[SQUEAKING]

[RUSTLING]

[CLICKING]

NANCY KANWISHER: So we're talking about navigation-- how you know where you are and how you can get from here to wherever else you want to go. And last time we talked about just the general problems that arise in navigation, and we talked about the parahippocampal place area and other parts of the brain that are involved in navigation.

So today we're going to continue that, but we're going to talk more about the actual populations of neurons in your head that are involved in doing this. And we'll talk about a particular aspect of the problem of navigation, which is called reorientation. That is what happens when you lose your bearings, and you need to figure out where you are again. Reset your internal map of where you are.

And then we'll talk about the idea that this whole system for navigation, cool as it is and fascinating as navigation itself is, is even more interesting because there's increasing evidence that we use that same system for lots of other aspects of high level cognition that have nothing to do with space per se. OK that's-- and then we'll have a quiz, a short quiz. That's the agenda. Here we go.

So the basic problems of navigation are, one, where am I? And two, how do I get from here to wherever else I want to go? And as I mentioned last time, we can break down each of these into a bunch of different components and facets of that question.

So when we want to know where we are, that can involve recognizing a familiar location. So if you see a photograph or you were plunked down spontaneously in an environment someplace you know, you would visually recognize it, and that would be one way to know where you were. Like, this is my living room.

Even if that location is unfamiliar and you're plunked down at random, you still have some idea of what kind of a place this is. Am I in a natural environment? An urban environment? Am I inside? Am I outside, et cetera?

And finally, you would have some sense of where you are with respect to the immediate bounding structures in your immediate environment. Like, for example, where you are in this room. As I'm talking to you right now, I'm aware that there's a wall behind me. That kind of immediate spatial location.

In terms of questions that arise when we have to figure out how do we get from here to wherever else we want to go. If you can directly see or hear your destination, then you have the simplest possible kind of navigation strategy. You just go toward that thing. OK, that's called beaconing, and it's like the minimalist case. Works great if you can see or hear your destination.

But when you can't, you need to know, where am I in my broader understanding of the layout of my environment and where is my goal. And for that, you need a mental map of your environment, and we'll talk more about that today. That's why it's in red.

You also need to know your current heading in that environment. It's not enough to know in my map of the world, I am here with a dot. You needs to know which way you're facing in that map of the world in order to plan your navigation, and we'll talk about that too.

We also need to know what routes are possible from here. So I may want to go over to Stata and get a cup of coffee. But I can't go this way. I've got to go around because I can't go through that glass.

OK, and so finally, this whole magnificent system that enables us to process all this stuff works pretty impressively. But every once in a while, something will go wrong, and it will get the wrong signal, and then we're lost. And so then we need a way to regain our bearings, and we'll talk about that too.

So last time I talked about a bunch of brain regions that are implicated in perceiving scenes and in navigation. We talked about the parahippocampal place area right here and this region over here, formerly known as TOS, now known as OPA. You don't need to remember all that. It's the bit that's out on the lateral surface that we can zap because it's out there. And both of those regions seem to be involved broadly in perceiving the shape of space around you.

We also talked a bit about retrosplenial cortex, that region that's hiding in the sulcus here that you can see better when you mathematically unfold the sulcus, there it is. Responds more to scenes than objects. And that region seems to be involved in something like getting your bearings-- that is the location and orientation of where you are with respect to your cognitive map and environment.

OK, so to make that a little more vivid, I gave you one description of a patient before, but here's from another study. Patients with damage to retrosplenial cortex-- so here's from a recent article-- in every case, the patient with this damage was able to recognize landmarks in their neighborhoods and retained a sense of familiarity. I know that place. That's the coffee shop five blocks from my house.

But despite that, none of those patients were able to find their way in familiar environments, and all but one were unable to learn new routes. So they can recognize the visual form of a particular place, but they don't know how to relate that to their cognitive map of the world and therefore plan a route from there. OK, so the part that I only alluded to at the end-- yes, question?

AUDIENCE: OK, is the retrosplenial cortex the home to the cognitive maps, or is it--

NANCY KANWISHER: Great question. We don't exactly know. The typical story is that the home of the cognitive map is the hippocampus, which we're about to talk about next for reasons I will tell you. But all of this is a very active area of research. It kills me every time I do these lectures. I look at my old notes, and I think here are these 10 other awesome studies, and then I try to fit them in, and then they just don't fit.

So actually one question I want to ask you guys after this lecture is, should I in future, either later in this course or in future courses, allocate even more time, or do you guys feel like OK, enough already with navigation. But I just think it's the coolest system. So there's lots of work exactly trying to answer that kind of question. And I'll give you a current snapshot of the approximate state, but all of this is in flux and very much actively investigated.

OK, so cognitive map, what do we mean by that? Just to remind you of this classic study from the 1940s in rats, where the rat, when they learned this route and then went up here and found their gold block, the rat immediately comes out and goes straight toward the goal. Telling you they've learned something much more interesting than the series of left and right turns to get to the goal. They must have done something much more like actually learned the layout of space and the relative position of that goal so they could come up with a new vector to get there when the original route was blocked.

OK, and you guys can do this too. When your route is blocked, you come up with a novel route. And you do that by having some knowledge of your environment, something tantamount to that in your head, some version of that. And further, you know where you are in that map. Like right now, you know where you are.

Now here's the cool thing-- specific neurons in your hippocampus right now are firing telling you that you are right there. So these neurons are called place cells, and this is what they do. OK, so I'll be a place cell, or rather what I'll do is I will act out the activity of a place cell by a series of clicks I will make as I walk around.

So imagine there's an electrode in my hippocampus, and you are hearing the activity of a single neuron in my hippocampus as I walk around. And here's what it would do. You'd hear background firing. So it's going to go click, click, click, click, click. Noisy background firing.

Click, click, click, click, click, click, click, click, click, click. Click, click, click, click, click, click, click, click, click, click, click, click, click, click. Click, click, click, click, click, click, click, click, click, click, click, click, click, click, click. Click, click, click, click, click, click, click, click.

Click, click, click, click, click, click, click, click. OK, I'm not going to go down there. Click, click, click, click, click, click, click, click. Click, click, click, click, click, click, click. Click, click, click, click, click, click, click, click. Click, click, click, click, click, click, click. Click, click, click, click, click, click, click, click, click, click, click, click, click, click.

So that's one neuron that fires only when I'm right over there, that place. It's not where I'm facing over there. It's not what I'm looking at particularly. It's when I'm right there. OK, that's a place cell.

