down from twigs. One type of octopus can even invert its countershading: if you suspend the octopus upside down, it uses pigment-producing cells called chromatophores in the skin, which are controlled by its vestibular input, to reverse its darker and lighter areas.

Charles Darwin noticed a striking example of nature's use of shading in the prominent eyelike spots on the long tails of argus pheasants. With the tail feathers at horizontal rest, the orbs are tinged from left to right. During the bird's courtship display, however, the tail feathers become erect. In this position, the spots are paler on top and duskier at bottom, so the disks seem to bulge out like shiny metallic spheres—the avian equivalent of jewelry.

That a few simple shaded circles can unveil the underlying assumptions of our visual systems—and even how such principles have played a role in shaping evolutionary adaptations—shows the power of visual illusions in helping us to understand the nature of perception. **M**

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Seeing in Black & White

Why it's not so cut-and-dried

BY ALAN GILCHRIST

HOW MANY TIMES have you heard people say that something is "black and white," meaning it is simple or crystal clear? And because black and white are so obviously distinct, it would be only natural for us to assume that understanding how we see them must be equally straightforward.

We would be wrong. The seeming ease of perceiving the two color extremes hides

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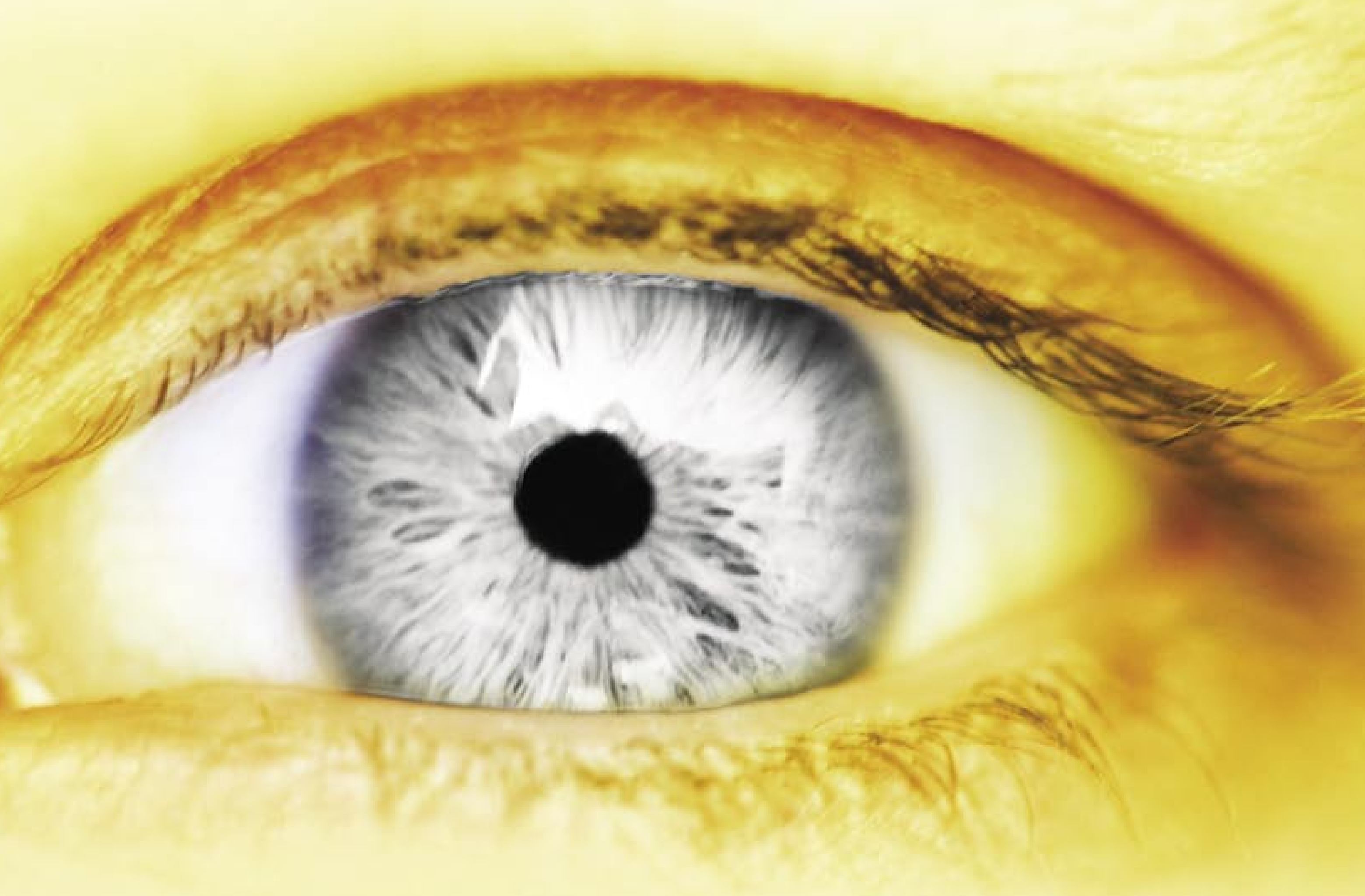

GETTY IMAGES

a formidable challenge confronting the brain every time we look at a surface. For instance, under the same illumination, white reflects much more light to the eye than black does. But a white surface in shadow often reflects less light to the eye than a black surface in sun. Nevertheless, somehow we can accurately discern which is which. How? Clearly, the brain uses the surrounding context to make such judgments. The specific program used to interpret that context is fraught with mystery for neuroscientists like me.

Recent studies of how we see black and white have provided insights into how the human visual system analyzes the incoming pattern of light and computes object shades correctly. In addition to explaining

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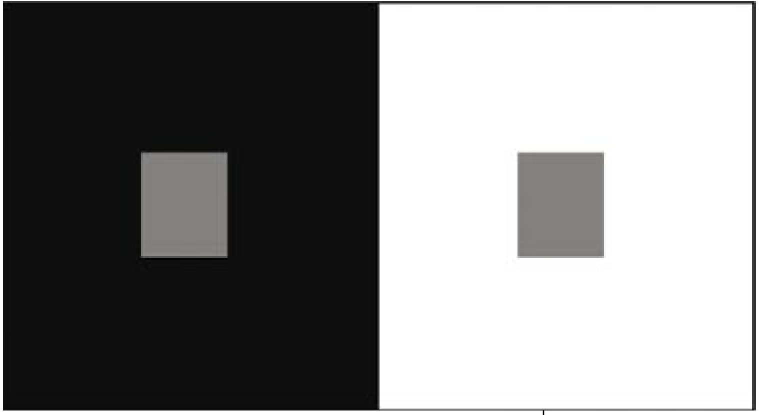

The gray rectangle in the black panel appears lighter than the identical gray surrounded by white.

more about how our own brains work, such research could help us in the design of artificial visual systems for robots. Computers are notoriously horrible at the kind of pattern recognition that comes so naturally to people. If computers could "see" better, they could provide more services: they could recognize our faces for keyless locks, chauffeur us around town, bring us the newspaper or pick up the trash.

Ask the Brains

Vision scientists force the brain to reveal its secrets using a method called psychophysics. Of course, the brain is not going to talk to us in lucid prose. Rather it is like a game of 20 questions. We ask the brain only yes or no questions: Do you work this way or that way? To get a clear answer, we must start with at least two competing hypotheses. Then we must carefully construct a test image that contains a critical "target" surface that should appear, let us say, light gray according to one hypothesis but dark gray for a competing explanation. Often these test images consist of delightful illusions, such as those you will see in this article.

To learn what the brain uses as an "anchor" against which to judge various patches of gray in images, the author and his colleagues hung a dome painted half black and half gray in a test apparatus (*right*). Volunteers who peered inside an opening in the enclosed device (*below*) saw the gray side as white and the black side as gray—proving that the brain's anchor is the lightest shade in a scene.

ALAN GILCHRIST

To appreciate the complexities of seeing a surface as black, white or gray, it helps to start with some basic physics. White surfaces reflect most of the light that strikes them—roughly 90 percent. In contrast (pun unintended), black surfaces reflect only about 3 percent of that light. When this reflected light enters the eye opening called the pupil, the lens focuses it onto the inner rear surface, or retina, much as light enters a simple box camera through a lens and then strikes the film. Photoreceptors in the retina can measure the amount of incoming light striking them.

So far, so good. But the light reflected from an object we look at, by itself, contains no hint of the shade of gray from which it was reflected. Here is where things get interesting.

The total amount of light reaching the eye depends far more on the level of illumination in any scene than it does on the percentage of light that any given surface reflects. Although a white surface reflects about 30 times as much light as a neighboring black shape in the same illumination, in bright sunlight that same white surface can reflect millions of times more light than it does in moonlight. Indeed, a black surface in bright light can easily send more light to the eye than a white surface in shadow. (This fact is why no robot today can identify the gray shade of an object in its field of view. The robot can measure only the amount of light that a given object reflects, called luminance. But, as is now clear, any luminance can come from any surface.)

Recognizing that the light reflected by the object itself contains insufficient information, psychologist Hans Wallach suggested in 1948 that the brain determines a surface's shade of gray by comparing the light received from neighboring surfaces. Wallach, a cousin of Albert Einstein, contributed a great deal to our knowledge of visual and auditory perception in studies he conducted

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Context matters: The “white” letters are actually darker than the “black” letters (*above*), as is clear when surroundings are removed (*inset*).

ALAN GILCHRIST

during his long tenure at Swarthmore College. He showed that a homogeneous disk could appear as any shade between black and white simply by changing the brightness of the light surrounding it, even though the disk itself never changes.

In a classic illusion, a gray square sits on a white background, and an identical gray square is on an adjacent black background [*see top illustration on opposite page*]. If the perceived lightness depended solely on the amount of light reflected, the two squares would look identical. The square on the black background looks lighter—which shows us that the brain compares neighboring surfaces.

More recent evidence has shown that this comparison of neighboring surfaces may be even simpler than Wallach imagined. Instead of measuring the intensity of light at each point in the scene, the eye seems to start by measuring only the change in luminance at each border in the scene.

Wallach’s work showed that the relative luminance of two surfaces is an important piece of the puzzle. But knowing just that property would still leave a lot of ambiguity. Put another way, if one patch of a scene is five times brighter than a neighboring patch, what does that tell the eye? The two patches might be a medium gray and black. Or they could just as well be white and gray. Thus, by itself, relative luminance can tell you only how different two shades are from each other but not the specific tint of either. To compute the exact gray of a surface, the brain requires something more: a point of comparison against which it can measure various hues, which researchers now call an anchoring rule.

Two anchoring rules have been proposed. Wallach himself, and later Edwin Land, inventor of instant photography, suggested that the highest luminance in a given scene automatically appears white. If this rule were true, it would serve as the standard by which the brain compared all lower

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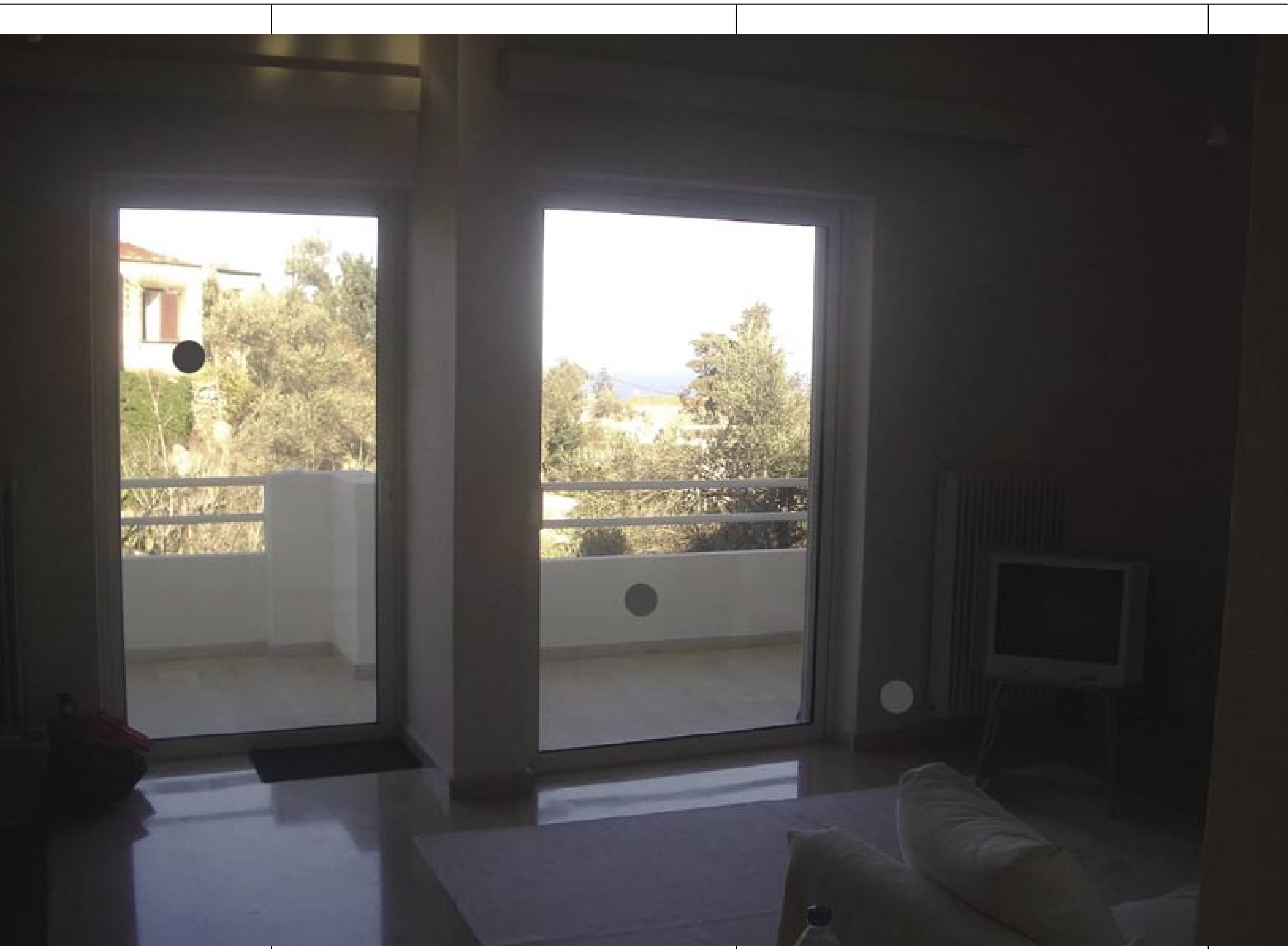
(The specific program used to interpret context is **fraught with mystery** for neuroscientists.)



ALAN GILCHRIST

Three identical disks pasted onto the photograph appear as different shades in different locations—showing how the brain applies a different anchor within each region of illumination.

luminances. Adaptation-level theory, created in the 1940s by psychologist Harry Helson, implied that the average luminance in a scene always appears middle gray. Lighter and darker gray shades would then be identified by comparing other luminances to this middle value. Researchers working in machine vision called this the "gray world assumption."

Which was right? In my laboratory we sought to find out in 1994. My colleagues and I at Rutgers University devised a way to test these rules under the simplest possible conditions: two gray surfaces that fill the entire visual field of an observer. We asked volunteers to place their head inside a large opaque hemisphere with its interior painted a medium shade of gray on the left and black on the right. We suspended the hemisphere within a larger rectangular chamber with lamps that created diffuse lighting for the viewer.

Remember, the brain does not yet know what these two shades of gray are—it has only relative luminance. If the brain's anchoring rule is based on the highest luminance, then the middle gray half should appear white and the black half should appear middle gray. But if the rule is based on the average luminance, then the middle gray half should appear light gray, whereas the black half should appear dark gray. The viewer would not see either side as being black or white.

The results were clear. The middle gray half

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appeared totally white; the black half, middle gray. Thus, our perceived gray scale is anchored at the "top," not in the middle. This finding tells us much about how the brain computes gray shades in simple scenes. The highest luminance appears white, whereas the perceived shade of gray of a darker surface depends on the difference—or, more precisely, the ratio—between its own luminance and that of the surface with the highest luminance.

Different Anchors

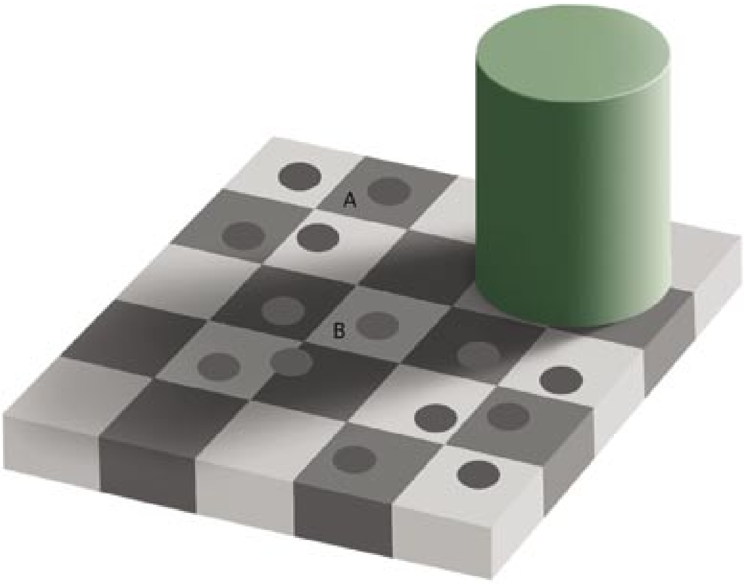
What about the much more complex scenes typical of everyday life? Does this simple algorithm work? At this point, the reader may not be surprised to learn that the answer is, "No, it is more complicated." If the brain compared only the luminance of each surface with the highest luminance in the entire scene, then a black surface in bright light would appear as the same shade as a white surface in shadow, given only that both have the same luminance, as often happens. But they do not: we can discern the difference between them. The visual system must, then, apply a different anchor within each region of illumination.

And indeed, research with many illusions shows that the anchor does vary. If I paste several identical gray disks onto a photograph with lots of brighter areas and shadows, the disks in the shadowed regions will appear much lighter than those in the sunlight [*see illustration on opposite page*]. I call these "probe disks," because they allow us to probe how the visual system computes gray shades at any location in the scene. Within any given region of illumination, the precise location of the disk matters little; the disk appears roughly the same shade of gray throughout the region.

Functionally, each region seems to have its own anchor—the luminance at which the brain perceives that a surface appears white. But programming a robot to process the image in this way presents a big challenge. Segmenting the picture into separate regions that have different illuminations requires the visual system to determine which edges in the image represent a change in the pigment of the surface and which, like the line formed by the outline of a shadow, mean an alteration in the illumination level. Such a program, for example, might classify an edge as the boundary between different regions of illumination if it is blurred or if it represents a planar break as, say, a corner.

Theorists such as Barbara Blakeslee and Mark McCourt of North Dakota State University argue that the human visual system need not use this kind of edge classification either. They argue for a less sophisticated process called spatial filtering. In our picture with gray disks, for instance, they would suggest that the gray shade of each disk depends mainly on the local luminance contrast at the edge of that disk (much as in Wallach's earlier proposal). They might note that the apparent shade of each disk in the photograph depends simply on the direction and strength of the luminance contrast between each disk and its immediate background.

We can test whether this simple idea works by placing some probe disks on a checkerboard with a shadow falling across it [*see illustration above*]. We find that disks with identical local contrasts will appear to have different shades. On the other hand, disks with different local contrasts may share the same shade of gray.



All the disks are identical, yet those in the shadow appear lighter gray. Disks on squares A and B appear to be different shades of gray, although they have identical local contrasts (squares A and B are identical in luminance, although they do not appear to be). Yet the two disks to the left and right of the letter B look the same (but have different local contrasts).

EDWARD ADELSON

All Together Now

Consider another visual trick, which sheds light on how the brain decides what elements to group together when it is sorting out patterns of light. Imagine a black "plus" sign, with two gray triangles [*see top right in box on next page*]. One of the triangles fits into the crook of the white area formed by the "elbow" of the plus; the oth-

(The Author)

ALAN GILCHRIST is a professor in the psychology department at Rutgers University. He studies visual perception, especially the "software" the visual system uses to decode the retinal image. He is also interested in child raising and critical thinking. His book *Seeing Black and White*, a 20-year effort, was published by Oxford University Press in 2006.

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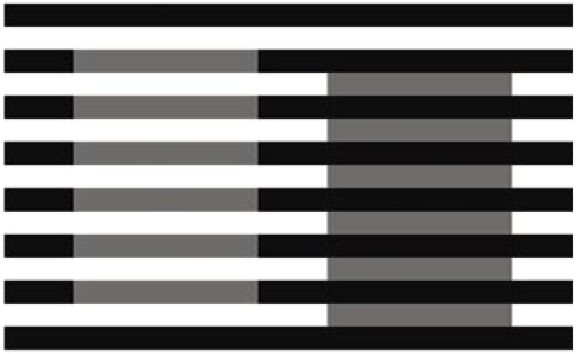
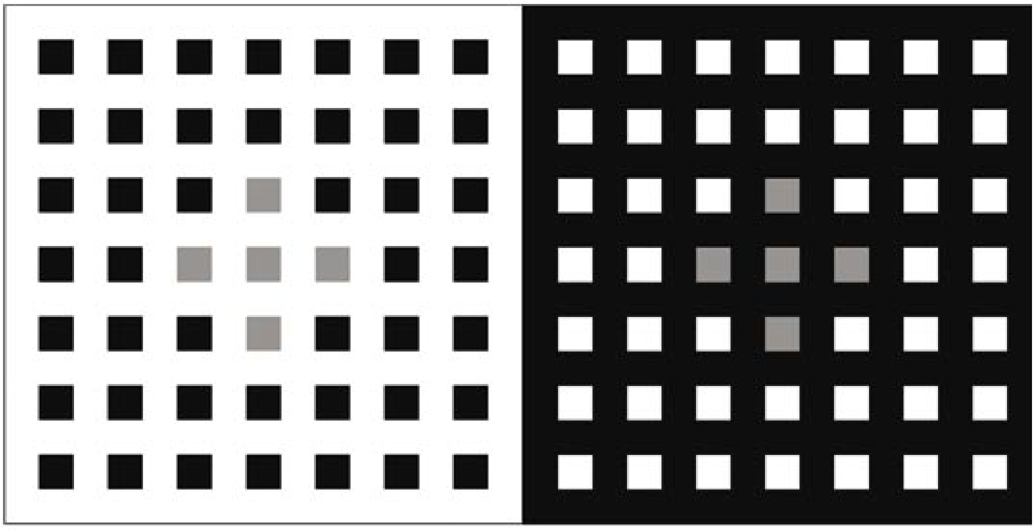
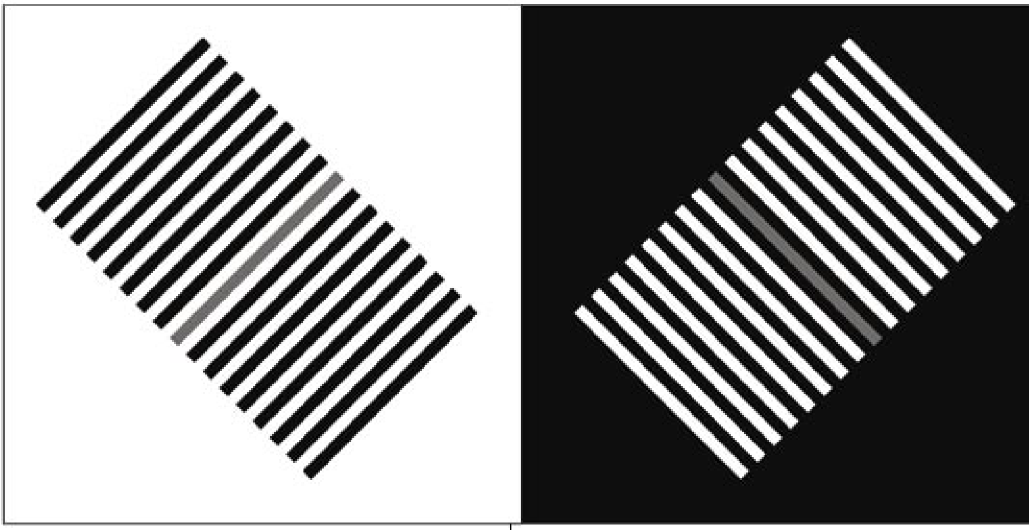
The Power of Groups

In each of the illusions below, identical gray regions appear different, depending on juxtapositions with their black or white surroundings. These effects cannot be attributed solely to contrast between neighboring regions, because contrast alone typically would make us perceive gray surrounded by white as darker than gray surrounded by black. Instead the critical factor for the brain's judgment of the gray shade seems to be which regions "belong" to one another.







