ERIC KANDEL: FROM MIND TO BRAIN AND BACK AGAIN

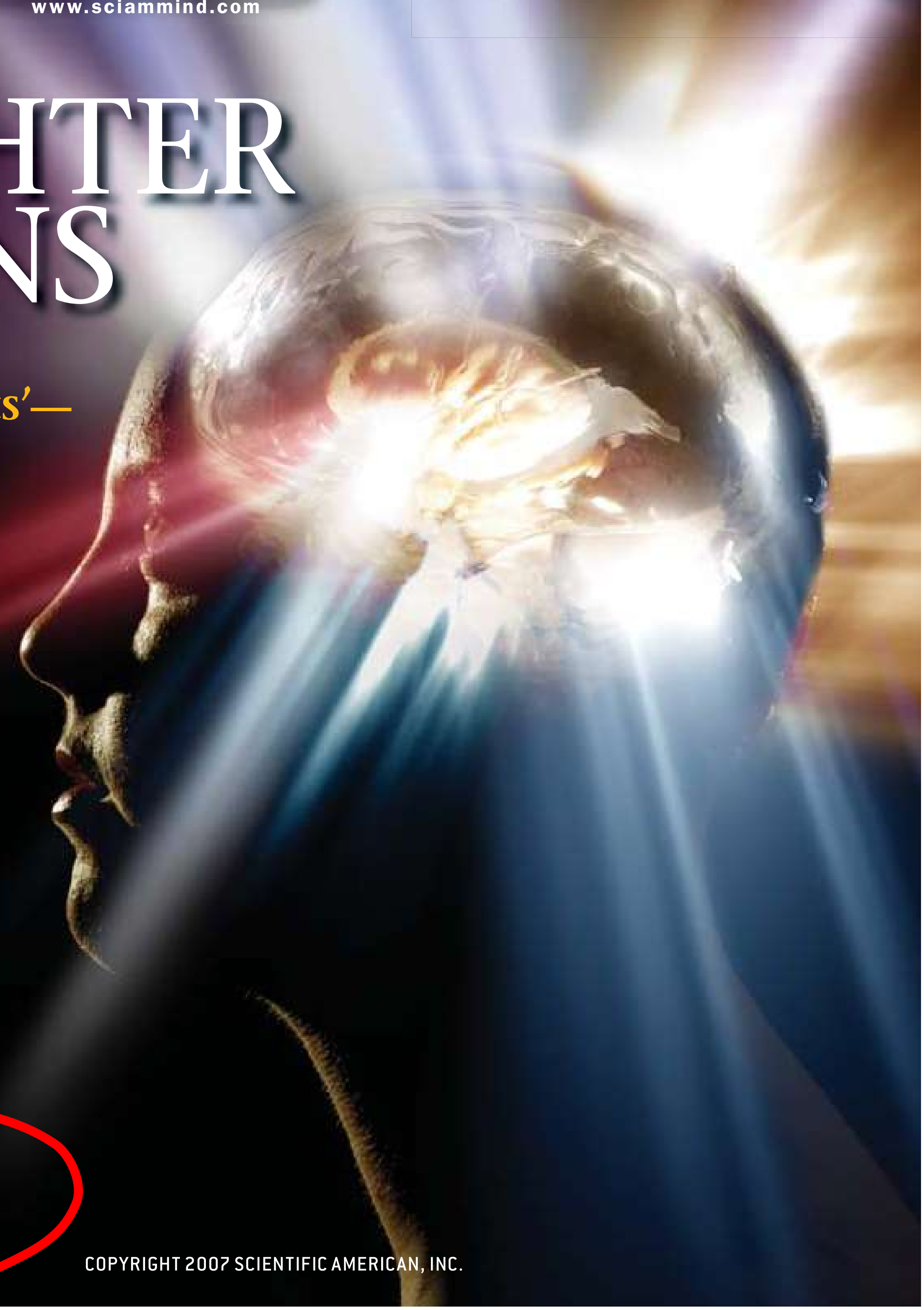
SCIENTIFIC AMERICAN MIND

THOUGHT • IDEAS • BRAIN SCIENCE

October/November 2007 www.sciammind.com

In Search of the God Spot

page 38



BRIGHTER BRAINS

Your IQ is higher than your parents'—which is higher than your grandparents'. Here's why.

