CONSCIOUSNESS RESEARCH

Visual System Provides Clues To How the Brain Perceives

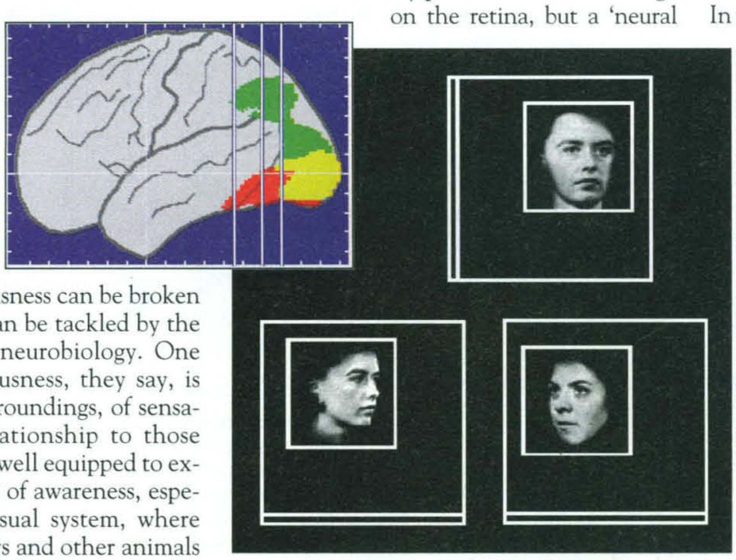
Most people would agree that consciousness is one of the great achievements—and great mysteries—of the human brain. But 10 years or so ago, any neurophysiologist who claimed to be looking for the neural basis of consciousness would have had a tough time being taken seriously. While everyone assumed that consciousness arises out of the activity of neurons in our brains, the concept seemed too ill-defined and tangled up with subjective self-awareness to be explored in a quantitative way. As California Institute of Technology (Caltech) neuroscientist Christof Koch puts it, a self-respecting neuroscientist had to "wait until after hours and drink several beers" before even discussing consciousness.

But that is changing, partly because of the efforts of Koch and his frequent co-author, Nobel laureate Francis Crick, to persuade neuroscientists that consciousness can be broken down into pieces that can be tackled by the techniques of modern neurobiology. One simple form of consciousness, they say, is awareness—of one's surroundings, of sensations, and of one's relationship to those stimuli. Researchers are well equipped to explore the underpinnings of awareness, especially in the brain's visual system, where years of work in monkeys and other animals have traced the pathways by which information from the retina enters the brain's cerebral cortex and is analyzed there.

Now, neuroscientists studying visual awareness are beginning to understand how neurons along the visual pathways come to represent what we "see"—not just what registers on our retinas—and how the brain itself influences those perceptions. The emerging picture, although still not clear in detail, suggests that "there is not one place where you have [perception], right at the top of the visual system," says Crick, but instead that the brain begins to select and alter the pure signals coming from the retina at early stages in the processing stream. The resulting picture in our mind's eye may be built up from contributions from all those processing levels.

Most of our understanding of visual processing pathways came from work done on anesthetized animals, who were not aware of the images, even though their visual systems were receiving information from the retina and extracting features such as color, movement, and form. In conscious animals, researchers expected the picture would be more complicated; psychological experiments had shown that an individual's mental state could alter visual awareness, enhancing certain features of a scene, for example, while downplaying others.

In the past decade, researchers studying the brains of fully conscious monkeys have learned that those changes are occurring at the level of neural activity in the visual cortex. "What we actually perceive is not the image on the retina, but a 'neural image' formed in the cortex," explains John Maunsell, who studies visual attention at Baylor College of Medicine in Houston. And that neural image, he adds, "is not a completely accurate representation of what is going on in the world; it has been adjusted."



Diverging paths. Identifying faces activates a human subject's "what" visual processing pathway (red); judging their location within the boxes activates the "where" path (green). Both tasks activate early areas (yellow) in the visual-processing stream.

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That adjustment can occur either by so-called "top-down" processes involving voluntary decisions—such as the choice to focus our attention on searching for a red book on the shelf, or a friend's face in a crowd—or by "bottom-up" influences over which we may have no control, such as the brain's involuntary mechanisms for resolving competition between conflicting interpretations of information it receives.