MICHAEL WHITE (*top left*); MAX WERTHEIMER AND WILHELM BENARY (*top right*); PAOLA BRESSAN *University of Padua* (*middle*); ELIAS ECONOMOU *University of Crete* (*bottom*)

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(Step by step, we will force the visual system to give up its secrets.)

er pokes inside the black area of one of the black bars. Here the two gray triangles are identical, and their immediate surroundings are identical. Each triangle borders white along its hypotenuse (the longest side) and black along the other two, equal-length sides. But the lower triangle, inside the black bar, "belongs" to the black cross, whereas the upper triangle seems to be part of its white background. Notice the boundary intersections. When the borders come together to form a kind of T junction, the brain seems to define the regions divided by the stem of the T as belonging together, but not the regions divided by the top of the T.

This interpretation of T junctions as a way for the brain to establish groups holds for another illusion, created by Australian artist Michael White. It has a series of horizontal black bars stacked with white spaces between them. In it, gray bars that are neighbored by black more than by white [*see top left in box on opposite page*] appear darker (not lighter) than the gray bars that are neighbored mostly by white. Here the T junctions at the corners of the gray bars suggest that the gray bars on the left lie in the same plane as the white background, whereas those on the right lie in the same plane as the black bars.

Paola Bressan in the psychology department at the University of Padua in Italy created a "dungeon" illusion, which further details the brain's grouping mechanisms. The gray squares at the middle right in the box on the opposite page, which are surrounded by black, appear darker than those at the middle left, which are enclosed by white.

This effect may occur because the gray elements on the right appear to lie in the same plane with the white background, rather than the black bars of the dungeon window. A reverse contrast illusion by University of Crete perception researcher Elias Economou makes the same point. The gray bar [*see bottom right in box on opposite page*], even though it is completely bordered by black, appears darker, apparently because it is a member of the group of white bars.

These fun illusions have a serious side. They show that the brain cannot compute the gray levels we perceive by simply comparing the luminances of two neighboring surfaces alone. Rather the surrounding context comes into play in a very sophisticated way. The fact that most people are unaware of the difficulty of the problem testifies to the remarkable achievement of the human visual system.

The Big Picture

Scientific consensus on how the brain computes black and white remains further down the road. Current theories fall into three classes: low, middle and high level. Low-level theories, based on neural spatial-filtering mechanisms that encode local contrast, fail to predict the gray shades that people see. High-level theories treat the computation of surface gray shades as a kind of unconscious intellectual process in which the intensity of light illuminating a surface is automatically taken into account. Such processes might be intuitively appealing but tell us neither what to look for in the brain nor how to program a robot. Middle-level theories parse each scene into multiple frames of reference, each containing its own anchor. These theories specify the operations by which black, white and gray shades are computed better than the high-level theories do, while accounting for human perception of gray surfaces better than the low-level theories do.

But before we can truly comprehend this aspect of vision—or program a robot to do what our human system does—we will need a better understanding of how boundaries are processed. The human eye, like the robot, starts with a two-dimensional picture of the scene. How does it determine which regions of the picture should be grouped together and assigned a common anchor? Vision scientists will continue to propose hypotheses and test them with experiments. Step by step, we will force the visual system to give up its secrets.

Decoding human visual computing may be the best way to build robots that can see. But more important, it may be the best way to get a grip on how the brain works. M

(Further Reading)

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Transparently Obvious

How the brain sees through the perceptual hurdles of tinted glass, shadows and all things transparent

BY VILAYANUR S. RAMACHANDRAN AND
DIANE ROGERS-RAMACHANDRAN

OUR ABILITY to perceive visual scenes effortlessly depends on intelligent deployment of built-in knowledge about the external world. The key word here is "intelligent," which raises the questions: Just how smart is the visual system? What is its IQ? For example, does the visual system know the laws of physics? Does it use inductive logic only (as many suspect), or can it perform deductions as well? How does it deal with paradoxes, conflicts or incomplete information? How adaptable is it?

Some insight into perceptual intelligence comes from the study of transparency, a phenomenon explored by Gestalt psychologist Fabio Metelli. He first drew attention to the fact that compelling illusions of transparency can be produced by using relatively simple displays.

The word "transparency" is used loosely. Sometimes it refers to seeing an object, such as a sunglass lens, and the objects visible through that object, and sometimes it means seeing something through frosted glass, known as translucency. Here we will restrict ourselves to the former, because the physical and perceptual laws pertaining to it are simpler.

Physics of Transparency

First let us consider the physics of transparency. If you put a rectangular neutral-density filter, such as dark glasses, on a sheet of white paper, the filter allows only a certain proportion of light through—say, 50 percent. Put another way, if the paper has a brightness, or luminance, of 100 candelas (cd) per square meter, the portion covered by the filter will have a luminance of 50 cd. If you then add a second such filter so that it partially overlaps the first, the overlapping region will receive 50 percent of the original 50 percent of the light—that is, 25 percent. The relation is always multiplicative.

So much for physics. What about perception? If, as in *a,* you simply have a dark square in the middle of a light square (with the former being 50 cd and the latter 100 cd), the inner square could be either a filter that cuts light by 50 percent or a darker square that reflects only 50 percent as much of the incident light as does the surrounding background. Without additional information, there is no way the visual system could know which condition exists; because the latter case is far more common in nature, that is what you will always see.

But now consider two rectangles that form a cross with an overlapping region in the middle. In this case it is not inconceivable—and, indeed,

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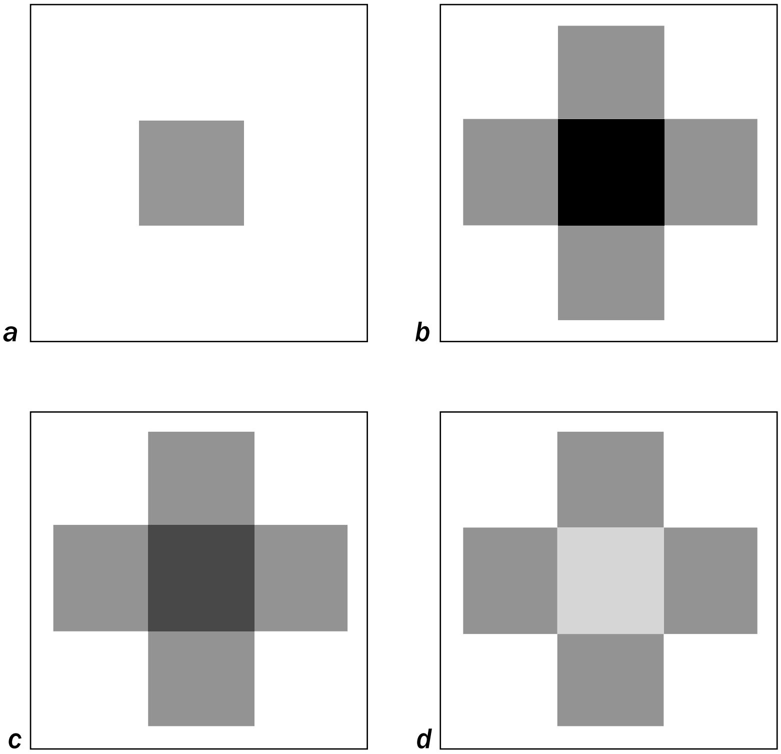

(Does the visual system know the **laws of physics**? How does it deal with paradoxes and incomplete information?)

it is more probable—that this configuration really does consist of two overlapping rectangular pieces of filters rather than five blocks arranged to form a cross. But if it is the former, then the luminance ratios must be such that the central square (the overlapping region) should be darker than the other squares and, of course, darker than the background. In particular, the central square's luminance should be a multiplicative function in terms of a percentage of the two filters. If the nonoverlapping regions of the two rectangles are, for instance, 66 and 50 percent of the background, respectively, then the inner square should be 50 percent of that 66 percent—or roughly 33 percent (that is, 33 cd, assuming the white paper is 100 cd).

Now the question is, Does the visual system have tacit "knowledge" of all these factors? We can find out by using a series of displays (*b, c, d*) in which the background and rectangles are of a fixed luminance (such as 100 and 50 cd, respectively) while the luminance of the inner square alone changes. In terms of the luminance that would exist with physical transparency, the inner square is set to be too dark (*b*), appropriately dark (*c*) or too light (*d*). If you look at these figures without knowing anything about physics, you see the rectangles as transparent in *c* but not in *b* or in *d*. It is almost as if your visual system knows what you do not know (or did not know until you read this article).

This experiment suggests that two conditions must be fulfilled for transparency to be seen. First, there must be figural complexity and segmentation to justify this interpretation (hence no transparency in *a*). Second, the luminance ratios have to be right (no transparency is visible in *b* or *d*).

SCIENTIFIC AMERICAN MIND (*top*); GETTY IMAGES (*bottom*)

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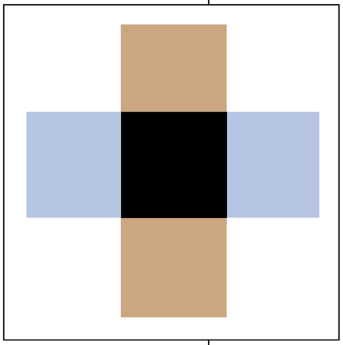
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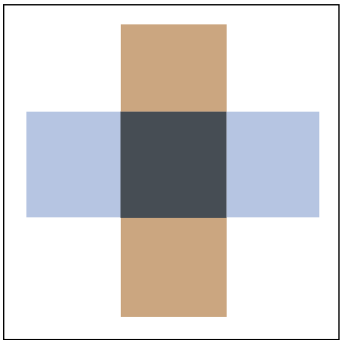
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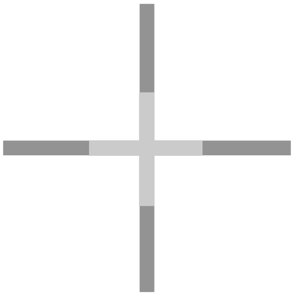
Shadowy Influences

Transparency is infrequent in nature, but shadows are not. It is possible that the "laws" of perception we have explored so far evolved primarily to deal with shadows and to distinguish them from "real" objects, which would also produce luminance differences in the visual scene as a result of differences in reflectance (for instance, a zebra's stripes or a white cat standing on a black surface).

The shadow cast by an object such as a tree could, in theory, be pitch black if there were a single distant light source, without scattering or reflections. Ordinarily, however, ambient light from the environment falls on the shadow so that a dark, but not black, shadow results. If the tree shadow falls on a sidewalk and darker grass (*e, on preceding page*), the manner in which the magnitude and sign of luminance vary along the shadow's boundary would be identical on both sides of the boundary, the shadow side and the light side. This covariation of luminance clues the brain that it is a shadow, not an object or texture.

It turns out that the luminance changes in transparency mimic those seen in shadows. The visual system may have evolved to discover and react appropriately to shadows rather than to transparent filters. If it could not do so, you might attempt to grab a shadow or gingerly step over it to avoid tripping, not realizing that it is not an object at all.

Interestingly, although our perceptual mechanisms seem to be aware of the physics of transparency pertaining to luminance, they appear to be blind to the laws pertaining to color "transparency." In *f* and *g*, we have two bars crossing each other, both with luminance of, say, 50 percent of the background. We have contrived it so that in *g*, the overlapping region has 25 percent of the background luminance, as it should if we were dealing just with luminance. But if the colors of the two filters are different—as they are—the overlap zone should be pitch black instead of gray. The reason is that the red filter transmits only long ("red") wavelengths when white light shines through it, and the blue filter transmits only short ("blue") wavelengths. Therefore, if you cross the filters, *no* light passes through; the overlap zone will be black. In fact, transparency is seen not when the midzone is black (*f*) but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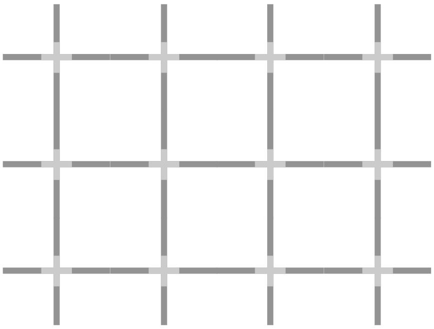
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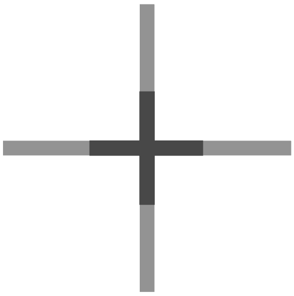
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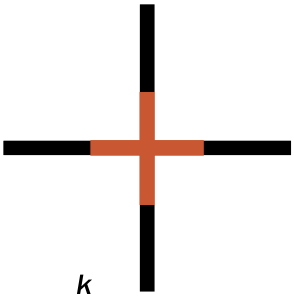
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(The visual system may have evolved to **discover and react** appropriately to shadows rather than to transparency filters.)

when it is 25 percent (*g*). Apparently, the visual system continues to follow the luminance rule and ignores the color incompatibilities.

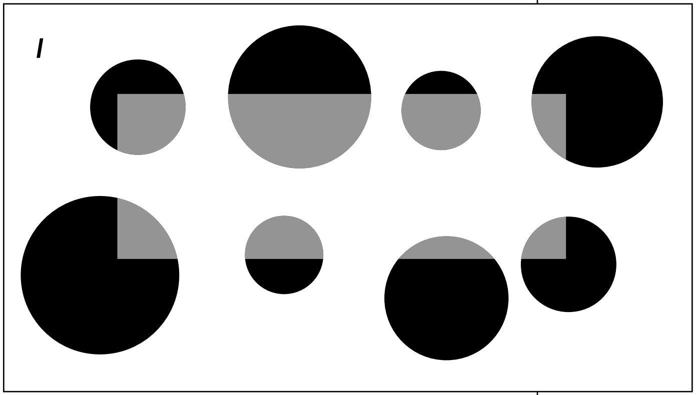
A curious effect occurs if you place a gray cross on a white background when the middle of the cross is a lighter shade of gray (*h*). Instead of seeing the lighter cross for what it is, the brain prefers to see it as if there were a circular piece of frosted glass or vellum superimposed on the larger gray cross. To achieve this perception, the brain has to "hallucinate" an illusory frosted glass spreading, even in the area surrounding the central region of the cross. The effect is especially compelling if you have a patch of several such crosses (*i*).

Once again the luminance ratios between the surround (white), the cross (dark gray) and the central region (light gray) have to be just right for the effect to occur; if they are wrong, the effect disappears (*j*). In other words, the ratios must be compatible with what would occur with actual translucent surfaces (for example, fog or frosted glass). The effect is even more striking if there is a chromatic component to the display (*k*).

Thus, even though the visual system does not know about color subtraction, if the luminance ratios are right, then the colors are "dragged along" with the spread of luminance.

Another intriguing effect is seen in *l*, invented by Italian psychologist Gaetano Kanizsa: the Swiss cheese effect. When you glance at it casually, you see a large opaque rectangle with holes in it superimposed on a smaller gray rectangle sitting on a black background. But with some mental effort, you can start to imagine the light-gray rectangle behind the holes as actually a translucent white rectangle in front of the holes and then start to perceive a transparent rectangle through which you see black spots in the background. This illusion demonstrates the profound effect of top-down influences on perception of surfaces; the transparency you see is not entirely driven bottom-up through serial hierarchical processing of the physical input on the retina.

Taken collectively, these demonstrations allow us to conclude that a remarkable degree of "wisdom" about the statistics and physical laws of transparency are wired into visual processing, through a combination of natural selection and learning. Yet there are limits to this wisdom. The visual system seems tolerant of incompatible colors. It is incapable of applying the physics of color subtraction, partly because color perception evolved much later in primates and did not get wired in adequately and partly because in the luminance domain, color overlap is much less common in the natural world than transparency and translucency are.



We may conclude that even though the visual system can make sophisticated use of such abstract properties as the physics of luminance ratios and the statistics of segmentation required for transparency, it is "dumb" with regard to other characteristics, such as color, because of the happenstance manner in which its hardware (or "squishy-ware") evolved through natural selection—strong evidence against "intelligent design." M

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With fond memories of Daniel J. Plummer (1966–2006), a dear friend and brilliant student of transparency and other phenomena.

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The Reality of Illusory Contours

How can an imaginary square look more real than a box with actual lines?

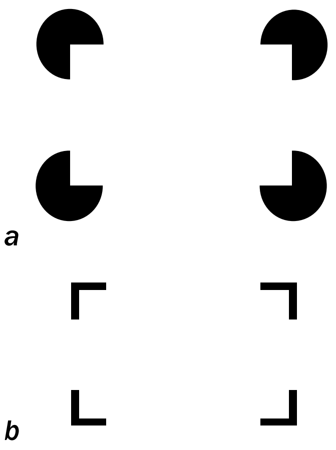
BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

COMPUTERS CAN calculate at staggering speed, but they cannot match the human visual system's uncanny ability to assemble a coherent picture from ambiguous fragments in an image. The brain seems to home in effortlessly on the correct interpretation by using built-in knowledge of the statistics of the world to eliminate improbable solutions.

This problem-solving aspect of perception is strikingly illustrated in *a* by the famous illusory rectangle of Italian psychologist Gaetano Kanizsa and neuropsychologist Richard L. Gregory of the University of Bristol in England. Your brain regards it as highly unlikely that some malicious scientist has deliberately aligned four Pac-men in this manner and instead interprets it parsimoniously as a white opaque rectangle partially covering four black disks in the background. Remarkably, you even fill in, or "hallucinate," the edges of the phantom rectangle. The main goal of vision, it would seem, is to segment the scene to discover object boundaries so that you can identify and respond to them.

Now, you might think that the mere presence of collinear edges is sufficient for the brain to "complete" the gap, but *b* demolishes this argument. Comparing the absence of illusory contours in *b* with their presence in *a,* we conclude that the critical cue is *implied* occlusion.

In *c* and *d,* we superimpose *a* on a background of bricks. Notice that in *d,* the illusory contours disappear. The brain realizes that a rectangle must be opaque to occlude the four black disks. But if it is opaque, how can the bricks be seen through it? So the brain rejects this percept.



In *c,* the bricks are aligned so that the edges coincide with the edges of the Pac-men. The occluding rectangle reemerges; indeed, it is actually more vivid than the illusory contour on its own. When multiple sources of information about an edge (in this case, the luminance-defined sides of the bricks and the illusory ones implied by occlusion) coincide spatially, the brain regards this coming together as compelling evidence that the edge is real.

How do we then explain the disappearance of the illusory rectangle in *e*—which could be logically interpreted as a textured rectangle occluding four gray disks in the background? To understand this anomaly, we need to invoke a "hardware" rather than "software" explanation. Notice that we have matched the mean luminance of the texture with that of the Pac-men. The neurons in your brain that extract the illusory edges can identify only those edges defined by luminance differences because of the way in which neurons evolved. Because the Pac-men in the display are defined by a difference of graininess, not luminance, no illusory contours are seen, even though the "logic" of the situation dictates that they should be.

In *f,* we superimpose an illusory circle on a simple gradient of luminance. Intriguingly, the region enclosed by the circle seems to bulge right out at you, especially if you squint your eyes to blur the image slightly. The brain deduces that the gradient must arise from a curved surface lit from above, and the illusory circle interacts with this impression to produce the final interpretation of a sphere. Yet if we superimpose a "real," thin,

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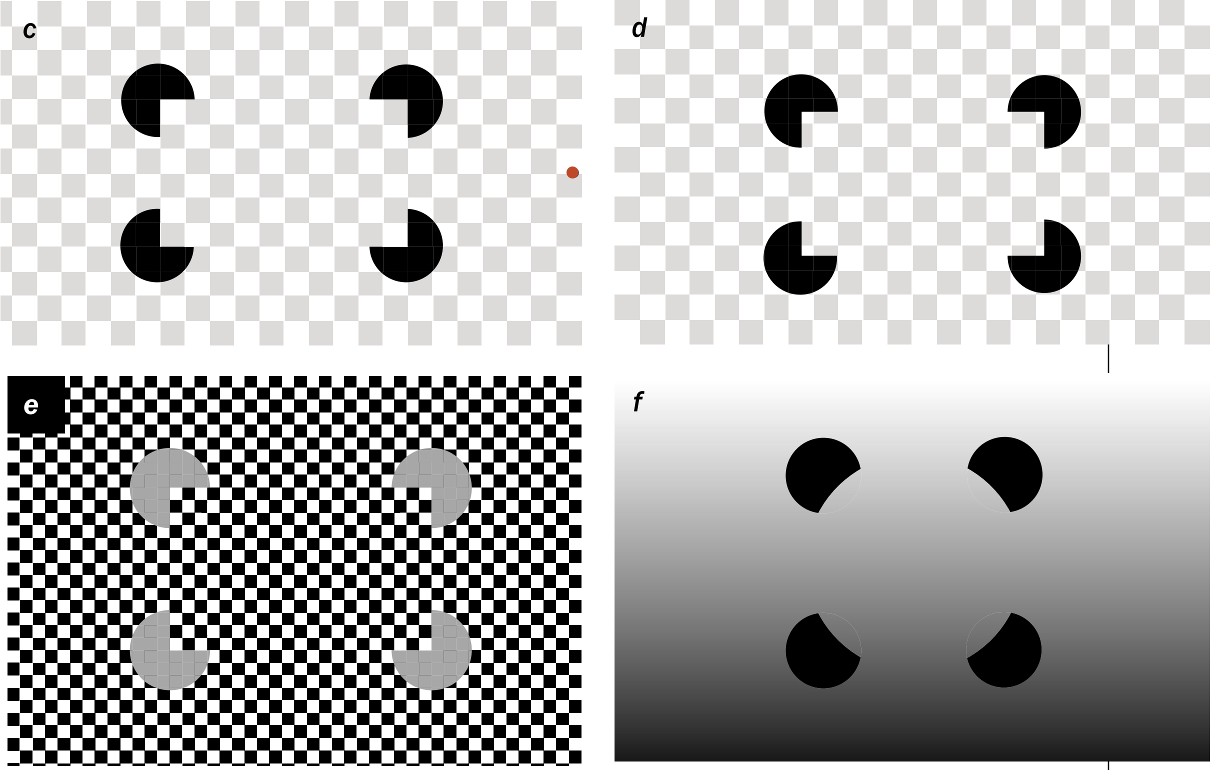

black-outline circle made of an actual luminance-based edge on the gradient, no bulge appears. This finding leads to a paradoxical aphorism that we invented to annoy philosophers—namely, that illusory contours seem more real than real contours. Such luminance edges can arise in the visual scene for any number of reasons—the edge of a shadow, for example, or the stripes of a zebra. They do not necessarily imply object boundaries.