And so there's lots of place cells in your hippocampus that do that, and they do it for different locations in your environment. And all of this was first worked out, of course, in rodents, who were running around who had electrodes in their hippocampus, but where those electrodes were connected with a loose tether so that the rodent could move around in their environment while recording from individual neurons in the hippocampus.

OK, so that's the setup. And so I'm going to show you a movie of an aerial view of a rodent moving around-- a rat moving around in its environment. Can you see the little rat there?

And what's happening is this video is tracing out the rat's path with the light gray. And every time that-- and it's recording from one neuron-- every time that neuron fires, it makes a red dot. So this is obviously sped up. But as the rat moves around in his environment, you see an accumulation like more firing when the rat is right there.

It's not which direction the rat is going through when he goes there. Just basically whenever he passes through that in any direction, neurons fire more than anywhere else. And then if we take that and blur it, as scientists like to do to make nice idealized pictures, that is the place cell for that neuron. That is the place in space that that animal has to be to make that neuron fire. Yeah, question.

AUDIENCE: Is it one dimension? I mean, can multiple places be mapped to the same neuron?

NANCY KANWISHER: That's complicated. In an immediate environment like this, generally not. OK, I'll show you some examples in a moment. It's more complicated if you follow that cell when the animal moves to a new location.

So let me say a few more things, and then if it's not clear, I'll take questions. Oops, we're going to see that again. OK, right so in answer to Sasha's question, here are a bunch of place cells from a rodent exploring the same environment.

So you might say, well, there's a hotspot here and a little sub one there. But in general, most of these cells respond with a hotspot in a particular single location in this particular environment. OK, did you have a different question about that?

AUDIENCE: Yes, so that all depends on the rat being conscious of the fact that it's in that place?

NANCY KANWISHER: Uh-huh. Uh-huh. If the rat was anesthetized or if he was blindfolded and you passively moved him around in that space and he had no idea-- no way to tell where he was, that wouldn't work. However, if the rat knows the environment and then you do this in a darkened room where he's actively locomoting around, these things will still work pretty well because rats are very good at keeping track of where they are, even without visual cues if they know the environment. They'll have other cues like tactile cues, and they will know how far they went in each direction.

Remember I talked briefly about the Tunisian ants doing dead reckoning. Keeping track of their vector and speed at each moment and integrating the whole thing to know where they are. That's called dead reckoning. Rats are pretty good at that too. Another question over here? Yeah.

AUDIENCE: For the place cells, do they have a map as well [INAUDIBLE].

NANCY KANWISHER: We'll get there. Great question. We'll get there. I'll just give you the answer. No, they don't. It's too bad.

They could have. They could have been all organized, but it's actually a little complicated. How would you organize them? What if you learned more stuff off of the edge of space? What if you had a whole other piece of your hippocampus? It would be inconvenient, so maybe that's why it doesn't work.

Whereas with visual space, your retinotopic information always stays the same. We don't have to suddenly add a whole new part of retinotopic space, thereby screwing up our retinotopic maps in the brain. I'm just making that up as a possible reason. I don't know if that's why. Yeah, sorry, behind you David, tell me your name.

AUDIENCE: Justice.

NANCY KANWISHER: Yeah, right, hi.

AUDIENCE: So I was wondering if you're in a smaller space comparatively or a bigger space, will areas of these specific place cells, what they're mapping to, will they also scale up right now?

NANCY KANWISHER: That's a great question. I don't know the answer. My guess is they'll scale according to the space. So if my fake place cell fields that I just acted out over there is maybe five feet across, if I was then confined to a little space, you'd probably have smaller ones for that space, but I don't know.

Let me say a little bit more about this. So just to cash this out, the place field is the location in space the animal has to be to make that hippocampal cell fire. OK, so let's distinguish that from a receptive field in visual cortex, which is a similar idea but a different one.

A receptive field and visual cortex is the location in the visual field where a stimulus has to be to make a visual neuron fire. Not where the animal itself has to be, where the stimulus has to be. So keep those ideas separate. They're related but different.

OK, so what about we and rodents tend to go around mostly on a 2D plane. That is we have buildings and trees and stuff. We sometimes go up in the z-axis, but mostly we live in a 2D plane, but that's not true of all animals.

So recall the bat that I mentioned last time. These amazing flyers and navigators who fly in 3D and complicated trajectories and yet have amazing abilities to keep track of where they are over 30 to 50 miles that they fly at night and even as they change their orientation.

Well, it turns out that in the hippocampus of bats, there's a bunch of work where people have put remote-- what do you call these things-- recording devices on bats, where you can remotely record neural activity in the hippocampus as the bat flies around. And it turns out that bats have place cells too, and their place cells, as they also can do this in a lab environment where they're flying around and you keep track of their location with cameras. So you know exactly where they are in 3D space.

And it turns out that place cells in bats are three dimensional because bats live in a three dimensional world. So whereas rodent-- these would be a bunch of schematized place cells for different hippocampal cells in a rodent, these are different place cells for different hippocampal cells in a bat. Make sense?

Bats need this. They need to know-- not making sense? OK, so the bat is moving around in three dimensions. Its place field isn't just like the one I did there. I can't act this out because I can't fly, but that place cell might fire over in that location. But then if the bat flew directly above it, it wouldn't. So it's got three dimensions. OK.

OK, so I said before that I had one of those, and I acted it out. But what's the evidence for that? The evidence in humans came way after the evidence in rodents. Because as you can imagine, it's harder to arrange to record from individual neurons in human hippocampus.

Nonetheless, as I've mentioned a few times there are occasional opportunities where a neurosurgeon has stuck an electrode in an interesting part of the brain for clinical reasons, and the patient and the neurosurgeon are nice enough to let scientists collect data. So I'm going to show you a really gross bloody picture. If that's going to bother you, just look away.

OK, so this is neurosurgery. You take the skull off, you take the dura off. That's the direct surface of the brain. The neurosurgeons stick electrodes right on top of there. And in this case, they put them deep inside the brain. OK, the gross pictures are gone. We have just a nice clean X-ray here.

So in these cases, this is a patient who's got an electrode sticking straight into the brain from the surface straight down n to the hippocampus. OK, kind of horrifying, but sometimes clinically called for. Seizures very often start in the hippocampus, so this is a commonplace for clinicians to put electrodes.

