

NEUROSCIENCE

Researchers Find Neurons That May Help Us Navigate

Walking a straight line or steering a car down a road may seem effortless, but your brain has to perform a difficult computation to keep you on course. Oncoming objects provide plenty of clues to where you are heading as their images appear to expand from a central point in the visual field. But that point doesn't stay fixed on your retina, because your eyes are continually moving about, drawn to street signs, interesting scenes, or people or animals crossing your path. Exactly how the brain compensates for these shifts, keeping track of your heading, has been unclear. Now results reported on page 1544 by a research team led by Richard Andersen at the California Institute of Technology and Martin Banks at the University of California (UC), Berkeley, may help clarify the mystery.

The researchers have found neurons that may serve as the brain's heading computation center. Working with monkeys, they have shown that the neurons in question, which are located in a part of the brain's visual system called the medial superior temporal (MST) area, can combine visual information with information about eye movements to calculate the correct heading. The result provides "a foot in the door toward understanding how the brain combines information from different sensory modalities ... to give you a sense of where you are going in space," says neurophysiologist Charles Duffy of the University of Rochester in New York. "The exciting thing about it," he adds, "is that these messages are being combined in single neurons to resolve complicated sensory information processing issues."

The finding builds on work done in the late 1980s, when cognitive scientist William Warren of Brown University in Providence, Rhode Island, followed within a few years by Berkeley's Banks and others, explored the question of how the brain computes a heading in human subjects. In the experiments devised by Warren's group, subjects were seated with their heads fixed motionless. They faced a wide computer screen that showed an expanding image, which gave them a sensation of moving through space. In some trials, the subjects were asked to move their eyes to track the movement of a marker across the screen. In those cases, although the expanding image from the computer screen was shifted on their retina by the eye movement, their brains made the necessary correction, and they could still identify the correct heading direction, as defined by the center of expansion on the screen.

In other trials, the experimenters eliminated any nonvisual clues that might come from the movement of the eyes. In this case, the subjects kept their eyes fixed on one spot on the screen, but the computer modified the screen image to simulate what the retinal image would look like if the eyes were sweeping across the screen. As in the first trial, the center of the expanding image was shifted on the subjects' retinas, but because there was no real eye movement, the brain had to rely solely on the movement of the retinal image to try to work out a heading.

Under some conditions, Warren found that the subjects could still correct for the simulated eye movement, even when their eyes didn't move. But under slightly different conditions, Banks found otherwise. When his subjects' eyes were still and the computer swept the expansion point across the image, they saw themselves traveling on a false path that curved away from the actual heading. From those experiments it is clear, says Warren, that "extraretinal information from eye movement makes a useful contribution" to the brain's heading calculation.

Andersen had spent the past 15 years studying how the brain combines eye movement information with visual information to locate stationary objects in space and suspected that the same sort of integration may be occurring when the brain calculates heading. So his group teamed up with Banks to search for neurons that might be making the heading computation. The researchers were drawn to the MST because Robert Wurtz and his colleagues at the National Eye Institute had found neurons there that had the necessary characteristics: They are sensitive to expanding images generated on the retina by movement through space and also to non-retinal information about eye movement. Wurtz's group hadn't shown how the MST neurons use that information, but Andersen

postdoc David Bradley says it seemed reasonable that "if a neuron were clever enough, it might be able to combine these two pieces of information to solve the heading problem."

To see whether the MST neurons are indeed clever enough, Bradley and his colleagues in Andersen's lab, graduate student Marsha Maxwell and postdoc Krishna Shenoy, recorded the electrical activity of the neurons in monkeys as the animals watched the same heading simulations shown to human subjects in earlier experiments.