In 1961 neurobiologists David H. Hubel and Torsten N. Wiesel, both then at Harvard University, discovered the basic alphabet of vision (they later shared a Nobel Prize in Physiology or Medicine for their efforts to understand information processing in the visual system); individual neurons in area 17 and area 18 (in the occipital lobe) fire only when lines of a certain orientation are displayed in a specific location on the screen (the "receptive field"). Many of them will respond only to a line of a specific length—if it is longer, they will stop firing ("end-stopped cells"). Neurophysiologist Rudiger von der Heydt of Johns Hopkins University suggested that these cells are signaling an implied occlusion that is effectively chopping off the line, and sure enough, the cells respond to illusory contours.

You can demonstrate the existence of such cells in your own brain. If you stare continuously at the red dot on the right in *c*, you will notice that after a few seconds, the illusory rectangle fades even though you still see the bricks and Pac-men. The cells signaling the illusory edges are "fatigued" by the steady fixation, which hyperactivates them and depletes them of their chemical neurotransmitters. If you move your eyes, they reappear, because a new set of cells is recruited. Apparently these illusory contour cells are more easily fatigued than those signaling the real edges of the bricks and Pac-men.

In more complex images, cells in the earliest stages of visual processing may signal illusory edges, but top-down modulation based on visual attention can reject or accept the contours depending on overall consistency with the scene. **M**

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The Quirks of Constancy

Even when we consciously know two lines are the same length, why can't we help seeing them as different?

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

ILLUSIONS ARE ANOMALIES that can reveal clues about the mysterious workings of the brain to neuroscientists in much the same way as the fictional Sherlock Holmes can solve a crime puzzle by homing in on a single out-of-the-ordinary fact. Think of the phrase "the dog that did not bark" (in Sir Arthur Conan Doyle's short story "Silver Blaze") or of the missing dumbbell (in Conan Doyle's novel *Valley of Fear*).

Perhaps the most famous examples of such visual tricks are the geometric optical illusions. In the Ponzo illusion (*a*), first demonstrated by Italian psychologist Mario Ponzo in 1913, one horizontal line looks shorter than the other one, although they are identical. In the Müller-Lyer illusion (*b, on page* 46), created by German psychiatrist Franz Müller-Lyer in 1889, the line bounded by the diverging arrowheads looks shorter than the one with converging arrowheads—although they, too, are identical.

These illusions are very familiar yet powerful; knowledge of true line length does not stop or diminish their effect. Do we have any idea what causes them? Why would the visual system persist in committing an error, in perceiving incorrectly something so simple even when we consciously know it is a trick? Before we explore those questions, let us introduce two more eye puzzles.

In *d*, on page 47, we have a field of shaded disks that are seen as eggs dispersed among cavities. The disks that are light on top look like bumps or eggs, the others like cavities. This

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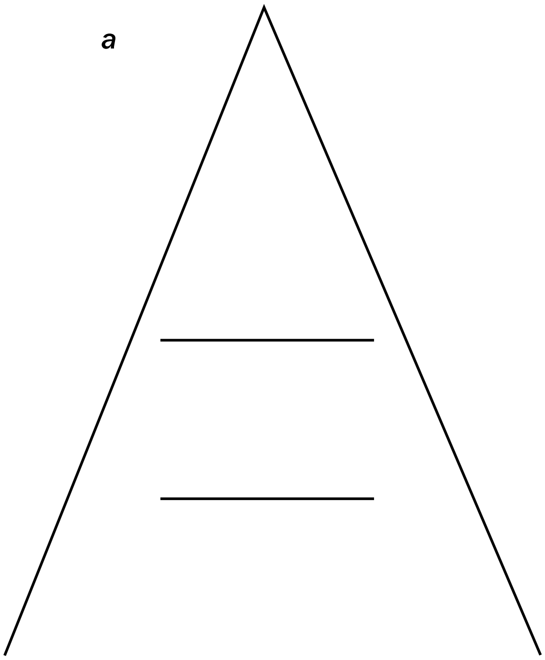
sense of depth comes from a built-in tendency for your visual system to assume that light shines from above (after all, we evolved on a planet with a single sun overhead). So the brain interprets the disks that are lighter on top as rounded like eggs and the light-on-bottom ones as cavities (because a hollow would be light on its bottom if lit from above). In *e,* on page 47, the shading gradient changes from left to right, and the depth is far less compelling (the tokens seem flatter) and more "bistable" (individual disks are equally likely to be seen as convex or concave, and the light source can be seen as arising from either side).

So far so good. But we also noticed that the perceived *gradient* of lightness—the apparent difference in brightness between the lightest and darkest parts of each disk—seems shallower for the spheres than for the craters. The brightness gradient also appears less steep for the light-on-top disks than for the light-on-side disks. Why? The physical gradient is exactly the same for each of the shaded disks (to convince yourself, rotate the paper).



(These illusions are **very familiar** yet powerful; knowledge of true line length does not stop or diminish their effect.)

Constancy Connection

These two sets of illusions, the geometric optical illusions and the gradient-steepness type, seem completely unrelated. But both reveal a basic principle in vision called perceptual constancy. This effect is the tendency to observe correctly an object as having constant physical attributes (size, shape, color, lightness, distance, and so on) despite tremendously variable retinal images that may occur for that object, which arise from changes in vantage point, distance, illumination and other variables. This point is not trivial. Unlike a video camera, our brains do not merely "read out" the retinal image to perceive an object. Rather we interpret it based on knowledge and context. For instance, constancy guides us despite changes in lighting. Believe it or not, the black ink of a newspaper has a higher absolute luminance (the physical light intensity measured by a photometer) when viewed in sunlight than white paper does when viewed in a well-lit room at night. Yet we recognize the true character of the objects and their comparative brightness: despite lighting conditions, we experience it as black type on white paper and do not—in fact, *cannot*—perceive the absolute luminance.

Another example, more relevant to our geometric illusions, is size constancy, or the tendency to identify an object as being constant in size whether it is near or far. If you watch a person running toward you, his image on your retina enlarges, although you do not see him expanding. Your brain unconsciously takes into account the distance and interprets size correctly. Similarly, if a person is lying on the ground with his feet extended toward you, the retinal image of his feet is twice the size of his head, but you do not see a microcephalic with giant feet. You see a normally proportioned person with his feet closer to you than his head.

But how does size constancy explain our geometric illusions? The phenomenon arises from a depth cue, called linear perspective, with which every visual artist is familiar. An object of constant size will throw a smaller image on your retina as it moves farther away. This shrinkage is just a simple consequence of optics; it has nothing to do with perception. Now consider what happens when you stand in the middle of parallel railway tracks and cast your gaze along their

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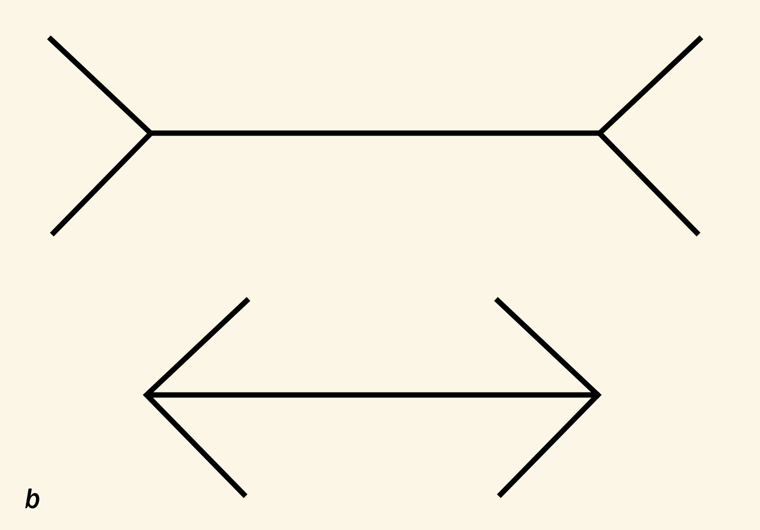
(Why do the top-lit eggs look **more uniform** in surface reflectance (lightness) compared with the side-lit disks?)

length. The rails remain parallel and the ties between them a constant size along their length, yet the resulting retinal image or indeed any 2-D projection of the tracks, such as a photograph or line drawing, shows the space between the rails and the corresponding size of the ties shortening with increasing distance. Again, this result is from simple optics, not perception. In the perceptual world, our brain largely corrects for this linear perspective, and we interpret the railroad as straight and parallel and the ties as being of a constant size. You correctly attribute the size changes to distance, not to changes in size.

Coming Together

Now take another look at the Ponzo illusion. Consider the converging lines; like railroad tracks, they suggest parallel lines extending far into the distance. Like the railroad ties, the horizontal segments are interpreted in the context of these converging lines and thus are seen to exist at different distances. In the Ponzo illusion, however, the two horizontal segments are drawn to be exactly the same length (unlike railroad ties, which get smaller with distance). Because they are interpreted in the context of converging lines and appear to lie at different distances, the brain applies a constancy correction, so that the top line looks longer than the bottom one. It is as if the brain reasons: “One horizontal line is farther away, so if it is the same physical length as the other horizontal line it should cast a smaller image in my eye. But because the image is the same size, it must be produced by a longer line that is farther away.” This correction occurs even though the viewer may not have any sense of depth from the converging lines.

Because the top line is deliberately drawn to be the same length as the bottom one, the brain *misapplies* this constancy rule, and you perceive it as looking abnormally long. The exact converse happens for the bottom line; it looks artificially short. Neuropsychologist Richard L. Gregory of the University of Bristol in England refers to this phenomenon as inappropriate constancy scaling. Your visual modules, concerned with depth, distance and size, perform the task on autopilot, without your conscious cogitation. Even if I use a ruler to show you that the two lines are the same, this high-level, conscious knowledge cannot “correct” what is signaled from the bottom up by constancy mechanisms.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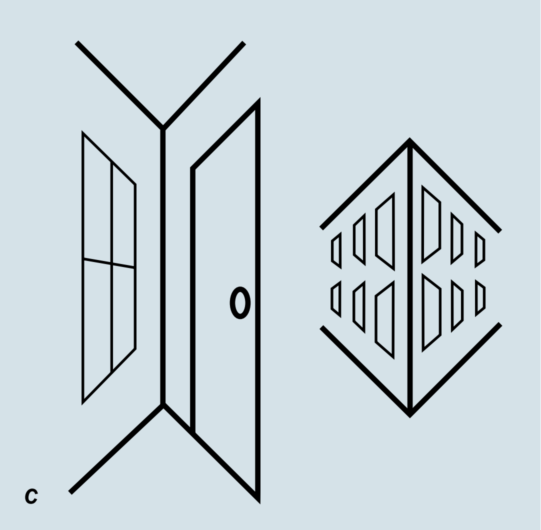
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Gregory has also proposed a delightful size-constancy explanation for the Müller-Lyer illusion (*b*). He points out that the contours of this illusion are identical to the contours one encounters when viewing the outside edge of a building or the inside corners of a room (*c*). In this two-dimensional projection of a three-dimensional world, the inside corner of the room is seen as farther away; size scaling is triggered and produces the misperception of different line lengths. As with the Ponzo illusion, whereas depth is implied by this figure, it need not be consciously

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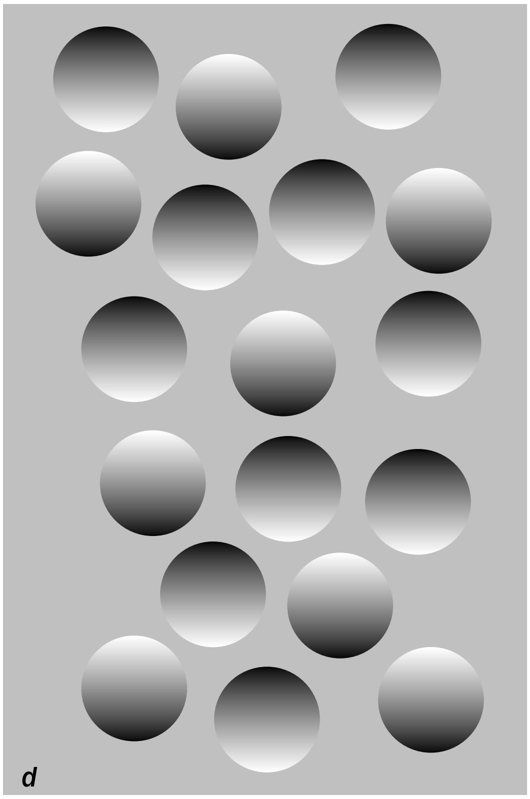

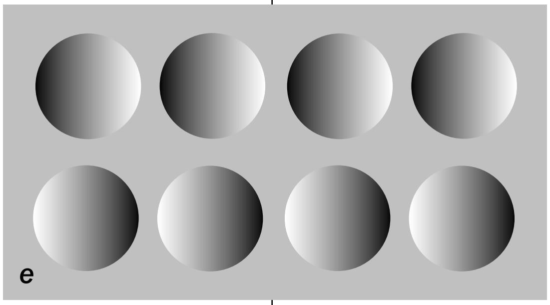

experienced. The perspective lines, Gregory proposes, directly set constancy scaling, so judgments of distance are unnecessary.

Let us now return to the eggs and cavities. We have explained the illusion of depth as being based on a built-in assumption that the light is shining from above. But why do the top-lit eggs look more uniform in surface reflectance (lightness) compared with the side-lit disks or the bottom-lit cavities? Here we need to invoke the analogous phenomenon of lightness constancy—the ability of the brain to extract the true reflectance of an object's surface, instead of variations in luminance caused by illumination.

First, consider a light-on-top egg. The brain assumes the sun is above you, and a real egg would convey exactly this pattern of luminance variation—a gradient of luminance decreasing gradually from top to bottom. So you see it as an egg or bump rather than as a flat, shaded disk; it is the "best-fit" hypothesis. But then the brain says, in effect: "The variation in luminance—light on top—is obviously not from the object itself but because of the way it is illuminated from above, so I will see it as uniform in reflectance." This effect of lightness constancy implies that if you did not see depth in the display, there would be no lightness constancy and you would in fact see the top as being much lighter and the bottom much darker than they seem now.

Now why does not the same argument apply to the light-on-side eggs seen in *e*, especially given that the luminance gradient is exactly the same? It is because the brain is not used to sideways illumination. Consequently, the impression of depth is weaker, and the correction for luminance variation (lightness constancy) is correspondingly weaker. The gradients of perceived lightness therefore appear steeper than they do for the top-lit eggs in *d*.

The same reasoning applies to the cavities. Because of the phenomenon of interreflection (light bouncing off the walls of the interior of a true cavity, partially nulling the gradient produced by illumination), the brain "expects" a smaller illumination gradient in cavities than in eggs. So it only weakly applies the constancy correction to the former. This milder correction would be sufficient in the real world, but the shading of the artificial cavities in *d* is physically identical (though inverted) to that of the eggs. Thus, the perceived gradient of lightness is higher than it is for the eggs. A second reason is that cavities are less common than bumps, and therefore the visual system is less adept at this constancy correction.

We have presented these complex arguments to emphasize that even extraordinarily subtle aspects of the statistics of the world are built into the visual system as rules. We can devise extremely simple displays from which we can use clues—like Sherlock Holmes—to help solve the mystery of visual perception. **M**

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Sizing Things Up

When you hoist two items of equal weight, your brain may be doing some heavy lifting

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

GETTY IMAGES

THE GREAT German physicist Hermann von Helmholtz not only discovered the first law of thermodynamics (the conservation of energy) but also invented the ophthalmoscope and was first to measure nerve impulse velocity. He is, in addition, widely regarded as the founding father of the science of human visual perception—and is, to both of us, an inspiration.

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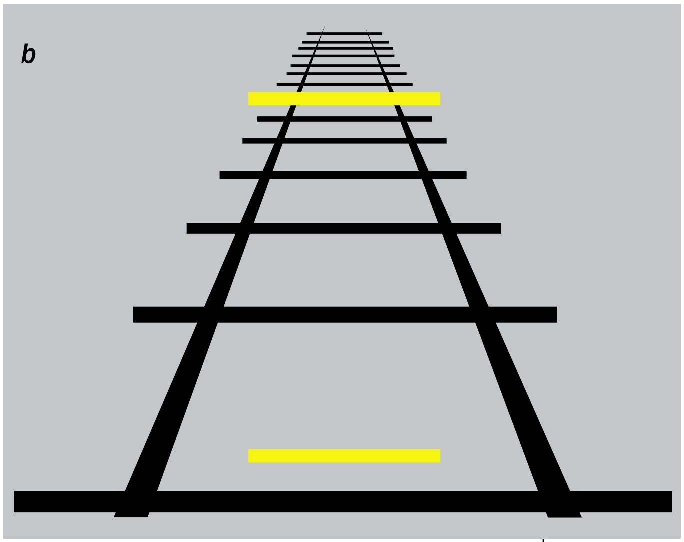
We have often emphasized in our writings that even the simplest act of perception involves active interpretation, or "intelligent" guesswork, by the brain about events in the world; it involves more than merely reading out the sensory inputs sent from receptors. In fact, perception often seems to mimic aspects of inductive thought processes. To emphasize perception's thoughtlike nature, Helmholtz used the phrase "unconscious inference." Sensory input (for example, an image on the retina at the back of the eye) is interpreted based on its context and on the observer's experience with, and knowledge of, the world. Helmholtz used the word "unconscious" because, unlike for many aspects of thinking, no conscious cogitation is typically required for perception. By and large it is on autopilot.



Because the two containers appear similar, except for size, one assumes the larger one is **proportionally heavier**.

Weighing the Evidence

A powerful demonstration of the predictive power of perception is seen with the size-weight, or Charpentier-Koseleff, illusion (conceptual representation in *a*), which you can easily construct and use to mesmerize your friends. This perceptual trick was one of Helmholtz's favorites, and we shall soon see why.

To set up, take two objects that are similar in shape, color and texture but different in size—such as hollow metal or plastic cylinders. Hide enough weight inside the smaller one so that its weight is identical to that of the larger object. Because the two containers appear similar, except for size, observers will naturally assume the larger one is proportionally heavier than the smaller one. Now ask a friend to pick them up and compare their weight.

She will surprise you by reporting that the objects are not equal in physical weight. She will insist the larger object feels much lighter than the smaller one. She will continue to assert this incorrect fact even if you tell her that you want her to report absolute weight, not density (weight per unit volume).

Try it yourself. Remarkably, even though you know the objects weigh the same (after all, you constructed them), you will experience the larger object as feeling considerably lighter than the smaller one. As with many illusions, knowledge of reality is insufficient to correct or override the misperception. We neuroscientists say that perception is immune to intellectual correction—that it is "cognitively impenetrable."

Impervious Illusion

Furthermore, the visual information continuously overrides the feedback from muscle signals telling you that the weights are physically identical. The illusion is impervious not only to high-level conceptual knowledge that the objects weigh the same but also to "bottom up" signals from other sources, such as feedback from muscle receptors, telling you they weigh the same. You can repeat this experiment many times, but you will still experience the illusion.

Why does the effect occur? When you reach out for the bigger object, you *expect* it to weigh more (given the assumption that it is made of the same stuff) and you exert greater lifting force. Because it weighs the same as the smaller object (which you expected to weigh less), however, you actually experience it as being lighter, relative to the smaller object.

As an analogy, imagine you run into someone who looks unintelligent and you initially expect him to be so. If he then starts talking normally, he seems even brighter than average! It is as if you calibrate your judgment of a person's capabilities by the way he looks, and therefore your final "reading" of his true skills—based on his verbal output—is an overestimate.

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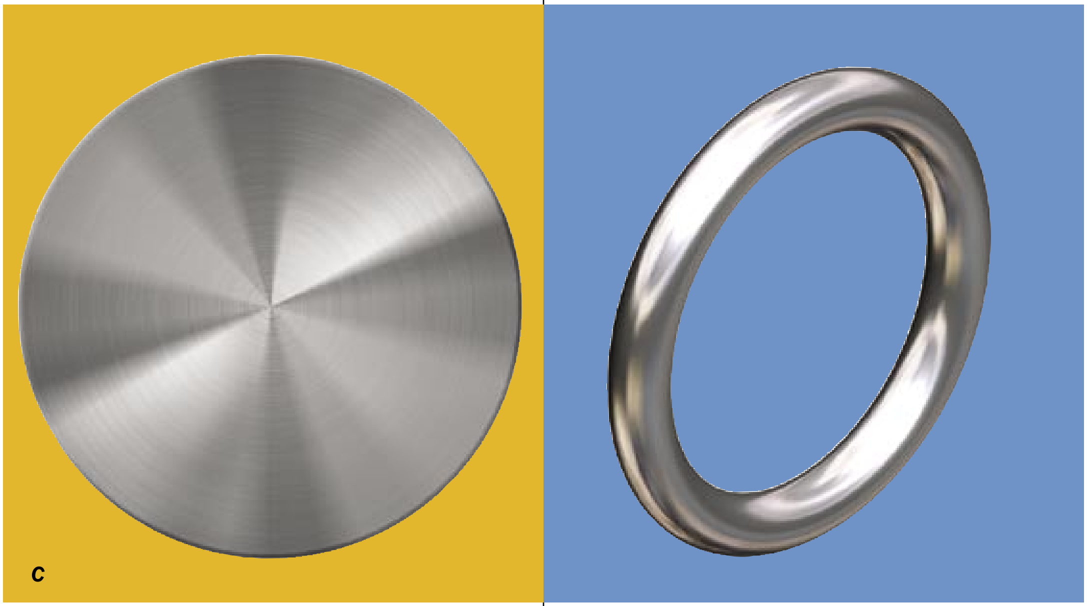

Insight from a Visual Trick

The size-weight illusion may be easier to understand if we couch it in terms of a more familiar visual illusion, the Ponzo, or railroad track, illusion (*b, on preceding page*). Two horizontal yellow bars are shown lying between two longer converging lines. Although the bars are identical, they are not seen as such: the top bar appears longer than the bottom bar. We can explain the illusion in terms of a visual effect called size constancy; if two objects of identical physical size are at different distances from a viewer, they are correctly perceived as being the same physical size, even though the images cast by them on the retina are different sizes. Quite simply, the brain "understands" there is a trade-off between retinal-image size and distance and, in effect, says, "That object's image is small because it is far; its actual size must be much bigger." To evaluate distance, the visual system uses various sources of information called cues, such as perspective, motion parallax, texture gradients and stereopsis. It then applies the appropriate correction for distance in order to judge true size.