And so what would you do if you had a patient who was willing to do your short experiment while hanging out in the hospital waiting to have a seizure with electrodes in their hippocampus? Well, you'd have them play a little game in a virtual space in some kind of-- you don't even need VR. You can use a pretty cheesy little video game, and I'm sure this one was quite cheesy. This study was done back in 2003.

So they had patients navigate through a space-- this is an aerial view of the space. The patients didn't see that. They saw this front view, and they navigated around with the joystick in that space. And there were three visually recognizable locations in that space, and they had to do things to go from one location to another. OK, details don't really matter. So all the while, Ekstrom and colleagues are recording from individual neurons in this patient's hippocampus.

OK, so here's an example of a place cell. So this is a diagram of the space I just showed you, with those three recognizable locations and other locations that the patient could virtually navigate through with the joystick. The red lines are the patient's trajectory as they moved around in that space. And the colors within each square are the average firing rate when the patient navigated through that location.

And so this is the place field of that individual cell in this patient's brain as they went through this space. Because the firing rate there was around five hertz compared to three hertz for some other locations and mostly lower than that. OK, does that make sense?

So just like the rodent experiment, but it's a person with a joystick looking at this space as they go through this virtual environment, and we're mapping out their place fields like that. OK, so that shows that humans have place fields in their hippocampus just as rodents and bats do. Yeah?

AUDIENCE: Well, this is independent of landmarks?

NANCY KANWISHER: That's a very complicated question. This patient had access to landmarks. They are seeing as they go through. So one could ask, for example, if you did it with your eyes closed and you had to go by dead reckoning remembering the left and right turns you had in a familiar environment, how well could these things go, they would go for at least a while.

They'd probably go for longer in rodents because rodents are more accustomed to navigating in the dark. And they rely less on visual cues and more on other cues. But yeah, place cells aren't just visually responsive.

So if we had, for example, if we set up a distinctive sound source in this corner of the room and a different-- like say somebody was singing quietly over here, and we tied a dog over there who was barking. And you walked around in this room with your eyes closed, you'd have a good way to keep track of your bearings as you moved around because you'd know that the singing was coming from here and the dog barking was coming from there.

You wouldn't be seeing anything. Your eyes would be closed, but your place cells would work pretty well. OK, so whenever you have some basis for knowing where you are, no matter what modality is telling you that-- and usually it's many modalities-- those place cells will go.

OK, so humans have these things too. So you can think of the place cell as the kind of "you are here" system that is the whole set of place cells. Any one place will only tell you are you in this particular location or not.

But you have a whole array of them, then collectively, that whole representation across all of those neurons can tell you where you are in your familiar environment. OK, but if you want to not just know where you are but you want to go somewhere else, like there, you also need to know your current heading as we discussed last time.

So it turns out that there is a whole other batch of cells that tell you what way you're heading. OK, these are called head direction cells, also first studied in rodents. And each head direction cell responds when that rodent is heading in a particular direction, not in another direction.

OK, so for example, if we're mapping along the x-axis different heading directions. So the rodent is facing in different directions in his environment. You map up the whole 360 degrees, this would be the response of one cell as that rodent moves around.

This one would be tuned to this particular direction. It would fire only when the rodent was facing this way, not when it was facing this way or this way or this way or this way. So does everybody get how where you are in space is different-- that's not a very good way to show this. Where you are in space is different from where you're aimed and headed in that location. OK, two orthogonal axes of relevant to your location. Yeah?

AUDIENCE: So this isn't the angle of the head in respect to the body, right? It's the entire--

NANCY KANWISHER: I think I meant to look that up again because this question always arises. I think that there's some muck about that in the literature, which is why I never remember a clear answer. Usually in a rodent, especially the same. Because rodents can turn their heads a little bit, but mostly they're going to keep it aimed the way they're moving.

So I don't know. This is a long, complicated excuse that I forget what the answer to that is. But send me an email, and I'll look it up. I meant to before this lecture. I just ran out of time.

OK, most of the time, they'll be the same. Actually, I'm pretty sure it's which way your body is facing. Because if I turn like this-- well, anyway, I'm not going that way. Yeah.

AUDIENCE: Have you found at least 360 cells for each angle?

NANCY KANWISHER: You mean, are there cells for each? Yes, yes, they pretty much evenly tile the 360 degrees around the animal. Yeah, so collectively, that whole set of cells, just as a collective set of place cells, is sufficient to tell the animal where it is. A collective set of head direction cells is sufficient to tell the animal which way it's oriented.

OK, I think we just said-- all these things are in a structure called the-- well, first found in the structure called the subiculum, which is part of the hippocampus. But since then, they've been found in lots of different regions. You don't need to remember that.

So they get input from lots of different information. There's many different ways to know which way we're oriented. For example, too bad we don't have a rotating chair. If we did, I would have done the following ridiculous thing. I would have sat one of you in it, and told you to close your eyes.

And I would suddenly turn it. And the person in the chair would notice that. That's your vestibular system that tells you if your body is being turned, even if you yourself don't decide to turn it. It will tell you if you get turned. That's another cue that provides input to the head direction cells, just as visual information does and potentially auditory information and lots of other kinds of information. So many different sources of information feed in to inform these head direction cells about the orientation of the animal.

All right, so you can think of this as the brain's compass telling the organism what way they're facing. And lots of organisms have versions of this. In the fly, there's an amazing structure that was discovered just a couple of years ago, where there's a whole layout of this little neural structure-- I forget what it's called.

But actually spatially in that structure, there's a little array of direction cells. So actually you can see it in a little spatial map of direction in that little structure in the fly. In humans and primates and rodents, it's not organized spatially like a literal map of direction.

OK, so now we have where you are and which way you're facing. One pool of cells, place cells for where you are. Another pool of cells for which way you're heading. But those are just-- we're just getting going here.

The coolest navigation-related cells are grid cells and entorhinal cortex. OK, so this is a slice of the brain like this, showing the hippocampus is folded up thing right here. And entorhinal cortex is just right next door.

OK, so an entorhinal cortex, these things were discovered around a dozen years ago, maybe 15 years ago. And I'm going to show you a video of a rodent moving around his environment mapping out activity, like we saw before. But now we're in entorhinal cortex, and this neuron is going to be a grid cell, and you'll see why as it moves around in its space. Maybe.

Come on. Here we go. OK, so there's a rodent. He's moving around. That's the tether taking the neural activity. The white dots are every time this one neuron fires, we're following one neuron this whole time. And the rodent is moving around, sped up video so you can see this happening.