PLUS:

Therapy 2.0

Smart Eating

Brain Stains

Skewed Vision

IMAGES.COM/CORBIS

Skewed Vision

Seeing things clearly, new evidence suggests, may be even harder than we thought

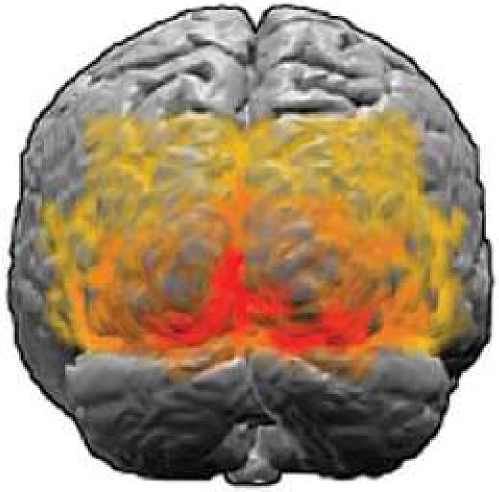
By Susana Martinez-Conde

My grade school in Spain had a color-coded system for test scores: "A" was red, "B" was blue, "C" was green and "F" was brown. So the color distribution in your academic chart revealed at a glance how well you were doing in your various classes. One result of this system was that red and brown became, respectively, my favorite and least favorite colors as a child.

This story is one of many examples of how an essentially neutral visual stimulus (the color red in this case) may become associated with a reward value (a good grade). From this information it is easy to predict that neurons in the brain's reward-processing system—a network of areas connecting the "thinking" cortex to the emotional centers in the brain's limbic system—may be activated by the physical properties of those sensory stimuli that come to be associated with rewards. We learn to associate certain stimuli with positive feedback; thus, my brain's reward centers learned to react happily to red.

(The Author)

SUSANA MARTINEZ-CONDE is director of the Laboratory of Visual Neuroscience at the Barrow Neurological Institute in Phoenix, where she studies visual perception, attention and visual illusions.



The primary visual cortex (*red*) was long thought to passively record unfiltered information from the eyes. New findings suggest that its role in the vision process is not quite so simple.

That this elemental learning system works so consistently is not terribly surprising. Less intuitive, however, is a phenomenon that was recently described in *Science* by cognitive neuroscientists Marshall G. Shuler and Mark F. Bear of the Massachusetts Institute of Technology. Working with rats, rat goggles and a water bottle, Shuler and Bear discovered that neurons in the brain's primary visual cortex—an area long thought to process purely sensory, value-free visual information before sending it on to other brain areas—can modulate their response as a function of expected reward. This finding sharply revises the standing view of vision's basic underlying mechanisms. Neurons in the primary visual cortex, once considered to be neutral collectors of features in the visual field, are in fact subject to complex cognitive influences. Even at the most fundamental level, it seems, our expectations shape how we view the world.

FAST FACTS

Believing Is Seeing

1» Scientists have long believed that the brain processes visual scenes in a series of hierarchical stages: from the simplest kinds of neutral assessments (such as color and contrast), made in the primary visual cortex at the outset of the visual-processing chain, to the more subtle value judgments that are made "higher" in the system.

2» New research shows that, in fact, the primary visual cortex is subject to complex cognitive influences.

3» Even at the most fundamental levels, our expectations shape how we view the world.

Hierarchy of Visual Understanding

Vision seems as if it is an immediate and simple system: you open your eyes and see. Yet the traditional view, established through decades of painstaking work, is that what we "see" is actually constructed by a hierarchical series of processing stages, each dealing with an increasingly complex aspect of perception. According to this scenario, neurons in the primary visual cortex—early in the visual-processing chain, just two stages after the retina becomes involved—are concerned primarily with distinguishing simple attributes such as contour and contrast. That information is then passed to higher visual areas that can process and interpret more complex stimuli such as hands and faces. Meanwhile neurons in "association areas" of the cortex integrate visual information with stimuli flowing in from other senses, such as hearing, and with cognitive processes such as attention, motivation or expectation.

Shuler and Bear challenge this traditional view by showing that neural activity in the brain's primary visual cortex, also known as V1, predicts with high accuracy the expected timing of rewards associated with various simple visual stimuli. In short, the visual cortex's response can vary depending on what the reward system expects, suggesting it plays a role in evaluating, rather than simply relaying, basic information. A supposedly clear window, as it were, turns out to be a sort of filter that colors what passes through it.