Bottom-up influences are responsible for certain illusions in which the brain is tricked into perceiving something distinctly different from the image received by the retinas. In one such illusion, called a "bistable percept," a single image produces two distinct perceptions that alternate involuntarily in the viewer's mind, although the image itself never changes. Familiar examples include the Necker cube, which creates the impression of a three-dimensional cube, alternately protruding from the page or recessed into it, and the well-known white-on-black picture that looks like either two faces or a vase.

Perceptual trickery. Behavioral experiments have shown that monkeys experience alternating perceptions when presented with bistable percepts just as humans do, and that has allowed researchers to use the illusions to search for neurons in a monkey's brain whose activity shifts with the monkey's perception, suggesting that they represent—and perhaps contribute to—that perception. In a recent experiment, Richard Andersen at Caltech, along with postdoc David Bradley and graduate student Grace Chang, found such neurons in the MT region of the monkey's visual system, which responds to movement.

The researchers showed monkeys a field of moving dots on a screen that appears to represent a cylinder that is rotating either clockwise or counterclockwise. "The stimulus is physically the same each time, and yet the monkey sees it either one way or another, as we do," says Andersen. As with the Necker cube or the faces and the vase, the perceived image alternates between the two possibilities every few seconds, and the monkeys were trained to indicate with an eye movement which way the cylinder appeared to be turning.

By recording from the animals' MT neurons, the team found that about half of the cells that fired vigorously in response to one percept, for example, when the monkey saw the dots as a clockwise-turning cylinder, would fire much less when the cylinder appeared to turn counterclockwise. That means, Andersen says, that about half of the neurons in MT reflect not the image on the animal's retina, which was the same for each trial, but what the animal perceives.

What distinguishes the neurons that shift with the percept from those that don't remains a mystery. One guess, says Crick, is that the shifting neurons are wired to other parts of the brain that direct the visual perceptions. What does appear clear, from experiments from the laboratory of Nikos Logothetis at Baylor, is that the percentage of neurons that reflect the animal's perception increases as visual information works its way up the visual processing pathway.

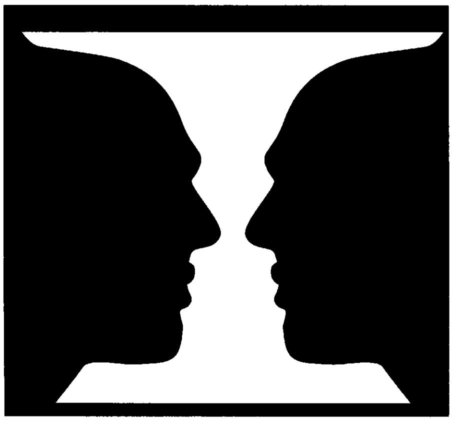
Logothetis's team subjected monkeys to binocular rivalry, a situation in which the two eyes are simultaneously shown completely different images, such as a tree and a face. Although each image is continually present on one of the viewer's retinas, the monkey, like a human viewer, is conscious only of one image at a time. The images alternate spontaneously, and monkeys can be trained to indicate which image they see.

In work over the past 8 years, Logothetis's team has sampled the activity of neurons in visual-processing areas ranging from the primary visual cortex, where retinal signals first enter the brain, to an area called IT, which is at the very end of one fork of the visual processing stream. In the primary visual cortex, only 18% of the tested neurons changed their response according to which image the animal was perceiving, suggesting that most of the neurons in that very early processing stage merely report what is happening on the retina. In areas midway in the processing stream, nearly half of the neurons' responses correlated with the animal's perception—a result comparable to what Andersen sees in MT, which is also a midway area. At the end of the line in IT, virtually all did. "There you have a perfect reflection of your perceived stimulus," says Logothetis.

Influences everywhere. The observation suggests that the "neural mechanisms underlying visual awareness are actually distributed over the entire visual pathway," Logothetis adds. "One could have thought that a sensory pathway just does its job, and awareness is the business of some other center, but this does not seem to be the case at all." However, the question remains: Are the neural responses that the researchers see throughout the visual cortex actually shaping the animal's perception, or are they somehow shaped by it?