And at first, it looks like completely random. But as a rodent keeps migrating around in his space there, you start to see that they're like blobs in there. It's not totally random. They're particular blobs that are clustered.

And oh my god, those blobs are organized in a hexagonal grid. It's a hexagon. Isn't that awesome? That's a grid cell. And whoops, here we go. We don't need to see it again. So this is a picture of what you just saw, the trajectory of the animal and the hot spots in that array. And here's a smoothed mathy version of where the firing is significant in that space, both showing you hexagonal grid cells.

OK, so this is at first glance a very weird thing. Why would it help to have essentially a place field that has multiple different places that make it fire? OK, and actually somebody else before whether place cells have two hot spots. Place cells generally have one, but grid cells, as you see, have many organized in this grid.

So the kind of circuitry and math of this whole system is mind blowing and super exciting, and the talk that I mentioned yesterday was on this topic. And many people are working on this, and they're working out like really deep interesting math about how you can take these cells, how they're arranged spatially in the brain at multiple scales and how you can use them to do path integration and keep track of how far an animal has gone along its trajectory.

It's a little bit much for this course, but I'll just say the current thinking is what these cells enable us to do is to keep track of how far we've gone in each direction, and that's really crucial in navigation. We need to know where we are, not just by the landmarks we see. We need to know how far we've gone in a given direction and the thought is that that's the function that these grid cells primarily serve in navigation. And so that's especially important for dead reckoning, like integrating where you've gone according to your trajectories.

OK, so you also need head direction cells at each point. So you can of the head direction cells as telling you the orientation of your vector and the grid cells of telling you the magnitude of the vector of how far you went. And then you take a whole bunch of those, and you integrate them, and you know where you've gone from your starting point. And lots of animals do all that math in their head. It's pretty complicated integrals, but they all do that.

OK, so this is super awesome work. And fittingly, the 2014 Nobel Prize was awarded to the Mosers, a then husband-wife team, who discovered the grid cells and also to John O'Keefe, who discovered place cells decades earlier. And it's a super exciting line of work and continuing to be very exciting one.

OK, so so far we've talked about place cells in the hippocampus, direction cells in the subiculum and lots of other places, and entorhinal grid cells and entorhinal cortex. And this is just a schematic diagram of where those locations are. The anatomy is complicated, and you don't need to know it. Know they're all in the hippocampus and its neighboring structures. That's good enough for here.

Well, OK, know that the grid cells are in entorhinal cortex and the place cells are in hippocampus. That's worth knowing. OK, direction cells are kind of all over.

OK, so that's cool, but there's one more cool kind of cell-- actually there's several more. The new one I never heard of was reported in this job talk yesterday, but we won't go there. We'll try to keep it simple.

Another well-established one is called a border cell. So these are the place fields of three different neurons from an animal moving around in this space. OK, so you see how these are very interesting kind of place fields. They're not just a nice round blob. They stretch around a whole order of the animal's environment.

OK, so does that make you think of anything? Does that ring any bells with other stuff we've talked about in here? I think we've talked a bunch about how the parahippocampal place area cares about the shape of space around you.

Well, you might think that you'd really want to have awareness of where you are with respect to navigational barriers. It turns out border cells respond not just to walls. If you put a rodent in an environment where there's a cliff they can't go off, the border cells also respond to the edge of that cliff. OK, so any navigational barrier basically telling you where you are with respect to navigational barriers.

OK, all right. Blah, blah, blah. OK, so as I mentioned in the last lecture when we talked about the parahippocampal place area, the shape of space around you has this kind of privileged role in many aspects of navigation. OK, so now we're going to talk about this problem of reorienting or regaining your sense of direction once you've been disoriented.

And so, again, I mentioned this before. But just to give you in give you the intuition of what we're talking about here, you come up from the subway in Manhattan or any other environment that's rectilinear that you know and you know which stop you're coming at up at. So you kind of know where you are, but you come out and you don't know which way to head. You don't know which way is which.

So that's a modern version of a classic problem that animals face in their environment. They may know where they are, but that doesn't tell them which way they're facing. So just to be really concrete about this, so here's an aerial view of a person. You're standing here.

You have a cognitive map in your mind, and your place cells are telling you your location in that map. OK, so you know where you are in that map. And you're looking down a street, so you know that you're oriented with respect to some external axis like this.

But you don't know how your mental maps should be aligned with that street. Are you facing like this, facing north in Manhattan, or are you facing south? All right, so that's the problem of reorientation is figuring out your particular orientation, not just your location but which way you're facing in a known environment.

And we've all faced some version of this presumably at some point, and it's annoying. It takes a while to figure out. And then I don't know if anybody's had this experience. I've had it only in Manhattan because that's where this arises for me, but I'm sure there are other locations.

Where you come up and you think you're going one way, and then all of a sudden, it's like your whole mental map goes kaboom. How many people have had that experience? It's very sudden and punctate. Yeah, it turns out that when that happens, all of your neurons flip together in unison.

Like they're all in cahoots. They have one version of this. When you have that experience, it's because they're all flipping together, and I'll show you some data on that in a second.

OK, all right. So there's a very evolutionary old system for solving just this problem. And it's a wonderful little piece of the literature that I'm going to spend a couple of minutes on because it's so classic and so cool. And this started with work by Randy Gallistel in the 1980s.

And so what he did was he studied this problem of reorientation-- that is figuring out your orientation in a known environment once you've been disoriented. It's a very particular aspect of the problem of navigation. So he put rats in a rectangular environment, and he had them explore the environment.

And then he hid some rat-relevant thing, like a little piece of food, say a chocolate chip in that corner. OK, rat sees that happen, rat is interested. Take rat out of box before they get to go take the chocolate chip, and then you disorient the rat.

You don't grab them by the tail and swing them around, but you do some slower version. You want to make them sick. You do some slower version of that so they've lost track of which way they're facing.

OK, now you put them in a new box-- new box because you don't want the smell to still be there, new box, and you see which way the rat goes. And you find that the rat goes 50-50 to those two corners. What does that mean the rat has encoded?

He doesn't go randomly to any corner. He goes to corners-- he knew it was in a corner. He doesn't go randomly to any corner. Yeah, Ben? Jack, I'm sorry.

AUDIENCE: Or you can turn it around to the left.

NANCY KANWISHER: Say again.

AUDIENCE: Like it's specifically in one of these directions. So the left [INAUDIBLE].

NANCY KANWISHER: You've got to say a little more than that. What's to the left? What's different about those two corners than the other two? Yeah, Isabel?