The experiment was quite clever. Shuler and Bear implanted rats with microelectrodes that recorded the activity of neurons in the primary visual cortex, then fitted the animals with head-mounted goggles that could create quick flashes of light in either eye. The researchers programmed the goggles to deliver a flash to the left eye or the right eye as the rats nuzzled a water tube. When the flash was presented, the animals had to lick the tube to obtain their reward: a drop of water. If the left eye was stimulated, water could be obtained more rapidly: the rats needed to lick the water tube half as many times as when the right eye was stimulated. Thus, the experimenters paired left-eye stimulation with a short wait for reward and right-eye stimulation with a relatively long wait.

In animals new to the experiment, all neuronal responses recorded were related to simply en-

It would be exciting to explore the ways in which the expectancy of reward may distort or bias perception.

coding the visual stimulus's physical properties, such as the onset of the flash, its duration, or which eye it flashed in. That is, the first couple of times the flash went off, the neurons responded to the stimulus—the flash—but did not differ in their response depending on which eye the flash was in or how long it took to get the reward. This result in naive rats (rats who had not learned the associations between flashes and reward timing) matched the classical conception of the primary visual cortex as a region that serves solely as a detector of visual features.

Primary Processing Gets Smart

After an animal had done the task three to seven times, however, about half its visual cortical neurons (43 percent on average) responded differently depending on whether the right or left eye got the flash; the neurons had learned that a flash in the left eye predicted a quicker reward than a flash in the right eye did. Once this expectation was established, the difference in neuronal activity occurred whether or not the actual reward appeared—that is, the V1 neurons responded differently to left and right flashes even if the water bottle did not deliver water.

Creating these unrewarded events was necessary because the lag between flash and bottle lick was often quite short (rats are fast), making it hard to know for certain that the rat was reacting to an expectation created by the flash rather than to the different reward itself. And indeed, these unrewarded flashes showed different responses, confirming a learned expectation. The primary visual cortex, in short, appeared to be able to exercise associative cognitive processes previously credited solely to higher cortical areas and wider networks. Those basic V1 neurons are pretty smart after all.

In a subsequent experiment, Shuler and Bear compared neuronal activity in "within-task" versus "outside-task" recording sessions, putting the experienced rats through trials in which the water tube was obstructed and in which no water reward was available. They wanted to see if the reward-response effect learned in the earlier trials would continue in that case. If it did, it would indicate not only that primary visual cortex circuits can create cognitive associations but also that those associations could be long-lasting. They found that these associations did persist. Once the tube was obstructed, the rats generally did not bother to approach it. Yet their previously trained primary visual cortical neurons continued to show reward-timing activity in response to the visual stimulation. This finding suggests that the alterations in neuronal responses produced by pairing a visual stimulus with a reward both persist and generalize to new contexts.

Hopes Spring Eternal—and Early

These discoveries hold multifaceted implications. As already noted, they challenge the traditional belief that the primary visual cortex is a visual area concerned strictly with low-level analyses of stimulus features. They also demonstrate that neurons in the primary visual cortex of adult animals have an unexpected degree of plasticity and can retain long-term effects.

I find especially intriguing a third aspect of this work. Reward expectation is a force driving our behavior: we tend to repeat actions that promise reward and avoid actions that promise no reward. Shuler and Bear have now shown that reward expectation plays a major role not just in shaping behavior but also in eliciting perceptual responses of neurons at the very early stages of visual processing. This demonstration suggests that our basic visual perception may be influenced at its most fundamental level by cognitive factors such as reward or attentional load. It would be exciting to see follow-up studies exploring ways in which the expectancy of reward may distort or bias perception or even create reward-based visual illusions. Such work could greatly improve our understanding of everyday decision making and of perceptual mistakes or anomalies. It could also throw light on impairments such as drug dependencies and other types of addictive behavior that involve the brain's reward pathways. That would be a rewarding result indeed. **M**

Each week in Mind Matters, www.sciammind.com's expert-written "blog seminar," researchers of mind and brain explain and discuss their disciplines' most notable recent findings. In this installment, Susana Martinez-Conde considers the finding that expectation colors what we see.

Mind Matters examines a new finding every week. Join the discussion at www.sciammind.com

(Further Reading)

- **Reward Timing in the Primary Visual Cortex.** Marshall G. Shuler and Mark F. Bear in *Science,* Vol. 311, pages 1606–1609; March 17, 2006.