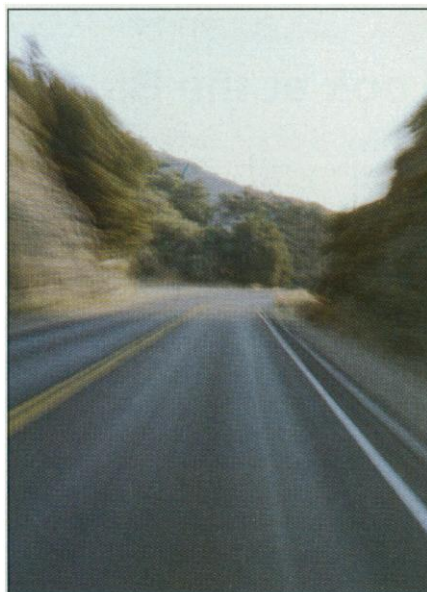
Each neuron fires most strongly when the center, or "focus," of an expanding retinal image is in a particular part of visual space, and its intensity of firing diminishes as the focus is shifted away from that area. So, in each run of the experiment, the team first identified the response of a given neuron to a particular heading, as defined by a focus location on the screen.

Next, while keeping the heading constant, they added either a real or simulated eye movement that shifted the focus by 30 degrees on the monkey's retina. Just as in the human experiment, the researchers got the monkeys to move their eyes by having them track a marker across the screen; for the simulated eye movement the monkey held its

eyes still, but the computer distorted the screen image to simulate the eye movement. If the neurons were compensating for the real or simulated eye movement, the researchers reasoned, they should continue responding as if the heading were unchanged; if they were not compensating, their firing should shift intensity as the image shifted on the retina.

In the trials in which the animals' eyes actually moved, nearly half of the neurons tested compensated for the eye movement and continued the same firing rate in response to the true heading being simulated by the computer. But when the monkeys' eyes were still, and the movement was just simulated by the screen image, the neurons' firing rate shifted, as if the neurons had lost track of the true heading. "These neurons [need] some sort of signal that tells them when the eye is moving," says Bradley. "If you deny them that signal, they can't compute the heading anymore."

"I'm sure they're right," said Rochester's



Fast forward. Brain neurons deduce our heading direction by sensing the center of an expanding visual image, such as this one.

D. BRADLEY

Duffy upon hearing of the experiment. Indeed, Duffy has good reason for saying that—he and Wurtz have an unpublished study with results similar to Bradley's.

To prove that these heading-sensitive neurons in the MST really are helping the brain compute heading, researchers in the field would like to see evidence that artificially changing the neurons' responses changes a monkey's perception of heading. They may soon get their wish. In recent unpublished experiments, UC Davis neurophysiologist Ken Britten put monkeys through tasks in which the animals had to discriminate between two simulated headings that were similar enough to make the animals very uncertain about the

answer. Under those conditions, Britten's group found they could bias the monkeys' answers toward a particular heading choice by stimulating the MST neurons known to prefer that heading. That is "pretty good evidence," says Warren, that MST neurons "play a functional role in that type of judgment."

How these neurons get their information about eye movements is still unclear, however. It might come in the form of a copy of the neural signal that tells the eyes to move, or alternately the signal could arise from neural sensors activated by the muscle contractions that actually move the eyes. And then there is the question of whether the MST neurons can compensate for the head move-

ments that normally accompany eye movements, a question that the teams of Andersen and Banks plan to address next.

But while not all the questions have been answered, the experiment has shown unequivocally, Andersen says, that the heading neurons "definitely use an eye movement signal to perform the computation." And that, says Warren, is a very satisfying result: "We have evidence [from the human experiments] that extraretinal information helps solve the problem, and they have now come up with a potential physiological basis for that." And therein may lie the answer to how you can enjoy the scenery without driving off the road.