But with the Ponzo illusion, the two horizontal bars are the same physical size on the retina. The converging lines provide a powerful trigger to read them—falsely in this case—as lying at different distances away (as though you are peering down a railroad track and see the railroad ties at increasing distance). Because your visual system "believes" the top bar is farther away, it infers that the top bar must really be larger than its size on the retina would indicate (relative to the other bar). You therefore perceive it as being larger.

To put it differently, size-constancy scaling enables you to perceive accurately the size of objects when you correctly perceive distance to those objects. In the Ponzo illusion, however, the misleading depth cue from the converging lines causes you to *misapply* the size-constancy algorithm so that the top bar is seen as being larger. Remarkably, the illusion overrides the visual signals from the retina informing the visual-size judgment centers in the brain that the two bars are exactly the same length. And because these mechanisms are all on autopilot, knowing that they are identical in size does not correct the illusion.

Brain Expectations

The situation with size and weight is analogous. (Read "actual weight signaled by muscles" for "actual retinal-image size.") Your brain says, "For the big object, I expect the muscle tension to be much greater in order to lift it." But because the muscle tension required is much lower than expected, the object is felt as unexpectedly light. This experience overrides your judgment of actual weight signaled by your muscles.

Remember that we said the size-weight judg-

STEVEN VAN SOLDT (*left*) AND STEVE O'CONNOR (*right*) *iStockphoto*

(We neuroscientists say that perception is immune to intellectual correction—that it is "**cognitively impenetrable**.")

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ment system is on autopilot. So we can ask how dumb or smart it is on its own. What if we now use as test objects a disk and a ring of the same outer diameter (*c*), and, as with the standard size-weight illusion, we adjust each of them so that they have the identical physical weight? Of course, as before, anyone picking up the ring will expect it to weigh much less because it looks as if it has less total volume. But you (the experimenter, aware of the size-weight illusion) would predict the reverse—that the hollow ring would be felt as being much heavier than the solid disk. In fact, in collaboration with Edward M. Hubbard, now at INSERM in France, we have found that a subject will experience *no* size-weight illusion; she will correctly judge the objects to be the same weight. The brain seems to merely utilize the *outer* diameter in making the judgment, rather than the overall volume. This experiment shows that the visual system is not sophisticated enough to understand that what is relevant is the total mass, not the outer diameter alone.

(What if we now use as test objects a disk and a ring of equal size and **identical weight**?)

In addition to size, the brain takes other factors into account for gauging anticipated weight. For example, if you pick up a plastic beer mug, it will feel unusually light. Again, this effect occurs because you expect it to be made of glass and, therefore, to be heavy. The original size-weight illusion may turn out to be largely hardwired (we do not know), but surely the beer mug–weight illusion must be learned. Our hominid ancestors were not exposed to mugs.

Felt vs. Real

What other insights can we gain from this illusion? Perhaps there is a practical application. Our house (which is very tall) has many stairs, and we expect to fatigue more quickly running up and down while carrying heavy loads than we would carrying light ones. Physical exertion increases when you are carrying greater weight; your heart beats faster, your blood pressure rises and you sweat. One typically assumes that this extra effort is because the muscles consume more glucose, and this information is fed back into the brain to generate the adaptive response of increased heart rate, blood pressure and sweating to allow for, and to anticipate, increased oxygen consumption resulting from hard work.

But is it conceivable that part of this preparation may also involve the *felt* weight of the object sending direct brain signals to the body? Imagine you run up and down a staircase with a large object and then compare the degree of tiredness you feel with that produced when carrying a much smaller object whose physical weight is the same as the larger item (and therefore *feels* heavier because of the illusion). Does the additional felt weight, as opposed to real weight, increase your sense of exertion or tiredness? In other words, is the fatigue determined by actual physical exertion? And would such imagined work actually increase your heart rate, blood pressure and sweating?

If so, the implication would be that merely feeling excess exertion causes the brain to send more signals to the heart to raise blood pressure, heart rate and tissue oxygenation. There have been sporadic reports that repeated imagined exercise can increase muscle strength, but precious little evidence. (We have started to explore this area in collaboration with neuroscientist Paul McGeoch of the University of California, San Diego.)

If it turns out that the felt weight determines how tired you feel, then next time you buy a suitcase for travel you should buy a large one; it will *feel* much lighter even if you stuff it with exactly the same amount of material! Quirks of perception have profound theoretical implications—but they can have practical consequences, too. **M**

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A Moving Experience

How the eyes can see movement where it does not exist

BY VILAYANUR S. RAMACHANDRAN AND
DIANE ROGERS-RAMACHANDRAN

THE GREAT RENAISSANCE SCHOLAR and artist Leonardo da Vinci left a legacy of paintings that combined beauty and aesthetic delight with unparalleled realism. He took great pride in his work but also recognized that canvas could never convey a sense of motion or of stereoscopic depth (which requires that two eyes simultaneously view slightly different pictures). He recognized clear limits to the realism he could portray.

Five hundred years later the limits of depicting depth in art remain true (except of course for "Magic Eye"–style prints, which, through multiple similar elements, basically interleave two views that the brain sorts out for each eye). But Leonardo could not have anticipated the Op Art movement of the 1960s, whose chief focus was to create the illusion of movement using static images. The art form grew wildly popular in the culture at large—the mother of one of us (Rogers-Ramachandran) even wallpapered an entire bathroom in a dizzying swirl of such black-and-white patterns.

The movement never really attained the status of sophisticated "high art" in the art world. Most vision scientists, on the other hand, found the images to be intriguing. How can stationary images give rise to motion?

Psychologist Akiyoshi Kitaoka of Ritsumeikan University in Kyoto, Japan, has developed a series of images called Rotating Snakes, which are particularly effective at producing illusory motion. As you gaze at *a,* you soon notice circles spinning in opposite directions. Viewing the image with your peripheral vision makes the motion appear more pronounced. Staring fixedly at the image may diminish the sense of movement, but changing your eye position briefly by looking to one side refreshes the effect. In this image, you see movement in the direction that follows the colored segments from black to blue to white to yellow to black. Yet the colors are merely added for aesthetic appeal and have no relevance to the effect. An achromatic version (*b, on page 54*) works equally well so long as it preserves the luminance profile of the colored version (in other words, as long as the relative reflected luminance of the different patches remains the same).

These delightful displays never fail to titillate adults and youngsters alike. But why does this illusion arise? We do not know for sure. What we do know is that the odd arrangements of luminance-based edges must somehow "artificially" activate motion-detecting neurons in the visual pathways. That is, the particular patterns of luminance and contrast fool the visual system into seeing motion where none exists. (Do not be alarmed if you don't see the movement, because some people with otherwise normal vision simply do not.)

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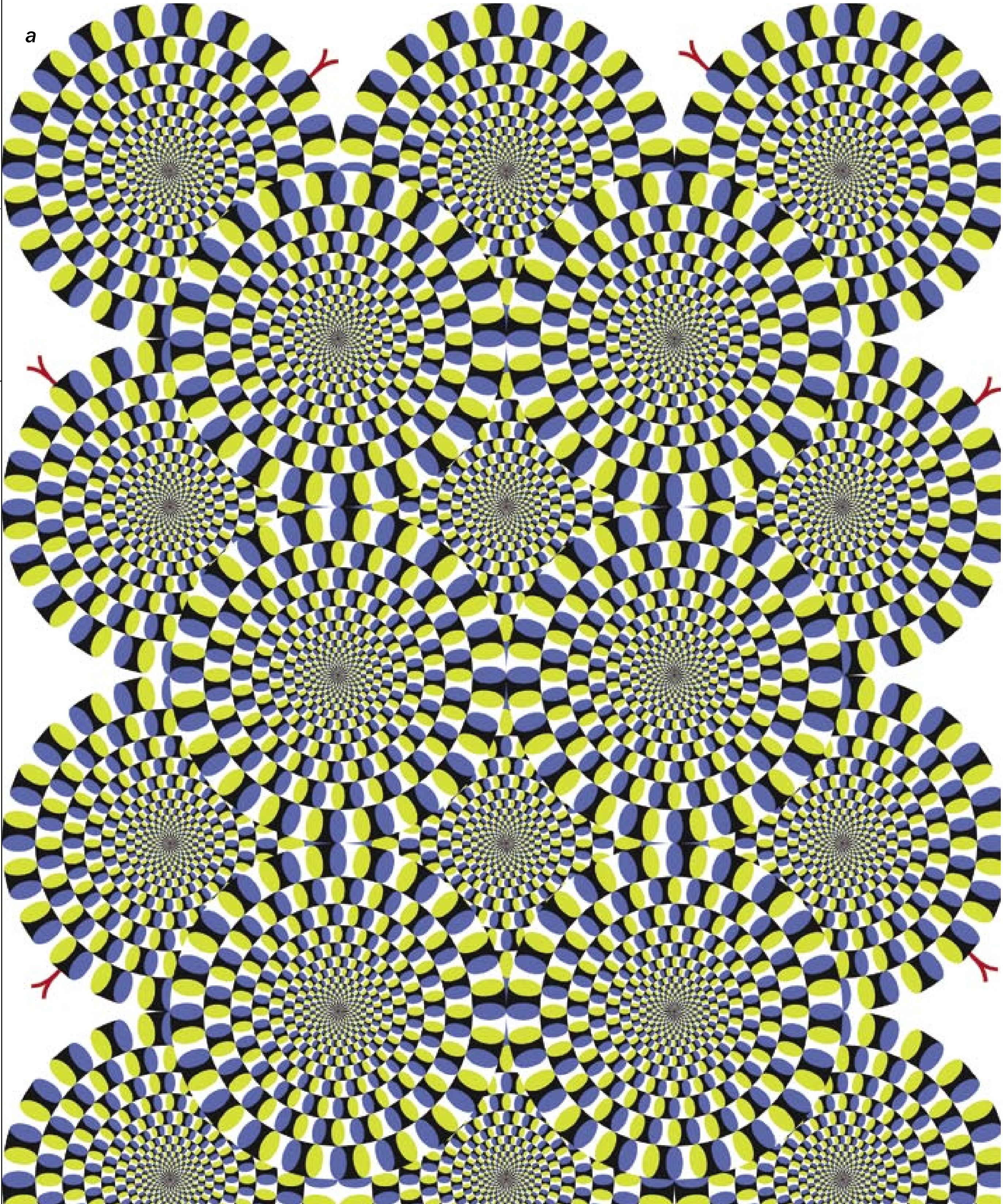
a



AKIYOSHI KITAOKA 2003

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How is a motion-detecting neuron in the brain **“wired up”** to detect the direction of motion?

To explore motion perception, scientists often employ test patterns of very short movies (two frames in length). Imagine in frame one a dense array of randomly placed black dots on a gray background. If, in frame two, you displace the entire array slightly to the right, you will see the patch of dots moving (jumping) to the right, because the change activates multiple motion-detecting neurons in your brain in parallel. This phenomenon is termed apparent motion, or phi. It is the basis for “motion” pictures in which no “real” motion exists, only successive still shots.

But if in the second frame you displace the dots to the right and also reverse the contrast of all the dots so that they are now white on gray (instead of black on gray), you will see motion in the opposite direction—an illusion discovered by psychologist Stuart M. Anstis, now at the University of California, San Diego. This effect is known as reversed phi, but we shall henceforth call it the Anstis-Reichardt effect, after the two vision scientists who first explored it. (The second person was Werner Reichardt, then at the Max Planck Institute for Biological Cybernetics in Tübingen, Germany.) We now know that this paradoxical reverse motion occurs because of certain peculiarities in the manner in which motion-detecting neurons, called Reichardt detectors, operate in our visual centers.

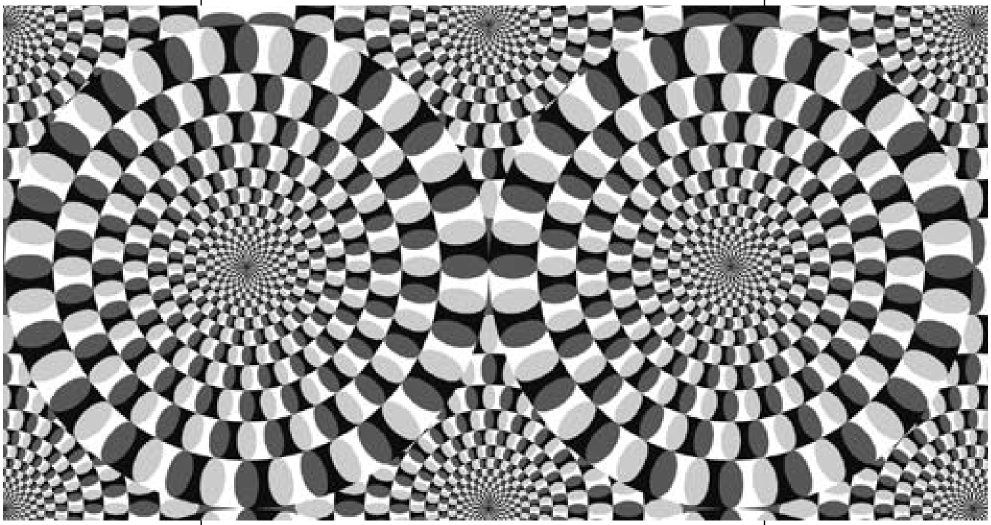
Wired for Motion

How is a motion-detecting neuron in the brain “wired up” to detect the direction of motion? Each such neuron or detector receives signals from its receptive field: a patch of retina (the light-sensing layer of tissue at the back of the eyes). When activated, a cluster of receptors in, say, the left side of the receptive field sends a signal to the motion detector, but the signal is too weak to activate the cell by itself. The adjacent cluster of retinal receptors on the right side of the receptive field also sends a signal to the same cell if stimulated—but, again, the signal is too weak on its own.

Now imagine that a “delay loop” is inserted between the first patch and the motion-detecting neuron but not between the second (right) patch and the same neuron. If the target moves rightward in the receptive field, the activity from the second patch of retina will arrive at the motion-detecting neuron at the same time as the delayed signal from the left patch. The two signals together will stimulate the neuron adequately for it to fire. Such an arrangement, akin to an AND gate, requires the circuit to include a delay loop and ensures direction as well as velocity specificity.

But this is only part of the story. In addition, we have to assume that for some reason we have yet to understand, stationary displays such as *a* and *b* produce differential activation within the motion receptive field, thereby resulting in spurious activation of motion neurons. The peculiar stepwise arrangement of edges—the variation in luminance and contrast—in each subregion of the image, combined with the fact that even when you fixate steadily your eyes are making ever so tiny movements, may be critical for artificially activating motion detectors. The net result is that your brain is fooled into seeing motion in a static display.

b



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Enhancing Motion

Finally, it is also known that patterns with a certain amount of regularity and repetitiveness will excite a large number of motion detectors in parallel, very much enhancing your subjective impression of motion. A small section of

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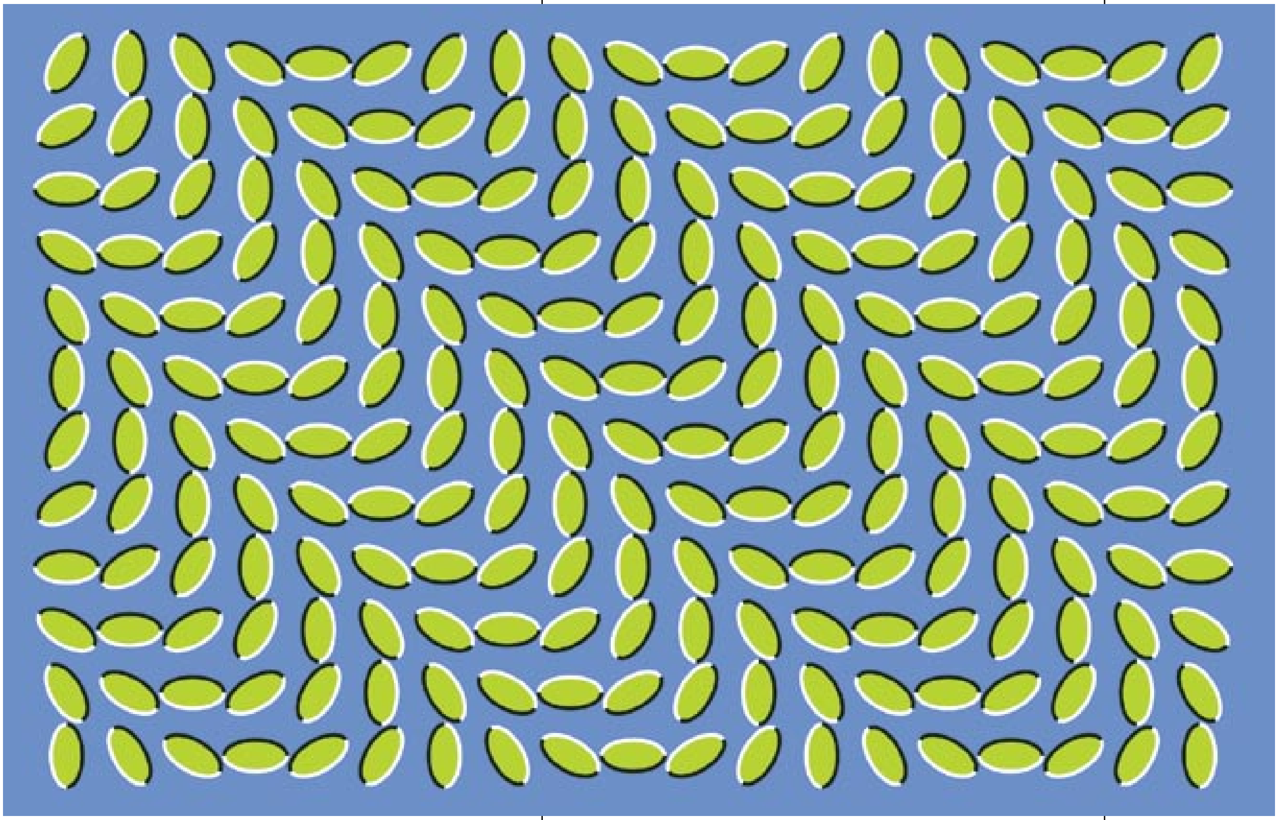

c

AKIYOSHI KITAOKA 2008

a display such as *c* is insufficient to generate noticeable motion, although the massively parallel signals from the highly repetitive patterns together produce strong illusory motion. Readers may want to conduct a few casual experiments themselves: Is the illusion any stronger with two eyes than with one? How many almondlike shapes or snakes are necessary to see them moving?

The manner in which stationary pictures work their magic to create tantalizing impressions of motion is not fully understood. We do know, however, that these stationary displays activate motion detectors in the brain. This idea has also been tested physiologically, by recording from individual neurons in two areas of the monkey brain: the primary visual cortex (V1), which receives signals from the retina (after being relayed through the thalamus), and the middle temporal area (MT) on the side of the brain, which is specialized for seeing motion. (Damage to the MT causes motion blindness, in which moving objects look like a succession of static objects—as if lit by a strobe light.)

The question is, Would static images like the rotating snakes "fool" motion-detecting neurons? The initial answer seems to be yes, as has been shown in a series of physiological experiments published in 2005 by Bevil R. Conway of Harvard Medical School and his colleagues.

Thus, by monitoring the activity of motion-detecting neurons in animals and simultaneously exploring human motion perception using cunningly contrived displays such as *a, b* and *c,* scientists are starting to understand the mechanisms in your brain that are specialized for seeing motion. From an evolutionary standpoint, this capability has been a valuable survival asset as an early warning system to attract your attention—whether to detect prey, predator or mate (all of which usually move, unlike stones and trees). Once again, illusion can be the path to understanding reality. **M**

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Ambiguities & Perception

What uncertainty tells us about the brain

BY VILAYANUR S. RAMACHANDRAN AND
DIANE ROGERS-RAMACHANDRAN

a

THE BRAIN ABHORS ambiguity, yet we are curiously attracted to it. Many famous visual illusions exploit ambiguity to titillate the senses. Resolving uncertainties creates a pleasant jolt in your brain, similar to the one you experience in the "eureka!" moment of solving a problem. Such observations led German physicist, psychologist and ophthalmologist Hermann von Helmholtz to point out that perception has a good deal in common with intellectual problem solving. More recently, the idea has been revived and championed eloquently by neuropsychologist Richard L. Gregory of the University of Bristol in England.

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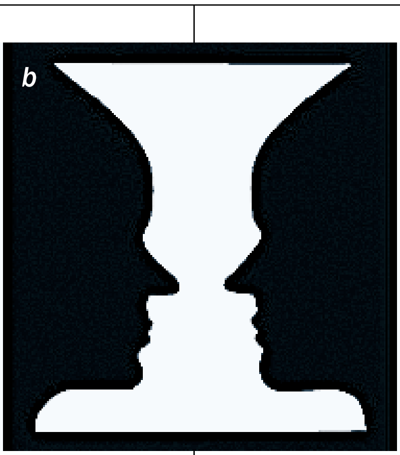
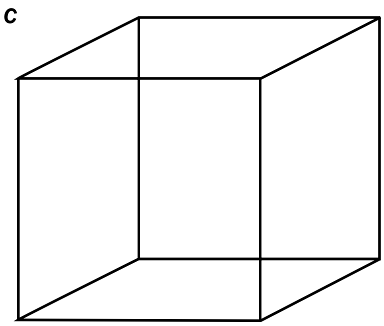
It is great fun when it flips spontaneously; it feels like an **amusing practical joke** has been played on you.





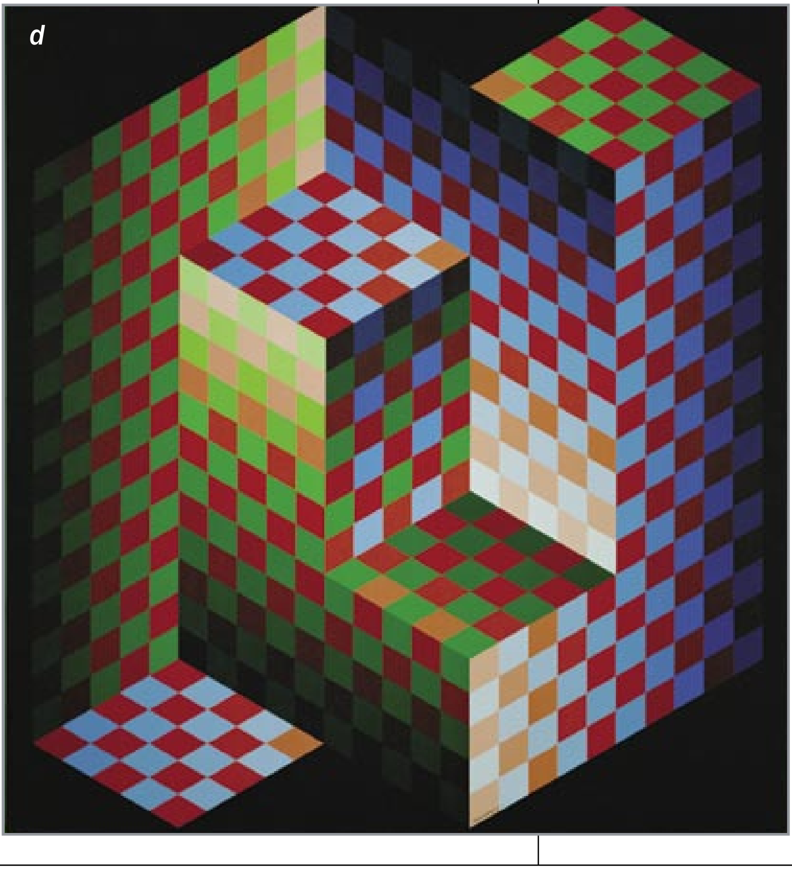
So-called bistable figures, such as the mother-in-law/wife (*a*) and faces/vase (*b*) illusions, are often touted in textbooks as the prime example of how top-down influences (preexisting knowledge or expectations) from higher brain centers—where such perceptual tokens as "old" and "young" are encoded—can influence perception. Laypeople often take this to mean you can see anything you want to see, but this is nonsense—although, ironically, this view contains more truth than most of our colleagues would allow.