AUDIENCE: Well, if he's looking at the shape of the room-- i.e. these two longer walls and two shorter walls-- he recognizes that the space [INAUDIBLE] he has to go to what looks like the right [INAUDIBLE].

NANCY KANWISHER: Exactly. He has to have encoded the axis-- the fact that the room is longer on one axis than another. And he's essentially encoded that chocolate chip was on the right side of the long wall or the left side of the short wall, and both of those corners are consistent with that. That's why he goes 50-50 to them.

He can't go 100% of the time to the right corner because he has no information that would tell him that in this experiment. OK, everybody clear? So it tells you he learned where the thing is with respect to the shape of the room and its particular aspect ratio.

OK, so now the plot thickens, and now they repeat the experiment. But this time, they make some very rat-salient asymmetry over here. You make a color and a texture, and you make other things to make this wall very saliently different.

So you would think the rat, motivated to find the chocolate chip, would now go 100% to that corner when we put them in the new box with the same landmark cue over there. But no, the rat goes 50-50 to the same two corners. And in control experiments, many control conditions, you can show-- and I'll show you one in a moment-- the rat absolutely knows about this wall. He's encoded the presence of that asymmetric wall, so he has the information that should enable him to break the symmetry, but he doesn't use it.

That's weird. You should be surprised. OK, everybody get why that's weird? He could have solved this one perfectly this time. He has the information. He's not using that information. OK, so that's weird.

But then Liz Spelke and her colleagues came along 10 years later and said, let's try this with infants. And so they did the infant version, where you put the infant in a room with a symmetrical-- in a rectangular room, and you hide the doors so the infant doesn't have any cues other than the shape of the room.

18 to 24-month-old infants, and then you hide a toy in a corner, and you see what the infant does. Actually what you do with the infant is you make this wall really salient in all kinds of ways. In one case, it was red velvet, and they first showed the-- and these are, I guess, toddlers.

They first show them that when you knock on the red wall, music happens. Totally cool, riveting for a little kid. They totally get it. They know all about the music wall. Very salient to them.

Nonetheless, you put them in this experiment, and they behave just like rodents. They go 50-50 to the two corners. Even though they notice the red music wall, and it could have solved the problem for them perfectly. And they were motivated, but they didn't use the information. Everybody get why that's kind of interesting and kind of surprising?

OK, now you might say, OK, rodents, infants, they're dummies. We wouldn't do that, us smart adult humans. Would we? But oh yes you would under certain circumstances. If we tied up your language system-- and there's lots of ways of doing that. One way is called shadowing.

So it's like simultaneous translation but you don't translate. Try this sometime. I do this occasionally when I'm bored in my car just because it's amusingly difficult. Turn on the radio, listen to somebody talking, and just repeat everything they say after they say it.

I'm not even translating. It's still demanding. So you have to be listening and producing. OK, running thing. OK, so that's called verbal shadowing, and it's an established way to really tie up your language system and take it offline so you can't really use it.

When you do this experiment on human adults, if they're verbally shadowing and their language system is tied up, they behave just like rodents and infants. That is they use the shape of the space, but they don't use salient landmarks that could help them solve it perfectly. They go 50-50 to the two corners. They become rats and infants. We become rats and infants.

OK, so Liz Spelke has spun a whole fascinating big theoretical story about what this really means. Well, let me just say a little bit more about this first before I do her whole big story. OK, yeah so the idea is-- so first of all, why would it make sense for rodents at least-- let's just consider the rats-- to use only the shape of space to reorient themselves when they're disoriented?

At first glance, that seems really crazy. But if you think about rodents in natural environments, the idea is that actually in natural environments, features change. Snow comes and goes. Plants come and goes. Odors change. All those kinds of features of the environment can change, but the shape of the environment, like that there's a slope like this and a barrier here and a cliff there, those are more stable features of the environment.

So it actually makes evolutionary sense for disoriented rodents at least to use the shape of space more than the features-- the colors and textures and odors of a space-- as landmarks to reorient themselves. Does that makes sense? And so the idea is that rodents have through evolution evolved this system for reorienting themselves when they lose their bearings that relies only on the shape of space so restrictively that even if another cube becomes relevant and important, they don't use it.

And the further idea is that we have some version of this system in our heads as well. And as smart adult humans, we learn all kinds of other strategies to get beyond this. We're not trapped with only being able to use this one system to solve it. We can use other systems-- possibly language to help us say things to ourselves, like it's on the left side of the short wall.

That's what Spelke thinks. There is some version in your head of, it's on the left side of the short wall, and that's why adults can do this when their language system isn't tied up. I don't think that's exactly right, but it's a beautiful story, and there's some evidence for it.

OK, anyway, part of the reason I go through this whole thing-- well, one, I think these experiments are cool, but it's also been the basis of a core idea in cognitive science, and that idea is called informational encapsulation. So think about, it's just lots of syllables for a pretty simple idea. That you have this system for reorientation, and it is designed to use the shape of space around you as the cue that you use to reorient yourself when you're disoriented.

That system is hardwired to do just that. And if some other part of your brain has information that could solve the problem, like the presence of a relevant feature that you could use, you don't have-- your re-orientation system doesn't have access to that information. It's informationally encapsulated. It only has access to the particular inputs that are hardwired into it.

And so 20 years ago, a lot of people went wild with this and said that all the brain regions that I've talked about and cognitive systems that we're considering in this course are informationally encapsulated. It's kind of an extreme idea that goes far beyond functional specificity to say the inputs are extremely restricted to each region, and that's probably not true.

But there's some limitations on the information that each of these processors were considering in this course has access to. And this is the classic evidence, behavioral evidence that some of those systems have very restricted inputs. Does that make sense, the idea of informational encapsulation? Not as an absolute truth about the brain, but as an idea that is interesting to consider individually for each of the systems we study.

There's been pushback about the extremeness of this claim that infants and rodents only use the shape of space. There are circumstances where you can get them to use other information, but it's definitely true that the shape of space is the dominant cue for reorienting in rodents and in infants.

All right, so when you're lost, as I've mentioned, there's two questions you need to answer-- where are you and which way you're oriented. This last stuff we were talking about is about which way you're oriented question. OK, and I just showed you some evidence for this general finding that the geometric cues, the shape of space are the dominant cues you use to reorient yourself, to get your heading back when you're disoriented.