Andersen notes that an experiment performed by William Newsome and his colleagues at Stanford University in 1991 suggests that neural activity in a midlevel area like MT can indeed influence perception. In that experiment, monkeys were given a task of telling whether, in a field of randomly moving dots, a subset of dots was moving up or down. The researchers deliberately made the task very difficult, so the monkeys were uncertain about the dots' movement, and got the answer wrong almost as often as they got it right. But Newsome's team found that stimulating neurons in MT that registered movement in a particular direction, "up," for example, biased the monkeys' decision in that direction, suggesting that these MT neurons actually shape perception. Stimulating MT neurons while the animal is viewing the bistable percept might shed light on whether MT is creating or just reflecting the monkey's perception in that case as well, Andersen suggests.

Researchers working on human perception can't use electrodes to determine whether individual neurons in the human visual system display the same traces of perception. But brain-imaging techniques such as positron emission tomography or functional magnetic resonance imaging offer a coarser look at activity in entire visual areas. And in at least one experiment, researchers have found activity in MT that correlates with the subjects' perceptions when they experience visual illusions, as Andersen and Logothetis found in monkeys.



The mind's eye. Monkey experiments suggest that the neural activity in the visual cortex changes when the image perceived shifts from the faces to the vase.

Several years ago, Roger Tootell and his colleagues at the Massachusetts General Hospital Nuclear Magnetic Resonance Center imaged the brains of subjects as they watched an expanding grid on a screen. When the grid stopped expanding, the subjects experienced an illusion called the "waterfall effect," the same effect experienced when you shift your gaze from a continuously moving image such as a waterfall to a stationary image: The new image appears to move in the opposite direction. The Boston researchers noticed that during the time the subjects experienced the illusion, activity continued in MT and other motion-sensitive areas of the brain. That, says Tootell, is consistent with the notion that the activity is creating, or at least contributing to, the illusion. Or, as he puts it, "the neural firing *is* the consciousness."

Top-down processes such as attention can shape perception just as powerfully as the involuntary bottom-up brain mechanisms that generate illusions. We all know the experience of paying such close attention to a gripping passage in a book or a friend's captivating conversation that we are oblivious to other activity going on around us. Indeed, one of the main things attention does is filter out unnecessary information and sharpen our perceptions of the things we are attending to. For the past decade, a number of labs have been working to understand how visual attention modifies neural responses to get this job done.

In 1985, Robert Desimone, of the National Institute of Mental Health (NIMH), and his then-student Jeffrey Moran were the first to show the influence of attention on neurons in the early processing stages of the visual cortex. They trained monkeys to keep their eyes fixed on a spot in the center of a screen, while the researchers recorded the electrical activity of individual neurons in the visual processing area called V4. This area contains neurons selective for color and form, and is one of the early stops for visual information as it makes its way along the so-called "what" pathway, which analyzes images for their identity.

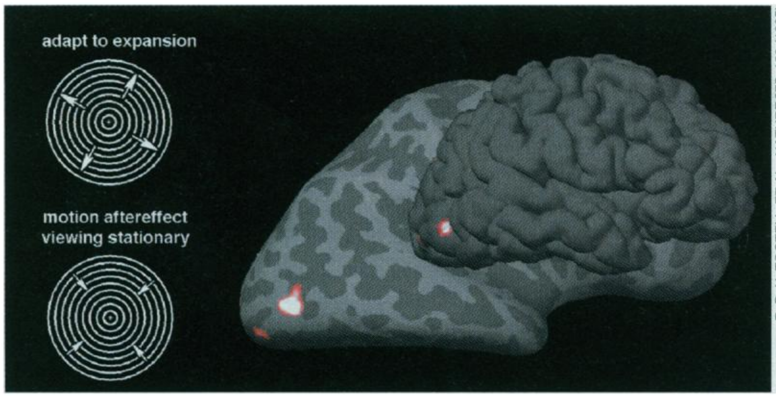
Color cues. Attention to red objects enhances a monkey neuron's response to the red bar in its receptive field (oval). When the monkey pays attention to green, the response to the red bar drops.

B. C. MOTTER, *J. NEUROSCIENCE* 14, 2178 (1994)

Neurons in V4, like all visual cortical neurons, have receptive fields—areas of the visual scene that they monitor for features they can respond to. In a typical experiment, Desimone and Moran adjusted the visual image on the computer screen so that two objects, one red, one green, lay within the receptive field of a red-sensitive neuron from which they were recording. Then they had the monkey perform a task that required it to pay attention to the red object. In that case, Desimone says, "the cell gave its normal good response to red." But in subsequent trials when the animal was required to attend to green, the neuron would be silent, a surprising result, because a red object was still in its receptive field. It was "as though the red had been filtered out" by the animal's attention to the green, Desimone says.