Fun Flips

Consider the simple case of the Necker cube (*c* and variation in *d*). You can view this illusion in one of two ways—either pointing up or pointing down. With a little practice, you can flip between these alternate percepts at will (still, it is great fun when it flips spontaneously; it feels like an amusing practical joke has been played on you). In fact, the drawing is compatible not only with two interpretations, as is commonly believed; there is actually an infinite set of trapezoidal shapes that can produce exactly the same retinal image, yet the brain homes in on a cube without hesitation. Note that at any time, you see only one or the other. The visual system appears to struggle to determine which of two cubes the drawing represents, but it has already solved the much larger perceptual problem by rejecting trillions of other configurations that could give rise to the retinal pattern we call the Necker cube. Top-down attention and will, or intent, can only help you select between two percepts; you will not see any of the other possibilities no matter how hard you try.

Although the Necker cube is often used to illustrate the role of top-down influences, it, in fact, proves the very opposite—namely, that perception is generally immune to such influences. Indeed, if all perceptual computations mainly relied on top-down effects, they would be much too slow to help you in tasks related to survival and the propagation of your genes—escaping a predator, for example, or catching a meal or a mate.

It is important to recognize that ambiguity does not arise only in cleverly contrived displays such as on these two pages and in *e*, on the next page, in which shading could make a surface feature on Mars appear to be convex or concave. In truth, ambiguity is the rule rather than the exception in perception; it is usually resolved by other coexisting bottom-up (or sideways, if that is the right word) cues that exploit built-in statistical "knowledge" of the visual world. Such knowledge



SCIENTIFIC AMERICAN MIND (*b* and *c*); VICTOR VASARELY, © ART RESOURCE, NEW YORK, PHOTOGRAPH BY ERICH LESSING, © 2007 ARTISTS RIGHTS SOCIETY, NEW YORK/ADAGP, PARIS (*d*)

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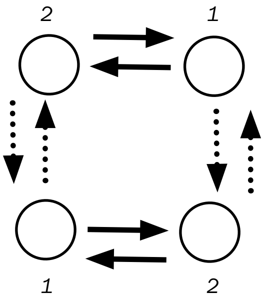
Mars crater or “island”? You can see it either way, but this bistable image is of the half-mile-wide Victoria Crater.

is wired into the neural circuitry of the visual system and deployed unconsciously to eliminate millions of false solutions. But the knowledge in question pertains to general properties of the world, not specific ones. The visual system has hardwired knowledge of surfaces, contours, depth, motion, illumination, and so on, but not of umbrellas, chairs or dalmatians.

f



Motion Control

Ambiguity also arises in motion perception. In *f,* we begin with two light spots flashed simultaneously on diagonally opposite corners of an imaginary square, shown at *1.* The lights are then switched off and replaced by spots appearing on the remaining two corners, at *2*. The two frames are then cycled continuously. In this display, which we call a bistable quartet, the spots can be seen as oscillating vertically (*dashed arrows*) or horizontally (*solid arrows*) but never as both simultaneously—another example of ambiguity. It takes greater effort, but as with the cube, you can intentionally flip between these alternate percepts.

We asked ourselves what would happen if you scattered several such bistable-quartet stimuli across a computer screen. Would they all flip together when you mentally flipped one? Or, given that any one of them has a 50 percent chance of being vertical or horizontal, would each flip separately? That is, is the resolution of ambiguity global (all the quartets look the same), or does the process occur piecemeal for different parts of the visual field?

The answer is clear: they all flip together. There must be global fieldlike effects in the resolution of ambiguity. You might want to try experimenting with this on your computer. You could also ask, Does the same rule apply for the mother-in-law/wife illusion? How about the Necker cube? It is remarkable how much you can learn about perception using such simple

NASA/JPL/UNIVERSITY OF ARIZONA (e); SCIENTIFIC AMERICAN MIND (f)

(In truth, **ambiguity is the rule** rather than the exception in perception.)

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It is almost as though perception involves selecting **the one hallucination** that best matches sensory input.

displays; it is what makes the field so seductive.

We must be careful not to say that top-down influences play no role at all. In some of the figures, you can get stuck in one interpretation but can switch once you hear, verbally, that there is an alternative interpretation. It is as if your visual system—tapping into high-level memory—"projects" a template (for example, an old or young face) onto the fragments to facilitate their perception. One could argue that the recognition of *objects* can benefit from top-down processes that tap into attentional selection and memory. In contrast, seeing contours, surfaces, motion and depth is mainly from the bottom up (you can "see" all the surfaces and corners of a cube, even reach out and grab it physically, and yet not know or recognize it as a cube). In fact, we have both had the experience of peering at neurons all day through a microscope and then the next day "hallucinating" neurons everywhere: in trees, leaves and clouds. The extreme example of this effect is seen in patients who become completely blind and start hallucinating elves, circus animals and other objects—called the Charles Bonnet syndrome. In these individuals, only top-down inputs contribute to perception—the bottom-up processes, missing because they are blind (from macular degeneration or cataracts), can no longer limit their hallucinations. It is almost as though we are all hallucinating all the time and what we call object perception merely involves *selecting* the one hallucination that best matches the current sensory input, however fragmentary. Vision, in short, is controlled hallucination.

But doesn't this statement contradict what we said earlier about vision being largely bottom-up? The answer to this riddle is "vision" is not a single process; perception of object*ness*—its outline, surface depth, and so on, as when you see a cube as cuboid—is largely bottom-up, whereas higher-level *identification* and categorization of objects into neurons or umbrellas do indeed benefit enormously from top-down, memory-based influences.

How and What

Physiology also supports this distinction. Signals from the eyeballs are initially processed in the primary visual cortex at the back of the brain and then diverge into two visual pathways: the "how" pathway in the parietal lobe of the brain and the "what" pathway, linked to memories, in the temporal lobes. The former is concerned with spatial vision and navigation—reaching out to grab something, avoiding obstacles and pits, dodging missiles, and so on, none of which requires that you identify the object in question. The temporal lobes, on the other hand, enable you to recognize what an object actually is (pig, woman, table), and this process probably benefits partially from top-down, memory-based effects. There are hybrid cases in which they overlap. For example, with the faces/vase illusion there is a bias to get stuck seeing the faces. But you can switch to seeing the vase without explicitly being told "look for the vase," if you are instead instructed to attend to the white region and see it as a foreground figure rather than as background.

Can the perception of ambiguous, bistable figures be biased in any way if they are preceded with other nonambiguous figures—a technique that is called priming? Priming has been explored extensively in linguistics (for instance, reading "foot" preceded by "leg" evokes the body part, but reading "foot" preceded by "inches" might suggest a ruler). Intriguingly, such priming can occur even if the first word appears too briefly to be seen consciously. Whether perception can be similarly primed has not been carefully studied. You might try it on friends.

Finally, as we note in one of our other articles, you can construct displays that are always ambiguous, such as the "devil's pitchfork" or the "perpetual staircase." Such paradoxical figures evoke wonder, delight and frustration at the same time—a microcosm of life itself. **M**

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Touching Illusions

Startling deceptions demonstrate how tactile information is processed in the brain

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

HUMANS, LIKE ALL PRIMATES, are highly visual creatures. Most of the back of our brain is devoted to visual processing, and half of the cortex is involved with sight. In addition, when visual inputs conflict with clues from other senses, vision tends to dominate. This supremacy is why, for example, ventriloquists are so compelling. We see the dummy talking, and we are fooled into hearing the voice coming from it—a case of what scientists call "visual capture." (With eyes closed, however, we can correctly localize the dummy voice to the ventriloquist.)

If information from vision and touch are incompatible, visual dominance may cause us to actually feel things differently than if we relied only on touch (without looking).

Curved Touch

In a simple but striking demonstration by James Gibson in the 1930s, a subject is first presented with a short, straight metal rod and asked to feel it with his eyes closed. Of course, he correctly feels it is straight. He then lets go of the rod and is asked to open his eyes and look down at it. Unbeknownst to him, it is the same rod but viewed through a wedge prism, which causes the rod to appear curved rather than straight. Not surprisingly, he now reports seeing a curved rod. But what happens when he reaches out and touches the rod while looking at it? Subjects reported nothing unusual: they noticed no rivalry, instability or averaging between the senses; the

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rod that they saw as curved they simply also felt as curved.

In short, vision redirects the tactile perception so that no conflict is experienced. Similarly, perception researcher Irvin Rock, then at Yeshiva University, showed in the 1960s that when shape or size perception for single simple objects was made to conflict between the senses (by the introduction of distorting lenses), perception conveyed by active touch was modified to conform to visual perception.

Yet another example of vision influencing touch occurs in patients with phantom limbs. After amputation of an arm, the vast majority of patients continue to feel vividly the presence of the missing arm, a phenomenon termed phantom limb in the late 1800s by physician and author Silas Weir Mitchell. Many people report that their phantom limb is frozen, paralyzed in a constant or fixed position, and that this experience is sometimes painful.

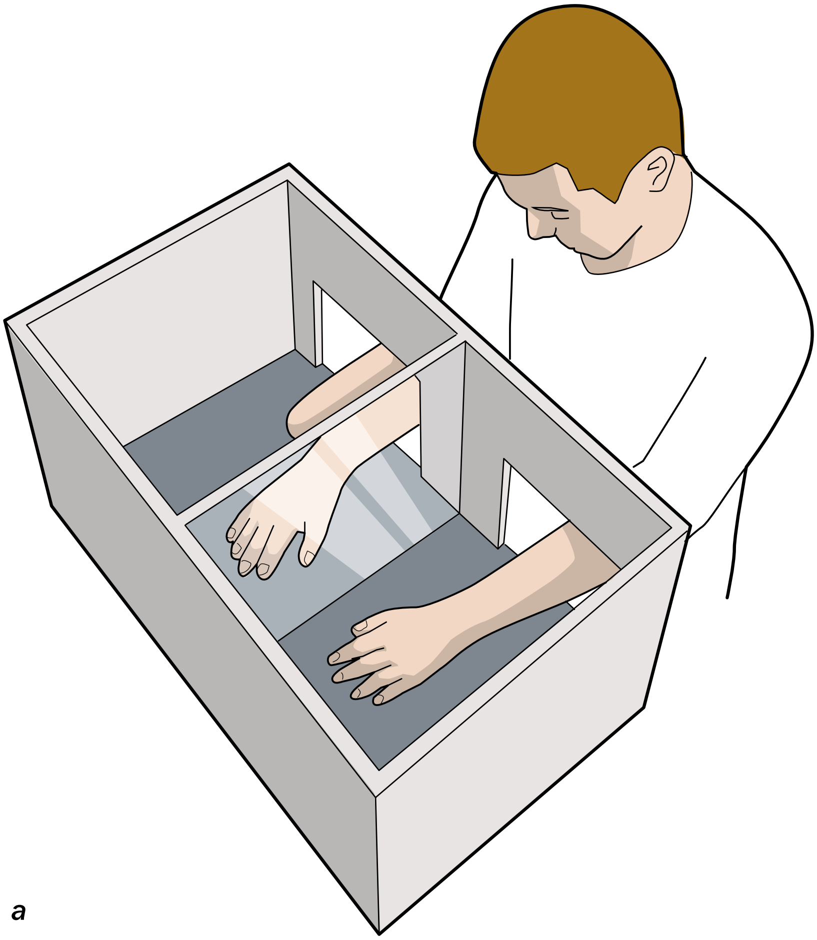
(When he looked at the reflection of his normal hand in the mirror, he felt the phantom being **visually resurrected**.)

We wondered whether touch sensations in the phantom arm could be influenced by visual input. We positioned a mirror on the table in front of a patient, along his midline, and asked him to position his intact arm and stump/phantom hand symmetrically on either side of the mirror (*a*). When he looked at the reflection of his normal hand in the mirror, he experienced the phantom being visually resurrected. Remarkably, if the patient moved his normal hand while looking at its reflection in the mirror, the previously frozen phantom seemed to become animated; he not only saw the hand but also *felt* it move. In some cases, this sensation seemed to alleviate the pain associated with the phantom.

The visual-capture effect also indicates our need for a single, sensible narrative of the world. That is, we (our brains) tend to reinterpret or discard some information, even when doing so may produce errors or illusions (as with the ventriloquist). This influence of vision has resulted in a kind of vision chauvinism in research, leading scientists to pay less attention to the other senses.

Touched in the Head?

The neural basis of these intermodality illusions has not been studied in detail. Recent work by Krish Sathian of Emory University and Alvaro Pascual-Leone of Harvard University suggests that somatosensory signals (those having to do with touch) may be seen in the primary visual cortex under certain circumstances—for example, in blind Braille readers. The tactile signals processed in the somatosensory centers of the brain may actually send feedback all the way to the very early stages of visual processing instead of being merely combined at some higher level. Studies on visual capture suggest that the converse may also be true—namely, that visual input may project to what is traditionally considered primary somatosensory cortex. These interactions between the senses, in addition to educating us about brain mechanisms for information processing, may also provide a useful tool in rehabilitation for neurological disorders.



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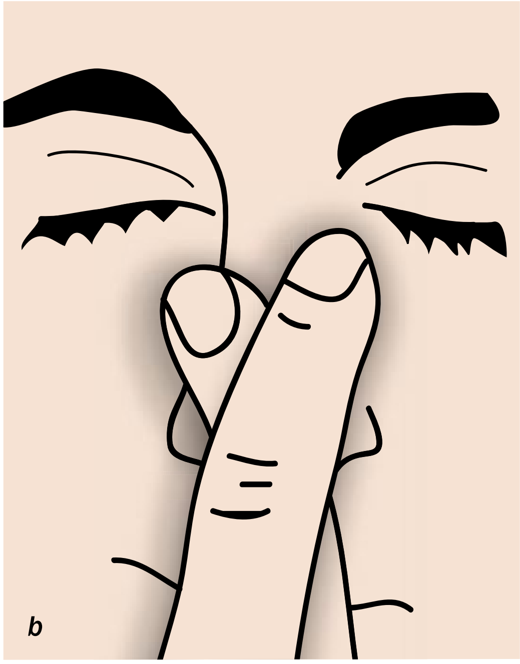

So the brain interprets the tactile experience as "I must have **two noses**."

We would like to consider here some tactile illusions that bear a striking similarity to visual illusions. Try the following experiment. Place two coins in your freezer till they are chilled (maybe 20 minutes). Remove them and place them on a table flanking a similar coin that has been kept at room temperature, so that the three coins now form a row. Now place the tips of the index and ring finger of one hand on the two cold coins and the middle finger on the middle coin. Amazingly, the middle finger feels equally cold. Perhaps the temperature-sensing pathways of the brain simply do not have the resolving power to discern two discrete sources. Yet the middle finger does not feel cold unless it is in contact with a neutral coin; if there are no tactile sensations emerging from it, the brain is reluctant to "fill in," or ascribe cold to, this region.

But how clever is this filling-in mechanism? What if the middle finger pressed against velvet or sandpaper rather than a coin? Does it have to be similar to what is being touched by the index and ring fingers? If so, how similar? And does this interpolation of cold occur early in sensory processing—for example, in the spinal cord or thalamus (the "gateway" for sensory inputs to the brain)? Or does it take place "higher up," in later processing stages in the brain?

One way to find out is to see what happens if you simply bend the middle finger upward and then put the middle finger *of the other hand* in its place. The illusion now disappears, suggesting that the filling in occurs at an early stage of tactile information processing, not at the higher level of space representation in the brain. (We know this occurs at an early stage because the sensory signals from two hands project to two separate hemispheres in the brain; information from them can be compared only at a relatively late stage of processing.)

What if the two outer coins were very hot and icy cold, respectively; would the middle coin take on the average temperature, or would it alternate between the two? What about an intermediate case? Say you crossed the index finger under the middle digit so that you formed a row with the index between the ring and middle fingers, the middle and ring fingers resting on the cold coins. Would the index finger now feel cold because of its intermediate location in space?

The reader might wish to dream up his or her own experiments: that is what makes the study of perception so much fun. You do not need to be an expert to do experiments that have far-reaching implications. If you attempt such an experiment, we would love to hear from you.

Let us try something different. Cross your left middle finger over your left index finger, making a small V at the end. Now close your eyes and place the V formed by the fingers on your nose (*b*). Astonishingly, many people who perform this "Aristotle illusion" maneuver report a distinct feeling of having two noses! How is this effect possible?

One way to interpret the phenomenon is to realize that given the normal, habitual spatial arrangement of the fingers, the only way the *left* side of your left middle finger will be stimulated simultaneously with the *right* side of your left index finger is when they are touching two objects. So the brain interprets the tactile experience as "I must have two noses." According to psychologist Stuart M. Anstis of the University of California, San Diego, the nose is not the only appendage in which perceptual doubling can be produced.

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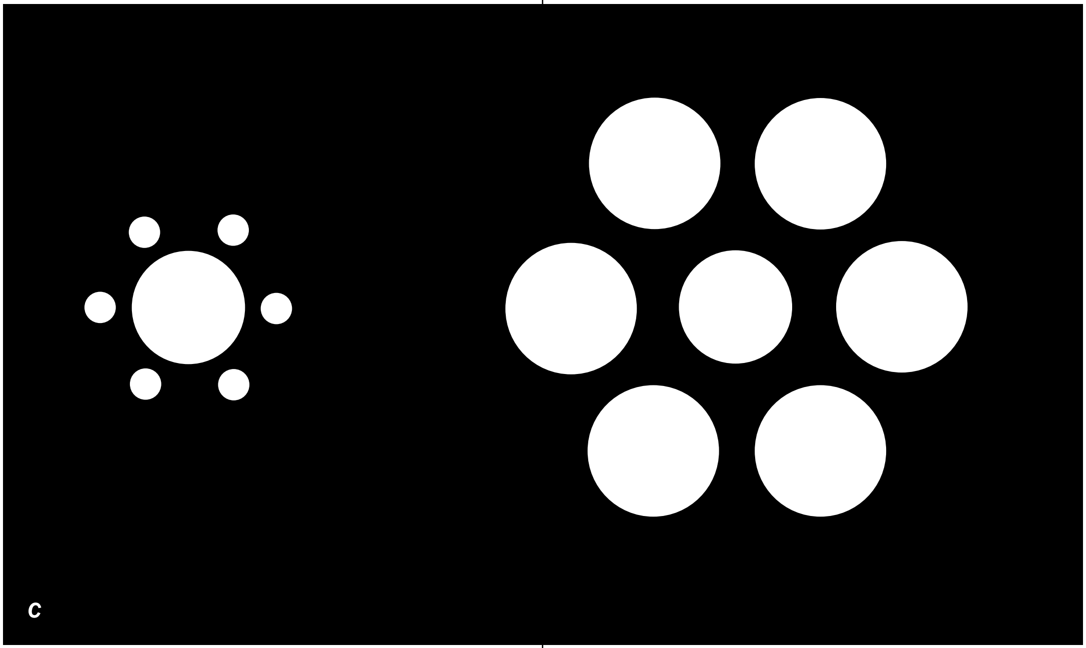
(The middle disk at left is the **same size** as the one at right, but the left looks larger because it is surrounded by small disks.)



Last, look at the visual illusion above (*c*). Believe it or not, the middle disk in the left panel of circles is the same size as the one on the right, but the left looks larger because it is surrounded by small disks. This optical trick is a powerful demonstration of the contextual nature of perception. (The skeptical reader may make a cardboard occluder with two holes to directly compare the two.) Is there an equivalent of this effect for touch?

Jelly or Velvet?

The following demonstration may be a related effect. Get some coarse chicken-cage mesh, preferably mounted in a wooden frame. Then hold the mesh between the palms of your hands. Nothing peculiar so far. Now start rubbing your palms against each other with the wire between them. Remarkably, your palms will feel like jelly or velvet. The cause of this striking illusion has yet to be determined. One possibility is that it has something to do with sensing and signaling the contrast between the sharp wire and the "neutral" touch sensations on the skin—the opposite of sharp being velvety or jellylike. A version of this illusion can be found in many science museums.

You can even get your hands to "float"—a well-known trick, sometimes called the Kohnstamm effect, reintroduced to us by our son, Jayakrishnan Ramachandran. Stand in the middle of an open doorway and use your arms to apply outward pressure on the two sides as if you were pushing them away from your body. After about 40 seconds, suddenly let go and relax, stand normally and just let your arms hang by your sides. If you are like most of us, your arms will involuntarily rise up as if pulled by two invisible helium balloons. The reason? When you apply continuous outward force, your brain gets used to this as the "neutral state"—so that when the pressure suddenly disappears, your arms drift outward.

This simple demonstration shows that the sensory areas of your brain are not the passive recipients of signals from your sense organs. Instead we should think of them as being in a state of dynamic equilibrium with the outside world, an equilibrium point that is constantly shifting in response to a changing environment. **M**

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The Phantom Hand

The feeling of being touched on a fake hand illuminates how the brain makes assumptions about the world

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

IN ONE VERY STRIKING ILLUSION, you can become convinced that you can feel a rubber hand being touched just as if it were your own. To find out for yourself, ask a friend to sit across from you at a small table. Use blocks or coffee cups to prop up a vertical partition on the table, as shown in the illustration on the opposite page. A flat piece of cardboard will do. Rest your right hand behind the partition so you cannot see it. Then, in view beside the partition, place a plastic right hand—the kind you can buy from a novelty shop or a party store around Halloween. Ask your assistant to repeatedly tap and stroke your concealed right hand in a random sequence. Tap, tap, tap, stroke, tap, stroke, stroke. At the same time, while you watch, he must also tap and stroke the visible dummy in *perfect synchrony.*

PHOTODISC/GETTY IMAGES

If he continues the procedure for about 20 or 30 seconds, something quite spooky will happen: you will have an uncanny feeling that you are actually being stroked on the fake hand. The sensations will seem to emerge directly from the plastic rather than from your actual hidden flesh.