—Marcia Barinaga

POPULATION

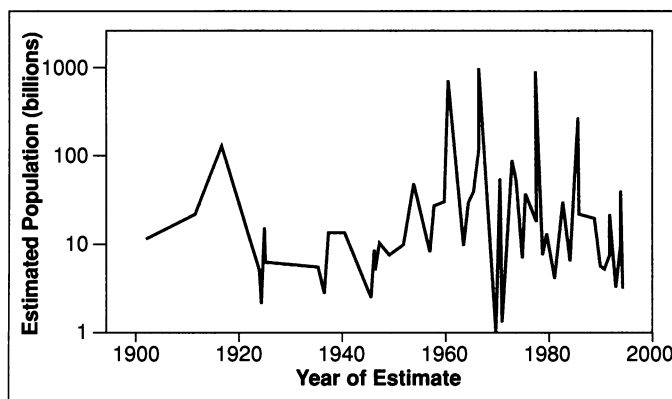
Ecologists Look at the Big Picture

How many people can the Earth support? The answer depends in part on how much land, water, and energy are available, so ecologists have often sought a solution using the same tools they apply to natural systems: looking at current patterns of food production and resource use, then extrapolating. But estimates have ranged from 1.5 billion to as many as 1 trillion people, depending on standard of living, new technologies, and so on.

At a crowded session on human population at the recent ecology meetings,* several speakers noted that resolution may come from a broader approach that includes social and economic dimensions. The bottom line, they say, is that human beings can choose to consume less and so boost Earth's carrying capacity. Such analyses are expected to yield a more realistic outlook and a bleak view of the choices ahead, suggesting, for example, that long-term prospects for maintaining the American lifestyle—or extending it to the nearly 6 billion people now on Earth—are grim.

This may seem all too obvious to some, but it is a novel idea when applied to this question, for most models of carrying capacity have assumed level or increased consumption, notes Cornell University agricultural scientist David Pimentel. The new analyses, he says, "are the first to consider reduced consumption as a realistic option for the future." And while previous models chiefly dealt with a defined set of

ecological resources, the new studies wrestle with a dizzying array of variables, from modes of transport to amount of waste generated. "The natural sciences are valuable," says population biologist Joel Cohen of Rockefeller University in New York City. "But they can't stand alone." Yet for all the touted virtues of interdisciplinary work, this new style of analysis has yet to yield hard estimates of just how



Crowd capacity. Estimates of how many humans can live on Earth have fluctuated from 1 billion to 1 trillion and show little sign of stabilizing.

many people can live on Earth.

Scientists anxiously watching population shoot up have been trying to calculate Earth's carrying capacity for centuries. But as Cohen noted in his talk, the resulting numbers haven't converged over time. For example, Stanford University biologists Paul Ehrlich, Anne Ehrlich, and Gretchen Daily recently estimated optimal population at about 1.5 billion, while in 1994 Paul Waggoner of the Connecticut Agricultural Experiment Station estimated that Earth could support 1 trillion people, assuming improved agriculture.

Cohen argues that many analyses have come up with wildly different figures because they rely on simple biological parameters, such as the amount of arable land per capita,

then extrapolate. That ignores the human choices that influence these parameters at least as much as natural constraints, he says. A billion beef-eaters require much more land than a billion vegetarians, for example, and people may change their preferences as resources become scarce. "Ecological limits appear not as ceilings but as trade-offs," says Cohen, who is now assessing the consequences of such trade-offs. For example, cotton clothes use fewer resources than wool, which requires land for raising sheep.

Similarly, population biologist William Rees of the University of British Columbia presented another type of model that takes into account how a society's choices may affect its "ecological footprint"—the area of productive land needed to support it. His analysis suggests that each American leaves at least a 5.0-hectare footprint, each Canadian 4.3 hectares, and most Europeans 3.5 hectares. To bring the developing world up to the living standard of Canada, assuming available technology, would require two more planet Earths, says Rees.

This approach, marrying natural constraints with human economic choices, gets high marks from some. "Mr. Cohen's reasoned resolution of the issues points the way to a reconciliation" of diverse estimates, says Harvard University sociologist Nathan Keyfitz.

But Cohen is so convinced that estimates of carrying capacity are elastic, depending on standard of living, that he won't give a numerical estimate—a position that draws scorn from other scientists. It's "not helpful in the policy arena," says Ehrlich, who claims that his own work also incorporates social variables, although not in the same detail. "Science draws conclusions, and he draws none," Ehrlich says. But there is at least one point on which Cohen and his critics can agree: There are some serious limits to sustaining the lifestyles common in the developed world.

—Anne Simon Moffat

* Meeting of the Ecological Society of America, 11–14 August, Providence, RI.