VISION RESEARCH

How the Brain 'Sees' Borders Where There Are None

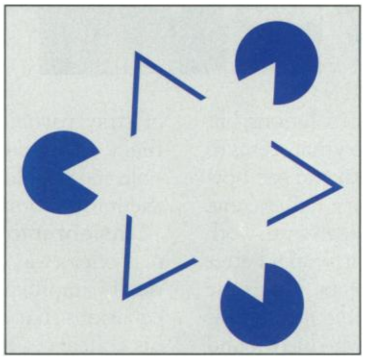
The mammalian brain has an amazing capacity for "seeing" objects under very unfavorable conditions. Take, for example, a backpacker hiking a forest trail who espies a dark brown object looming up ahead. Is it just another tree trunk among many? Or is it a bear whose outline is partially obscured by the tree trunk behind it? The answer could be vital to the hiker's continued existence—and so it's fortunate that the brain can provide it. Cognitive scientists, who for decades have been studying the problem of how the brain performs this feat, thought they had a pretty good idea about the solution. But a group of visual neuroscientists has recently come up with some surprising results on how we see objects that do not have clearly defined borders, and these findings are causing researchers to rethink some long-held notions.

Psychologists had thought that we use contrast—such as that between the sky and the parts of the bear not obscured by the tree—to figure out what we are looking at when portions of an object's border blend in with its background. This would be akin to deciphering a word from just a few letters in a game of hangman and would require the activity of the brain's higher cognitive centers. But the new results, which come from Robert Shapley's group at New York University (NYU),* show for the first time that specific cells in the primary visual cortex of monkey brains can respond to "illusory contours" (the term used to describe borders where no contrast exists). Those cells, which are low in the hierarchy of neurons involved in visual processing and not involved in higher order reasoning, were not supposed to have that ability. "This violates the standard dogma," says psychologist Glenn Meyer of Lewis and Clark College in Portland, Oregon. While the findings don't eliminate a role for the brain's higher reasoning activities, they do mean that perception of illusory contours begins at a much lower level in the visual system than expected.

Although psychologists interested in visual perception first began drawing illusory contour figures at the turn of the century, the standard dogma that recognition of the contours requires higher cognitive activity originated about two decades later with the work of the Gestalt psychologists, who formulated laws for how people group visual elements in space.

*The data were presented at the annual meeting of the Association for Research in Vision and Ophthalmology, which was held from 3 to 8 May in Sarasota, Florida.

The modern era of illusory contour studies began, however, in the 1950s, when psychologist Gaetano Kanizsa of the University of Trieste devised a series of striking figures to illustrate illusory contours, such as the "Kanizsa triangle" (see figure at right). Following the ideas of the Gestalt psychologists, Kanizsa believed the perception of contours arose from the human brain's tendency to assemble disparate visual features into complete and simple forms. And because illusory contours appear under a wide variety of conditions, he thought that the perception of the contours could not be explained by specific contour-detecting cells.



Illusory contour. Kanizsa triangle.

Nevertheless, hints that should have alerted researchers to the possible existence of such cells began appearing in the 1970s. That's when cognitive researchers found, for example, that illusory contours disappear when elements of the figures are changed in ways that should not interfere with the formation of "good" forms, if these forms are indeed inferred by the brain's reasoning capabilities. The Kanizsa triangle itself provides an illustration: Color the "pacman" figures red and their background a shade of green that has the same luminance, and the triangle is no longer seen. Such findings are best explained by the existence of specific visual cells involved in processing illusory contours that do not respond when the stimulus is altered appropriately.

Low contrast. The border between the outer two profiles resembles those used to detect V1 cells that respond to illusory contours.

These hints grew much stronger in 1984, when researchers obtained the first direct evidence that neurons in the visual cortex play a role in the perception of illusory contours. By implanting fine electrodes in single cells of the visual cortex of monkey brains, Rüdiger von der Heydt, Esther Peterhans, and Günter Baumgartner at University Hospital in Zurich, Switzerland, were able to detect cells that could respond to several types of illusory contours.