Why does this happen? Matthew Botvinick and Jonathan Cohen, then at the University of Pittsburgh and Carnegie Mellon University, who reported the so-called rubber-hand illusion in 1998, have suggested that the physical similarity between your real hand and the model is sufficient to fool the brain into attributing the touch sensations to the phony fingers. They believe this illusion is strong enough to overcome the minor discrepancy of the position of your real hand signaled by your body's joint and muscle receptors versus the site of the plastic hand registered by your eyes.

But that is not the whole story. At about the same time that Botvinick and Cohen observed the rubber-hand effect, we and our colleagues William Hirstein and Kathleen Carrie Armel of the University of California, San Diego, discovered a further twist: the object your helper touches does not even need to resemble your palm and digits. He can produce the same effect if he just pets the table. Try the same experiment, but this time have your acquaintance rub and tap the surface in front of you while making matching movements on your real, concealed hand. (If using the table alone does not work, practice on a dummy hand first before graduating to furniture.) You may have to be patient, but you will eventually start feeling touch sensations emerge from the wood surface before you. The illusion is even better if you have a rubber sheet covering the tabletop to mimic the tactile qualities of skin.

Assimilating the Hand

This illusion is extraordinarily compelling the first time you encounter it. But how can scientists be certain that you have now perceptually assimilated the table into your body image (rather than merely assigning ownership to it the same way you own a house)? In 2003 Armel and one of us (Ramachandran) learned that once the illusion has developed, if you "threaten" the table or dummy by aiming a blow at it, the person winces

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(You will have the uncanny feeling that you are actually being stroked **on a fake plastic hand**.)

and even starts sweating, as she would if she were facing a real threat to her own body. We demonstrated this reaction objectively by measuring a sudden decrease in electrical skin resistance caused by perspiration—the same galvanic skin response used in lie detector tests. It is as if the table becomes incorporated into a person's own body image so that it is hooked up to emotional centers in the brain; the subject perceives a threat to the table as a threat to herself.

These illusions demonstrate two important principles underlying perception. First, perception is based largely on extracting statistical correlations from sensory inputs. As you feel your unseen hand being tapped and stroked and see the table or dummy hand being touched the same way, your brain in effect asks itself, "What is the likelihood that these two sets of random sequences [on the hidden hand and on the visible table or dummy] could be identical simply by chance? Nil. Therefore, the other person must be touching *me*."

Second, the mental mechanisms that extract these correlations are based on automatic processes that are relatively impervious to higher-level intellect. With information gathered by sensory systems, the brain makes its judgments automatically; they do not involve conscious cogitation. Even a lifetime of experience that a table is not part of your body is abandoned in light of the perceptual decision that it is. Your "knowing" that it cannot be so does not negate the illusion (just as some people cling to superstitions even while recognizing their absurdity).

Question Assumptions

The experiment was inspired by earlier work we had done with patients who had phantom limbs. After a person loses an arm from injury or disease, he may continue to sense its presence vividly. Often the phantom seems to be frozen in a painfully awkward position. We asked a patient to put his phantom left arm on the left side of a mirror propped vertically on a table in front of him. He then put his intact right arm on the right side, so its reflection was seen in the mirror superimposed on the phantom, creating the visual illusion of having restored the missing arm. If the patient now moved his right arm, he saw his phantom move. Remarkably, this "animated" the phantom so it was felt to move as well—sometimes relieving the cramp. Even more surprising: in some cases, if the physician touched the real hand, the patient not only saw his phantom being touched but experienced the touch as well. Again the brain regards this combination of sensory impressions as unlikely to be a coincidence; therefore, it quite literally feels the touch emerging from the phantom hand.

If an assistant taps and strokes your hidden real hand and a visible fake hand in synchrony, the sensations will seem to come from the plastic.

Consider what these illusions imply. All of us go through life making certain assumptions about our existence. "My name has always been Joe," someone might think. "I was born in San Diego," and so on. All such beliefs can be called into question at one time or another for various reasons. But one premise that seems to be beyond question is that you are anchored in your body. Yet given a few seconds of the right kind of stimulation, even this axiomatic foundation of your being is temporarily forsaken, as the table next to you seems to become part of you. As Shakespeare aptly put it, we are truly "such stuff as dreams are made on." **M**

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It’s All Done with Mirrors

Reflections on the familiar and yet deeply enigmatic nature of the looking glass

ERIK VON WEBER *Getty Images*

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

Mirrors have held a peculiar fascination for people ever since one of our early hominid ancestors looked at her reflection in a pool and noticed an uncanny correlation between her own muscle movements—sensed internally—and the visual feedback. Even more mysterious—and perhaps not unrelated—is our ability to “reflect” on ourselves as the first introspective primates. This ability displays itself in ways as different as the mythical Narcissus looking at his reflection in a lake to Internet pioneer Jaron Lanier’s invention of virtual reality to transport you outside your own body.

Intriguingly, neuroscientists have discovered a new class of brain cells called mirror neurons that let you “adopt another’s point of view,” both literally and metaphorically (“I see what you mean”). Perhaps such neurons even allow you to look at yourself from another’s vantage point, so you become “self conscious” of what you are doing or wearing or even of who you are. It is as if the brain were peering into its own internal mirror.

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We take all these abilities for granted, but about a decade ago Eric L. Altschuler and Steve Hillyer, both then at the University of California, San Diego, and one of us (Ramachandran) described a new neurological syndrome called mirror agnosia in which a patient with a small right hemisphere stroke cannot tell that a mirror reflection is not a physical object. Amazingly, these patients will repeatedly try to reach for, pick up or grab the reflection (which they claim is a real item) located in the mirror. Mentally, such patients are otherwise perfectly normal; they continue to have abstract knowledge of mirrors and the nature of their optics. Such patients give us a glimpse into the surreal no-man's-land between reality and illusion, and they help us realize how tenuous our hold on reality is. Mirrors are familiar yet deeply enigmatic.

It will feel as if you are looking at **your real left hand**, even though you are not.

Mirror Magic (No Smoke)

You can play with mirrors to explore their magic. Begin by constructing the mirror box [*see illustration on this page*]. We initially designed this box to treat patients with phantom limbs and stroke (more on this therapy later), but you can have fun experimenting on yourself and your friends. Alternatively, for a quick start, use the swinging, mirror-covered door of a bathroom medicine cabinet or simply prop up a mirror using books or bricks.

Normally our senses, such as vision and proprioception (muscle and joint sense), are in reasonably good concordance. The messages from different senses converge in the angular gyrus and supramarginal gyrus in the parietal lobe, where you construct your "body image." These two gyri were originally fused as one gyrus (the inferior parietal lobule) in apes. Given the importance of intermodality (cross-sensory) interactions, however, in humans the lobule became enormous and split into two. From such humble beginnings, we evolved into a hairless ape capable of vast technological sophistication—an ape that not only can reach for peanuts but also can reach for the stars.

Let us return to the mirror box. Start with the reflective side facing rightward. Put your left hand on the left side of the mirror, so it is hidden from view, and place your right hand on the right side so that it exactly mimics the posture and location of the hidden left hand. Now look into the mirror at the reflection of your right hand; it will feel as if you are looking at your real left hand, even though you are not.

While looking in the mirror, begin to move both hands synchronously—in circles or by opening and closing your fingers, for example—so that the reflected and hidden hand are in lockstep. Now, here is the clever bit: stop moving just the left (hidden) hand as you continue moving the right hand. Move your right hand *slowly;* rotate or wave it about and wiggle your fingers but keep your left hand still. For a moment you will now *see* the left hand moving but *feel* it remaining still. Most people experience a jolt of surprise; the brain abhors contradictions.

Even more discombobulating: move your hidden left hand while keeping the right one still. This time you get an even bigger jolt when vision and proprioception "clash." Next, while still looking in the mirror, have a friend stroke your right hand with his finger. You will see your "virtual left hand" being stroked—but your actual left hand, behind the mirror, is not being touched.

The mirror box can create the illusion of a restored limb, helping to treat phantom pain.

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BLAISE HAYWARD *Getty Images*

With this peculiar sensory conflict, your left hand may seem to be anesthetized—because you see, but do not feel, the touch.

Spooky Hand

Another quite different type of incongruence, which we have observed with Altschuler, occurs if you look at your hand through a minimizing—that is, concave—lens (novelty or science museum shops are good places to purchase inexpensive plastic sheets of these lenses). The hand, when viewed through this type of lens, looks much longer and smaller than it should be, which feels odd. But if you now move your hand and wiggle your fingers, the sensation becomes even more paradoxical and spooky. You feel that the hand does not even *belong* to you; you have a temporary out-of-body experience, as if you were manipulating some other person's hand!

The same happens if you look down through the lens at your own feet as you walk. They feel long, skinny and rubbery, as if they were detached from you or you were a giant inspecting his own feet. Even our sense of "willing" a hand or leg to move or of being anchored in our body, it turns out, is built on shaky foundations.

Such parlor games are amusing, but they are also of considerable interest both theoretically and clinically. When an arm is amputated, a patient continues to feel its presence vividly, a syndrome called phantom limb. Oddly enough, many patients believe that they can move their phantom freely ("it answers the phone," "it waves goodbye," and so on).

How does this illusory feeling happen? When you move your hand, motor command centers in the front of the brain send a signal out, down the spinal cord to the muscles on the opposite side of the body. At the same time, a copy of the command (like an e-mail CC) goes to the parietal lobe. As we already noted, this area gets both visual and proprioceptive (body-position sense) feedback that can be compared with the motor command, thereby forming a feedback loop to ensure accuracy. If the arm is lost, there is no proprioceptive feedback, but the copy of the command is nonetheless sent to the parietal lobe and sensed by the patient's brain as movements of the phantom.

For reasons we do not fully understand, some patients are unable to move their phantom—they say it is "paralyzed." And often they report that the phantom limb is painful or frozen in a peculiar, unnatural posture.

How can a phantom be paralyzed? It turns out that many of these patients have had a preexisting injury to the nerves that exit the spinal cord and innervate arm muscles, such that the arm was intact but paralyzed. During that phase, every time the premotor cortex in the front of the brain sent a command to move the arm, it received visual and proprioceptive feedback say-

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(Would it be possible to **"unparalyze" a phantom** by giving the patient visual feedback?)

ing, "No, it is *not* moving." Eventually this message gets stamped into the brain as a form of "learned paralysis," a kind of memory that is carried over into the phantom.

The Mirror Cure

Would it be possible to "unparalyze" a phantom by giving a patient visual feedback every time he attempted to move his phantom? Would this strategy provide pain relief? In a 1996 paper we described the technique of using the mirror box. The patient "puts" his clenched, paralyzed phantom on one side and his normal hand on the other, then looks in the mirror while performing mirror-symmetric movements (opening and closing the fist, clapping, and so on). The mirror box gives the visual illusion that the phantom has been resurrected and is actually moving in perfect synchrony with the brain's commands.

Incredibly, the phantom also *feels* as if it is moving, and in many patients the cramping sensation goes away for the first time in years. In some patients the phantom vanishes completely and permanently, along with the pain; it is the brain's way of dealing with sensory conflict. (We suggested in that same paper that such procedures may also be helpful for other conditions such as stroke or focal dystonia, a neurological condition that causes involuntary muscle contractions.) These effects on phantoms have now been confirmed in clinical trials on patients and elegantly explored with brain-imaging studies by neuropsychologist Herta Flor of the University of Heidelberg's Central Institute of Mental Health in Mannheim, Germany.

Phantom pain is bad enough, but it is uncommon compared with an equally disabling disorder, stroke, which is a leading cause of disability in the U.S. Damage to the fibers that go from the cortex to the spinal cord caused by a vascular lesion can lead to complete paralysis of the opposite side of the body. We wondered if there is a component of learned paralysis in stroke; perhaps the initial swelling and inflammation cause a temporary interruption of signal transmission. This interruption, combined with visual evidence of paralysis, leads to a form of learned paralysis in addition to the real paralysis caused by nerve damage.

In 1999, in collaboration with Altschuler, we turned to the mirror box to treat stroke paralysis. Testing nine patients, we found striking recovery of function, which was remarkable given that stroke paralysis is usually considered incurable. We postulated that multimodal cells (cells hooked up directly to vision, proprioception and motor output—similar to mirror neurons) that had been rendered dormant by the stroke were being revived by the illusory visual feedback from the mirror. This result, too, has been replicated in controlled trials by two independent groups led by psychologist Jennifer A. Stevens, then at Northwestern University and the Rehabilitation Institute of Chicago, and neurologist Christian Dohle of Düsseldorf University Hospital and the Godeshöhe Neurological Rehabilitation Center in Germany.

We also know that even though most motor fibers from the cortex cross over to the opposite side of the body (that is, contralateral), some fibers go directly to the same side (ipsilateral). It has long been a puzzle why intact fibers cannot "substitute" for the damaged ones if there is a stroke. Perhaps they are being "recruited" by the use of the mirror. If so, we may conclude that mirrors (and smoke) are not only useful to magicians. They also can reveal deep insights into how the brain integrates different sensory inputs. Equally important, visual feedback—whether from mirrors or virtual reality—can even be clinically useful in promoting recovery of function from neurological deficits that have long been considered incurable. **M**

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Paradoxical Perceptions

How does the brain sort out contradictory images?

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

HISTORICAL PICTURE ARCHIVE *Corbis*

PARADOXES—IN WHICH THE SAME information may lead to two contradictory conclusions—give us pleasure and torment at the same time. They are a source of endless fascination and frustration, whether they involve philosophy (consider Russell's paradox, "This statement is false"), science—or perception. The Nobel Prize winner Peter Medawar once said that such puzzles have the same effect on a scientist or philosopher as the smell of burning rubber on an engineer: they create an irresistible urge to find the cause. As neuroscientists who study perception, we feel compelled to study the nature of visual paradoxes.

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Let us take the simplest case. If different sources of information are not consistent with one another, what happens? Typically the brain will heed the one that is statistically more reliable and simply ignore the other source. For example, if you view the inside of a hollow mask from a distance, you will see the face as normal—that is, convex—even though your stereovision correctly signals that the mask is actually a hollow, concave face. In this case, your brain's cumulative experience with convex faces overrides and vetoes perception of the unusual occurrence of a hollow face.

> If different sources of information are **not consistent** with one another, what happens?

Most tantalizing are the situations in which perception contradicts logic, leading to "impossible figures." British painter and printmaker William Hogarth created perhaps the earliest such figure in the 18th century (*a*). A brief view of this image suggests nothing abnormal. Yet closer inspection reveals that it is logically impossible. Another example is the "devil's pitchfork," or Schuster's conundrum (*b*). Such impossible figures raise profound questions about the relation between perception and rationality.

In modern times, interest in such effects was partly revived by Swedish artist Oscar Reutersvärd. Known as the father of impossible figures, he devised numerous geometric paradoxes, including the "endless staircase" and the "impossible triangle." These two were also independently developed by Lionel and Roger Penrose, the famous father-and-son scientists; *c*, on the next page, shows their version of what is now commonly called the Penrose triangle.

Dutch artist M. C. Escher playfully embedded such figures in his engravings exploring space and geometry. Consider Escher's staircase (*d, on next page*): no single part of the staircase is impossible or ambiguous, but the entire ensemble is logically impossible. You could be climbing the staircase upward forever and yet keep going in circles, never reaching the top. It epitomizes the human condition: we perpetually reach for perfection, never quite getting there!

Is this staircase truly a perceptual paradox? That is, is the brain unable to construct a coherent percept (or token of perception) because it has to simultaneously entertain two contradictory perceptions? We think not. Perception, almost by definition, has to be unified and stable at any given instant because its whole purpose is to lead to an appropriate goal-directed action on our part. Indeed, some philosophers have referred to perception as "conditional readiness to act," which may seem like a bit of an overstatement.

Despite the common view that "we see what we believe," the perceptual mechanisms are really on autopilot as they compute and signal various aspects of the visual environment. You cannot choose to see what you want to see. (If I show you a blue lion, you see it as blue. You cannot say, "I will choose to see it as gold because it ought to be.") On the contrary, the paradox in *d* arises precisely because the perceptual mechanism performs a strictly local computation that signals "ascending stairs," whereas your conceptual/intellectual mechanism deduces that it is impossible logically for such an ascending staircase to form a closed loop. The goal of perception is to compute rapidly the approximate answers that are good enough for immediate survival; you cannot ruminate over whether the lion is near or far. The goal of rational conception—of logic—is to take time to produce a more accurate appraisal.

Genuine or Not?

Are impossible figures (aside from the triangle, to which we will return) genuine paradoxes within the domain of perception itself? One could argue that the perception itself remains, or appears to remain, internally consistent, coherent and stable and that a genuinely paradoxical percept is an oxymoron. The staircase is no more a paradox than our seeing a visual illusion such as the Müller-Lyer (*e, on page 73*)—in which two lines of equal length appear to differ—but then measuring the two lines with a ruler and convinc-


b

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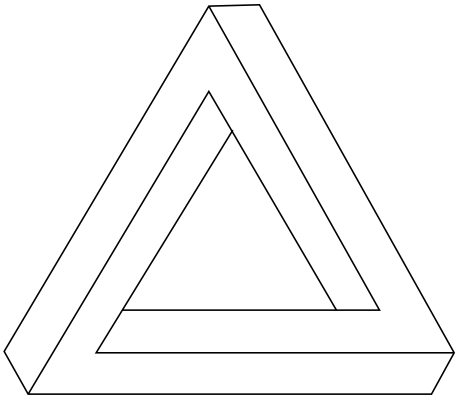
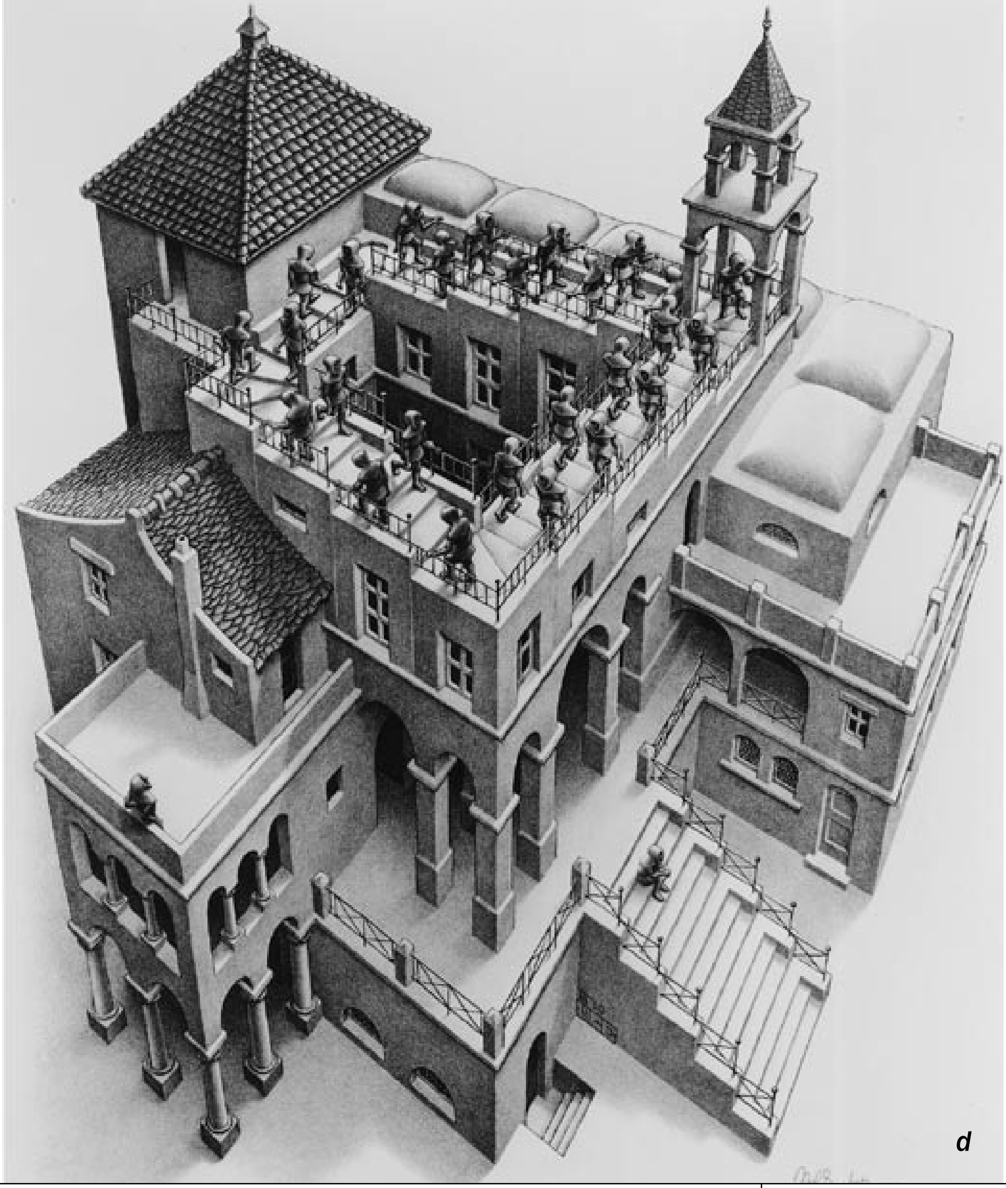


c

ing ourselves at an intellectual level that the two lines are of identical length. The clash is between perception and intellect, not a genuine paradox within perception itself. On the other hand, "This statement is false" is a paradox entirely in the conceptual/linguistic realm.

Another compelling perception is the motion aftereffect. If you stare for a minute at stripes moving in one direction and then transfer your gaze to a stationary object, the object appears to move in the opposite direction that the stripes moved. This effect arises because your visual system has motion-detecting neurons signaling different directions, and the stripes constantly moving in one direction "fatigue" the neurons that would normally signal that direction. The result is a "rebound" that makes even stationary objects appear to move in the opposite direction.

Yet curiously, when you look at the object, it seems to be moving in one direction, but it does not seem to get anywhere; it does not progress to a goal. This effect is often touted as a perceptual paradox: How can something seem to move but not change location? But once again, the percept itself is not paradoxical; rather it is signaling with certainty that the object is moving. It is your intellect that deduces it is not moving and infers a paradox.



d

Consider the much more familiar converse situation. You know (deduce) that the hour hand of your clock is moving, even though it looks stationary. It is not moving fast enough to excite motion-detecting neurons. Yet no one would call a clock hand's movement a paradox.

