NEUROSCIENCE

The Mapmaking Mind

Studies in monkeys are revealing how the brain manipulates maps of sensory information to guide our movements through the world around us

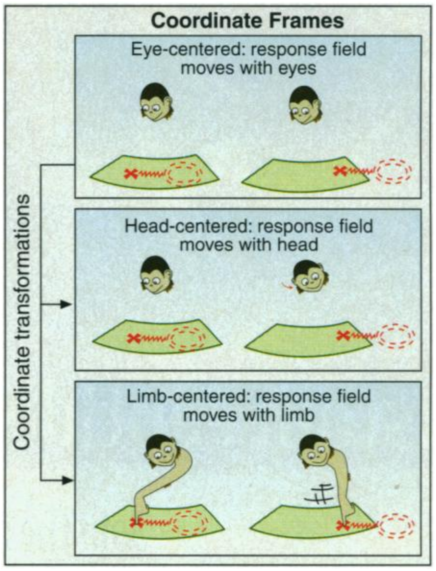
You are eating a meal. Never shifting your gaze from your dinner companion, you spot your wine glass out of the corner of your eye, reach for it, and take a drink. Casting a glance to your plate, you spear a piece of meat with your fork and bring it to your mouth. Making these movements seems simple—just a matter of using your eyes to direct your hands. But that impression belies the complex manipulations of visual information that your brain must perform before it can guide your activity.

"If you could only process information that came out of the optic nerve, you would never be able to localize objects in space," says neuroscientist David Sparks of Baylor College of Medicine in Houston. That's because the images that fall on your retina are of limited use for finding the objects themselves, unless the brain knows the orientation of your eyes in your head, and of your head on your shoulders. The same is true for information received through other senses, such as hearing: Each one delivers a map of the world that must be transformed before it can guide motor activity.

In a series of recent experiments, including one described on page 257 of this issue, neuroscientists eavesdropping on neurons in monkeys are learning how the brain manages this feat. They are finding that as the brain passes information along the pathway from sensation to movement, it modifies the maps, adding information to them and replotting them in coordinates that are useful for the movements it needs to direct. The experiments have pinpointed areas where the transformation is largely complete, and areas where it appears to be in process. And they suggest that the default frame of reference in the primate brain seems to be the visual world, perhaps reflecting an overriding importance of vision among the senses.

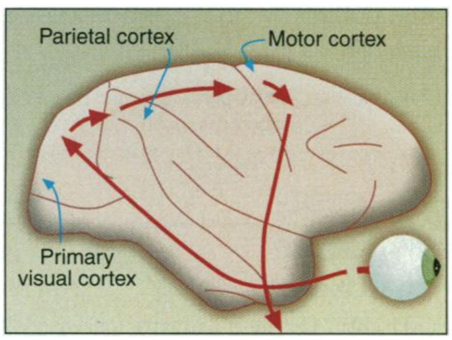
"It is a fascinating area" of research, says neuroscientist Richard Andersen of the California Institute of Technology, the senior author on the *Science* paper. "It has to do with the whole issue of how we perceive the world as stable, and how we can adjust our movements" to interact with it, even though our eyes and bodies are never still.

Researchers have known for decades that many of the brain areas that first receive sensory information are organized spatially in a way that resembles a map of the sensory world. Sensory neurons have so-called "receptive fields"—locations that they survey and to which they respond. Visual neurons, for example, respond to particular patches of the retina, and all their receptive fields together describe a map of the retina. In brain areas that respond to touch, the neurons' receptive fields map out the surface of the skin; auditory neurons map the three-dimensional space around the head. But, just as a street map won't help you find the highest spot in town unless someone adds elevation data, those sensory maps don't have all the information the brain needs to direct the body's interactions with the world.



Frames of reference. The brain contains maps of the world in various coordinate frames.

Indeed, even keeping track of an object in the visual world requires constant remapping, as eye movements shift the position of the object on the retina. Early evidence of this remapping came in 1980, when Sparks, then at the University of Alabama, and postdoc Lawrence Mays were studying neurons in the superior colliculus, a part of the brain stem that directs eye movements. The neurons there have a memory for visual targets, which the brain uses to direct the eyes to objects. For example, when monkeys are trained to shift their gaze toward a target that flashed somewhere in their peripheral vision a moment earlier, collicular neurons begin to fire as soon as they detect the target in their receptive fields, and they keep firing even when the target disappears, holding the memory of its location in retinal map coordinates. The brain uses those remembered coordinates to calculate the direction and distance it needs to shift the eyes to look at the spot.