In primate vision, nerve signals are passed from one cortical area to another. And the Zurich group detected the responding cells in an area called V2, but they found no sign of them in the primary visual cortex (V1) where Shapley's team have now detected their responsive cells. Although researchers don't fully understand the roles played by the different parts of the cortex in processing visual signals, cells in V1, the first area the signals reach, were supposed to detect simple contrast, while V2 cells, which come in later, might accomplish more complex aspects of contour perception. Thus, von der Heydt's findings were less of a challenge to the notion that illusory contour perception depends primarily on higher cognitive functioning.

Two years later, however, Christoph Redies and his colleagues at the Max Planck Institute for Biophysical Chemistry in Göttingen, Germany, also using single-cell recording techniques, obtained evidence that cells in the primary visual cortex of the cat respond to illusory contours. Shapley says those results inspired him and his postdoc David Grosof to take another look at the responses of V1 cells in monkeys to illusory borders. Because other projects in the lab kept them busy, however, those experiments, which were done in collaboration with NYU colleague Michael Hawken, didn't get under way until late 1990.

The first decision Shapley and Grosof had to make was what kind of patterns to test. They settled on two types, one with a border formed by two different textured patterns and the other where the border was between a texture and a blank region. All the patterns had to be adjusted so that there was no contrast difference across the borders, Shapley says, to be sure that the V1 cells were in fact responding to illusory contours and not to the contrast differences they were already known to detect. The researchers then passed each pattern individually in front of a monkey's eyes, while recording the responses of single V1 cortical cells with microelectrodes.

The results: Of the total of 25 cells recorded in five monkeys, about half sent out bursts of impulses every time a border crossed its receptive field, which is the region of visual space that a cell "sees." The cells did not respond appreciably to the interior of the textured re-

SOURCE: SPRINGER-VERLAG ILLUSTRATIONS: SUSAN NOWOSLAWSKI gions. The rest of the cells tested responded to contrast-defined borders, as expected, but weakly or not at all to the illusory borders.

The work shows, Shapley says, that some V1 cells can respond to borders and not just to contrast differences and indicates a previously unsuspected role for these cells in contour and form processing. "If the findings hold up, it suggests that V1 processing is more complex than we thought, that more is going on than just a simple filtering based on orientation, motion, and color," agrees Lewis and Clark's Meyer.

As for why Shapley's group found that some V1 cells can respond to borders, while his group didn't, von der Heydt suggests it's because he used a different type of pattern. In contrast to the texture borders tested by the New York group, the illusory contours in von der Heydt's patterns appeared in gaps of empty space between visual elements. It's possible, he asserts, that V1 cells do not respond to the gap type of contour, although this remains to be proven. Indeed, says vision scientist Norma Graham of Columbia University, the patterns employed by Shapley are a "more powerful tool" for trying to understand how cells see contour because they enable researchers to gather precise data that can help verify or refute various models of how the visual system works.

In any event, the existence of a novel class of contour-sensitive cells in V1 suggests to Shapley a new cellular mechanism for how the brain processes information about forms in the initial stages of seeing. He proposes that V1 contains at least two types of cells, each with a different function in perceiving forms against a visual background. The classic V1 cells enable us to perceive local areas of contrast within an object or across its border with the background. The novel cell type, meanwhile, may be responsible for our ability to see an object's contours, whether or not there is contrast difference between the object and its background.

Shapley tailored his proposed mechanism, he says, to fit with the natural way people perceive an object's borders, which are seen separately from its brightness or shading. "If you have an object with a gradation in contrast across it, the brightness of the object tends to be determined by the local contrast across the border. But the object stands out from the background independent of what the local brightness is," he explains.