Perception-Cognition Boundary

There are borderline cases, as exemplified by the devil's pitchfork. In this display, some people can "see" the whole in a single glance. The local and global perceptual cues themselves are perceived as a single gestalt with internal contradictions. That is, one can ap-

SCIENTIFIC AMERICAN MIND (c); M. C. ESCHER'S *ASCENDING AND DESCENDING*, © 2008 THE M. C. ESCHER COMPANY-HOLLAND. ALL RIGHTS RESERVED. WWW.MCESCHER.COM (d)

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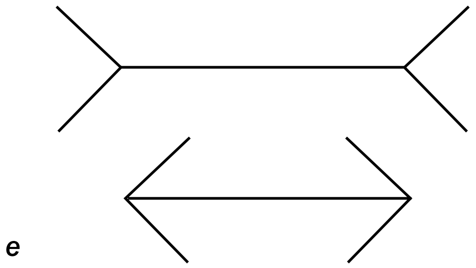
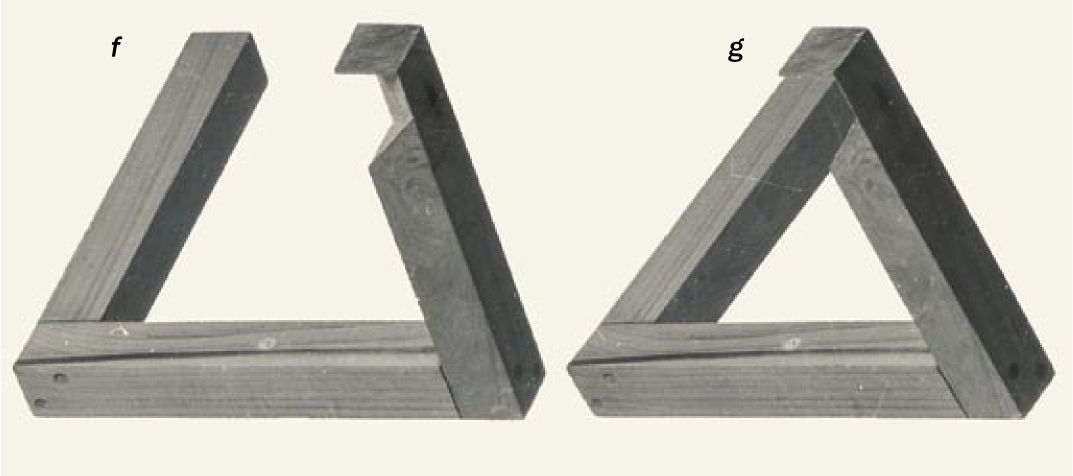
> (Perception is **virtually instantaneous**, whereas rational conception—logic—takes time.)





SCIENTIFIC AMERICAN MIND (*e*); COURTESY OF RICHARD L. GREGORY *University of Bristol* (*f* and *g*)

prehend the whole in a single glance and appreciate its paradoxical nature without thinking about it. Such displays remind us that despite the modular quasi-autonomous nature of perception and its apparent immunity from the intellect, the boundary between perception and cognition can blur.

The impossible triangle is similar. As shown by neuropsychologist Richard L. Gregory of the University of Bristol in England, you can construct a complicated 3-D object (*f*) that would produce the image in *g* only when viewed from one particular vantage point. From that specific angle, the object appears to be a triangle confined to a single plane. But your perception rejects such highly improbable events, even when your intellect is convinced of their possibility (after being shown the view at *g*). Thus, even when you understand conceptually the unusual shape of object *f*, you continue to see a closed triangle when viewing *g*, rather than the object (*f*) that actually gives rise to it.

How would one test these notions empirically? With the Escher staircase, one could exploit the fact that perception is virtually instantaneous, whereas cogitation takes time. One could present the display briefly—a short enough time to prevent cognition from kicking in—say, a tenth of a second followed by a masking stimulus (which prevents continued visual processing after removal of the test figure). The prediction would be that the picture should no longer look paradoxical unless the stimulus duration were lengthened adequately. The same could be tried for the devil's pitchfork, which is more likely to be a genuine perceptual paradox. In this case, the mask may not be able to "dissect" it into two distinct (perception or cognition) stages. It may boil down to a matter of scale or complexity.

Whatever paradoxes' origins, no one can fail to be intrigued by these enigmatic displays. They perpetually titillate our senses and challenge all our notions of reality and illusion. Human life, it would seem, is delightfully bedeviled by paradox. M

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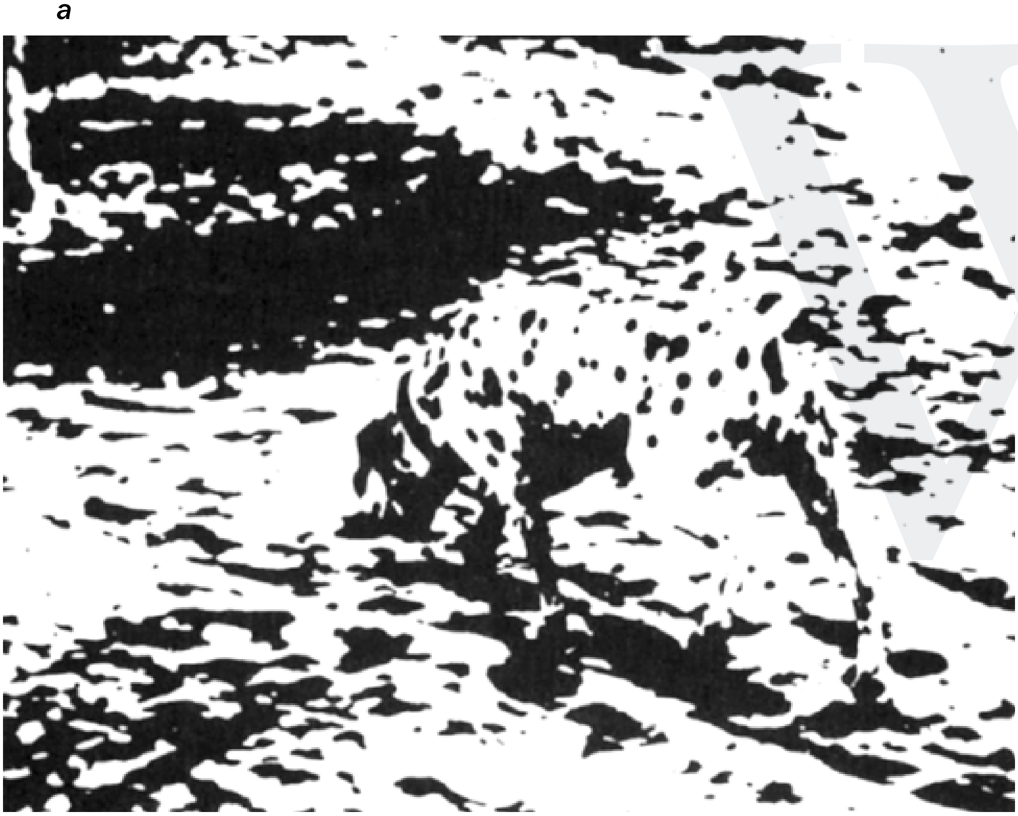
The Neurology of Aesthetics

How visual-processing systems shape our feelings about what we see

BY VILAYANUR S. RAMACHANDRAN AND
DIANE ROGERS-RAMACHANDRAN



COURTESY OF RICHARD L. GREGORY *University of Bristol*

WHAT IS ART? Probably as many definitions exist as do artists and art critics. Art is clearly an expression of our aesthetic response to beauty. But the word has so many connotations that it is best—from a scientific point of view—to confine ourselves to the neurology of aesthetics.

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Aesthetic response varies from culture to culture. The sharp bouquet of Marmite is avidly sought after by the English but repulsive to most Americans. The same applies to visual preferences; we have personally found no special appeal in Picasso. Despite this diversity of styles, many have wondered whether there are some universal principles. Do we have an innate "grammar" of aesthetics analogous to the syntactic universals for languages proposed by linguist Noam Chomsky of the Massachusetts Institute of Technology?

The answer may be yes. We suggest that universal "laws" of aesthetics may cut across not only cultural boundaries but across species boundaries as well. Can it be a coincidence that we find birds and butterflies attractive even though they evolved to appeal to other birds and butterflies, not to us? Bowerbirds produce elegant bachelor pads (bowers) that would probably elicit favorable reviews from Manhattan art critics—as long as you auctioned them at Sotheby's and did not reveal that they were created by birdbrains.

In 1994, in a whimsical mood, we came up with a somewhat arbitrary list of "laws" of aesthetics, of which we will describe six: grouping, symmetry, hypernormal stimuli, peak shift, isolation and perceptual problem solving. For each law, we will explain what function it might serve and what neural machinery mediates it.

Pay Attention!

Let us consider grouping first. In *a*, you get the sense of your visual system struggling to discover and group together seemingly unrelated fragments of a single object, in this case a dalmatian. When the correct fragments click into place, we feel a gratifying "aha." That enjoyable experience, we suggest, is based on direct messages sent to pleasure centers of the limbic system saying, in effect, "Here is something important: pay attention"—a minimal requirement for aesthetics. Fashion designers understand the principle of grouping. The salesclerk suggests a white tie with blue flecks to match the blue of your jacket.

Grouping evolved to defeat camouflage and more generally to detect objects in cluttered environments. Imagine a tiger hidden behind foliage (*d, on page* 77). All your eye receives are several yellowish tiger fragments. But your visual system assumes that all these fragments cannot be alike by coincidence, and so it groups them to assemble the object and pays attention. Little does the salesperson realize that he or she is tapping into this ancient biological principle in selecting your tie.

Evolution also had a hand in shaping the appeal of symmetry. In nature, most biological objects (prey, predator, mate) are symmetrical. It pays to have an early-warning alert system to draw your attention to symmetry, leading quickly to appropriate action. This attraction explains symmetry's allure, whether for a child playing with a kaleidoscope or for Emperor Shah Jahan, who built the Taj Mahal (*b*) to immortalize his beautiful wife, Mumtaz. Symmetry may also be attractive because asymmetrical mates tend to be unhealthy, having had bad genes or parasites in their early development.

Let us turn now to a less obvious universal law, that of hypernormal stimuli. Ethologist Nikolaas Tinbergen of the University of Oxford noticed more than 50 years ago that newly hatched seagull chicks started begging for food by pecking at their mother's beak, which is light brown with a red spot. A chick will peck equally fervently at a disembodied beak; no gull need be attached to it. This instinctive behavior arose because, over millions of years of evolution, the chick's brain has "learned" that a long thing with a red spot means mother and food.

Tinbergen found that he could elicit pecking without a beak. A long stick with a red spot would do. The visual neurons in the chick's brain

MICHAEL FREEMAN *Corbis*

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GUSTAV KLIMT, "STUDY OF A NUDE." PHOTOGRAPH BY GÉRARD BLOT *Réunion des Musées Nationaux/Art Resource, NY*

are obviously not very fussy about the exact stimulus requirements. But he then made a remarkable discovery. If the chick viewed a long, thin piece of cardboard with three red stripes, it went berserk. The chick preferred this strange stimulus to a real beak. Without realizing it, Tinbergen had stumbled on what we call a "superbeak." (He later shared the 1973 Nobel Prize in Physiology or Medicine for his work on animal behavior patterns.)

We do not know why this effect occurs, but it probably results from the way in which visual neurons encode sensory information. The way they are wired may cause them to respond more powerfully to an odd pattern, thereby sending a big "aha" jolt to the bird's limbic system.

What has a superbeak got to do with art? If gull chicks had an art gallery, they would hang a long stick with stripes on the wall, and they would likewise adore it and pay dearly to own one. Art, similarly, stirs collectors to plunk down thousands of dollars for a painting without understanding why it is so compelling. Through trial and error and ingenuity, modern artists have discovered ways of tapping into idiosyncratic aspects of the brain's primitive perceptual grammar, producing the equivalent for the human brain of what the striped stick is for the chick's brain.

A related principle, called peak shift, plays a role in the appreciation of caricature or even good portraiture. Features that make a particular face (for example, George W. Bush's) differ from the "average" of hundreds of male faces are amplified selectively so the result looks even more Bush-like than Bush himself. In 1998 philosopher William Hirstein of Elmhurst College and I (Ramachandran) suggested that cells in the monkey brain that are known to respond to individual faces (such as Joe, the alpha male) will do so even more vigorously to a caricature of the face than the original. This strong response has now been confirmed in experiments by Doris Tsao of Harvard University.

Why Less Is More

We turn to the next two related principles: isolation and perceptual problem solving, or peekaboo. Any artist will tell you that sometimes in art "less is more"; a little doodle of a nude is much more beautiful than a full-color 3-D photograph of a naked woman. Why? Doesn't this phenomenon contradict peak shift?

To resolve this particular contradiction, we need to recall that our brains have limited attentional resources—an attentional bottleneck results because only a single pattern of neural activity can exist at a time. Here is where isolation comes in. A cleverly contrived doodle or sketch (*c*) allows your visual system to spontaneously allocate all your attention to where it is needed—namely, to the nude's contour or shape—without being distracted by all the other irrelevant clutter (color, texture, shading, and so on) that is not as critical as the beauty of her form conveyed by her outlines.

Evidence for this view comes from autistic children with savant skills such as Nadia. She produced astonishingly beautiful drawings, perhaps because, while most of her brain was functioning suboptimally, she may have had an island of "spared" cortical tissue in her parietal lobe, which is known to be involved in one's sense of artistic proportion. Hence, she could spontaneously deploy all her attentional resources to this one spared "art module." (Once she grew up and gained other social skills, her artistic skills vanished.) Bruce Miller of the University of California, San Francisco, has shown that even some adult patients who develop a degeneration of their frontal and temporal lobes (called fronto-

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(Evolution has had a hand in shaping the **appeal of symmetry**.)

temporal dementia) suddenly develop artistic talents, possibly because they can now allocate all their attention to the parietal lobes.

A related "law" of aesthetics is peekaboo. In the ninth century A.D. Indian philosopher Abhinavagupta discovered this effect, which Austrian-British art historian Sir Ernst Gombrich rediscovered in the 20th century. An unclothed person who has only arms or part of a shoulder jutting out from behind a shower curtain or who is behind a diaphanous veil is much more alluring than a completely uncovered nude. Just as the thinking parts of our brains enjoy intellectual problem solving, the visual system seems to enjoy discovering a hidden object. Evolution has seen to it that the very act of searching for the hidden object is enjoyable, not just the final "aha" of recognition—lest you give up too early in the chase. Otherwise, we would not pursue a potential prey or mate glimpsed partially behind bushes or dense fog.

Every partial glimpse of an object (*d*) prompts a search—leading to a mini "aha"—that sends a message back to bias earlier stages of visual processing. This message in turn prompts a further search and—after several such iterations and mini "ahas"—we arrive at the final "aha!" of recognition. The clever fashion designer or artist tries to evoke as many such mini "ahas," ambiguities, peak shifts and paradoxes as possible in the image.

We have barely touched on more elusive aspects of aesthetics such as "visual metaphor," a pleasing resonance between the visual and symbolic elements of an image. Between the aesthetics of gull chicks and the sublime beauty of a Monet, we have a long journey ahead to truly understand visual processing in the brain. Meanwhile our studies have given us tantalizing glimpses of what the terrain might look like, inspiring us to continue our pursuit. **M**

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THEO ALLOFS *Corbis*

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Cracking the da Vinci Code

What do the *Mona Lisa* and Abraham Lincoln have in common?

BY VILAYANUR S. RAMACHANDRAN AND DIANE ROGERS-RAMACHANDRAN

SPANISH PAINTER EL GRECO often depicted elongated human figures and objects in his work. Some art historians have suggested that he might have been astigmatic—that is, his eyes' corneas or lenses may have been more curved horizontally than vertically, causing the image on the retina at the back of the eye to be stretched vertically. But surely this idea is absurd. If it were true, then we should all be drawing the world upside down, because the retinal image is upside down! (The lens flips the incoming image, and the brain interprets the image on the retina as being right side up.) The fallacy arises from the flawed reasoning that we literally "see" a picture on the retina, as if we were scanning it with some inner eye.

PHILIPPE G. SCHYNS *University of Glasgow* AND AUDE OLIVA *Massachusetts Institute of Technology*; ADAPTED FROM "DR. ANGRY AND MR. SMILE: WHEN CATEGORIZATION FLEXIBLY MODIFIES THE PERCEPTION OF FACES IN RAPID VISUAL PRESENTATIONS," BY P. G. SCHYNS AND A. OLIVA, IN *COGNITION*, VOL. 69, NO. 3; 1999 *(opposite page)*

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No such inner eye exists. We need to think, instead, of innumerable visual mechanisms that extract information from the image in parallel and process it stage by stage, before their activity culminates in perceptual experience. As always, we will use some striking illusions to help illuminate the workings of the brain in this processing.

Angry and Calm

Compare the two faces shown in *a*. If you hold the page about nine to 12 inches away, you will see that the face on the right is frowning and the one on the left has a placid expression.

But if you move the figure so that it is about six or eight feet away, the expressions change. The left one now smiles, and the right one now looks calm.

Up close, one face frowns and the other looks calm. Viewed from farther away, **the two faces change**. How?

How is this switch possible? It seems almost magical. To help you understand it, we need to explain how the images were constructed by Philippe G. Schyns of the University of Glasgow and Aude Oliva of the Massachusetts Institute of Technology.

A normal portrait (photographic or painted) contains variations in what neuroscientists such as ourselves term "spatial frequency." We will discuss two types of spatial frequency: The first is "high"—with sharp, fine lines or details present in the picture. The second is "low"—conveyed by blurred edges or large objects. (In fact, most images contain a spectrum of frequencies ranging from high to low, in varying ratios and contrasts, but that is not important for the purposes of this article.)

Using computer algorithms, we can process a normal portrait to remove either high or low spatial frequencies. For instance, if we remove high frequencies, we get a blurred image that is said to contain "low spatial frequencies in the Fourier space." (This mathematical description need not concern us further here.) In other words, this procedure of blurring is called low-pass filtering, because it filters out the high spatial frequencies (sharp edges or fine lines) and lets through only low frequencies. High-pass filtering, the opposite procedure, retains sharp edges and outlines but removes large-scale variations. The result looks a bit like an outline drawing without shading.

These types of computer-processed images are combined together, in an atypical manner, to

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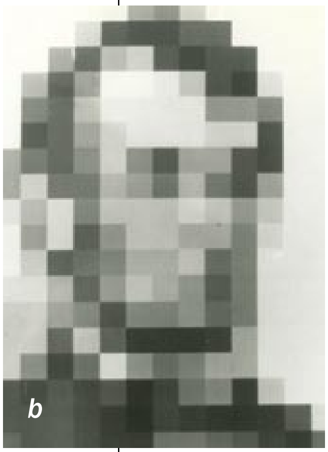

create the mysterious faces shown in *a*. The researchers began with normal photographs of three faces: one calm, one angry and one smiling. They filtered each face to obtain both high-pass (containing sharp, fine lines) and low-pass (blurred, so as to capture large-scale luminance variations) images. They then combined the high-pass calm face with the low-pass smiling face to obtain the left image. For the right image, they overlaid the high-pass frowning face with the low-pass calm face.

What happens when the figures are viewed close-up? And why do the expressions change when you move the page away? To answer these questions, we need to tell you two more things about visual processing. First, the image needs to be close for you to see the sharp features. Second, sharp features, when visible, "mask"—or deflect attention away from—the large-scale objects (low spatial frequencies).

So when you bring the picture near, the sharp features become more visible, masking the coarse features. As a result, the face on the right looks like it is frowning and the one on the left like it is relaxed. You simply do not notice the opposite emotions that the low spatial frequencies convey. Then, when you move the page farther away, your visual system is no longer able to resolve the fine details. So the expression conveyed by these fine features disappears, and the expression conveyed by low frequencies is unmasked and perceived.

The experiment shows vividly an idea originally postulated by Fergus W. Campbell and John Robson of the University of Cambridge: information from different spatial scales is extracted in parallel by various neural channels, which have wide ranges of receptive field sizes. (The receptive field of a visual neuron is the part of the visual field and corresponding tiny patch of retina to which a stimulus needs to be presented to activate it.) It also shows that the channels do not work in isolation from one another. Rather they interact in interesting ways (for example, the sharp edges picked up by small receptive fields mask the blurred large-scale variations signaled by large receptive fields).

Honest Abe

Experiments of this kind go back to the early 1960s, when Leon Harmon, then working at Bell Laboratories, devised the famous Abraham Lincoln effect. Harmon produced the picture of Honest Abe (*b*) by taking a regular picture and digitizing it into coarse pixels (picture elements). Even when viewed close-up, there is enough information in the blocky brightness variations to recognize Lincoln. But these data, as we noted already, are masked by the sharp edges of the pixels. When you move far away from the photograph or squint, the image blurs, eliminating the sharp edges. Presto! Lincoln becomes instantly recognizable. The great artist Salvador Dalí was sufficiently inspired by this illusion to use it as a basis for his paintings, an unusual juxtaposition of art and science (*c*).

> Squint, and the image blurs, eliminating the sharp edges. **Presto!** Lincoln becomes instantly recognizable.

REPRINTED WITH PERMISSION OF LUCENT TECHNOLOGIES, INC./BELL LABS (*b*); *GALA CONTEMPLATING THE MEDITERRANEAN SEA WHICH AT TWENTY METRES BECOMES THE PORTRAIT OF ABRAHAM LINCOLN (HOMAGE TO ROTHKO)*; MUSEO DALÍ/BRIDGEMAN ART LIBRARY; © 2006 SALVADOR DALÍ, GALA-SALVADOR DALÍ FOUNDATION/ARS, NEW YORK (*c*)

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The **elusive smile** can be seen only when you look away from the mouth. Attend to it out of the corner of your eye.

MARGARET LIVINGSTONE *Harvard Medical School*

Mysterious *Mona Lisa*

Finally, consider the mysterious smile of Leonardo da Vinci's *Mona Lisa*. Philosophers and art historians who specialize in aesthetics often refer to her expression as "enigmatic" or "elusive," mainly because they do not understand it. Indeed, we wonder whether they prefer not to understand it, because they seem to resent any attempts to explain it scientifically, apparently for fear that such analysis might detract from its beauty.

But neurobiologist Margaret Livingstone of Harvard Medical School made an intriguing observation; she cracked the da Vinci code, you might say. She noticed that when she looked directly at Mona Lisa's mouth (*d, center panel*), the smile was not apparent (quite a disappointment). Yet as she moved her gaze away from the mouth, the smile appeared, beckoning her eyes back. Looking again at the mouth, she saw that the smile disappeared again. In fact, she noted, the elusive smile can be seen only when you look away from the mouth. You have to attend to it out of the corner of your eye rather than fixating on it directly. Because of the unique shading (placement of low spatial frequencies) at the corners of the mouth, a smile is perceived only when the low spatial frequencies are dominant—that is, when you look indirectly at the masterpiece.

To confirm this notion, she performed a low-pass filtering (*left panel*) and a high-pass filtering (*right panel*) of the *Mona Lisa*. Notice that with the low-pass (blurred) image the smile is more obvious than in the original—it can be seen even if you look directly at the mouth. With the high-pass (outlinelike) image, however, no smile is apparent, even if you look away from the mouth. Putting these two images back together restores the original masterpiece and the elusive nature of the smile. As with the changing faces, we can now better appreciate what Leonardo seems to have stumbled on and fallen in love with—a portrait that seems alive because its fleeting expression (thanks to quirks of our visual system) perpetually tantalizes the viewer.

Taken collectively, these experiments show that there is more to perception than what meets the eye. More specifically, they demonstrate that information at different scales, such as fine versus coarse, may be extracted initially by separate neural channels and recombined at different stages of processing to create the final impression of a single unified picture in your mind. **M**

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Illusory Color & the Brain

Novel illusions suggest that the brain does not separate perception of color from perception of form and depth

BY JOHN S. WERNER, BAINGIO PINNA AND LOTHAR SPILLMANN

Autumn leaves and reflections in a fountain highlight the way color contributes to perception. Much of the depth and detail disappears in a black-and-white version of the scene.