From seeing to acting. Pathways in the brain.

CREDITS: (TOP) CHRIS HEDRICK; (BOTTOM) AARON BATISTA

Sparks wondered what would happen to that memory of retinal position if the monkey's eyes took a detour on their way to the target location, rather than going there directly. Such a move would shift the position of the remembered target relative to the retina, so that it would fall on a different patch of retina, surveyed by different collicular neurons. The brain would need to incorporate that shift into its memory of the target, in order to move the eyes correctly to the spot where the target had been.

To see how the brain would compensate for the shift, Sparks trained monkeys in a task that inserted an intermediate eye movement. While they sat with eyes fixed ahead, two spots appeared in their peripheral vision and then disappeared. After a brief wait, the monkeys looked first to the location of one spot, then to the location of the other.

While the monkeys did this, Mays recorded the activity of a particular set of neurons, those whose receptive fields covered the spot on the retina where the second remembered target would fall once the monkeys' eyes had made the first move. Those neurons never actually sensed the spot of light, because by the time the eyes moved, it was gone from the screen. But they seemed to get the message that the location of the remembered target had shifted into their receptive fields, because as soon as the eyes moved, they began to fire, marking the new retinal position of the target. That result, Sparks says, showed that collicular neurons receive information about the position of the eyes and use it to adjust their map of the world, providing "an updated signal of the movement required to look to the spot."

Such remapping within an eye-based reference frame may be all the brain needs to shift the eyes to a visual target. But how does an animal direct its eyes to an object it has heard, not seen? In 1984, Martha Jay, a student with Sparks, found that the superior colliculus transforms other types of sensory information into an eye-based reference frame, apparently in preparation for moving the eyes. She trained monkeys to look toward the source of a sound in a dark room while she recorded from sound-responsive collicular neurons. If those neurons were behaving like pure auditory neurons, and simply localizing the sound source with respect to the head, it shouldn't matter where the animals' eyes were looking, Sparks says. "But that's not what we found."

Brain power. Maps in body coordinates help these soccer players head the ball.

CREDIT: O. MARTINEZ/ALLSPORT MEXICO

When Jay got the animals to shift their gaze, neurons that had responded to the sound in previous trials gave no response, and other neurons instead became active. That finding suggested that the neurons used data on eye position to generate an eye-based map of the sound source, containing the information necessary for the monkey to look to the sound.

More recently, researchers have studied how the brain remaps sensory information into frames of reference tied to a limb—which is what has to happen before you can, say, reach for a glass of wine. In 1994, Michael Graziano, working with Charles Gross at Princeton, mapped the receptive fields of monkey neurons in the premotor area, which helps control limb movements. Others had shown that neurons in this area respond both to visual stimuli and to touch, and Graziano found that the responses were closely linked. If a neuron responded to touches on a particular area of the body, it also fired when visual objects came within 20 centimeters of that area. "The neuron seems to be interested in a chunk of space near the body, near the tactile representation," says Graziano. "Anything entering that chunk of space will activate the neuron."

When Graziano then had the monkey shift its gaze to a different place, the same neurons continued to respond to objects near the same locations on the animal's arm, even though the image of those objects now fell on a different part of the retina. "[Normally] a visual receptive field would move when the eye moves," says Graziano. "But these don't. The visual receptive field is anchored to the tactile receptive field." Such maps aren't limited to the hands and arms; Graziano and Gross checked the premotor area that controls head and facial movements, and found similar maps there. Soccer players provide a good example of how important this information can be, he says. In the midst of play, he notes, "they have to encode the position of the ball relative to each of their body parts—head, knee, foot," and premotor maps such as those he found can help them to do just that.

Discoveries like these show that, in many cases, by the time sensory information reaches brain areas near the end of the sensation-to-movement path, it has been translated into map coordinates that can guide the movements those areas control. But earlier in the processing path, in a brain area called the parietal cortex, researchers have found a fascinating mixed-bag of transformations.