More recent experiments by neuroscientist Brad Motter at the Veteran's Affairs Medical Center in Syracuse, New York, have traced this attention-driven shift in real time by having monkeys switch their attention from one color to another in the middle of an experimental trial. That "showed in a very impressive way that you can have these effects switch on and switch off," Baylor's Maunsell says. And Maunsell and his then-postdoc Stefan Treue last year detected the neural effects of attention in another branch of the visual system, known as the "where" pathway because it focuses on an object's location in space.

Indeed, following Desimone and Moran's milestone experiment came a flood of studies confirming that an animal's choice of how to direct its attention influences the responses of neurons throughout the visual-processing pathways. Researchers don't all agree on how that happens, and labs are busy testing the competing hypotheses. But there is a common thread: "The monkey's sensory processing is being controlled by an idea of what it is looking for," says Motter.



R. B. H. TOOTELL *ET AL.*, *NATURE* 375, 139 (1995)

Traces of an illusion. The movement-sensitive visual area, MT, is active in human subjects experiencing an illusion of movement after staring at a moving grid *(left)*. In the larger brain view, the folds have been flattened.

As with the perception experiments, the monkey results on attention have been paralleled in humans. In a 1990 experiment, Steven Petersen of Washington University in St. Louis and then-postdoc Maurizio Corbetta presented human subjects with a collection of moving colored objects and asked them to discriminate among them based either on shape, color, or movement. Although the images were the same in all cases, the brain activation pattern varied depending on which feature the subjects were attending to. Paying attention to motion caused the greatest activation in the apparent human equivalent of MT; when the subjects attended to color, the area thought to be the human equivalent of V4 lit up brightest; and when shape was the focus, the researchers found that the greatest activation was elsewhere along the "what" pathway.

Other researchers have added to that finding. For example, Leslie Ungerleider, James Haxby, and their colleagues at the NIMH showed subjects sequential sets of faces and asked them to determine whether the faces belonged to the same person, or alternatively whether they were in comparable positions relative to the edges of the box that framed them. When the subjects were paying attention to the identity of the faces, their "what" pathway was more active, and the "where" pathway lit up brightest when the position of the faces was key.

Seeking the command center. But where in the brain does the attention-directing command come from? Attention, says Caltech's Koch, can be thought of as a way to "provide a compact representation of what is currently important to me in my environment, and to make this accessible to my planning" of whatever task needs to be done. And so, he and Crick reason, the orders telling the rest of the brain what to pay attention to must originate in the areas in the front of the brain that are responsible for planning, such as the prefrontal cortex.

Following up on this idea, Koch and Crick have hypothesized that the neurons in the visual cortical areas whose responses are changed by attention are the ones that receive inputs from the front of the brain. There is no evidence yet to support that hypothesis, but Motter says the timing in his experiments is consistent with such an idea. When he prompted monkeys to switch their attention, he says it took 150 to 300 milliseconds for the neurons in V4 to shift their responses. That, he notes, was ample time for a visual signal to "go quite a ways into the system," for example, up to the prefrontal cortex or other attention-directing areas and then back down to V4.

Where the attention signal comes from and how it is broadcast to the various visual processing areas are only some of the countless questions that have been raised by the experiments so far. Indeed, the results, which show that attention can shift neural responses in relatively early visual processing stages like MT and V4, combined with the findings from the illusion experiments that the activity of neurons in those areas correlates with actual perceptions, create the tantalizing suggestion that those neurons are, at least in part, responsible for driving our perceptions. But so far, that is only a correlation; proof would require selectively silencing or stimulating those neurons, extremely difficult experiments that are just getting under way.

"We don't claim to have answered the problem of how you are visually aware of things," says Baylor's Logothetis. "But we are quite happy with the answers we have so far." And focusing on visual awareness has not only brought researchers one small step closer to understanding the mysteries of consciousness; it has finally given the word a legitimate place in the neurobiologists' lexicon.

–Marcia Barinaga

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