A WORLD WITHOUT COLOR appears to be missing crucial elements. And indeed it is. Colors not only enable us to see the world more precisely, they also create emergent qualities that would not exist without them. The color photograph at the left, for example, reveals autumnal leaves in the placid water of a fountain, along with the reflections of trees and of a dark-blue afternoon sky behind them. In a black-and-white picture of the same scene, the leaves are less distinct, the dark-blue sky is absent, the reflections of the light are weak, the water itself is hardly visible, and the difference in apparent depth among the sky, trees and floating leaves is all but gone.

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Yet this role for color, and even the true nature of color, is not well recognized. Many people believe that color is a defining and essential property of objects, one depending entirely on the specific wavelengths of light reflected from them. But this belief is mistaken. Color is a sensation created in the brain. If the colors we perceived depended only on the wavelength of reflected light, an object's color would appear to change dramatically with variations in illumination throughout the day and in shadows. Instead patterns of activity in the brain render an object's color relatively stable despite changes in its environment.

Most researchers who study vision agree that color helps us discriminate objects when differences in brightness are insufficient for this task. Some go so far as to say that color is a luxury and not really needed: after all, totally color-blind people and many species of animals seem to do well without the degree of color perception that most humans have. The pathway in the brain that serves navigation and movement, for example, is essentially color-blind. People who become color-blind after a stroke appear to have normal visual perception otherwise. Such observations have been taken as support for the insular nature of color processing, suggesting it has no role in processing depth and form—in short, that color is only about hue, saturation and brightness.

But the study of illusory colors—colors that the brain is tricked into seeing—demonstrates that color processing in the brain occurs hand in hand with processing of other properties, such as shape and boundary. In our decade-long attempt to discern how color influences perceptions of other properties in objects, we have considered a number of novel illusions, many created by us. They have helped us understand how the neural processing of color results in emergent properties of shape and boundary. Before we begin our discussion of these illusions, however, we need to recall how the human visual system processes color.

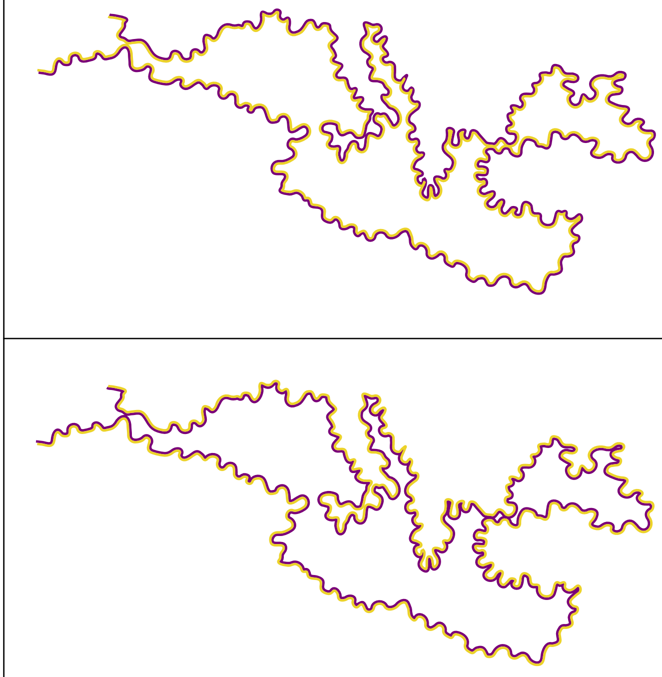
Pathways to Illusions

Visual perception begins with the absorption of light—or, more precisely, the absorption of discrete packets of energy called photons—by the cones and rods located in the retina [*see box on next page*]. The cones are used for day vision; rods are responsible for night vision. A cone photoreceptor responds according to the number of photons it captures, and its response is transmitted to two different types of neurons, termed on and off bipolar cells. These neurons in turn provide input to on and off ganglion cells that sit side by side in the retina.

The ganglion cells have what is called a center-surround receptive field. The receptive field of any vision-related neuron is the area of space in the physical world that influences the activity of that neuron. A neuron with a center-surround receptive field responds differently depending on the relative amount of light in the center of the field and the region around the center.

An on ganglion cell fires maximally (at a high rate) when the center is lighter than the surround, firing minimally when the receptive field is uniformly illuminated. Off cells behave in the opposite way: they fire maximally when the center is darker than the surround and minimally when the center and surround are uniform. This antagonism between center and surround means that ganglion cells respond to contrast and in this way sharpen the brain's response to edges and borders.

Most of the ganglion cell axons (fibers) relay their signals to the brain, specifically to the lateral geniculate nucleus of the thalamus (near the



Watercolor effect, in which the lighter of two colors seems to spread, shows how important color can be in delineating the extent and shape of a figure. The map of the Mediterranean Sea emerges at once when the tint that at first seems to cover the sea (*top*) spreads to the land area.

JOHN S. WERNER, BAINGIO PINNA AND LOTHAR SPILLMANN (*this page and opposite page*)

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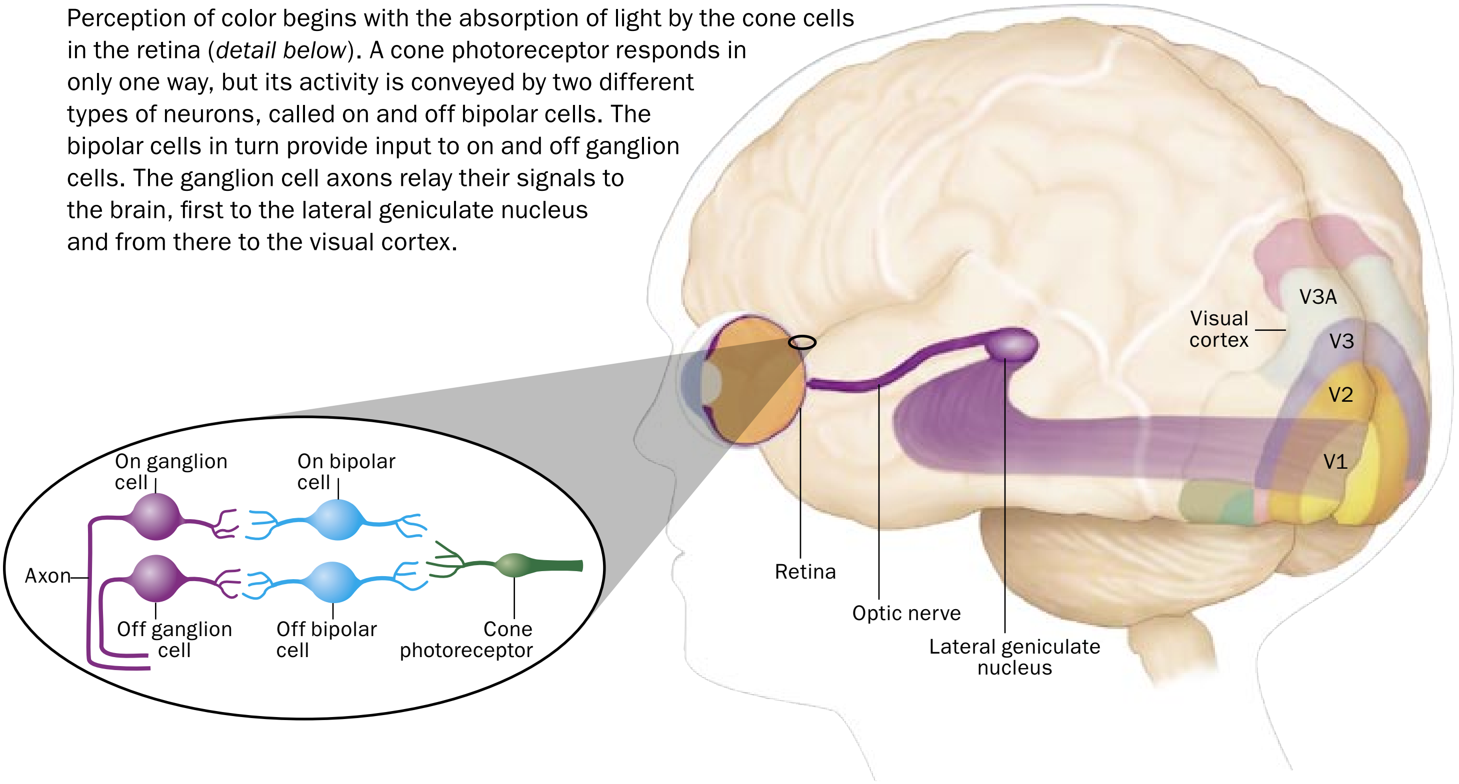
Seeing Color

Perception of color begins with the absorption of light by the cone cells in the retina (*detail below*). A cone photoreceptor responds in only one way, but its activity is conveyed by two different types of neurons, called on and off bipolar cells. The bipolar cells in turn provide input to on and off ganglion cells. The ganglion cell axons relay their signals to the brain, first to the lateral geniculate nucleus and from there to the visual cortex.



MELISSA THOMAS

center of the brain) and from there to the visual cortex (at the back of the brain). Different populations of ganglion cells are sensitive to somewhat different features of stimuli, such as motion and form, and their fibers conduct signals at different velocities. Color signals, for example, are carried by the slower fibers.

About 40 percent or more of the human brain is thought to be involved in vision. In the areas stimulated early in visual processing (parts of the visual cortex called V1, V2 and V3), neurons are organized into maps that provide a point-to-point representation of the visual field. From there, visual signals disperse to more than 30 different areas, interconnected by more than 300 circuits. Each of the areas has specialized functions, such as processing color, motion, depth and form, although no area mediates one perceptual quality exclusively. Somehow all this information is combined, in the end, into a unitary perception of an object having a particular shape and color. Neuroscientists do not yet understand the details of how this comes about.

Interestingly, bilateral damage to certain visual areas leads to deficits in the perception of form as well as color, which offers another piece of evidence that color is not disembodied from the other properties of an object. The intermingling of color signals in the brain with signals carrying information about the form of objects can result in perceptions not expected from an analysis of the wavelengths of light reflected from those objects—as our illusions make startlingly clear.

The Watercolor Effect

One of our early experiments with illusory color illustrates how important color can be in delineating the extent and shape of a figure. Un-

FAST FACTS

Color Vision

1» Vision researchers have long held that color processing in the brain is separate from the processing of other features, such as depth and form.

2» The study of illusory colors, however, demonstrates that the perception of color generates emergent properties of form and depth.

3» In particular, the authors have adapted a figure called the Ehrenstein illusion to reveal how color, shape and form are linked in the brain's perception of the visual world.

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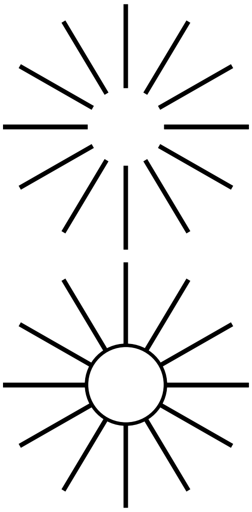
der certain conditions, color changes in response to the surrounding color; it can become more different (called contrast) or more similar (called assimilation). The spreading of similar color has been described only over rather narrow areas, in agreement with the finding that most connections among visual neurons in the brain are relatively short range. We were therefore surprised to find that when an uncolored area is enclosed by two differently colored boundary contours—with the inner contour lighter than the outer contour—tint emanates from the inner contour, spreading across the entire area, even over rather long distances [*see illustration on page 83*].

Because the color resembles a faint veil such as that seen in watercolor painting, we call this illusion the watercolor effect. We found that the spreading requires the two contours to be contiguous so that the darker color can act as a barrier, confining the spreading of the lighter color to the inside while preventing it from spreading to the outside. The figure defined by the illusory watercolor appears dense and slightly elevated. When the colors of the double contour are reversed, the same region appears a cold white and slightly recessed.

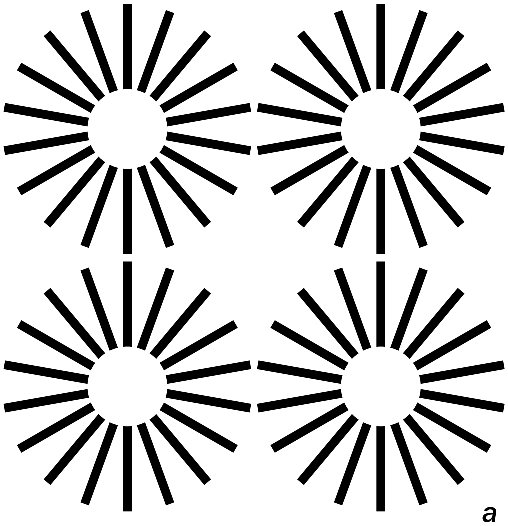
The watercolor effect defines what becomes figure and what becomes ground even more powerfully than the properties discovered by the Gestalt psychologists at the turn of the 20th century, such as proximity, smooth continuation, closure, symmetry, and so on. The side of the double contour that has the lighter color fills in with watercolor and is perceived as figure, whereas the side that has the darker color is perceived as ground. This asymmetry thus helps to counteract ambiguity. The phenomenon is reminiscent of the notion of Edgar Rubin, one of the pioneers of figure-ground research, that the border belongs to the figure, not the ground.

A possible neural explanation for the watercolor illusion is that the combination of a lighter contour flanked by a darker contour (on an even lighter background) stimulates neurons that respond only to a contour that is lighter on the inside than the outside or to a contour that is darker on the inside than the outside, but not to both. Border ownership most likely is encoded at early stages of processing in the visual cortex, such as in brain areas V1 and V2. In experiments with monkeys, neurophysiologists have found that approximately half the neurons in the visual cortex respond to the direction of contrast (whether it gets lighter or darker) and therefore could delineate the border. These same neurons have a role in depth perception that might contribute to figure-ground segregation.

Our investigations showed that wiggly lines produce stronger watercolor spreading than straight ones do, probably because the undulating borders engage more neurons responsive to



Ehrenstein figure (*top*), developed by German psychologist Walter Ehrenstein in 1941, provides the foundation for the illusions that follow. Adding a circle (*bottom*) destroys the illusion of a bright central disk.



Bright circular patches fill the central gap of an Ehrenstein figure modified to enhance that illusion.

JOHN S. WERNER, BAINGIO PINNA AND LOTHAR SPILLMANN

(The Authors)

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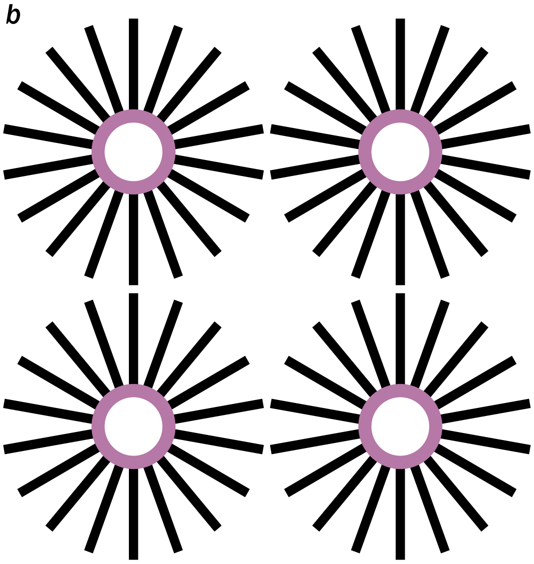
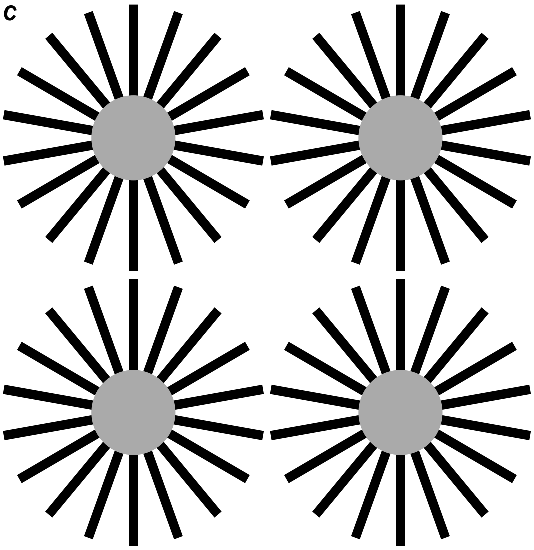
b



Anomalous brightness induction: the addition of colored rings makes the illusory patches appear even whiter.

c



Scintillating luster: gray disks cause shimmering circular patches to fill the central gap.

orientation. The color signaled by these uneven edges must be propagated across regions of cortex that serve large areas of the visual field, continuing the spread of color until border-sensitive cells on the other side of the enclosed area provide a barrier to the flow. Color and form are thus bound together inextricably in the brain and perception at this level of cortical analysis.

Radial Lines

The radial line illusion offers further evidence of the role color plays in distinguishing figure from ground. In 1941 German psychologist Walter Ehrenstein demonstrated that a bright circular patch conspicuously fills the central gap between a series of radial lines. The patch and the circular border delineating it have no correlate in the physical stimulus; they are illusory. The bright illusory surface seems to lie slightly in front of the radial lines [*see top illustration on preceding page*].

The length, width, number and contrast of the radial lines determine the strength of this phenomenon. The spatial configuration of the lines necessary for the illusion to take effect implies the existence of neurons that respond to the termination of a line. Such cells, called end-stopped neurons, have been identified in the visual cortex, and they may explain this effect. These local signals combine and become inputs to another (second-order) neuron, which fills in the central area with enhanced brightness.

In our studies of the Ehrenstein illusion, we evaluated variations in the number, length and width of the radial lines, and the examples we present in this article use the most striking combination that we found [*see lettered illustrations*]. We show four copies of each pattern, arranged as a quartet, to enhance the effects. Once we determined the characteristics for the radial lines that produced the brightest central circle (*a, on preceding page*), we experimented with variations in the chromatic properties of the central gap. First we added a black annulus, or ring, to the Ehrenstein figure, and the brightness of the central gap disappeared entirely—the illusion was destroyed, as Ehrenstein had already noticed. We suspect that this effect arises because the ring silences the cells that signal line terminations.

If the annulus is colored, however, other cells may be excited by this change. When we added a colored annulus, the white disk not only appeared much brighter (self-luminous) than it did in the Ehrenstein figure, it also had a dense appearance, as if a white paste had been applied to the surface of the paper (*b*). This phenomenon surprised us; self-luminosity and surface qualities do not ordinarily appear together and have even been considered to be opposing, or mutually exclusive, modes of appearance. We call this phenomenon anomalous brightness induction. As occurs with the watercolor effect, cells in early cortical areas are candidates for causing this illusion.

Next we inserted a gray disk into the central gap of an Ehrenstein figure (*c*). Another phenomenon, called scintillating luster, arose, in which illusory brightness gives way to the perception of a glossy shimmer that occurs with each movement of the pattern or of the eye. The scintillation, or flashing, may come about by a competition between the on and off systems: line-induced

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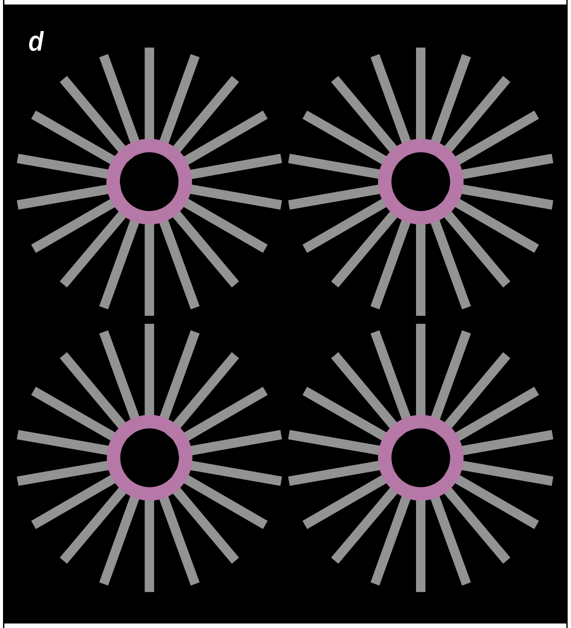
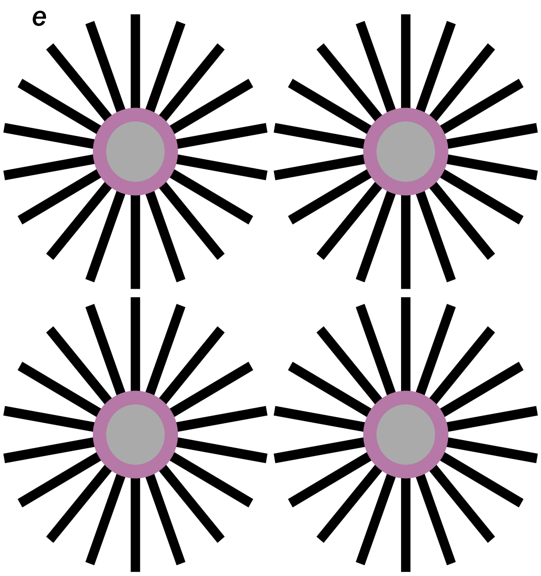


Anomalous darkness induction (*d*): black disks within a colored ring appear much blacker than the physically identical surrounding black.



Flashing anomalous color contrast (*e*): gray disks ringed in purple appear as greenish-yellow flashing lights when the pattern or the eye moves back and forth.

brightness (illusory increment) competes with the dark gray of the disk (physical decrement). When we replaced the central white disks within the colored ring with black disks and used a black background (*d*), the disks looked even darker than the physically identical surrounding area. Instead of appearing self-luminous, as white disks do, blackness seems to generate a void, or a black hole, that absorbs all the light.

When the central disk within the chromatic ring was gray instead of white or black, the disk appeared to become tinted with the complementary color of the annulus—for example, greenish-yellow when the surrounding ring was purple (*e*). Furthermore, the disk appeared to flash with each eye movement, or when the pattern moved back and forth, and to move in relation to its surround. Flashing anomalous color contrast depends on radial lines and a chromatic annulus the way the other effects do, but it also has unique qualities that do not appear to be a simple combination of the other known effects. In this illusion, the induced color appears both self-luminous and scintillating. Strikingly, it appears to float above the rest of the image. The surface color and the self-luminous color do not mix; instead one belongs to the disk on the page, and the other emerges from a combination of the other characteristics of the stimuli.

In flashing anomalous color contrast, the radial lines may activate local end-stopped neurons, as has been proposed for the filling in of gaps by illusory contours, but activity by those cells does not account completely for the combined flashing and complementary color. It is not clear whether the radial lines have a direct effect on color contrast or whether the vividness of the color is derived indirectly from the luster and scintillation caused by the combination of radial lines and the gray center.

Current understanding of the brain cannot explain all the things going on in this illusion. The complexity of the illusion suggests that it is unlikely to result from a single unitary process but may represent an attempt by the brain to reconcile competing signals from multiple specialized pathways. Scientists clearly have much more to learn about how the brain perceives the physical world. Fortunately, ongoing work on illusory colors will continue to offer a tantalizing portal into the complexities of the human visual system. **M**

(Further Reading)

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