In some cases, major map transformations have been made by the time the information reaches the parietal cortex. Last year, for example, Jean-René Duhamel and Carol Colby, then postdocs with Michael Goldberg at the National Eye Institute, found a radically transformed visual map in a parietal area called the ventral intraparietal area (VIP). This location seems to be involved in locating objects with respect to the head and face. Some neurons in VIP respond to touch sensations on the head and face, and also have visual receptive fields that—like those Graziano and Gross found in the premotor area—"remain tied to a portion of the skin surface" regardless of which way the eyes are looking, says Colby, who is now at the University of Pittsburgh.

In other cases, the parietal maps seem only partially transformed, like a work in progress. Brigitte Stricanne and Pietro Mazzoni, students in Andersen's lab when he was at the Massachusetts Institute of Technology, reported in 1996 that sound-sensitive neurons in the lateral intraparietal area (LIP), which keeps track of objects that are possible targets for eye movements, encode the location of a sound source in eye-based coordinates. Although that finding is reminiscent of Jay's and Sparks's results in the superior colliculus, this map seemed to be incomplete. "It was predominantly eye-centered, and that was consistent with what was found in the colliculus," says Andersen, "but there were also cells that weren't in eye-centered coordinates … and there were cells that were intermediate. That suggested to us that the transformation could actually be taking place there. But we don't know that for sure."

Andersen and his team expected they would also find at least a partial remapping of visual information in the parietal reach region (PRR). Identified in 1997 by Larry Snyder, then a postdoc in Andersen's lab, this region seems to specialize in tracking objects that the animal can reach out and grasp. Some PRR neurons track those objects visually, and Andersen and Snyder expected that these neurons' receptive fields would be "limb-centered"—linked to a spot on the animals' arms or hands. After all, says Andersen, "to move your hand to a target, you need the location of the target with respect to the limb." But as the team reports in this issue, that turned out not to be the case.

Graduate student Aaron Batista and postdocs Snyder and Chris Buneo trained monkeys to hold their eyes still while one of several buttons in front of the monkeys lit up briefly, and then—after a pause—to reach out and push that button. The researchers identified PRR neurons that fired during the waiting period, marking the location of the target. Then they had the monkeys fix their eyes in a new direction and repeated the task two ways. In one case, they had the monkey reach to the same button. That used the same arm movement as before, but because the animal's eyes had moved, it put the target at a different retinal location. In the other case, the monkey reached to a different button, chosen because its image fell in the same place on the retina as the first button had before the eyes moved.

The results, reported on page 257, show that after the eye movement, the same neurons responded only when the reach target occupied the same retinal location, even though the direction of the reach had changed. That shows the PRR neurons' receptive fields are tied to retinal, not limb, coordinates. The findings may reflect an economy on the part of the brain, says Snyder, who is now at Washington University in St. Louis. The PRR pays attention to objects that might be targets for reaching, he says, but it "makes perfect sense" that "if there are 20 things out there that you can reach for, you aren't going to want to transform every one of those into reach coordinates" before you know which one you're actually going to reach to. The brain might wait until later in the processing stream to make the transformation, when there's been a decision to reach for a particular object.

Other things being equal, in fact, the primate brain seems to favor keeping its maps in visual coordinates. An unpublished study from Andersen's lab underscores the dominance of vision in mental mapmaking: Former postdoc Yale Cohen, now at Dartmouth, trained a monkey to reach toward a sound rather than a visual target. Even though the information was coming in via the auditory system and going out as a reach, it was encoded in the PRR in visual coordinates. The neurons that responded to the sound shifted when the animal moved its eyes, even though neither the source of the sound nor the direction of the reach had changed.

This preference for eye-based maps may reflect the fact that "vision is the dominant sense in primates, and it seems to provide a common framework for coding all kinds of spatial information," says Colby. What's more, she notes, we generally first move our eyes to something that has drawn our attention, regardless of what we are going to do next. "It may be that in the parietal reach region, things are in eye-centered coordinates because you normally look at the thing you are reaching for," Colby says.

A big question that remains is just how such sense-based maps ultimately get redrawn. The brain can get information about the position of the eyes, head, and limbs from neurons in the motor areas that control them, says neuroscientist Jennifer Groh of Dartmouth College. She and others have developed computer models that suggest how the brain could incorporate that information into new maps that reflect the body as well as its environment. Those models will help researchers devise experiments to tackle the question, and take the next step toward understanding how the mind maps the world.