But do we really know that those cues are different for place recognition and for heading direction? So I've said, here are two different parts of the problem. But do they function differently? Do we really use different cues? Do we use the shape of space more for heading direction and maybe other cues for place recognition, for knowing where we are?

OK, so I'm going to show you a very elegant behavioral experiment in mice that does this all at once in one experiment. So this is Josh Julian, a former lab tech in my lab. I get no credit for this whatsoever. I'm proud even though I shouldn't be proud. He was just an endogenously smart guy who went on and did an awesome experiment after he left my lab and went off to grad school, and here's his awesome experiment.

OK, so he said, let's get mice to do both of these tasks. They have to know where they are and which way they're oriented. OK, we're going to do the same disorientation thing. Take them out, turn them around till they're disoriented. But these mice have to learn two different environments. OK, one environment has the vertical stripes on the short wall, on one of the short walls. The other environment has horizontal stripes on the short wall.

So you do the same experiment. You bait one corner, and you see where the rodent goes does. Does he go to the two opposite corners? Exactly the same experiment, but he has to remember which room is-- to solve the problem, he has to know-- he has to discover, rediscover the vertical stripes or the horizontal stripes and act accordingly.

Because when he's in the vertical context, the thing gets hid. He does this over repeated trials. The food gets hid on the-- hang on, let me get this right. Long wall on the left. Do, do, do. Yeah, right.

Yeah, so when the long wall is on the left of the rodent. OK, that corner, the long wall is on the left. Everybody oriented? Whereas when he's in the blue context, the reward here, the long wall is on the right. OK, so he has to learn those two different environments and that the relevant shape cues are opposite in each. OK, everybody got that?

OK, now what you find is that the rodent can learn that just fine. OK, so this shows that when you put the rodent in the vertical context in a room like this, they go more to these two corners than those two corners. Whereas when you put him in a horizontal context with horizontal stripes, he goes more to those two corners than those two corners.

That tells you the rodent has used the orientation of the stripes to figure out which room he's in and hence, which two corners are the right ones. Everybody got that? But here's the amazing thing-- even though in this experiment, the very same animals in the very same trials, are using those stripes to figure out which room they're in, they don't use those stripes at all to break the symmetry and to go only to the correct corner, which they could do but don't.

So once you've trained the rodents on these two things that the reward is here in the vertical context and they're in the horizontal context, you disorient them, you put them back in. You find that when you have vertical stripes, they go to these two corners-- I'm just repeating the data. When there are horizontal stripes, they go to those two corners. OK, they've learned that.

But why do they go to those two corners? They learned the damn stripes. They used them to know which room they're in, but they don't use them to break the asymmetry and decide which is the correct corner.

OK, so this is like a microcosm of everything I've been saying so far all in one experiment. The rodents are noticing those feature cues, using them to figure out which room they're in, where are they, but failing to use those features, the orientation of the stripes, to figure out which of the two corners is the correct one. They're not even encoding food is near stripes. Like, duh, that should have been easy.

All right, so this is a beautiful-- I mean, this is more evidence for informational encapsulation of this system. Because it shows us on the very same trial, they used the stripe information to know which room. They failed to use it to figure out their orientation in that room.

Is this sort of making sense? I realize it's kind of subtle. It's sort of simple and subtle at the same time. Yeah?

AUDIENCE: So with cells that you showed us in the very first maps--

NANCY KANWISHER: What are they doing here?

AUDIENCE: Yeah, exactly.

NANCY KANWISHER: Great question. Let's look at that. That's what we're doing next. It's a great question. What are the damn place cells doing here? Great question.

OK, let's say a little bit more, and then we'll think about what the place cells are doing. OK, so let me just restate, cash out the findings here. The mice are using the features to figure out which place they're in. Are they in this one or that one?

But they are failing to use those features to figure out which is a correct corner. They're still 50-50 for the two corners, even though logically they have that information, and they could use it, and they should use it, they don't. So that means the mice are using features-- in this case, orientation-- for place recognition, but not for regaining their orientation within that place. I'm just repeating what I said before. Is that making sense?

OK, so now David's question, what are the place cells doing here? Great question. Let's look. It's mice, so we can do that or Keinath et al. can do that and Josh Julian, my amazing former lab tech. So again, I get no credit whatsoever.

So what do they do? They allow the mice to forage for crumbs in a box like this. OK, they disorient the mouse before each trial. Take them out, turn them around so he doesn't know which way he's facing. Put them in the box.

And they find that place cells have a particular location in that box. Not surprising. That's what place cells do. So here are two different trials-- two different cells that were mapped out in a rodent doing this.

This cell responds always in that corner. Another cell responds only in that corner. OK, these are just place cells like we described before doing what place cells do. But now, sometimes those place cells are off by 180 degrees, even though the stripes should resolve the ambiguity. OK, so those same cells on other trials respond to the opposite corner.

So the place cells are doing just what the rodent is doing. The place cells are confused. Am I facing-- I am oriented like this, or am I oriented like that? The place cells don't know, and the rodent doesn't know.

And the coolest thing about this experiment is that these things are linked. On the trials where the rodent goes to the wrong corner, the place cells are also in the wrong corner. OK, they systematically determine which way the animal will go.

Oh, and also as I mentioned before, all those cells are in cahoots. They're all in sync going the same way. So when one of the cells rotates to the opposite corner, all the other ones rotate to the opposite corner.

So it's as though somehow on trial to trial, the rodent thinks he's oriented in one way, he's actually 50-50 which way he's oriented. He's not using the feature cues, and his behavior according to where he looks for the food exactly follows that way he's oriented and so do all of his place cells. OK, that's that whole system goes together.

That tells you that those place cells are relevant behaviorally. They are the system that either directly determines or is tightly linked to the system that determines which way the animal thinks he's facing. OK, I realize this is a little bit complicated.

Does it make sense to you that as we've been talking about with reorientation, even though the animals should know from this stripe the difference between that corner in this corner, he doesn't know behaviorally. He's looking for food right there, and yet he goes 50-50. Weird and stupid, right? Place cells do the same thing. And further, the place cells and the behavior go together. Yeah, Sasha?

AUDIENCE: So if you're reading information off of place cells, can you zap it? Can you [INAUDIBLE]?

NANCY KANWISHER: Wouldn't that be nice? Turns out you can't for the reason someone over here asked a long time ago. You, I think. And that's because they're all interleaved together.

And if you zap just one, you're not going to have-- one cell, you're not going to have an effect. And if you zap a whole region, you get all of them and you get muck. So you can't do that manipulation unfortunately. You need some kind of topography to do the manipulation.