The findings of Shapley's team reveal a new beginning for the process by which the brain extracts forms from visual scenes. But what happens later on—how strips of contour are integrated into perception of a whole object—remains a mystery. "What we've seen in neurons are just signals that indicated pieces of a certain orientation and location," von der Heydt says. "As yet, we don't have evidence for the perception of a whole figure such as a closed rectangle," an analysis with which Shapley agrees. "We have no idea about that at all—at least, from a physiological point of view."

He speculates, nevertheless, that the new visual work may also be related to sensory processing generally. "We see that there are these very sophisticated and specific wiring tasks being performed," notes Shapley. He suggests that similarly specific processes may be operating to cull out relevant features from other sensory "spaces," such as those we perceive by listening to, or touching, the world. But, of course, tracing out the exact tasks performed at each stage of sensory processing will take much more probing of the brain.

–Ingrid Winckelgren

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PALEOANTHROPOLOGY

An About-Face for Modern Human Origins

When the Chinese and American anthropologists looked at two 350,000-year-old skulls found recently in China, the two researchers had a flash of self-recognition: The unusually complete skulls have flattened faces that look remarkably like those of modern humans—even though some of the skulls' other features appear sufficiently ancient that they have been classified as belonging to *Homo erectus*, a primitive hominid that spread from Africa at least 1 million years ago. And those modern-looking features have stirred up a controversy: They prompted archeologist Li Tianyuan of the Hubei Institute of Archeology and Dennis Etler, a paleoanthropologist who is a doctoral candidate at the University of California, Berkeley, to propose in the 4 June *Nature* that ancient hominids living in Asia could have been among the ancestors of modern humans.

UC/BERKELEY

Flat face. A skull from China may shed light on the evolution of modern humans.

The suggestion is controversial because it flies in the face of a leading, albeit embattled, theory that modern humans evolved only in Africa as recently as 150,000 years ago. According to this "Out of Africa" hypothesis, early modern *Homo sapiens* left Africa about 100,000 years ago, rapidly moving around the globe and displacing other, more archaic hominids in Europe and Asia. This theory, based on fossils and the analysis of mitochondrial DNA, already suffered a major blow earlier this year when problems were found with the way the genetic data were analyzed (*Science*, 7 February, pages 686 and 737). And now come Li and Etler with the claim that the recently discovered skulls provide fossilized evidence to support another theory—that modern humans evolved in several places through much of the Old World, including Asia.

The new fossils, which were excavated in 1989 and 1990 near the Han River in Yunxian in Hubei province, were found crushed in sediments that are tough to date. Based on preliminary indications from associated fauna, however, Chinese archeologists have determined that they are least 350,000 years old, which would make them the most complete skulls of such great age ever found in Asia.

Last year, Li traveled to Berkeley to compare them with casts of fossils of similar age. While he was there, he teamed up with Etler, who went to China in the summer of 1991 to study the skulls with Li. They concluded that the shape of one of the skulls and its long, low cranial vault made it *Homo erectus*. But "the facial structure is much more modern looking than what you see in hominids that were living at the same time in Africa and Europe," says Etler. "This shows that modern features were emerging in different parts of the world."

Not so fast, say some other paleoanthropologists. "I'm skeptical of their claim across the board," says *Homo erectus* expert Philip Rightmire of the State University of New York at Binghamton, a leading proponent of the Out of Africa theory. The dating is poor, he claims, and the specimens need more preparation, such as cleaning and putting the crushed pieces together in a proper reconstruction.

Equally skeptical is another proponent of the Out of Africa hypothesis, paleoanthropologist Christopher Stringer of the Natural History Museum in London. Stringer says that "modern" features described by Li and Etler also appear in African fossils of equal age. "I would say the facial features they're talking about are primitive," he asserts. Such flattened features also are found in the Ndutu hominid fossil from Tanzania, a specimen from Thomas Quarry in northern Africa, and an upper jaw from Broken Hill in Zambia, he says. More work must be done on the Chinese skulls before claims can be made about their unique modern features, he says: "It's very important material, but I think it's far too early to say if it really changes the arguments about the origins of modern humans."

–Ann Gibbons