–MARCIA BARINAGA

MEETING

DNA and Field Data Help Plumb Evolution's Secrets

MADISON, WISCONSIN—By the shores of Lake Mendota from 22 to 26 June, biologists at Evolution '99 revealed some surprising twists in nature's evolutionary course, from the ills of inbreeding to a complex three-way relationship among plants and moths.

Evolutionary Ménage à Trois

For insects, as for people, the way to get the most out of life is often to form partnerships. In the case of several nondescript white moths, the partner is a desert plant, the yucca. At first glance, the relationship seems quite amiable: the moth pollinates yucca flowers and then lays its eggs there, where nascent seeds nourish the developing larvae.

But moths, like people, sometimes cheat on their partners when a third party enters the relationship, evolutionary biologist Olle Pellmyr from Vanderbilt University in Nashville, Tennessee, reported at the meeting. When two kinds of moths depend on the same yucca, "it's a different game," he says, opening the way for one moth to become a parasite of both the yucca and the other moth. "The bottom line is one [moth] can turn into a cheater if it can get another moth to carry the [pollination] burden," says Pellmyr.

The work "is an exquisite demonstration," showing "a deep understanding of evolutionary interactions," says Douglas Futuyma, an evolutionary biologist at the State University of New York, Stony Brook. "Even in mutualistic interactions, there are conflicts" over each partner's share of seeds, for example, "and this can lead to the evolution of parasitism."

Since 1992, Pellmyr and his colleagues have been documenting relations between 35 yucca species and the 13 moths that tend them. The system seems elegantly balanced: The moths have evolved large, specialized mouth parts to gather yucca pollen, and the plant guards against the moth larvae eating too many seeds by monitoring the egg load and dropping flowers with too many eggs before the seeds and fruit mature (*Science*, 25 August 1995, p. 1046). Some moths specialize on one yucca; others visit several species. But two of the moth species are different. They are "cheaters": They no longer have the pollen-gathering mouth parts, and they lay their eggs late, directly into the fruit or seed after the seed is set—thus avoiding the yucca's defense.

Slacker. Some moths that depend on the yucca plant have shifted from pollinators (*left*) to parasites (*right*).

Pellmyr and his colleagues have now analyzed the cheaters' DNA, which shows that they evolved separately, and studied their ecology. The fieldwork shows that the cheaters flourish only where there is another moth also depositing its eggs on the same yucca species. Pellmyr concludes that a three-way relationship drove the moths to cheat. With two moths going after the same flowers, egg overload could be rampant. But if one moth species showed up late, it could bypass the plant's ability to drop off flowers containing too many moth eggs and could rely on the other, hard-working moth for pollinating duty.

For example, in Florida, where two moth species, *Tegeticula yuccasella* and *T. cassandra*, head for the same yucca, a new cheater species has split off from *T. cassandra*. Both moths inject their eggs just under the surface of yucca fruit, but *T. cassandra* deposits its eggs on day 1, and the cheater waits until 5 days later, Pellmyr reported. Furthermore, this cheater has not only stopped spending its energy growing special mouth parts and pollinating, but it has also lost its dependence on a single yucca species, and has spread westward, taking advantage of other moth-yucca partnerships all the way to New Mexico, Pellmyr says.

The other cheater also arose from a situation in which two moths depended on the same yucca. This second cheater visits a variety of yuccas in its southwestern U.S. habitat and is "a little more evolved," Pellmyr notes. It arrives very late, encountering 3-week-old fruit, and has a special knifelike appendage that it uses to place eggs deep into the hard fruit, directly onto the seeds.

Though the two cheaters originated in very different parts of the United States, Pellmyr's team has now found plants in New Mexico with both cheaters as well as a faithful pollinator. "We're itching to go study this more," he says. He also expects that this yucca has some additional means of keeping the parasite in check, because otherwise the cheaters could overwhelm the plant, and the yucca and its faithful pollinator would likely go extinct. No matter what turn the moth-yucca soap opera takes, says Futuyma, "the work is rapidly becoming a classic in evolutionary ecology."

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