OK, so I just said how all this-- I got ahead of myself-- how it relates to behavior, but just to go through that quickly. So what we've done here is they've trained the mouse on this classic reorientation task. They disorient the mouse before each trial while recording from hippocampal place cells.

As before, given cell flips 180 degrees from trial to trial, despite the fact that the stripes should disambiguate it and tell them which way he's oriented. And by the way, head direction cells and the grid cells also flip in the same way in cahoots with the place cells. But you can tell which corner the animal will go to by looking at what the place cells respond.

And so when this place cell represents that location, the animal searches first there. And when it flips around, they search in the opposite corner. OK, so all of that just shows this really strong link between the place cells and behavior.

So to recap, we've talked about four different kinds of cells involved in representing space and navigating around in it. Place cells that are like the "you are here," they respond when you're in a particular location. Direction cells that respond when you're heading in one direction, not in another direction.

Border cells that fire when you're near a particular border in the environment. I have border cells going right now throughout this whole lecture. I've got a batch of border cells that are going.

Grid cells that do this amazing thing of firing when the animal is in multiple different locations, and those locations that make it fire are arranged in a hexagonal grid. Think of it as a kind of ruler telling the rodent how far he's gone in this space, and those grid cells are like the rulers. Yeah, right. Those are the four kind we've talked about.

So now, here's the cool thing. All this stuff-- navigation is awesome. We need it, it's important. All mobile animals need it for the reasons we've been talking about. But we can use this whole system for so much more than just navigation.

Once you have this fancy system in your head to keep track of your location, to keep track of your direction, to keep track of where things are, how you're moving through that space, you can use that whole magnificent system in other ways. And in the last three or four years, there's just a huge number of studies that are really starting to take this very seriously, particularly the grid cells and thinking about how the grid cells-- I mean, probably the whole system, but people have been focusing on the grid cells and how they're used in multiple different situations.

So here's one. OK, this is a cool study where what these guys did was they stuck a little device hanging around people's necks, the subjects' necks. Have a little camera aiming forward. It takes pictures at random intervals and records the person's GPS location.

OK, so you send them off for a few months with this little device, and you do something to protect people's privacy. I don't know exactly how they maneuver that, but I'm sure they found a way. And so then they get this set of photographs taken from this person's front view of wherever they were over several months as they went wherever they went in their lives with a little GPS tag for each photograph.

OK, so then what they do is they bring the subjects in and pop them in the scanner and show them some of those pictures. And they asked people to relive the experience that they had when they were looking at that thing. Put this on me, it'd be my monitor like all the time, and I wouldn't know which experience to relive, but I guess these people had richer lives let's hope.

OK, so now what they do is they use multiple Voxel pattern analysis in the hippocampus while people are reliving those experiences in the scanner by looking at those images taken from their front facing cameras. And then they asked, is the pattern of response in the hippocampus, like some bunch of voxels, here is some pattern, is it more similar for events the subject remembers that were nearby in space?

OK, so you do this for me, it's like yes, I occasionally go to the Stata cafeteria, and I occasionally go to the Koch Center cafeteria, and I spent a lot of time at home, and those two things are closer to each other than my home thing. Are the patterns more similar for nearby locations than for more distant locations? And they were. So this is the distance on a log scale between two patterns that result from the subject looking at two different images, and this is the similarity of the pattern in the hippocampus.

Now some of you might be wondering, and in fact, I wonder this too. I think this is a cool study so I'm presenting it, but it doesn't make sense to me because everything we know about the hippocampus is those place cells are pretty interleaved. So how you manage to get a pattern response reading out a systematic location out of the hippocampus is a mystery to me. So they can't be fully-- there must be some kind of structure in there to the layout of those cells to enable them to get this information.

OK, does everybody get how it's telling you that the hippocampus is remembering and reliving some representation of the locations of where you had those experiences? Everybody get how this shows us? But then they asked another interesting question, and they said, oh, does it also represent time?

So we've been talking about space for the last two lectures, but now we're going straight off the deep end. And our first step, not even near the deep end yet is, does it do not just space but time? So they can take all those photographs and say, OK, how far apart in time were these two photographs taken? And they can do the same graph, and yes, they get a relationship with time as well. The farther apart in time people saw those two patterns, the more different the patterns in the hippocampus. Isn't that cool?

OK, so that's one example showing that the hippocampus holds some kind of large scale representation of not just space but also time. And so there's a lot of work on how this gives structures to our memories for distances over the range of 100 meters and times between 15 hours and a month. I'm going to run out of time, so unless it's a clarification question, I'm going to keep going. Yeah, OK.

AUDIENCE: Are different states confounded for time?

NANCY KANWISHER: Yeah, yes. If you just did it like that-- so you have to do something to pick out time things that aren't confounded with space. You have this big sample of pictures, and you take a subset where you balance for it. Absolutely. They would have to do that. I can't actually remember, but they must have done that. Imperfect as peer review is, you'd never get through peer review if you didn't take care of that problem.

OK, so that's the first thing. Here's another even more radical example. So people have shown that grid-like representations-- and I'm skipping over most of the details here to give you the gist because actually the details are a bit complicated. But they've shown that people seem to use their grid cell system when they are thinking about conceptual spaces, not just physical spaces.

OK, so there's one classic experiment in which these guys taught subjects a conceptual space. They taught them about different kinds of birds, and these birds differed on two dimensions. They could vary in neck length or in leg length. And these things were orthogonal varied, so they made some artificial birds that filled up that space.

And so here are some of the birds. This one has short legs, and OK, here's one with short legs and a long neck. And here's one with a longer neck and shorter-- wait, let's see. Longer legs and shorter neck right there. OK, so you've got every possible combination.

They didn't show people a space like that. They just taught them things about these different birds. They had to remember their names and various facts about them. And so the idea is that when people learn about those birds, they mentally construct a 2D space. Because, in fact, those birds were generated from a 2D space, varying neck length and leg length.

And so then when they scan subjects, they found essentially a neural signature of a grid system representing that 2D space. So even though the grid system presumably evolved to enable us to navigate around in a 2D space and keep track of where we are in that 2D space, it seems like it's now getting co-opted and being used for all kinds of representations of 2D spaces, including extremely abstract, artificial learned 2D spaces that you weren't even taught explicitly as a 2D space. You were just taught these birds. So that's pretty amazing.

In another recent study, they had subjects do a role-playing game while in the scanner. And in the role-playing game, they're interacting with virtual characters. And those virtual characters had different kinds of social power and different affiliations with other individuals.

So here's another-- the social space that was invented by the experimenters, and the subjects are playing this game, interacting with other virtual individuals who vary in social dominance and their affiliation to others. And they find place cell activity that seems to echo the position of another person in that social space.

I mean, that's extremely abstract. And yet again, parts of the navigation spatial system are being co-opted to do this. I'm not giving you the details on how all this is done. I'm just telling you that studies have shown that these systems are being co-opted for other uses.

Here's another very charming non-spatial use-- well, sort of spatial use-- of place cells. So those bats, turns out, are extremely social organisms. They have very sophisticated social structures, and they care a lot about each other and who's related to whom and who's doing what to whom.

And it turns out that there are social place cells in bats. That is, cells in this bat's brain, if I were a bat, that would be representing your location, Jack. OK, so not the usual thing where my place cells are just saying where am I. I'm watching you, and my place cells are telling me, where are you. Something social organisms care a lot about, including bats.

So they have an observer bat here hanging upside down, and he's watching this bat fly over to there and back. And then in this experiment, he subsequently flies that same path. That's how we know that he's watching that path because he has to mimic the bat's path that he just observed.

But while he's watching that bat fly on that path, what you see is here's a cell right here. Here is the path flown by the bat, like out and back. And this is when the bat is flying out and back himself, and this is when the other bat is flying out and back.

That blurred a little bit. Here's the place field for self and the place field for other. They're not the same. A given cell doesn't represent the same location when it's me who's there and when it's the person or bat I'm watching who's there. But they're place fields in both cases. Social place cells.

I'm going to keep going because otherwise I'm going to run out of time, but I'll hang around after. OK, so this whole system is used not just for representing social status. What kind of bird this is in this abstract bird space, but actually for making decisions, for thinking.

OK, so as rats run in mazes, you can record-- we've shown this already-- you can show multiple hippocampal place cells. And can you guys imagine that if we were recording from several different hippocampal cells at the same time, we could read out those cells and make a guess about where the rat is in its location. It's just like MVPA but done across neurons. So we have a pretty good sense of where the rat is.

So now we have a rat navigating around in this maze, and what I'm going to show you, the white circle is where the rat actually is. And the little color thing is telling you where the simultaneous readout from several place cells in that rat's hippocampus would predict where the rat is. Like can we tell where the rat is by looking at its place cells?

OK, so right here they're in the same place. It makes sense. The rat is right there, and we're reading it out. OK, so far so good. But now what we're going to do is watch what that place cell location does as the rat moves around in his environment and makes decisions about where to go next.

OK, so what we're going to see is the rat is going to come up to an intersection of the maze-- I think it's right here. And he's going to decide, am I going to go this way? Am I going to go that way?

And as the rat stays there deciding which way to go and the white stays there as he sits there thinking, huh, should I do this? Should I do that? You could call it neural deliberation. We will see what his place cell activity shows you.

So here we go. Rat starts there-- whoops, how do I play this here? OK, so rat is heading up there, and so are his place cells. He comes up to the intersection. He stays in one place, but look what his place cells are doing. Should I go over there? I'm just interpreting what this means, but it sure looks like neural deliberation to me.

And that's what he decided. Everybody get what we just saw? While he's standing there, he's in one place, but he's clearly deciding where to go next. And while he's deciding, those place cells are essentially apparently running simulations of where he might go next.

OK, so we started with this big long list of things you need to know to navigate around in the world. And the neural basis of all this is really not understood yet, but I've shown you what I think are a bunch of tantalizing snippets. Which lead to the idea that our best current guess about the neural locus of these things, which is very far from the actual understanding of how they work, is that the perception of the layout of space around us, the PPA and the occipital place area are very involved in that.

Also in saying for an unfamiliar place what kind of place is this. I didn't show you those data, but you can, in fact, decode whether you're looking at a scene or a beach by looking at the pattern of response and the PPA. We talked about the idea that the retrosplenial cortex may be involved in recognizing familiar locations-- that's a bit of a question mark.

That the idea that your map of the world is represented in your hippocampus by way of place cells, which also say where you are in that world. That your heading direction in humans-- I didn't give you all the evidence for this, but in humans, there's quite a bit of evidence that retrosplenial cortex is very involved in heading direction. I guess I did give you evidence-- patients who have had damage there and can recognize places but not know how they're oriented there.

That planning routes around boundaries in your environment involves the occipital place area and the parahippocampal place area and that this business of reorientation seems to particularly involve heading direction cells in humans, most likely in retrosplenial cortex. So you don't need to memorize all. I mean, I don't care that much about the locations.

What I want you guys to understand is what are these problems that are involved in navigation and what kinds of things can we learn with different kinds of behavioral and neural measures. And you may have noticed in the last couple of lectures that I presented lots of behavioral data, because actually so far, the richest insights about how the system actually works still come-- or many of the rich ones come from behavioral data.

OK, quiz is in two minutes. Does anybody want to ask me a question before the quiz? Yeah?

AUDIENCE: Do you know that the [INAUDIBLE]?

NANCY KANWISHER: Yeah, so you have to do lots of controls to work that out. And I didn't show you any of the details of the data. But yeah, these guys are pretty careful, and there are all these things-- there are many different ways in which people are watching hippocampal neurons and decoding trajectories from hippocampal neurons.

You may have heard about replay, which is a big thing in this department. Tonegawa and Wilson labs study this, where you have a rodent moving around in one trajectory during the day, and then you record from those neurons at night, and you see replay of the trajectories that the rodent went through in the previous day. And so there you have to be really careful to say, OK, there's a lot of data and a lot of noise, and is this really more than the noise? And it is, but it takes a lot of statistical work to show that. Yeah?

AUDIENCE: [INAUDIBLE] scenario be like a place that I know. With the neurons, the same neurons would fire if I go back to that environment, I assume, or like the place?

NANCY KANWISHER: Yeah, yep.

AUDIENCE: But then you can't really have that, or you can't reserve neurons for those [INAUDIBLE].

NANCY KANWISHER: It's a good question. How do we have enough neurons? Yeah, especially for some place we go every six months. Are they sitting around waiting for us to go back there?

No, there's some recycling of neurons across very different locations. So within that location, they'll be consistent. But yes, you do recycle. So the same neuron will have one place cell in this environment, and it may or may not have a place cell in another environment. That's a good question.